



# Basteria

TIJDSCRIFT VAN DE NEDERLANDSE MALACOLOGISCHE VERENIGING

VOLUME 80 (4-6) | 10 DECEMBER 2016

A late Holocene forest fauna  
in the dunes of Noordwijk,  
The Netherlands,  
with *Spermodea lamellata*  
(p.195)



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ISSN-0005-6219

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Printed by HIGH TRADE, Zwolle, The Netherlands

# Notes on Enidae, 8. Systematics of some Turkish Enini previously assigned to *Imparietula* and *Pseudochondrula*, with the description of two new genera (Gastropoda, Pulmonata)

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## INTRODUCTION

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We have investigated the genital system of several Enidae taxa from the northeastern part of Turkey that have previously been assigned to the genera *Imparietula* and *Pseudochondrula*. Four distinct groups can be recognized, which are mainly characterized by the inner structure of the penis and to a lesser extent on the shell. These are *Imparietula* (the flattened lobe is attached to the penis wall; penial papilla absent; the shell without a parietalis and a columellaris but with a palatalis superior), *Pseudochondrula* (the elongated lobe is free from the penis wall; penial papilla absent; the shell with a well-developed parietalis, columellaris and palatalis superior), *Anatolya* gen. nov. (presence of a penial papilla that is covered with irregular folds and narrow grooves; the shell without a parietalis and a columellaris but with an indistinct thickening at the height of the palatalis superior), and *Pseudojaminia* gen. nov. (two parallel V-shaped lobes that are partially attached to the penis wall; penial papilla absent; shell with or without a parietalis, columellaris and/or palatalis superior). These four groups are considered to have genus status; the latter two are described as new to science.

Key words: Gastropoda, Pulmonata, Enidae, *Anatolya*, *Pseudojaminia*, anatomy, Turkey.

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The land snail family Enidae B.B. Woodward, 1903 (1880) can be subdivided into two subfamilies, viz. Buliminusinae Kobelt, 1880, and Eninae (e.g. Bank & Neubert, 1998; Hausdorf, 2001). The Buliminusinae are characterized by the presence of a penial caecum (missing in the Eninae) and the long epiphallar flagellum (short or absent in the Eninae). Furthermore, an epiphallar caecum is missing, whereas it is mostly present in the Eninae. The following genera belong to the Buliminusinae: *Buliminus* Beck, 1837 (synonyms: *Bulimina* Ehrenberg, 1831; *Petraeus* Albers, 1850; *Sestertia* Bourguignat, 1884); *Pene* Pallary, 1929; *Paramastus* P. Hesse, 1933 (with the subgenus *Cyrenaeus* Heller, 1971) and *Iranopsis* Bank & Neubert, 1998 (with the subgenus *Mordaniella* Bank & Neubert, 2016 = a nomen novum for *Mordania* Bank & Neubert, 1988 [non Dworakowska, 1979]).

The subfamily Eninae can be subdivided into three tribes, viz. the Chondrulinini Wenz, 1923, the Multidentulinini Schileyko, 1978, and the Enini. The Chondrulinini are characterized by a well developed penial papilla with an open groove and by the penis wall that is decorated with small papillae. In the Multidentulinini the penis wall is smooth, and the penial papilla is perforated (i.e. with an open canal). Finally, in the Eninae the penis wall is smooth or decorated with longitudi-

nal rolls, and the penial papilla is absent or, when present, not perforated.

The Chondrulini consists, when one follows the above given diagnostic criteria, the following genera: *Thoanteus* Lindholm, 1925; *Peristoma* Krynicki, 1833, *Caucasicola* P. Hesse, 1917 (synonyms: *Medea* O. Boettger, 1883 [non Eschscholtz, 1825]; *Helle* P. Hesse, 1916 [non Osten-Sacken, 1896]); *Zebrina* Held, 1838 (synonym: *Zebrinus* Westerlund, 1887); *Georginapaeus* Schileyko, 1998; *Rhabdoena* Kobelt & Moellendorff, 1902; *Chondrus* Cuvier, 1817 (synonym: *Antichondrus* Lindholm, 1925); *Brephulopsis* Lindholm, 1925 (synonym: *Ramusculus* Lindholm, 1925); *Ayna* Pál-Gergely, 2009; *Leucomastus* A.J. Wagner, 1928 (synonym: *Aschera* Pallary, 1939 [nomenclaturally invalid name]); *Chondrula* Beck, 1837 (synonyms: *Gonodon* Held, 1838; *Eucore* Charpentier, 1837; *Chondrulus* Westerlund, 1887; *Dentistomus* M. von Kimakowicz, 1890); *Mastus* Beck, 1837 (synonyms: *Pseudomastus* O. Boettger, 1889; *Amphitrorsus* M. von Kimakowicz, 1890); *Meijeriella* Bank, 1985 (synonym: *Borlumastus* Örstan & Yıldırım, 2004) and *Eubrephulus* A.J. Wagner, 1928.

We assign to the Multidentulini, following the above given diagnostic criteria, the following genera: *Euchondrus* O. Boettger, 1883 (synonym: *Multidentinia* Lindholm, 1925); *Multidentula* Lindholm, 1925 (synonyms: *Bollingeria* Forcart, 1940; *Tokatia* Hudec, 1972; *Improvisa* Schileyko, 1978; *Senaridenta* Schileyko, 1978); *Chondrulopsina* Lindholm, 1925; *Siraphoroides* Schileyko, 1977; *Pentadentula* Suvorov, 2006 and *Merdigera* Held, 1838.

The Enini exhibit a multitude of genera, some of them being very rich in species, ranging from the Canary Islands, Europe, North Africa, and a large part of Asia (ranging from Turkey/Caucasus to Japan and from Kazakhstan to Indonesia). A considerable number of these taxa is poorly known. Here we will discuss some Turkish taxa that have previously been assigned to the genera *Imparietula* Lindholm, 1925, and *Pseudochondrula* P. Hesse, 1933.

The type species of *Imparietula* and *Pseudochondrula* is *Bulimus leucodon* L. Pfeiffer, 1846, and *Buliminus florenskii* Rosen, 1914, respectively. *Imparietula leucodon* is a species known from a restricted area in the north-eastern part of Turkey (Vilayets Trabzon and Rize), whereas *Pseudochondrula armeniaca florenskii* lives in a small area around Ardanuç in the Vilayet Artvin. The outer morphology of the genital system of *florenskii* has been described by Hesse (1933: 171, fig. 13), but nothing has been reported on the important internal structure of the penis. A short remark has been given on the genital system of *leucodon*, including the internal structure of the penis, by Hausdorf (1999: 153). We have investigated several species taxa that have been

assigned to *Imparietula* and *Pseudochondrula*. Much to our surprise it turned out that both genera have to be redefined, and that it is necessary to establish two new genera in order to accommodate taxa that have previously been classified under *Imparietula* or *Pseudochondrula*.

All species that are anatomically examined by us share the following traits: penis appendix well-developed, long, its retractor inserts on the distal end of the organ around the boundary of A1 and A2; the retractor muscle of the penial appendix and the penis attach on the diaphragm next to each other; penis moderately long, the insertion of the penial retractor is on the penis; epiphallus long, usually cylindrical, usually with a small epiphallar caecum; the distal portion of the epiphallus (= the portion situated closer to the penis) is usually more slender than the proximal part; the proximal, thicker epiphallar portion is internally decorated with transversal slit-like pockets, which probably play a role in forming the spikes of the spermatophore; flagellum very short or absent; bursa copulatrix without diverticulum. In the following, we refrain from detailed descriptions of the genitalia, but highlight the observed diagnostic features, with special focus on the inner structure of the penis.

#### SYSTEMATIC PART

Family Enidae B.B. Woodward, 1903 (1880)

Subfamily Eninae B.B. Woodward, 1903 (1880)

Tribus Enini B.B. Woodward, 1903 (1880)

##### *Imparietula* Lindholm, 1925

*Imparietula* Lindholm, 1925: 30, 39. Type species (by monotypy): *Bulimus leucodon* L. Pfeiffer, 1846.

The history regarding the identity of *leucodon*, the type species of *Imparietula*, is complex. Forcart (1940: 206) synonymized *Buliminus* (*Brephulus*) *lasistanicus* Lindholm, 1914 with *leucodon*, although he did not possess shells of either *lasistanicus* or *leucodon*. The anatomy (jaw, radula, outer morphology of the genital system) of *lasistanicus* was described by Hesse (1933: 169-170, fig. 11) based on syntypes provided by Lindholm; this description was placed by Forcart under *leucodon*. Forcart redefined *Imparietula* based on this synonymy, and placed several taxa under *Imparietula*, namely the monotypic taxa *leucodon*, *adjarica* Retowski, 1914, *tetrodon* Mortillet, 1853, and *brevior* Mousson, 1876, as well as the polytypic taxa *blanda* L. Pfeiffer, 1853, *se-ductilis* Rossmässler, 1837, and *armeniaca* Mortillet, 1854. As a consequence, *Pseudochondrula* was considered a synonym of *Imparietula* by Forcart. Gittenberger (1967: 130-137) followed the opinion of Forcart, and

added the monotypic *altenai* Gittenberger, 1967 and *pelidne* Biggs, 1946 to *Imparietula*. Akramowski (1976: 154–158) also followed Forcart, and included in addition *pupoides* Krynicki, 1833, and *sieversi* Mousson, 1873, into *Imparietula*. The latter two species belong to *Multidentula* Lindholm (tribus Multidentulini) and *Ljudmilena* Schileyko, 1984 (tribus Enini), respectively. Schileyko (1984: 288, 306) separated *Pseudochondrula* from *Imparietula*, and described (1984: 307–308, fig. 220) the external and internal morphology of the genital system of *brevior* under *Imparietula*, as the anatomy of *leucodon* was at that time unknown. Later on, Schileyko (1998: 205) synonymized *Imparietula* with *Spaniodonta* Kobelt & Moellendorff, 1902 (type species: *Buliminus (Chondrula) diodon* Retowski, 1883), and characterized *Spaniodonta* on the basis of the anatomy of *brevior*, as the anatomy of *diodon* is unknown. Sysoev & Schileyko (2009: 58–59) once more changed their opinion, and considered *Imparietula* a genus on its own, with the inclusion of *brevior*. Hausdorf (1999: 153) made a brief remark on the anatomy of the true *leucodon*, and synonymized *Pseudochondrula* with *Imparietula*. Bank & Neubert (1998: 81) restricted *Imparietula* to *leucodon*, *brevior*, *pelidne* and *altenai*, and placed *seductilis*, *blanda*, *armeniaca* and *tetrodon* into *Pseudochondrula*. In his latest edition of the Turkish land snails, Schütt (2010: 97–99) included *altenai*, *pelidne*, *leucodon* (and included *lasistanicus* as its synonym) and *brevior* into *Imparietula*, and included in addition *ridvani* Schütt, 1995, to it. He also separated *Pseudochondrula* from *Imparietula*, and treated, amongst others, *blanda*, *seductilis*, *tetrodon*, and *armeniaca* as being representatives of *Pseudochondrula*.

From the above it can be concluded that the anatomical characterization of *Imparietula* with respect to the internal morphology of the penis is essentially based on *brevior*, whereas the anatomy of the type species *leucodon* remained to a large extent unknown (with the exception of the short remark given by Hausdorf (1999: 153)). During a conchological revision of the Turkish Enidae by Bank et al. (in preparation), it was found that *lasistanicus* is not a synonym of *leucodon*; the anatomy of *leucodon* as described by Forcart (1940: 207) belongs therefore to *lasistanicus*. Below we describe the anatomy of *leucodon* into detail, as well as that of *pelidne*, *altenai* and *ridvani*, and show that all these taxa belong to *Imparietula*. Furthermore, we assign *lasistanica* to *Imparietula*; in addition, Bank, Menkhorst & Neubert (2016) recently described a new *Imparietula* species, namely *inflexa*. The taxon *brevior* turned out not to be a representative of *Imparietula*, but belongs to a hitherto undescribed genus, which we name *Anatolya* gen. nov.

The genus *Imparietula* should anatomically be di-

agnosed as follows: the genital system lacks a diverticulum, the spermathecal reservoir is somewhat to markedly swollen, the epiphallar caecum is located in the middle of the epiphallus or slightly subterminal, a normal penis appendix is present, the penis is relatively slender, a penial papilla is absent, and the inner surface of the penis is decorated with a large lobe that is divided in the middle. The large to middle-sized shell is dextral or sinistral, with a more or less well-developed palatalis superior; there is no columellaris or parietalis.

*Imparietula leucodon* (L. Pfeiffer, 1846)  
(Figs 1, 10A; Pl. 1 Fig. 1)

*Bulimus leucodon* L. Pfeiffer, 1846, in Philippi: 114–115, pl. XII.5  
fig. 7 (shell). Type locality: "inter Trapezuntum et Gu-

mushana".

*Bulimus leucodon* – Reeve, 1849: pl. 63 fig. 432 (shell, syntype).

*Buliminus leucodon* – Kobelt, 1880: 52, pl. 200 fig. 2013 (copy  
from Pfeiffer).

*Chondrula leucodon* – Kobelt, 1899: 567–568, pl. 89 figs 1–2 (copy  
from Pfeiffer).

*Imparietula leucodon* – Zilch, 1959: 183, fig. 630 (copy from Pfeif-  
fer); Bank & Neubert, 1998: 81, fig. 8 (shell); Hausdorf, 1999:  
153; Schütt, 2010: 98, figs a–d (shell) [partim, without *lasis-  
tanicus* as synonym].

*Spaniodonta leucodon* – Schileyko, 1998: 208, fig. 257B (drawn  
after Bank & Neubert, 1998).

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Genital system. – One specimen was examined (TR,  
Vil. Trabzon, Çatak, at Çatak-2 bridge, 400 m (rocks),  
40°48.030'N, 39°35.013'E, leg. Fehér, Ishibe, Ohara,  
Okubo, Otani & Pál-Gergely, 06.vii.2012). The penial  
appendix is long and inserts close to the base of the  
penis; internal penial wall with a flattened lobe,  
which is entirely attached to the penial wall; this lobe  
has a wavy edge, and two grooves starting from the  
direction of the epiphallus; one of the grooves reaches  
the end of the lobe, but the other one stops around  
the middle; the grooves divide the lobe into three  
parts, of which the middle one bears a papilla.  
Epiphallar caecum relatively well-developed,  
rounded, papilla-like; flagellum present but short,  
blunt.

Remarks. – This dextral species is known from the  
Vilayets Trabzon and Rize (Turkey) only.

*Imparietula lasistanica* (Lindholm, 1914) (Pl. 1 Fig. 4)

*Buliminus (Brepulus) lasistanicus* Lindholm, 1914: 36–38. Type  
locality: "In der näheren Umgebung von Lomaschen (Gouv.  
Batum)".

*Pseudochondrula lasistanica* – Hesse, 1933: 169–170, fig. 11 (geni-  
tals).



Remarks. – A lectotype has been designated by Baker (1963: 203); it is present in ANSP 248139a. This dextral species is known from the surroundings of Artvin (Vilayet Artvin) down to Tortum (Vilayet Erzurum), in the valley of the Çoruh Nehri and the Tortum Çayı (Turkey).

*Imparietula pelidne* (Biggs, 1946)  
(Figs 2, 9C; Pl. 1 Fig. 5)

*Ena (Ena) pelidne* Biggs, 1946: 223-224 + fig. (shell). Type locality: "Near Maçka, Trebizond Province, Asia Minor".

*Imparietula pelidne* – Schütt, 2010: 97, figs a-b (shell).

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**Plate 1 (Previous page)**

**Fig. 1.** *Imparietula leucodon* (L. Pfeiffer, 1846), Vil. Trabzon, 3 km S. Maçka, H. Menkhorst leg., 8.viii.1992 (H = 16.7 mm). **Fig. 2.** *Imparietula ridvani* Schütt, 1995, Senckenberg Natural History Museum Frankfurt am Main (SMF) # 318787 (holotype *ridvani!*), Vil. Erzurum, Tortum Selâlesi near Çagliyan (H = 17.1 mm). **Fig. 3.** *Imparietula ridvani* Schütt, 1995, Vil. Erzurum, 9 km SW. Uzundere, 2 km S. exit to Dikmen, H. Menkhorst leg., 13.viii.1992 (H = 15.7 mm, sinistral; H = 14.7 mm, dextral). **Fig. 4.** *Imparietula lasitanica* (Lindholm, 1914), Vil. Erzurum, 9 km N. Tortum, 1450 m, H. Menkhorst leg., 13.viii.1992 (H = 17.8 mm). **Fig. 5.** *Imparietula pelidne* (Biggs, 1946), Vil. Trabzon, Trabzon, 50 km towards Gümüşhane, left part of the valley, 1250 m, E. Neubert leg., 7.ix.1989 (H = 16.3 mm). **Fig. 6.** *Imparietula altenai* E. Gittenberger, 1967, Vil. Trabzon, 1 km S. Hamsıköy, H. Menkhorst leg., 8.viii.1992 (H = 22.9 mm). **Fig. 7.** *Pseudochondrula armeniaca armeniaca* (Mortillet, 1854), Vil. Gümüşhane, 6 km N. Arpalı (= 22 km NW. Bayburt), H. Menkhorst leg., 11.viii.1992 (H = 19.0 mm). **Fig. 8.** *Pseudochondrula armeniaca armeniaca* (Mortillet, 1854), SMF 318782 (holotype *controversial!*), Vil. Artvin, Su kavuşumu 4 km SW. Sebzeciler, near the outlet of the Oltu Çay into the Çoruh Nehri (H = 16.8 mm). **Fig. 9.** *Pseudochondrula armeniaca armeniaca* (Mortillet, 1854), Vil. Artvin, tunnel 5 km S. Zeytinlik, H. Menkhorst leg., 20.vii.1988 (H = 19.6 mm). **Fig. 10.** *Pseudochondrula armeniaca florenskii* (Rosen, 1914), Vil. Artvin, 2 km NW. Ardanuç, H. Menkhorst leg., 22.vii.1988 (H = 14.7 mm). **Fig. 11.** *Pseudochondrula armeniaca florenskii* (Rosen, 1914), Vil. Artvin, cleft 47 km NNE. crossing Demirkent/Ayvalı/Yusufeli, 600 m, H. Menkhorst leg., 8.vii.1986 (H = 15.7 mm). **Fig. 12.** *Pseudojaminia arcospira* (Mousson, 1874), Vil. Tunceli, 13 km NE. Tunceli, Pülümür Çayı, E. Neubert leg., 16.vii.1986 (H = 19.0 mm, dextral; H = 18.4 mm, sinistral). **Fig. 13.** *Anatolya brevior* (Mousson, 1876), Zoologisches Museum Zürich #513649 (syntype *brevior!*), Araxes, collection Mousson ex Sievers 1875 (H = 11.5 mm). **Fig. 14.** *Anatolya brevior* (Mousson, 1876), Vil. Ağrı, Patnos, 1700 m, H. Menkhorst leg., 19.viii.1992 (H = 11.5 mm). If not stated otherwise, all shells in the collection of the Naturhistorisches Museum der Burgergemeinde Bern (NMBE).

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Genital system. – One specimen was examined (TR, Vil. Trabzon, 4 km S of Hamsıköy, 1405 m, 40°41.323'N, 39°27.505'E, leg. Fehér, Ishibe, Ohara, Okubo, Otani & Páll-Gergely, 06.vii.2012). The penial appendix is long and inserts close to the base of the penis; internal penial wall with a low, irregular thickening, which is probably homologous with the flattened fleshy lobe of *I. leucodon*. Epiphallar caecum not found; flagellum present but very short, blunt.

Remarks. – This dextral species is known from the Vilayets Trabzon and Rize (Turkey) only.

*Imparietula altenai* E. Gittenberger, 1967  
(Figs 9B, 9I; Pl. 1 Fig. 6)

*Imparietula altenai* E. Gittenberger, 1967: 42 (13): 130-134, fig. 2 (shell), 3-4 (genitals). Type locality: Turkey, "3 km südlich von Hamsıköy, etwa 45 km südsüdwestlich von Trabzon; 1750-1900 m; in einem feuchten Wald mit Picea und Fagus". *Imparietula altenai* – Schütt, 2010: 97 + 2 figs (shell).

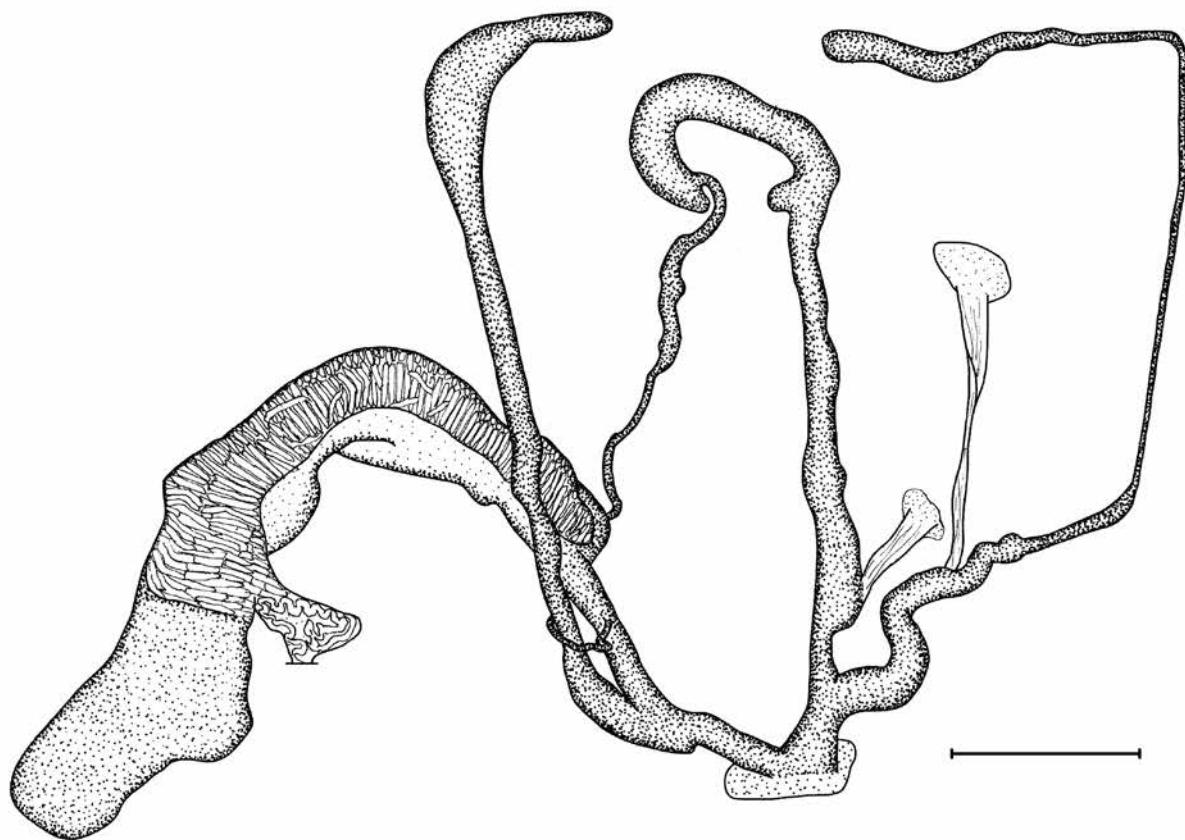
Genital system. – One specimen was examined (TR, Vil. Trabzon, Hamsıköy, along the road to Çıraklı Köyü, 1262 m (rocks), 40°40.818'N, 39°28.953'E, leg. Fehér, Ishibe, Ohara, Okubo, Otani & Páll-Gergely, 06.vii.2012). Our results of the habitus of the genitalia agree with those of Gittenberger (1967: fig. 3), therefore we do not present a drawing of the whole genitalia. The penial appendix is long and inserts close to the base of the penis; internal penial wall with a lobe, which is very similar to that of *I. leucodon*; the only differences are that the edge of the lobe is not waved in *I. altenai* and the shorter groove is longer. Epiphallar caecum small, rounded; flagellum present but short, blunt.

Remarks. – This dextral species is known from Ayvasilhan and Hamsıköy (Vilayet Trabzon, Turkey) only.

*Imparietula ridvani* Schütt, 1995  
(Figs 3, 9D; Pl. 1 Figs 2-3)

*Imparietula ridvani* Schütt, 1995: 162-164, pl. 1 fig. 3 (shell). Type locality: "Türkei, Vilayet Erzurum, Tortum şelalesi, Wasserfall am Ende des Tortum Gölü bei Çağlayan". *Imparietula ridvani* – Schütt, 2010: 99 + fig. (shell, paratype).

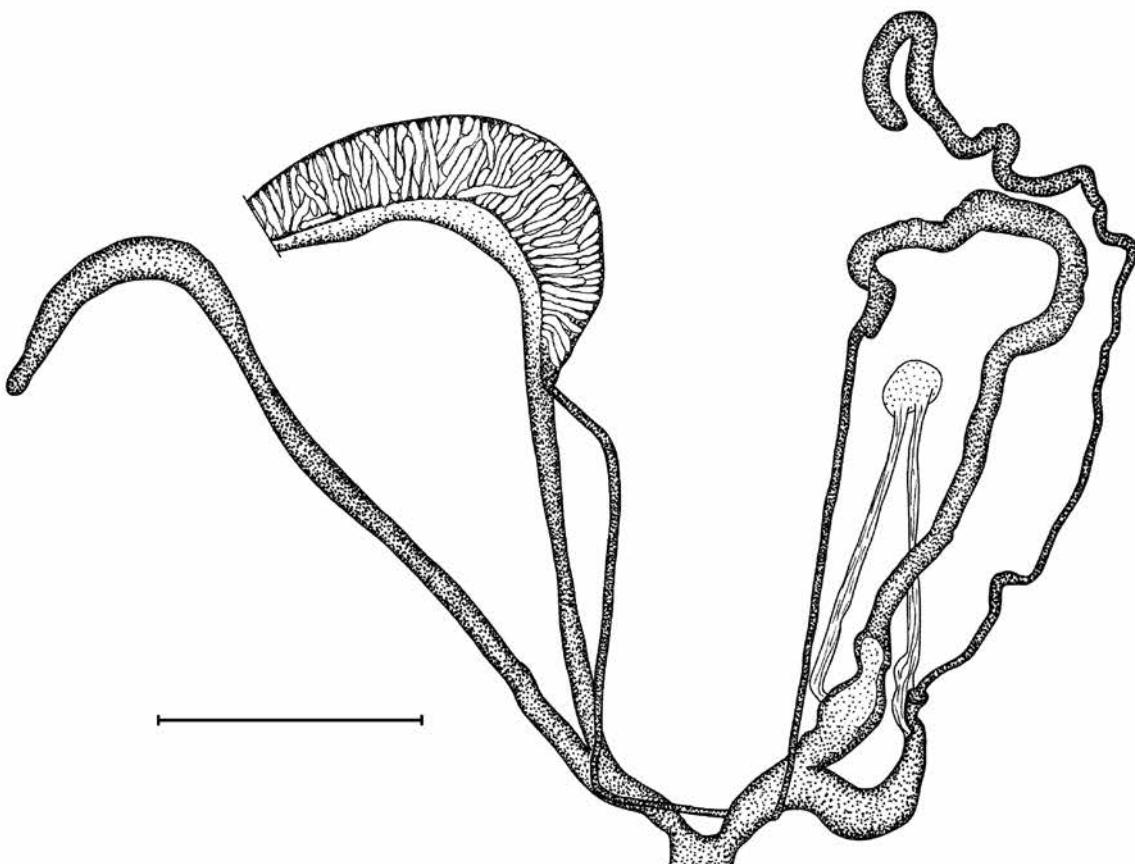
Genital system. – One sinistral specimen was examined (TR, Vil. Artvin, 1 km S of Kinalıçam (towards Erzurum), 40°44'06.5"N, 41°39'53.9"E, leg. Páll-Gergely, B. 06.vii.2011). The long penial appendix inserts close to the base of the penis; internal penial wall with a flattened lobe which is entirely attached to the penial wall; this lobe has a straight edge, and is divided by a main groove; the proximal end is some-

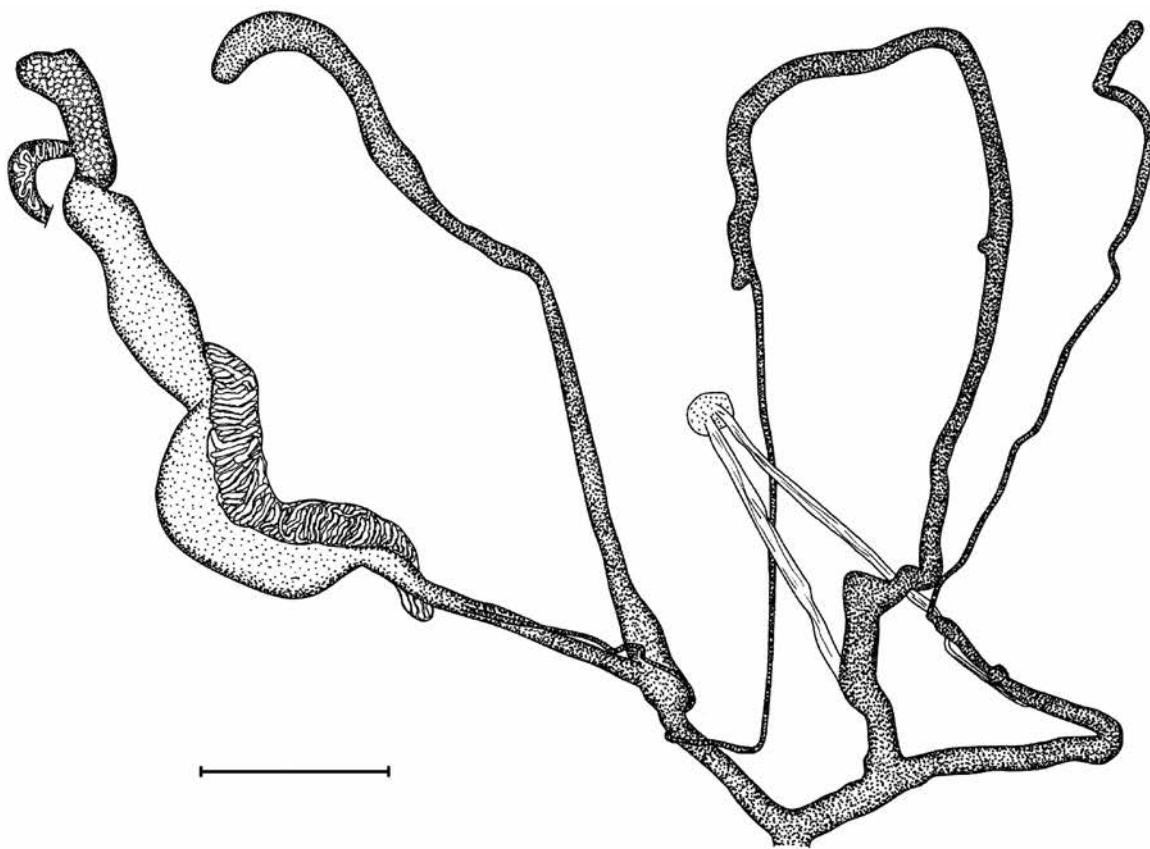


**Fig. 1 (above).** Genital system of *Imparietula leucodon* (L. Pfeiffer, 1846). Vil. Trabzon, Çatak, at Çatak-2 bridge, 400 m (rocks). Scale bar represents 2 mm.

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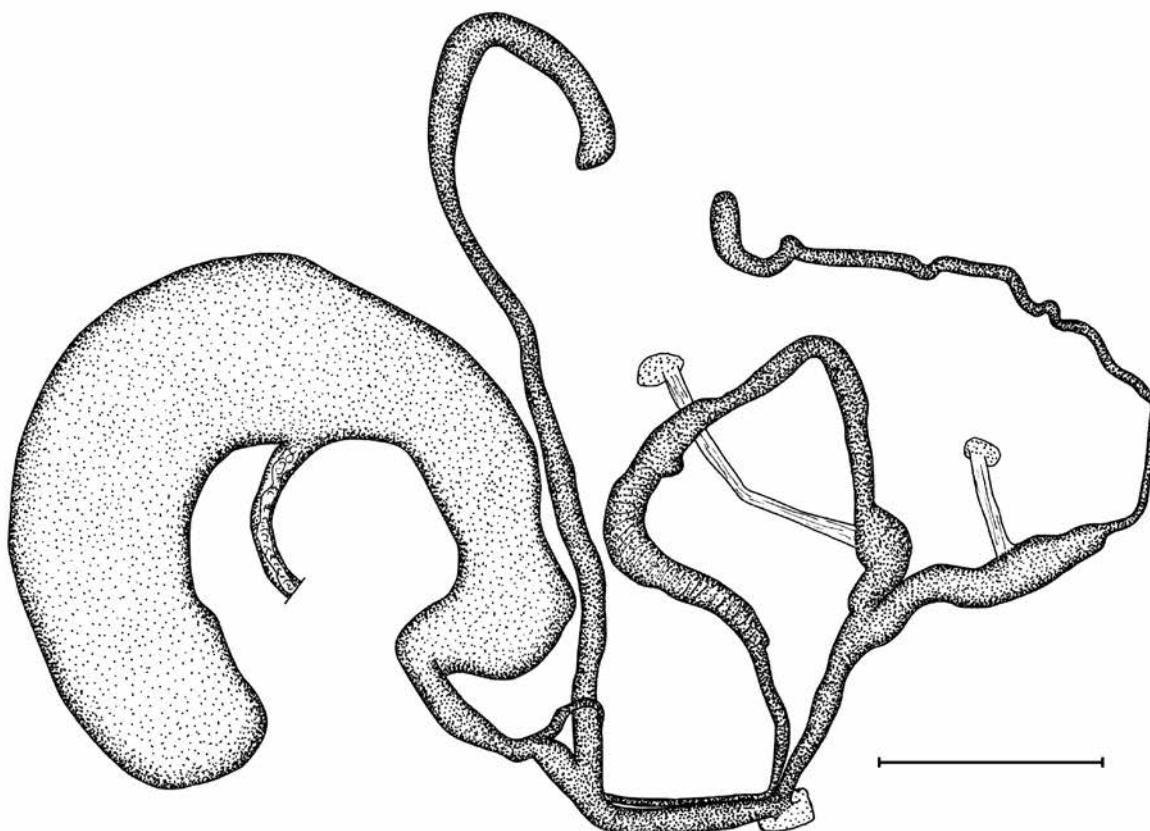
**Fig. 2 (below).** Genital system of *Imparietula pelidne* (Biggs, 1946). Vil. Trabzon, 4 km S of Hamsiköy, 1405 m. Scale bar represents 2 mm.

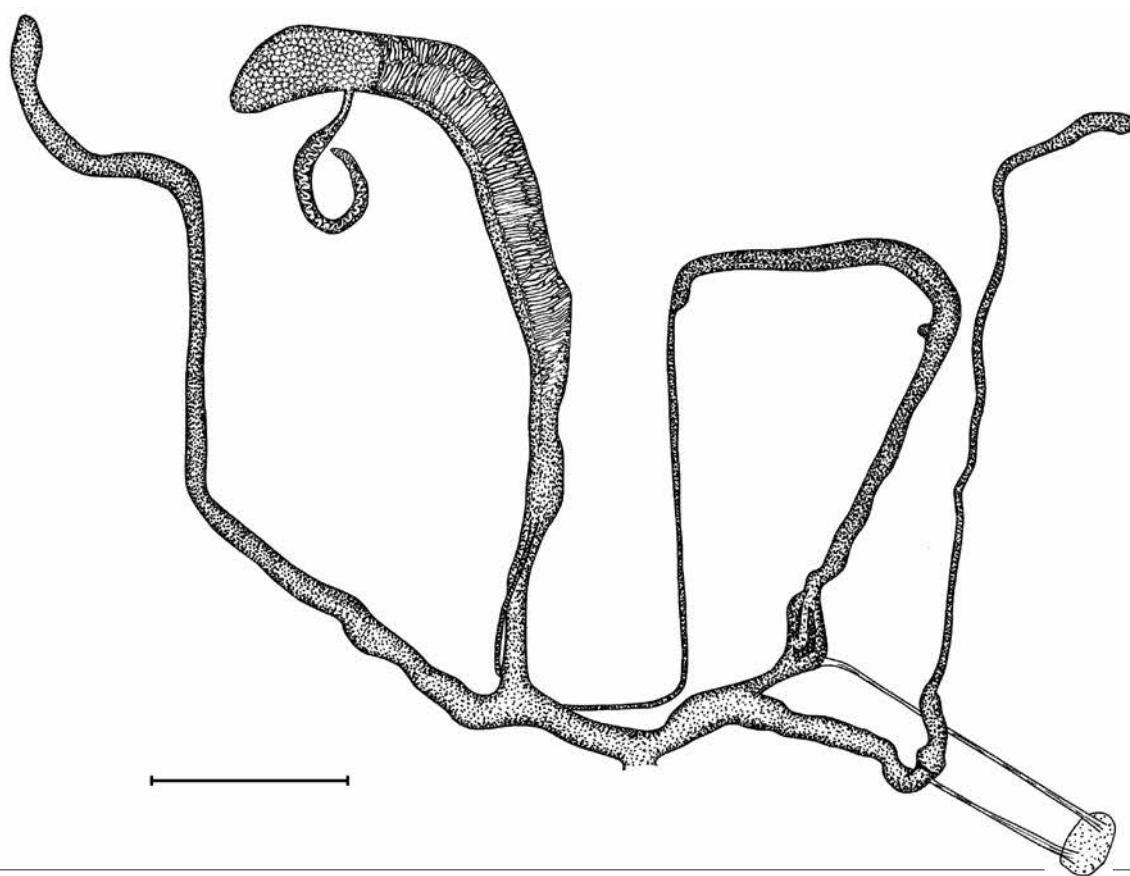




**Fig. 3 (above).** Genital system of *Imparietula ridvani* Schütt, 1995. Vil. Artvin, 1 km S of Kinalıçam (towards Erzurum) (sinistral specimen). Scale bar represents 2 mm.

**Fig. 4 (below).** Genital system of *Pseudochondrula armeniaca armeniaca* (Mortillet, 1854). Vil. Erzurum, İspir, castle hill, NW-part (sinistral specimen). Scale bar represents 2 mm.

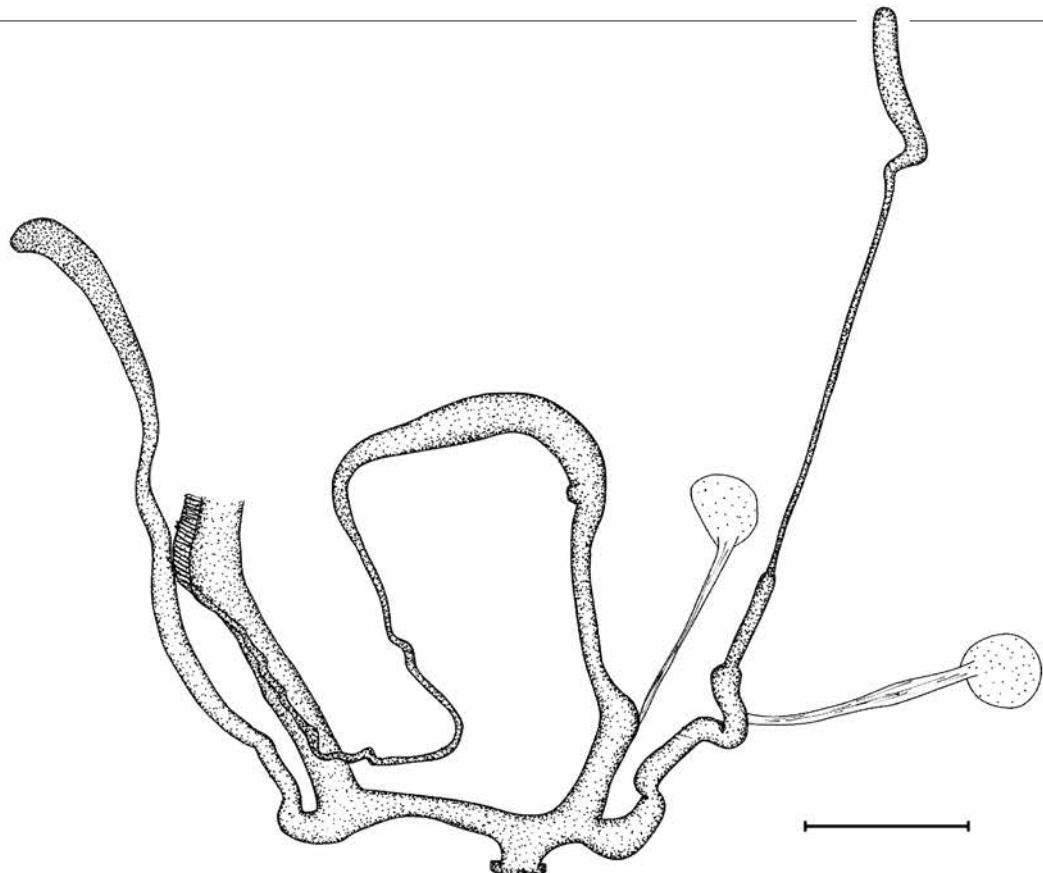


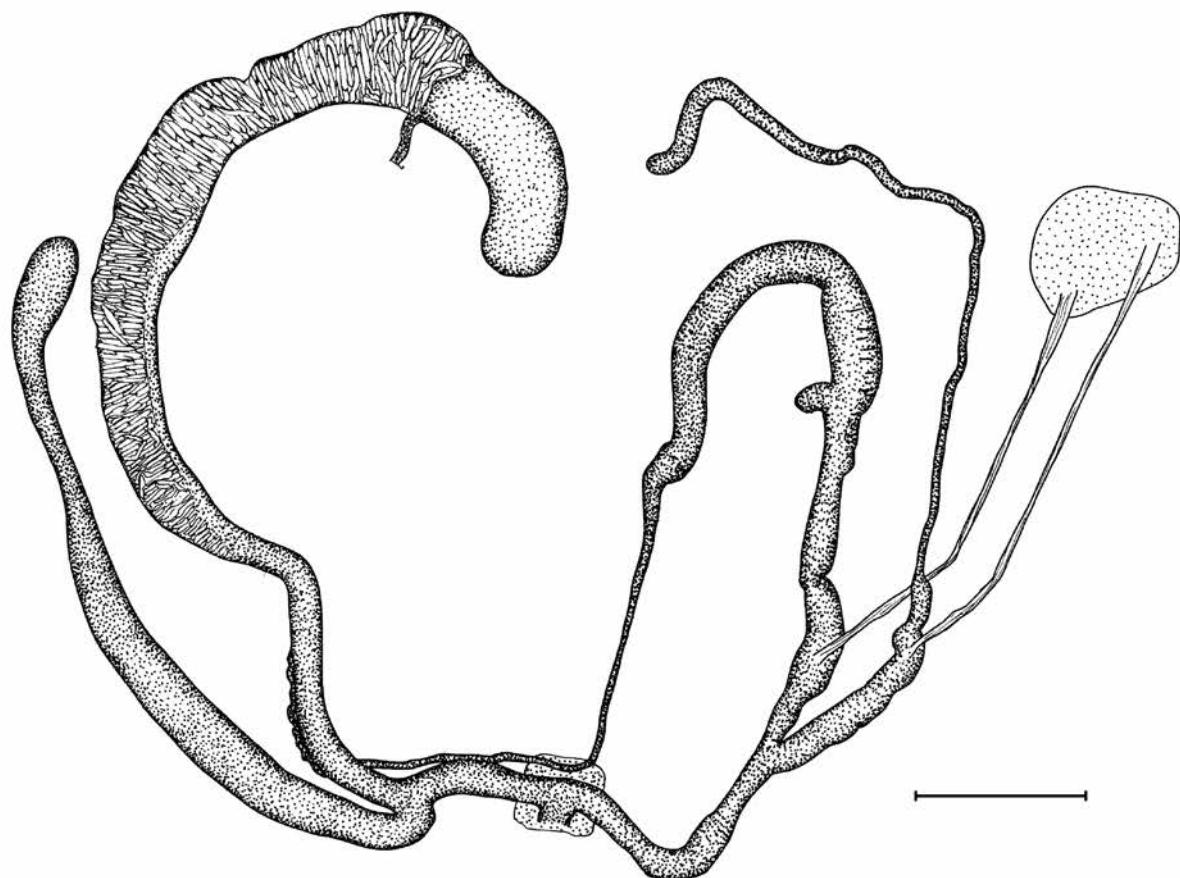


**Fig. 5 (above).** Genital system of *Pseudochondrula armeniaca armeniaca* (Mortillet, 1854). Vil. Artvin, 1 km N of Havuzlu junction (Erzurum--Artvin road), 50 m (rocks) (dextral specimen). Scale bar represents 2 mm.

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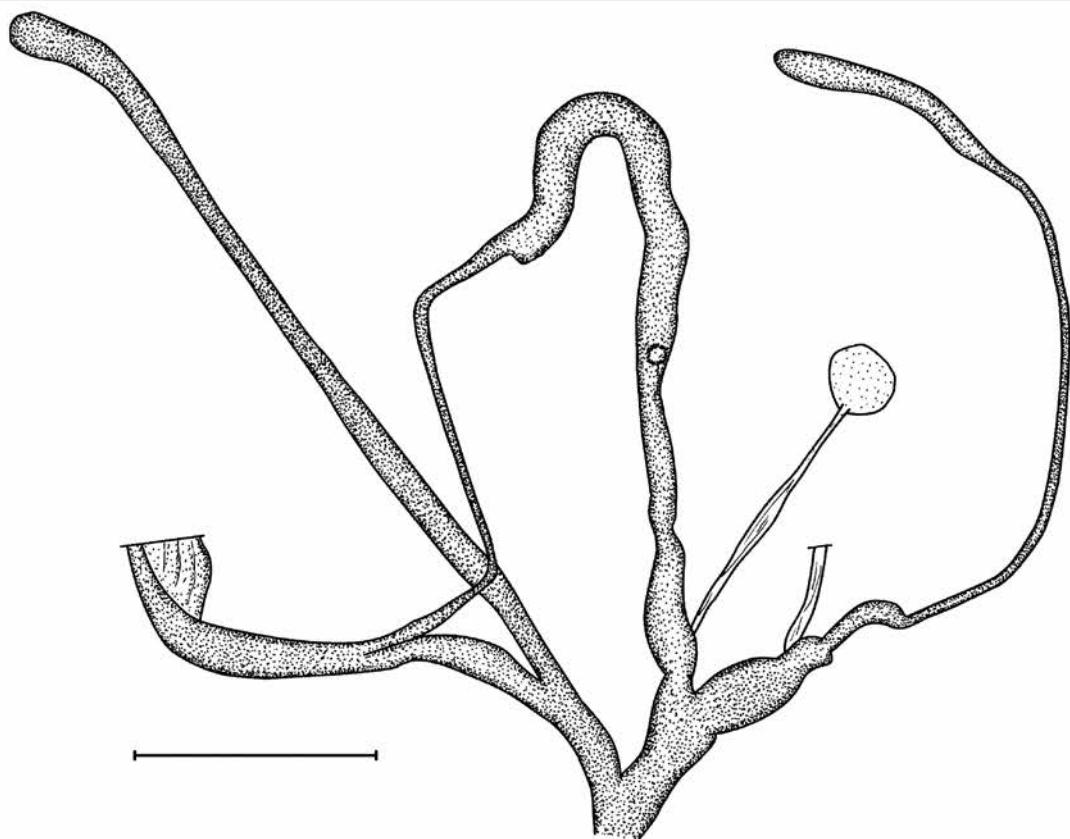
**Fig. 6 (below).** Genital system of *Pseudojaminia blanda* (L. Pfeiffer, 1853). Vil. Bayburt, 5 km N of Bayburt, 1525 m (rocks). Scale bar represents 2 mm.

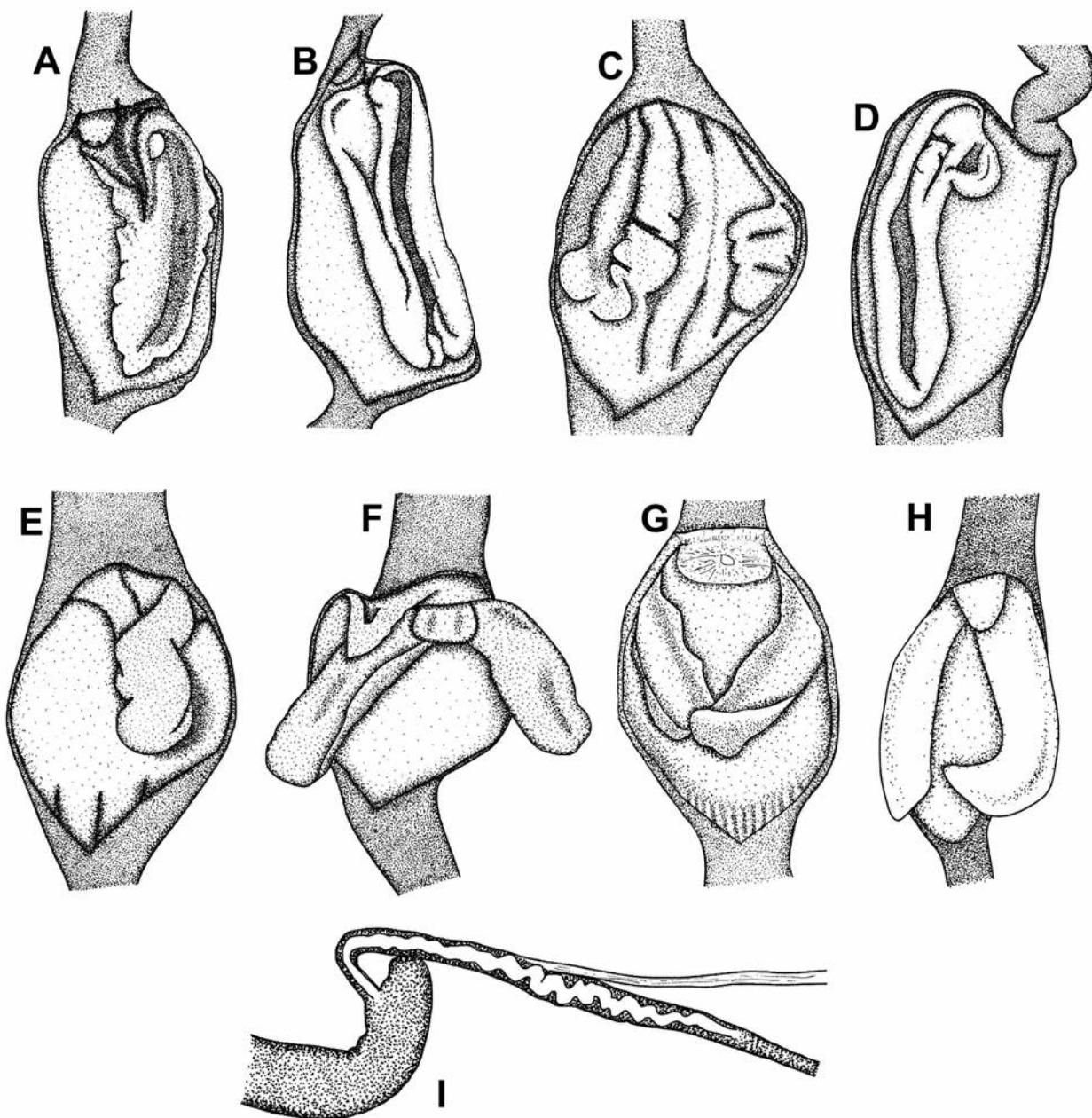




**Fig. 7 (above).** Genital system of *Pseudojaminia arctespira* (Mousson, 1874). Vil. Tunceli, N of Tunceli, 990 m a.s.l. Scale bar represents 2 mm.

**Fig. 8 (below).** Genital system of *Pseudojaminia seductilis scapa* (L. Pfeiffer, 1853). Vil. Bayburt, between Aşkale and Bayburt, about 7 km from Aşkale, 1630 m a.s.l. Scale bar represents 2 mm.





**Fig. 9.** Inner structure of the penis (A–H) and flagellum of Turkish Enidae (not to scale). (A) *Imparietula leucodon*; (B) *Imparietula altenai*; (C) *Imparietula pelidne*; (D) *Imparietula ridvani*; (E) *Pseudochondrula armeniaca armeniaca*; (F) *Pseudojaminia arctespira*; (G) *Pseudojaminia se-ductilis scapa*; (H) *Pseudojaminia blanda*. (I) *Imparietula altenai*, TR, Vil. Trabzon, Hamsiköy, along the road to Çirali Köyü, 1262 m (rocks).

what complicated, and one of the divided parts branches off to three branches. Epiphallar caecum small, rounded, papilla-like; flagellum present but short, blunt.

**Remarks.** – This species can be either dextral or sinistral and is known from the Vilayet Erzurum (Turkey) only.

#### *Anatolya* gen. nov.

Type species (by monotypy): *Buliminus (Petraeus) brevior* Mous-  
son, 1876.

**Diagnosis.** – The genital system lacks a diverticulum, the spermathecal reservoir is voluminous, the epiphallar caecum is located in the middle of the epiphallus, a normal penis appendix is present, the penis is short but markedly thickened, the penial papilla is covered with irregular folds and narrow grooves, and the inner surface of penis is decorated with a circular fold or with vestigial V-shaped pilasters. The middle-sized shell is dextral without any apertural barriers (or with an indistinct thickening at the height of the palatalis superior).

**Remarks.** – The type species has mostly been

placed within *Imparietula*. However, in *Imparietula* a penial papilla is missing, the penis is more slender, and the inner surface of the penis is decorated with a large lobe that is divided in the middle.

Derivatio nominis. – Named after the Russian malacologist Anatoly Schileyko, who contributed so much to our knowledge of the Enidae.

*Anatolya brevior* (Mousson, 1876) (Pl. 1 Figs 13-14)

*Buliminus (Petraeus) brevior* Mousson, 1876: 34-35, pl. 2 fig. 5 (shell). Type locality: "éjections de l'Araxe supérieur".  
*Buliminus brevior* – Kobelt, 1877: 72-73, pl. 137 fig. 1364 (shell).  
*Chondrulus brevior* var. *viator* Westerlund, 1897: 44. Type locality: "Erivan".  
*Chondrula brevior* – Kobelt, 1899: 599, pl. 92 figs 7-8 (shell – copy from Kobelt, 1877)  
*Pseudochondrula brevior* – Hesse, 1933: 172, fig. 14 (genitals).  
*Imparietula brevior* – Forcart, 1940: 226-227, pl. 2 fig. 58 (shell); Akramowski, 1976: 156, fig. 71A (genitals), pl. 7 fig. 76 (shell); Schileyko, 1984: 307-308, fig. 219/I (shell), 220 (genitals); Sysoev & Schileyko, 2009: 59, fig. 24A (shell).  
*Spaniodonta brevior* – Schileyko, 1998: 208, fig. 257C (shell), 257D-E (genitals – copy from Schileyko, 1984).

Remarks. – Hudec & Lezhawa (1967: 75-77, fig. 3, pl. 1 fig. 2) described under *Imparietula brevior* the anatomy of a species from Georgia ("Gebirgskamm Trialetskij chrebet im Kleinen Kaukasus") (= Trialetis Kedi in Samtsche-Dzjavacheti). However, the depicted shell belongs to the taxon *lederi* O. Boettger, 1883 (considered a synonym of *brevior* by Hudec & Lezhawa), a species that is restricted to Georgia (it was originally described from "Ezeri", about 43.0185°N 42.564°E). The anatomy that Hudec & Lezhawa describe is remarkable, as a small diverticulum is present, which was not found by Schileyko (1984: 292-294, fig. 208/I-III); also the penial appendix shown by Hudec & Lezhawa is extremely long. The concept of *brevior* by Schütt (2010: 99) is also wrong, as he synonymized *lederi* and *tuberifera* O. Boettger, 1879, with *brevior*, although both *lederi* and *tuberifera* are species on their own (e.g. Sysoev & Schileyko, 2009: 62, 63). Also the shell shown by Schütt does not seem to fit with *brevior*.

*Anatolya brevior* is known from Turkey (Vilayets Ağrı, Artvin, Erzincan, Gümüşhane and Van), as well as from Georgia and Armenia. It is likely that it also lives in the most northwestern part of Iran, but it has so far not been recorded from this country.

*Pseudochondrula* P. Hesse, 1933

*Pseudochondrula* P. Hesse, 1933: 152, 167-168. Type species (by original designation): *Buliminus florenskii* Rosen, 1914.

As is the case with *Imparietula*, the story with respect to *florenskii* (the type species of *Pseudochondrula*) is confusing. Hesse (1933: 171) considered it a species of its own, whereas Forcart (1940: 209-210) treated it as a subspecies of *armeniaca*. Schileyko (1978a: 521; 1978b: 845; 1998: 205) synonymized *florenskii* with *seductilis*. This opinion was maintained by Schileyko (1984: 289) and Sysoev & Schileyko (2009: 63), and added also *armeniaca* as a synonym to *seductilis*. In contrast, *florenskii*, *armeniaca* and *seductilis* are treated as full species by Schütt (2010: 92, 94, 95). Other Turkish taxa that have often been assigned to *Pseudochondrula* are *tetrodon* (e.g. Schileyko, 1984: 290-292; Bank & Neubert, 1998: 81; Schütt, 2010: 96) and *blanda* (e.g. Bank & Neubert, 1998: 81; Schütt, 2010: 92).

The anatomical characterization of *Pseudochondrula* with respect to the internal morphology of the penis is based on *seductilis* as described by Schileyko [1978a: 521, fig. 5-II; copied by Schileyko (1984: 289-290, fig. 206 and Schileyko (1998: 205, fig. 254B-C)]. During a conchological revision of the Turkish Enidae by Bank et al. (in preparation) it was found that *seductilis* and *armeniaca* are two different species, and that *florenskii* is a subspecies of *armeniaca*. The external morphology of the genital system of *florenskii* has been described by Hesse (1933: 171, fig. 13). Below we describe the anatomy of the nominotypical *armeniaca* in detail, and show that *seductilis* belongs, together with *blanda* and *tetrodon*, to a hitherto undescribed genus, which we name *Pseudojaminia* gen. nov. (see below). The genus *Pseudochondrula* as we define it currently consists of a single taxon only, the polytypic *armeniaca*.

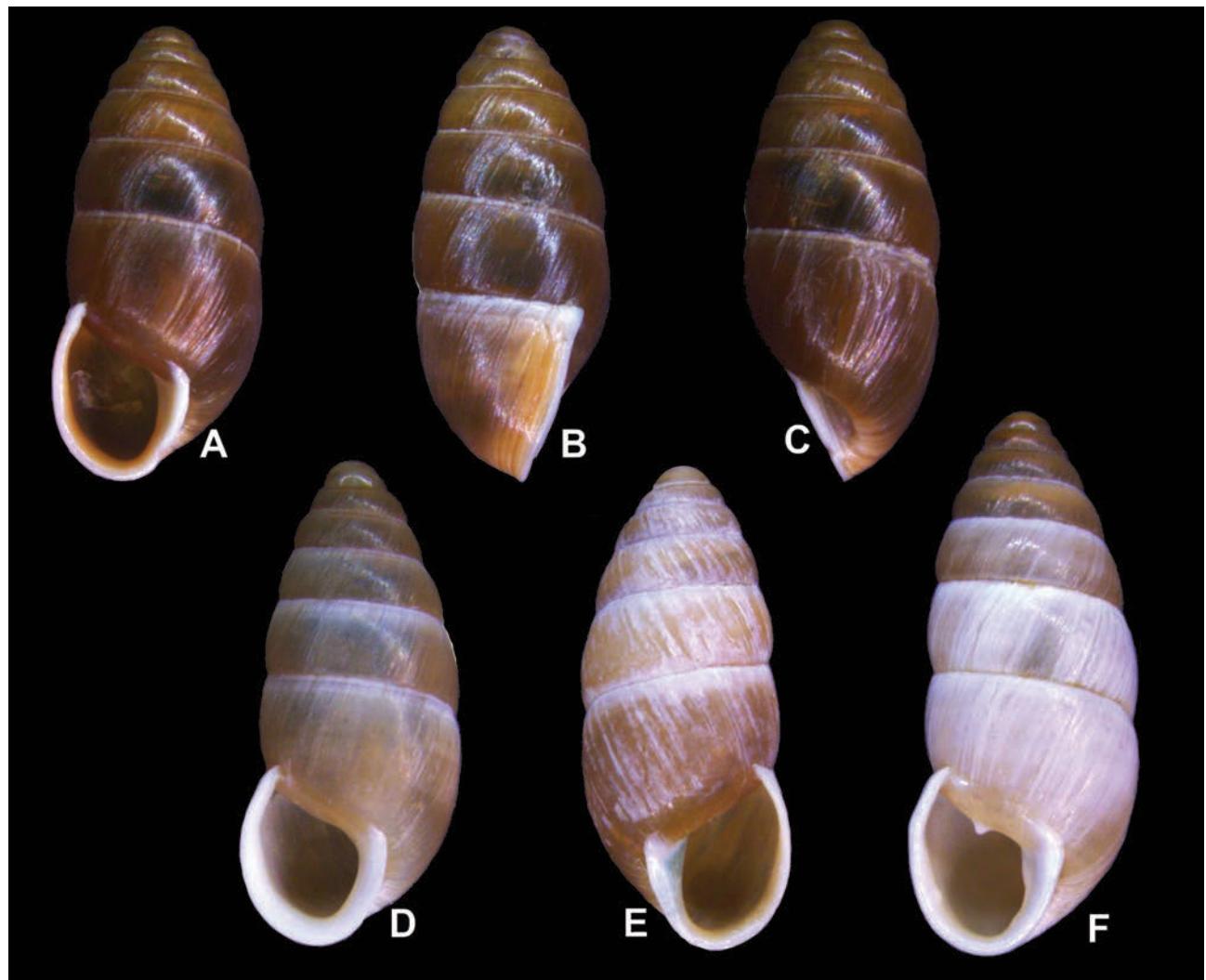
*Pseudochondrula* should anatomically be characterized as follows: the genital system lacks a diverticulum, the spermathecal reservoir is somewhat swollen, the epiphallar caecum is approximately located in the middle of the epiphallus, a normal penis appendix is present, the penis is relatively slender, a penial papilla is absent, and the inner surface of the penis is decorated with a single, elongated, fleshy lobe, which is free from the penial wall. The rather large shell is dextral or sinistral with a prominent palatalis superior, a well-developed parietalis and a mostly well-developed columellaris.

*Pseudochondrula armeniaca armeniaca* (Mortillet, 1854)  
(Figs 4-5, 9E; Pl. 1 Figs 7-9)

*Bulimus (Pupa) seductilis* var. *armeniaca* Mortillet, 1854: 8. Locus typicus: "Ispir, pachalick d'Erzéroum, sur les débris de la citadelle".

*Buliminus (Chondrula) kollyi* Retowski, 1889: 249-250. Type locality: "im Auswurfe des Tschorok bei Batum".

*Chondrula kollyi* – Kobelt, 1903: 35-36, pl. 283 fig. 1819 (shell, holotype)



**Fig. 10.** *Pseudojaminea seductilis scapa* from Vil. Bayburt, between Aşkale and Bayburt, about 7 km from Aşkale, 1630 m a.s.l. (A-C) typical shells; (D) light coloured shell; (E) dextral individual (2 shells out of 229); (F) rare individual with weakly developed teeth (only 3 shells out of 124).

*Imparietula armeniaca armeniaca* – Forcart, 1940: 209, pl. 2 fig. 40 (shell, synotype).

*Pseudochondrula armeniaca* – Schütt, 1995: 161, pl. 1 fig. 2 (shell); Schütt, 2010: 92, figs a-b (shell).

*Pseudochondrula controversa* Schütt, 1995: 161-162, pl. 1 fig. 1 (shell). Type locality: "Türkei: Vilayet Artvin, Su kavusumu bei Yusufeli am Zusammenfluß des Çoruh Nehri mit dem durch den Tortum Çay verstärkten Oltu Çay".

*Pseudochondrula controversa* – Schütt, 2010: 94 + fig. (shell, paratype).

Genital system. – Two specimens were examined: one sinistral specimen of typical *armeniaca* (TR, Vil. Erzurum, İspir, castlehill, NW-part, 40°28'55.52"N, 40°59'45.79"E, leg. Páll-Gergely, 05.vi.2011) and another of "*controversa*" (dextral specimen) (TR, Vil. Artvin, 1 km N of Havuzlu junction (Erzurum--Artvin road), 50 m (rocks), 40°51.530'N, 41°41.891'E,

leg. Fehér, Ishibe, Ohara, Okubo, Otani & Páll-Gergely, 10.vii.2012) were anatomically examined. The penial appendix inserts close to the base of the penis; internal penial wall with a single, elongated, fleshy lobe, which is free from the penial wall. Epiphallar caecum small, rounded, papilla-like; flagellum extremely short, only slightly indicated.

Remarks. – The nominotypical subspecies, which is both sinistral and dextral, is known from a few localities in the Vilayets Artvin, Erzurum and Gümüşhane (Turkey) only, namely in the Çoruh Nehri valley from Arpalı to Artvin. At the type locality of *controversa* both sinistral and dextral specimens were collected, although Schütt did not mention this in his original description of *controversa*. A sinistral specimen from Su Kavuşumu was figured by Schütt (2010: 92, fig. b) under the name *armeniaca*, whereas in the same book a dextral specimen from

the same locality (paratype!) was figured on page 94 under the name *controversa*. There can be no doubt that the dextral *controversa* is the same as the dextral *kollyi*. The latter taxon was not known by Schütt, who (2010: 96) wrongly synonymized it with *tetrodon*, apparently following Schileyko (1984: 291) and Sysoev & Schileyko (2009: 63).

*Pseudochondrula armeniaca florenskii* (Rosen, 1914)  
(Pl. 1 Figs 10-11)

*Buliminus florenskii* Rosen, 1914: 188-189, pl. 2 fig. 10 (shell). Type locality: "bei Ardanuç".

*Pseudochondrula florenskii* – Hesse, 1933: 171, fig. 13 (genitals).

*Imparietula armeniaca florenskii* – Forcart, 1940: 209-210, pl. 2 fig. 41a-b (shell, syntype).

Genital system. – A juvenile specimen (TR, Vil. Artvin, 1 km S of Ardanuç, 41° 07.673' N 42° 03.165' E, leg. Páll-Gergely, 06.vi.2011) was examined, which had a blunt, low epiphallar caecum and lacked a flagellum; the inner wall of penis was not examined, because the whole genital system was insufficiently developed.

Remarks. – The subspecies *florenskii*, which is both sinistral and dextral, is known from the surroundings of Ardanuç only (Vilayet Artvin, Turkey). It should be stressed that the concept of *florenskii* by Schütt (2010: 94, figs a-b) is wrong; the shells on the picture, that were collected far away from Ardanuç, belong to *Pseudojaminia arctespira*.

***Pseudojaminia* gen. nov.**

Type species (by original designation): *Bulimus blandus* L. Pfeiffer, 1853.

Diagnosis. – The genital system lacks a diverticulum, the spermathecal reservoir is hardly to markedly swollen, the epiphallar caecum is located in the middle of the epiphallus or slightly subterminal, a normal penis appendix is present, the penis is relatively slender, a penial papilla is absent, and the inner surface of the penis is decorated with two parallel, V-shaped lobes that are partially attached to the penis wall. The medium-sized to rather large shell can be sinistral or dextral. The shell can have a palatalis superior, a parietalis and a columellaris. However, all these apertural folds can be absent or highly reduced, even within a single species (e.g. *tetrodon*, see Bank & Neubert, 2016: pl. 6 figs 6-9). The columellaris is, when present, situated as an oblique triangle at the basal part of the columellar peristome. In some species a robust columellar ledge is present.

Notes. – The following species are, based on the genital system, assigned to *Pseudojaminia*: *blanda* (L.

Pfeiffer, 1853), *arctespira* (Mousson, 1874), *seductilis* (Rossmässler, 1837), *tetrodon* (Mortillet, 1853), *lederi* (O. Boettger, 1883), *tuberifera* (O. Boettger, 1879) and ?*sinistrorsa* (Kokotschashvili & Schileyko, 1984). In the Georgian species *sinistrorsa* the V-shaped lobes are less well developed. The Iranian taxon *purus* Westerlund, 1890 seems to belong to *Pseudojaminia* as well, but so far only shells are known.

Derivatio nominis. – Sinistral shells of *Pseudojaminia* often resemble those of the true *Jaminia* species (*quadridens* O.F. Müller, 1774; *loewii* Philippi, 1844; *thiesseanus* Westerlund, 1879).

*Pseudojaminia blanda* (L. Pfeiffer, 1853)  
(Figs 6, 9H)

*Bulimus blandus* L. Pfeiffer, 1853b: 149. Type locality: "prope Amasia".

*Chondrula hedjinensis* Kobelt, 1907: 34, pl. 348 fig. 2165 (shell).

Type locality: "bei Hedschine in Cilicien". Note: a syntype has been figured by Forcart (1940: pl. 2 fig. 43a-b) as *Imparietula blanda hedjinensis*.

*Buliminus (Chondrulus) scapus* var. *cylindrata* Nägele, 1906: 27.

Type locality: "Balian-Keuy, Euphr. super.". Note: a syntype has been figured by Forcart (1940: pl. 2 fig. 54a-b) as *Imparietula seductilis cylindrata*.

*Buliminus (Chondrulus) antitauricus* Nägele, 1910: 150. Type locality: "Antitaurus in Cilicien". Nomen nudum.

*Imparietula blanda sebasteana* Forcart, 1940: 212-214, fig. 9 (genitals), pl. 2 fig. 45 (shell). Type locality: "Strasse Sivas-Malatya ca. 5 km von Sivas entfernt, 1350 m ü. M."

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Genital system. – Two dextral specimens were examined (TR, Vil. Bayburt, 5 km N of Bayburt, 1525 m (rocks), 40°18.119'N, 40°13.814'E, leg. Fehér, Ishibe, Ohara, Okubo, Otani & Páll-Gergely, 07.vii.2012). The penial appendix inserts close to the base of the penis; internal penial wall with two independent, parallel lobes having rather pointed ends; the proximal part of these lobes are attached to the penial wall; additionally to these, there is a blunt, small, rather pointed "velum" (cf. Schileyko's drawing of *P. seductilis*) at the border with the epiphallus; the opening of the epiphallus is "under" the velum. Epiphallar caecum small, papilla-like; flagellum not found.

Remarks. – The genital system of *P. blanda* has previously been investigated by Forcart (1940: 212-213, fig. 9 – as *Imparietula blanda sebasteana*). The shell of *P. blanda* is extremely variable; both sinistral and dextral populations occur. The identity of *Imparietula blanda lycia* FORCART, 1942 (type locality: "Vilayet Antalya, zwischen Elmali und Oberli, 1100-1300 m ü. M.") needs verification; this taxon is most likely a synonym of *Orculella bulgarica bulgarica* (P. Hesse, 1915).

*Pseudojamina arctespira* (Mousson, 1874)  
(Figs 7, 9F; Plate 1 Fig. 12)

*Chondrus arctespira* Mousson, 1874: 29-30. Type locality: "entre Haleb et Biredschek, à Nisib et jusqu'à Siverek".

*Chondrus blandus vasvarii* H. Wagner, 1938: 771. Type locality: "Malatya".

*Imparietula blanda arctespira* – Forcart, 1940: 214-215, pl. 2 figs 46-47 (shell; 47 = syntype *vasvarii*).

*Pseudochondrula arctespira* – Schütt, 2010: 91, figs a-c.

Genital system. – One dextral specimen was examined (TR, Vil. Tunceli, N of Tunceli, 990 m a.s.l., 39° 11.547' N 39° 42.318' E, leg. Páll-Gergely & Németh, 04.vi.2011). The penial appendix inserts far from the base of the penis; internal penial wall with two independent, parallel lobes having rather pointed ends; the proximal part of these lobes are attached to the penial wall; additionally to these, there is a blunt, small "velum". Epiphallar caecum relatively well-developed, somewhat elongated, blunt; flagellum not found.

Remarks. – As is the case with *P. blanda*, this species can be both sinistral and dextral in the same population (see also Schütt, 2010: 91, figs b-c). The shells designated by Schütt (2010: 94, figs a-b) as *Pseudochondrula florenskii* belong to *Pseudojamina arctespira*.

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*Pseudojamina seductilis scapa* (L. Pfeiffer, 1853)  
(Figs 8, 9G, 10A-F)

*Bulimus scapus* L. Pfeiffer, 1853a: 358-359. Type locality: "in Asia minore".

*Bulimus sagax* L. Pfeiffer, 1853b: 148-149. Type locality: "prope Amasia Asiae minoris".

*Buliminus (Chondrula) incertus* Retowski, 1883: 55. Type locality: "am Strande bei Sudak .... im Anspüllicht des Meeres".

*Buliminus (Chondrulus) moveradi* Westerlund, 1892: 35-36. Locus typicus: "Kleinasien, bei Angora".

*Chondrulus incertus* var. *proprius* Westerlund, 1897: 55. Type locality: "Persia ad Tokat".

Genital system. – Two sinistral specimens were examined (TR, Vil. Bayburt, between Aşkale and Bayburt, about 7 km from Aşkale, 1630 m a.s.l., 39°56.473'N, 40°36.763'E, leg. Páll-Gergely, 05.vi.2011). The penial appendix inserts close to the base of the penis; internal penial wall with two independent, parallel lobes having rather pointed ends; additionally to these, there is a blunt, small "velum". Epiphallar caecum very small, papilla-like; flagellum small, only indicated.

Remarks. – The genital system of *P. seductilis scapa* has previously been investigated by Hesse (1933: 169,

fig. 10 – as *Pseudochondrula scapus*). The genital system of the nominotypical subspecies has been reported by Hesse (1933: 173, fig. 15A-C), Akramowski (1976: 158, fig. 71D), Schileyko (1978: 521, fig. 5/2 – copied by Schileyko, 1984: fig. 206 and Schileyko, 1998: fig. 254B-C), and Grossu (1987: 346-347, fig. 206).

*Pseudojamina seductilis* is a polytypic species. In Turkey, three subspecies are living: *P. seductilis seductilis*, *P. s. scapa*, and *P. s. komarowi* (O. Boettger, 1880). A synonym of the latter is *Buliminus (Chondrula) lindholmi* Retowski, 1915 (type locality: "prope Artvin"). A syntype of *komarowi* has been figured by Forcart (1940: pl. 2 fig. 55a-b).

*P. seductilis scapa* usually lives in rocky areas; its shell can be both sinistral and dextral. The shell does not vary much within a single population, but there can be major differences in slenderness or apertural barriers. A well-developed parietalis, palatalis and columellaris can be present, but populations occur with a reduced armature, or that lack one, two or all three apertural barriers. We encountered a well-delimited form of *P. seductilis scapa* from the following localities: (1) Vil. Bayburt, Masat, meadow along the road, 1720 m a.s.l., 40°11.392'N, 40°26.901'E, leg. Németh & Páll-Gergely, 04.vi.2011 (> 70 ex.); (2) Vil. Bayburt, between Aşkale and Bayburt, about 7 km from Aşkale, 1630 m a.s.l., 39°56.473'N, 40°36.763'E, leg. Németh & Páll-Gergely, 05.vi.2011 (> 220 ex.); (3) Vil. Erzurum, 7 km NW of Aşkale, 1652 m, 39°56.472'N, 40°36.395'E, leg. Fehér, Ishibe, Ohara, Okubo, Otani & Páll-Gergely, 08.vii.2012 (11 ex.); Vil. Bayburt, S of Çalidere (10 km S Maden), 1760 m, 40°06.724'N, 40°25.444'E, leg. Fehér, Ishibe, Ohara, Okubo, Otani & Páll-Gergely, 08.vii.2012 (1 ex.). This form is interesting because nearly all specimens lack apertural barriers (see Fig. 10), and because it inhabits wet meadows together with other hygrophilous species, such as *Succinella oblonga* (Draparnaud, 1801), *Zonitoides nitidus* (O.F. Müller, 1774), *Pseudotrichia rubiginosa* (Rossmässler, 1838) and *Orculella bulgarica* (P. Hesse, 1915). We consider this form an ecophenotype of *Pseudojamina seductilis scapa*, but further studies should be performed, e.g. with the help of sequencing, to decipher whether this statement is correct.

#### ACKNOWLEDGEMENTS

We are grateful to Ir. Henk P.M.G Menkhorst (Krimpen aan de IJssel) for placing his collected material from Turkey at the disposal of the second author, and to Dr. Ronald Janssen (Senckenberg Natural History Museum, Frankfurt am Main) for allowing the second author to study type material of *Imparietula ridvani* and *Pseudochondrula controversa*. The photo-

graphs of plate 1 in this work have been taken/ processed by MSc. Estée Bochud and Dr. Eike Neubert (NMBE) which we greatly acknowledge here.

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