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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.

Introduction

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; Sestria Bourguignat, 1884); Pene Pallary, 1929; Paramastus P. Hesse, 1933 (with the subgenus Cyrenaecus 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 Chondrulini Wenz, 1923, the Multidentulini Schileyko, 1978, and the Enini. The Chondrulini 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 Multidentulini 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: *Thoantaeus* Lindholm, 1925; *Peristoma* Krynicki, 1833, *Caucasicola* P. Hesse, 1917 (synonym: *Medea* O. Boettger, 1883 [non Eschscholtz, 1825]; *Helle* P. Hesse, 1916 [non Osten-Sacken, 1896]); *Zebrina* Held, 1838 (synonym: *Zebrina* Westerlund, 1887); *Georginapaeus* Schileyko, 1998; *Rhabdoena* Kobelt & Moellendorff, 1902; *Chondrus* Cuvier, 1817 (synonym: *Antichondrus* Lindholm, 1925); *Brefhulopsis* 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; *Eucere* Charpentier, 1837; *Chondrula* Westerlund, 1887; *Dentistomus* M. von Kimakowicz, 1890); *Mastus* Beck, 1837 (synonyms: *Pseudomastus* O. Boettger, 1889; *Amphitrorsus* M. von Kimakowicz, 1890); *Meijeriella* Bank, 1985 (synonym: *Bolunastus* Örstan & Yıldırım, 2004) and *Eubrefhulus* 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; *Impariva* Schileyko, 1978; *Senaridenta* Schileyko, 1978); *Chondrulopsisina* Lindholm, 1925; *Siraphoroides* Schileyko, 1977; *Pentadentula* Suvorov, 2006 and *Meraligera* 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 *Impariva* Lindholm, 1925, and *Pseudochondrula* P. Hesse, 1933.

The type species of *Impariva* and *Pseudochondrula* is *Balimus leucodon* L. Pfeiffer, 1846, and *Balimus florenski* Rosen, 1914, respectively. *Balimus leucodon* is a species known from a restricted area in the north-eastern part of Turkey (Vilayets Trabzon and Rize), whereas *Pseudochondrula armeniaca florenski* lives in a small area around Ardanuç in the Vilayet Arvin. The outer morphology of the genital system of *florenski* 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 *Impariva* 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 *Impariva* 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)

*Impariva* Lindholm, 1925

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

The history regarding the identity of *leucodon*, the type species of *Impariva*, is complex. Forcart (1940 : 206) synonymized *Balimus* (*Brefhulus*) *lasistianicus* Lindholm, 1914 with *leucodon*, although he did not possess shells of either *lasistianicus* or *leucodon*. The anatomy (jaw, radula, outer morphology of the genital system) of *lasistianicus* 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 *Impariva* based on this synonymy, and placed several taxa under *Impariva*, namely the monotypic taxa *leucodon*, *adjacra* Retowsky, 1914, *tetrodon* Mortillet, 1853, and *brevior* Mousson, 1876, as well as the polytypic taxa *blanda* L. Pfeiffer, 1853, *seductilis* Rossmässler, 1837, and *armeniaca* Mortillet, 1854. As a consequence, *Pseudochondrula* was considered a synonym of *Impariva* 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 *sieserisi* 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 & Møllendorff, 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. Syssoev & 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 *Imparietula*, 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, Schütz (2010: 97-99) included *altenai* and *leucodon* (and included *lasistanicus* as its synonym) and *brevior* into *Imparietula*, and included in addition *ridvani* Schütz, 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 terminal, 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).

*Bulimus 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* – Zülch, 1959: 183, fig. 630 (copy from Pfeiffer); Bank & Neubert, 1998: 81, fig. 8 (shell); Hausdorf, 1999: 153; Schütz, 2010: 98, figs a-d (shell) [partim, without lasistanicus as synnym].


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)

*Bulimus (Brephulus) lasistanicus* Lindholm, 1914: 36-38. Type locality: “In der näheren Umgebung von Lomaschen (Gouv. Batum)”.

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

ials).
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 Çay (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).

**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 rätsend), Vil. Erzurum, Tortum Şelâlesi near Çağlayan (H = 17.1 mm). **Fig. 3.** *Imparietula ridvani* Schütt, 1995, Vil. Erzurum, 9 km SW. Uzungere, 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 lasistonica* (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. Hamsiköy, 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 controverse!), Vil. Artvin, Su kavuşumu 4 km SW. Sebzeciler, near the outlet of the Otlu 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.1988 (H = 15.7 mm). **Fig. 12.** *Pseudojaminia arctespira* (Mousson, 1874), Vil. Tunceli, 13 km NE. Tunceli, Pulümür Çaylı, E. Neubert leg., 16.vii.1986 (H = 19.0 mm, dextral; H = 18.4 mm, sinistral). **Fig. 13.** *Anatolyla brevior* (Mousson, 1876), Zoologisches Museum Zürich #513649 (syntype brevior), Araxes, collection Mousson ex Sievers 1875 (H = 11.5 mm). **Fig. 14.** *Anatolyla 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 (NMHB).

Genital system. – One specimen was examined (TR, Vil. Trabzon, 4 km S of Hamsiköy, 1405 m, 40°13.323’N, 39°27.505’E, leg. Feher, Ishibe, Ohara, Okubo, Otani & Päll-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 Hamsiköy, 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, Hamsiköy, along the road to Çirali Köyü, 1262 m (rocks), 40°40.818’N, 39°28.953’E, leg. Feher, Ishibe, Ohara, Okubo, Otani & Päll-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 against the 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.

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 rideani* 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.

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 Ağskale and Bayburt, about 7 km from Ağskale, 1630 m a.s.l. Scale bar represents 2 mm.
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 Mousson*, 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 pilaisters. 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

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**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 pelidiæ*; (D) *Imparietula rideouti*; (E) *Pseudochondrula armeniaca armeniaca*; (F) *Pseudojaminia arctespira*; (G) *Pseudojaminia seductilis scapa*; (H) *Pseudojaminia blandula*. (I) *Imparietula altenai*, TR, Vil. Trabzon, Hamsi Köy, along the road to Çıralı Köyü, 1262 m (rocks).
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)

*Balimnus* (Petrus) *brevior* Mousson, 1876: 34-35, pl. 2 fig. 5 (shell). Type locality: "éjections de l'Araxe supérieur".

*Balimnus brevior* – Kobelt, 1877: 72-73, pl. 137 fig. 1364 (shell).

*Chondrula 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* – Hesse, 1933: 172, fig. 14 (genitals).

*Imparietula brevior* – Forcart, 1940: 226-227, pl. 2 fig. 58 (shell):

Akromowski, 1976: 156, fig. 71A (genitals), pl. 7 fig. 76 (shell); Schileyko, 1984: 307-308, fig. 219I (shell), 220 (genitals); Sysoev & Schileyko, 2009: 59, fig. 264A (shell).


Remarks. – Hudec & Lezhawa (1967: 75-77, fig. 3, pl. 1 fig. 2) described under *Imparietula brevior* the anatomy of a species from Georgia ("Gebirgskamm Trialeitkis chrebet im Kleinen Kaukasus") (= Trialeitis 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. 208I-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, Gümüşhan 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


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 columnellars.

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


*Balimnus* (*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)
Imparietula armeniaca armeniaca – Forcart, 1940: 209, pl. 2 fig. 40
(shell, synytype).
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 an-
other 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; fla-
gellum extremely short, only slightly indicated.
Remarks. – The nominotypical subspecies, which
is both sinistral and dextral, is known from a few lo-
calities in the Vilayets Artvin, Erzurum and
Gümüşhane (Turkey) only, namely in the Çoruh
Nehri valley from Arpalı to Artvin. At the type local-
ity of controversa both sinistral and dextral specimens
were collected, although Schütt did not mentioned
this in his original description of controversa. A sinis-
tral 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

Fig. 10. Pseudojaminia 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).
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 kolfy. The latter taxon was not known by Schütz, 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)

_Bulimus 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 Schütz (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 col umellaris peristome. In some species a robust columellar ledge is present.

Notes. – The following species are, based on the genital system, assigned to _Pseudojaminia: blandus_ (L.

Pfeiffer, 1853), _arctespira_ (Mousson, 1874), _seductilis_ (Rossmässler, 1837), _tetrodon_ (Mortillet, 1853), _lederi_ (O. Boettger, 1883), _tuberculosa_ (O. Boettger, 1879) and _sinistrosa_ (Kokotschashvili & Schileyko, 1984). In the Georgian species _sinistrosa_ 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; _thesisanus_ Westerlund, 1879).

_Pseudojaminia blandus_ (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 blandula hedjinensis_.

_Bulimus (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_.

_Bulimus (Chondrulus) antitauricus_ Nägele, 1910: 150. Type locality: "Antitaurus in Cilicien". Nomen nudum.

_Imparietula blanda sebastana_ Forcart, 1940: 212-214, fig. 9 (genitals), pl. 2 fig. 45 (shell). Type locality: "Strasse Sivas-Malaty ca. 5 km von Sivas entfernt, 1350 m ü. M."
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, 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; 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 *Pseudojaminia arctespira*.

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

*Baliminus scapus* L. Pfeiffer, 1853a: 358-359. Type locality: ‘in Asia minoris’.

*Baliminus sagus* L. Pfeiffer, 1853b: 148-149. Type locality: ‘prope Amassia Asiae minoris’.

*Baliminus* (*Chondrula*) *incertus* Retowski, 1883: 55. Type locality: ‘am Strande bei Sudak .... im Anspülicht des Meeres’.


*Chondrula* *incertus* var. *propris* 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* 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).

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

*P. s. 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, 04.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 Çalıdere (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* (O. Boettger, 1880). We consider this form an ecophenotype of *Pseudojaminia seductilis scapa*, but further studies should be performed, e.g. with the help of sequencing, to decipher whether this statement is correct.

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