

The genus *Ena* in Turkey, with remarks on its phylogenetic relationships (Gastropoda: Buliminidae)

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The Turkish species of *Ena* are revised. There are three species: *Ena nogellii* (Roth) is widespread in the western Pontic region of Turkey; *Buliminus ponticus* Retowski is a synonym of *Ena nogellii* (Roth); *Ena menkhorsti* Hausdorf and Bank, sp. n. is widespread in the eastern Pontic region of Turkey; *Ena dazimonensis*, sp. n. is restricted to the surroundings of Tokat. *Ena* is transferred from the Eninae *sensu* Schileyko into the Pseudonapaeinae Schileyko. Therefore, Pseudonapaeini Schileyko is a synonym of Enini Woodward and the Eninae *sensu* Schileyko must be called Chondrulini Wenz.

KEYWORDS: Gastropoda, Buliminidae, Ena, Turkey.

Introduction

Forcart (1940), in his pioneer monograph of the Buliminidae of Turkey, included five Turkish species in the genus Ena Turton, 1831, namely Ena (Ena) frivaldskyi (L. Pfeiffer, 1847), Ena (Ena) nogellii (Roth, 1850), Ena (Ena) andronakii (Lindholm, 1913), Ena (Sesteria) gallandi (Bourguignat, 1884) and Ena (Sesteria) biplicata (Retowski, 1889). Zilch (1959) separated Sesteria Bourguignat, 1884 (type species: Sesteria gallandi Bourguignat) and Clausilioides Lindholm, 1925 (type species: Buliminus biplicatus Retowski) from Ena as genera. They usually differ from Ena in the presence of a columellar lamella. The anatomy of *Sesteria gallandi* is unknown, while the external morphology of the genitalia of *Clausilioides biplicatus* has been described by Hesse (1933). However, the internal structures of the penis of *Clausilioides biplicatus*, which would be essential for its classification, are also unknown. Because of their divergent shell characters and their geographical distribution it is likely that Sesteria and Clausilioides are related neither to each other nor to Ena. Schütt (1993) quoted the data from Forcart (1940) on the species of Ena sensu stricto and added Ena (Ena) obscura (O. F. Müller, 1774) as an additional Turkish species. He neglected the fact that Schilevko (1984) had transferred Ena obscura to a distinct genus Merdigera Held, 1838. Furthermore, he overlooked that Bank (1985) had pointed out that Ena frivaldskyi probably belongs to Meijeriella Bank, 1985. Gittenberger and Menkhorst (1993) included Ena andronakii (= Turanena yusufelensis Gittenberger and Menkhorst, 1993; see Schütt, 1996) in Turanena Lindholm, 1922, while Schütt (1996) referred this species to Akramovskiella Schileyko, 1984. Finally, Schütt (1995) described a new species, Ena yildirimi Schütt, 1995 from Turkey. However, this species has a palatal tooth and does not belong to Ena but, like B. frivaldskyi, to Meijeriella (a revision of Meijeriella is in preparation by R. A. Bank, Hoofddorp). Thus, Ena nogellii (Roth) is at present the only Ena species known from Turkey.

In the following, it will be shown that *Ena nogellii sensu* Forcart is a composite species. Furthermore, it will be shown that *Buliminus ponticus* Retowski, 1887 which was included in *Mastus* by Forcart (1940) is a synonym of *Ena nogellii* (Roth). The three Turkish species of *Ena* will be described and their distribution data will be summarized. The phylogenetic relationships and the delimitation of *Ena* will be discussed.

Material and methods

The counting of the shell whorls follows Kerney and Cameron (1979: 13). The terms proximal and distal refer to the position in relation to the gonad. In the descriptions of the genitalia the division of the penial appendix in five sections as proposed by Schileyko (1984) is adopted. In the locality lists the localities are arranged according to vilayets (Turkish provinces). Within the vilayets the localities are ordered alphanumerically according to the UTM-code. The material on which this study is based is kept in the collections listed under the following abbreviations: FMNH, Field Museum of Natural History, Chicago; HAU, Collection B. Hausdorf; IZPAN, Polska Akademia Nauk, Instytut Zoologii, Warszawa; MEN, Collection H. P. M. G. Menkhorst; NBE, Collection E. Neubert; NMB, Naturhistorisches Museum, Basel; NNM, Nationaal Natuurhistorisch Museum, Leiden; SMF, Senckenberg-Museum, Frankfurt a. M.; ZMH, Zoologisches Museum der Universität Hamburg; ZSM, Zoologische Staatssammlung, München.

Additional abbreviations: alt.=altitude; D =shell diameter; det. anat.= anatomically determined; H =shell height; leg.=collected by; V.=Vilayet.

Systematics

Family BULIMINIDAE Kobelt, 1880

The family name Buliminidae Kobelt, 1880 (type genus *Buliminus* Beck, 1837) is a junior homonym of the name Buliminidae Jones, 1875 (Foraminifera, type genus *Bulimina* d'Orbigny, 1826). Therefore, Woodward (1903) replaced the name Buliminidae Kobelt, 1880 by Enidae Woodward, 1903. Nevertheless, the name Buliminidae Kobelt, 1880 is still being used by several authors (e.g. Schileyko, 1984; Hausdorf, 1994, 1999; Alonso *et al.*, 1995; Bank and Neubert, 1998). Bank and Neubert (1998) proposed a classification of the Buliminidae into two subfamilies, the Bulimininae and the Eninae. The Bulimininae include four genera for which no family-group name besides Buliminiae Kobelt, 1880 is available. Cases in which the homonymy between family-group names results from similarity but not identity of the names of their type genera are to be referred to the International Commission on Zoological Nomenclature for a ruling (Article 55.3 ICZN). In accordance with Article 55.3 ICZN, an amendment of the stem of Buliminidae Kobelt, 1880 will be applied for to the International Commission on Zoological Nomenclature to remove

the homonymy. If this application is successful, the name Buliminidae Kobelt, 1880 can be used further on (in the amended form) and no new replacement name for Bulimininae Kobelt, 1880 will be necessary. The existing usage is maintained pending a ruling of the Commission.

Subfamily ENINAE Woodward, 1903

Genus Ena Turton, 1831

Ena Turton, 1831: 80. Type species (Herrmannsen, 1847: 421): Bulimus montanus Draparnaud, 1801.

Diagnosis. A genus of Buliminidae which is characterized by a large, brownish, elongated oval shell without apertural teeth, the palatal insertion of the peristome which does not distinctly approach to the columellar edge, a usually well-developed imperforate penial papilla (which is rudimentary only in *Ena dazimonensis* sp. n.; see below), a penial appendix, the lack of a penial caecum, a caecum at the middle section of the epiphallus, a more or less short flagellum, and a diverticulum to the bursa copulatrix.

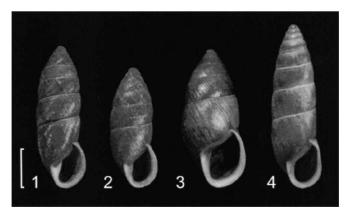
Ena nogellii (Roth, 1850)

(figures 1, 2, 5, 8, 13)

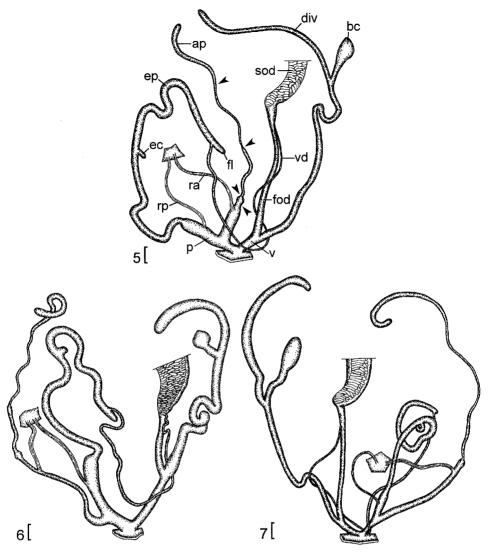
Bulimus Nogellii Roth, 1850: 341. Terra typica: 'Kolchis'.
Bulimus Nogelli [sic]: L. Pfeiffer, 1856: 56, pl. 16 figures 7, 8.
Buliminus (Petraeus) ponticus Retowski, 1886: 28, pl. 1 figure 9. Locus typicus: unknown (published in 1886 according to Westerlund, 1887: 30).
Buliminus (Napaeus) ponticus: Westerlund, 1887: 30.
Buliminus (Petraeus) Nogelli [sic]: Westerlund, 1887: 61.
Buliminus (Napaeus) ponticus: Kobelt, 1888: 33, pl. 99 figure 564.
Buliminus (Napaeus) ponticus: Retowski, 1889: 249.
Ena (Ena) nogelli [sic]: Forcart, 1940: 129 [partim], figure 2, pl. 1 figure 3.

Chondrula (Mastus) pontica: Forcart, 1940: 248, pl. 3 figure 82.

Ena (Ena) nogelli [sic]: Gittenberger, 1967: 137.

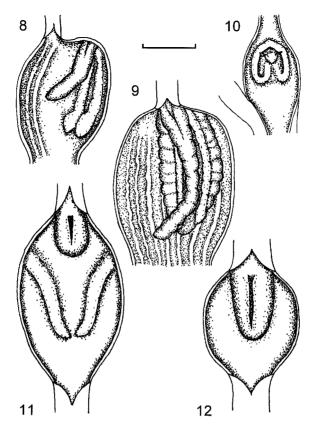


FIGS 1–4. Ena spp., shells: (1) Ena nogellii (Roth), 'Kolchis' (holotype ZSM 19960564);
(2) Ena nogellii (Roth), V. Zonguldak: Amasra 4km towards Cide (ZMH 2809);
(3) Ena menkhorsti Hausdorf and Bank, sp. n., V. Giresun: 5km N of Tamdere (holotype NNM); (4) Ena dazimonensis, sp. n., V. Tokat: Tokat (holotype ZMH 2807). Scale bar = 5 mm.



FIGS 5–7. Ena spp., genitalia: (5) Ena nogellii (Roth), V. Kastamonu: Kapõu 3.5 km towards Cide (HAU); (6) Ena menkhorsti Hausdorf and Bank, sp. n., V. Giresun: 5 km N of Tamdere (holotype NNM); (7) Ena dazimonensis, sp. n., V. Tokat: Tokat (holotype ZMH 2807). Abbreviations: ap=appendix; bc=bursa of the bursa copulatrix; div= diverticulum of the bursa copulatrix; ep=epiphallus; ec=epiphallic caecum; fl=flagellum; fod=free oviduct; p=penis; ra=retractor appendicis; rp=retractor penis; sod= spermoviduct; v=vagina; vd=vas deferens. The arrows point to the boundaries of the appendix sections. Scale bar=1 mm.

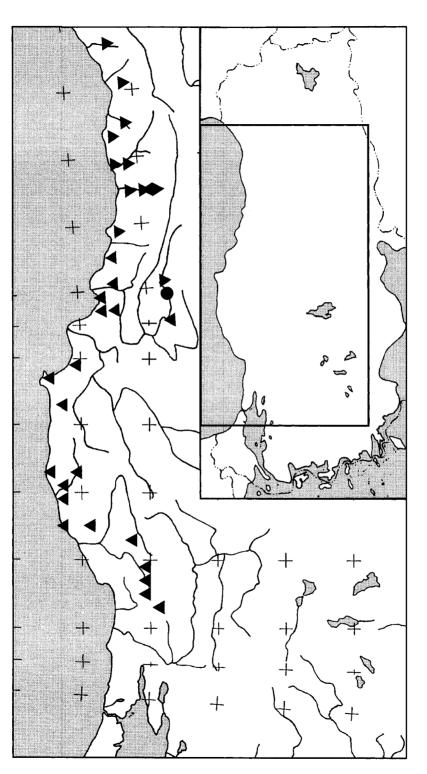
Shell (figures 1, 2). Elongated oval; with 7–8.25 slightly inflated whorls; moderately thick-walled; teleoconch with coarse growth ridges crossed by irregular incised spiral striae producing a granulated sculpture; brownish corneous; subtranslucent; the body whorl does not ascend towards the aperture; aperture oval, edentate; peristome slightly expanded, reflexed and moderately thickened on the inside; palatal insertion of the peristome connected with the columellar edge by a thin callus; rimate or umbilicus open.

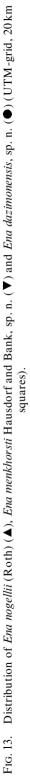


FIGS 8–12. Ena spp., internal structure of the penis: (8) Ena nogellii (Roth), V. Kastamonu: Kapõsu 3.5 km towards Cide (HAU); (9) Ena menkhorsti Hausdorf and Bank, sp. n., V. Giresun: 5 km N of Tamdere (paratype NNM); (10) Ena dazimonensis, sp. n., V. Tokat: Tokaţ (holotype ZMH 2807); (11) Ena concolor (Westerlund), Yugoslavia, Crna Gora: Čakor pass (HAU); (12) Ena monticola (Roth), Greece, Etolia: Golemion 1 km towards Katafigion (HAU). Scale bar = 1 mm.

Measurements. Various localities (n=30): D: 5.2–6.7 mm, mean = 5.7 \pm 0.3 mm; H: 13.0–21.8 mm, mean = 15.3 \pm 1.8 mm; D/H: 0.307–0.408, mean = 0.374 \pm 0.025.

Genitalia (figures 5, 8). The penial appendix inserts at the distal section of the penis. The appendix sections A_1 , A_2 and A_3 are distinctly delimited, whereas there is no marked boundary between the sections A_4 and A_5 . The appendix retractor inserts at the proximal half of section A_1 . The penial retractor inserts at the proximal section of the penis. Both retractors insert close to each other at the diaphragm. An imperforate penial papilla inserts at the proximal end of the penis. There is a short groove in the proximal part of the penial papilla facing the opening of the epiphallus. There is a longitudinal fold at each side of the penial papilla. The two folds converge and become higher towards their distal ends, which are detached from the penis wall. Opposite to these structures, there are two indistinct longitudinal ridges, which run towards the opening of the epiphallus. Besides, the penial wall is irregularly sculptured. There is a spur-shaped caecum at the middle section of the very long epiphallus. The flagellum is moderately short. The vagina is shorter than the penis. The free oviduct is longer than the vagina. The diverticulum of the bursa copulatrix is more than twice as long as the bursa and its duct proximally of the branching point.





Remarks. According to Forcart (1940: 118), *Ena nogellii* and *Chondrula pontica* differ in the ratio D/H. *Ena nogellii* is said to be characterized by a ratio lower than 0.345, whereas the ratio is said to be greater than 0.345 in *Chondrula pontica*. In 30 specimens measured for this study, the ratio D/H varies almost continuously between 0.307 and 0.408. There are no constant differences between the specimens identified as *Ena nogellii* and those identified as *Chondrula pontica* by Forcart (1940). The two figures of Retowski (1886: pl. 1 figure 9) which Forcart (1940) identified as the two distinct species show only a smaller and a larger specimen of *Ena nogellii*.

In Forcart's (1940: figure 2) figure of the genitalia of *Ena nogellii* the diverticulum of the bursa copulatrix is shorter than the bursa and its duct proximally of the branching point. A re-examination of Forcart's specimen has shown that the diverticulum is torn off. The rest of the diverticulum is still attached to the spermoviduct. Moreover, the position of the atrium is not correctly indicated in the figure; therefore the vagina appears very long.

Most of the 12 examined syntypes of *B. ponticus* Retowski, 1886 (IZPAN; SMF 63752, 63753, 63754, 103922) belong to *Ena nogellii*. However, one of the specimens in the Retowski collection in the IZPAN belongs to a *Mastus* species. Therefore, a lectotype of *B. ponticus* Retowski, 1886 (IZPAN, coll. Retowski, measurements: D = 5.6 mm, H = 14.6 mm) has been designated to clarify the application of that name.

Napaeus ponticus var. *rugosus* Westerlund, 1897 has no affinities to *Ena nogellii*. A syntype (Naturhistoriska Museet in Göteborg, NMG 1894) (probably the holotype) belongs to a *Mastus* species from Crete (R. A. Bank, personal communication). Consequently, the type locality given by Westerlund (1897), 'Tauria' (=Crimea), must be wrong.

Distribution and material (figure 13). Ena nogellii is widespread in the Pontic region of Turkey between the V. Bolu in the west and the V. Giresun in the east.

Ena nogellii certainly does not live in 'Kolchis'. *Euxinastra iberica* (Roth, 1850), which is described in the same publication with the wrong distribution record 'Georgien', is known only from the Vilayets Samsun and Ordu (Bank and Menkhorst, 1994). I suppose that both species were collected by M. Wagner near Samsun, where his ship landed on its way to the Caucasus.

V. Bolu: Cinler 1.5 km towards Mudurnu, UK38 (det. anat.; HAU); Kaynaslõ UL51 (MEN); Boludağo Gecidi, 900m alt., UL61 (det. anat.; MEN); Karacasu, 750 m alt., UL80 (IZPAN); Eskiçaga 3 km towards Mengen, VL22 (HAU). V. Zonguldak: 10km NNE Kocanoz between Safranbolu and Barton, VL59 (NNM); Amasra 4km towards Cide, VM52 (HAU; ZMH 2809). V. Kastamonu: Kapõu 3.5 km towards Cide, VM83 (det. anat.; HAU); Cide 4 km towards Grebolu, WM03 (HAU); Azdavay 2km towards Ulus, WM20 (HAU); Belyaka near Doganyurt 0.5 km towards Cide, WM35 (det. anat.; HAU). V. Sinop: Türkeli 20 km towards Sinop, XM23 (NBE); Sinop, XM75 (SMF 14489, specimens to Retowski, 1889); 16 km SE of Gerze, 100 m alt., XM91 (MEN). V. Samsun: Cukurbük, 450 m alt., BF65 (det. anat.; NMB 4480b, specimens to Forcart, 1940); Samsun 15km towards Havza, 400m alt., BF66 (NMB 4516a, specimens to Forcart, 1940); 17km SW of Samsun, BF66 (MEN); Samsun, BF77 (SMF 14488, 103923, 103924, specimens to Retowski, 1889 and Forcart, 1940); Tekkeköy, BF86 (det. anat.; FMNH 279868; IZPAN); Dervent Burnu, 10 m alt., BF87 (NMB 4480a, specimens to Forcart, 1940); Yenice 25 km SSW of Çarşamba, CF04 (IZPAN). V. Ordu: Curiköyü 7 km W of Ünye, CF55 (NNM, specimens to Gittenberger, 1967); Ünye, CF55 (MEN). V. Giresun: 5km N of Tamdere, DE48 (MEN). V. Tokat: Turhal, BE57 (MEN).

B. Hausdorf

'Kolchis' (holotype of *B. nogellii* Roth: ZSM 19960564). Debris of the Black Sea near Koktebel, Crimea (lectotype (design. nov.) of *B. ponticus* Retowski: IZPAN; paralectotypes of *B. ponticus*: IZPAN; SMF 63752, 63753, 63754, 103922).

Ena menkhorsti Hausdorf and Bank, sp. n. (figures 3, 6, 9, 13)

Shell (figure 3). Elongated oval; with 6.5–8.5 slightly inflated whorls; moderately thick-walled; teleoconch with more or less coarse growth ridges crossed by irregular incised spiral striae producing a granulated sculpture; brownish corneous; sub-translucent; the body whorl does not ascend towards the aperture; aperture oval, edentate; peristome slightly expanded, reflexed and moderately thickened on the inside; palatal insertion of the peristome connected with the columellar edge by a thin callus; rimate or umbilicus open.

Measurements. 5 km N of Tamdere (n = 10): D: 6.9–8.0 mm, mean = 7.5 \pm 0.3 mm; H: 15.5–19.5 mm, mean = 17.2 \pm 1.1 mm; D/H: 0.395–0.516, mean = 0.439 \pm 0.035.

Genitalia (figures 6, 9). The penial appendix inserts at the distal section of the penis. The appendix sections A_1 , A_2 and A_3 are distinctly delimited, whereas there is no marked boundary between the sections A_4 and A_5 . The appendix retractor inserts at the proximal section of section A_1 . The penial retractor inserts at the proximal section of the penis. Both retractors insert close to each other at the diaphragm. A very long and slender imperforate penial papilla inserts at the proximal end of the penis. There is a short groove in the proximal part of the penial papilla facing the opening of the epiphallus. There is a V-shaped structure with two longitudinal ridges at the penial wall behind the penial papilla. The lateral and distal wrinkled margins of this structure are detached from the penial wall. Besides, the penial wall is sculptured with irregular longitudinal ridges. There is a spur-shaped caecum at the middle section of the very long epiphallus. The flagellum is moderately short. The vagina is shorter than the penis. The free oviduct is longer than the vagina. The diverticulum of the bursa copulatrix is more than twice as long as the bursa and its duct proximally of the branching point.

Remarks. Ena menkhorsti differs from *Ena nogellii* (Roth) in the broader shell with a usually slightly weaker sculpture, and in the inner structures of the penis, especially the V-shaped structure behind the very long penial papilla. No constant differences have been found between the proportions of the various sections of the genitalia, which are very variable in both species.

The two converging folds in the penis of *Ena nogellii*, which are distally detached from the penis wall, are in the same position as the V-shaped structure in the penis of *Ena menkhorsti* and are therefore probably homologous to that structure. A detachment of such structures is not known from other *Ena* species or related genera. Therefore, the distal detachment of these structures is a synapomorphy of *Ena menkhorsti* and *Ena nogellii*, indicating that they are sister species.

B. Hausdorf and R. A. Bank (Hoofddorp, The Netherlands) are joint authors of this new species.

Etymology. The species is named in honour of Dipl.-Ing. Henk P. M. G. Menkhorst, Krimpen aan de Ijssel, who discovered it.

Type locality. V. Giresun: rocks 5km N of Tamdere, DE48.

Distribution and material (figure 13). Ena menkhorsti is widespread in the eastern Pontic region of Turkey between the Vilayets Tokat and Ordu in the west and the V. Rize in the east. Several specimens of *Ena menkhorsti* and of *Ena nogellii* have been found sympatrically at rocks 5 km N of Tamdere in the V. Giresun.

V. Ordu: 12 km N of Gürgentepe, CF92 (MEN). V. Giresun: 5 km N of Tamdere, DE48 (det. anat.; holotype NNM, leg. H. Menkhorst, 23 July 1990, measurements: D = 7.7 mm, H = 17.2 mm; MEN; ZMH 2810); Giresun 49 km towards Şebin Karahisar, 800 m alt., DE49 (det. anat.; NBE); Giresun 75 km towards Şebin Karahisar, 1500 m alt., DE57 (NBE); 8 km S of Dereli, DF50 (MEN); 12 km S of Giresun, DF51 (MEN); 15 km S of Giresun, DF51 (NBE); 7 km S of the mouth of the Doğankent Çayõ DF83 (NBE); mouth of the Doğankent Çayõ 30 km towards Torul, DF91 (NBE). V. Trabzon: 3.5 km N of Tonya, EF22 (IZPAN); 10–13 km SSE of Maçka, EF51 (IZPAN); 35 km S of branch from OF towards Bayburt, S of Ataköy, FF00 (NBE). V. Rize: 21 km S of Çamlihemşin, 870 m alt., FF62 (NBE). V. Tokat: Gökdere, CE08 (MEN).

Ena dazimonensis, sp. n.

(figures 4, 7, 10, 13)

Bulimus (Petraeus) nogelli [sic]: Nägele, 1894: 106 [non Roth, 1850]. Ena (Ena) nogelli [sic]: Forcart, 1940: 129 [partim, non Roth, 1850], pl. 1 figure 4.

Shell (figure 4). Elongated oval; with 8–9.25 very slightly inflated whorls; moderately thick-walled; teleoconch almost smooth, with only irregular, fine growth ridges; brownish corneous; subtranslucent; the body whorl does not ascend towards the aperture; aperture oval, edentate; peristome slightly expanded, reflexed and distinctly thickened on the inside; the thickening of the peristome gets abruptly weaker in the sinulus; palatal insertion of the peristome connected with the columellar edge by a thin callus; rimate or umbilicus open.

Measurements. Tokat (n=30): D: 5.6–6.7 mm, mean = 6.1 ± 0.3 mm; H: 18.2–22.6 mm, mean = 20.1 ± 1.0 mm; D/H: 0.265–0.346, mean = 0.307 ± 0.020 .

Genitalia (figures 7, 10). The penial appendix inserts at the distal section of the penis. There is neither a marked boundary between the appendix sections A_1 and A_2 nor between the sections A_3 , A_4 and A_5 . The appendix retractor inserts at the proximal section of the extraordinarily long section A_1 . The penial retractor inserts at the diaphragm. There is a horseshoe-shaped ridge with ends which bend inwards in the proximal section of the penis. There is a small, conical hump, which is probably a rudiment of the penial papilla, in the middle of the horseshoe-shaped structure. There is a heel-shaped caecum at the middle section of the very long epiphallus. The flagellum is very short. The vagina is more than half as long as the penis. The free oviduct is four times as long as the bursa and its duct proximally of the branching point.

Remarks. Ena dazimonensis differs from *Ena nogellii* (Roth) and *Ena menkhorsti* Hausdorf and Bank, sp. n. in the almost smooth shell which has on average more whorls that are hardly inflated, and by the distinctly thickened peristome. The genitalia of *Ena dazimonensis* are especially characterized by the heel-shaped epiphallial caecum, the very short flagellum and the inner structures of the penis, especially the horseshoe-shaped ridge and the rudimentary penial papilla.

The inner structure of the penis of *Ena dazimonensis* resembles that of *Pseudonapaeus chodschendicus* Schileyko, 1978.

Etymology. The species is named after the ancient village Dazimon (the modern Tokat), the type locality of the species.

Type locality. V. Tokat: Tokat, rocks above the cemetery, BE96.

Distribution and material (figure 13). Ena dazimonensis is known only from the surroundings of Tokat.

V. Tokat: Tokat, BE96 (det. anat.; holotype ZMH 2807, leg. B. Hausdorf, 5 October 1987, measurements: D = 6.1 mm, H = 20.4 mm; HAU; NMB 4480d; SMF 14486, 63751, 104386, 104387, 104388, 202962, 237583, specimens to Nägele, 1894 and Forcart, 1940; ZMH 2808); 3.5 km S of Tokat, BE96 (HAU); 5 km S of Tokat, BE96 (MEN).

Delimitation and phylogenetic relationships of Ena

Until recently, the separation of Merdigera Held, 1838 from Ena Turton, 1831 proposed by Schileyko (1984) had not been accepted in most studies (e.g. Bank and Menkhorst, 1992; Schütt, 1993). This separation is based on the inner structures of the penis, especially the penial papilla, which is perforated by the seminal duct in Merdigera, whereas there is an imperforate penial papilla at one side of the opening of the epiphallus in *Ena*. However, the inner structure of the penis is known only from a single *Ena* species so far, namely *Ena montana* (Draparnaud, 1801), the type species of the genus (Schileyko, 1984). It is not known how variable the penial structures of *Ena* are or whether the species which have been included in *Ena* so far actually belong to Ena or whether they belong to Merdigera. Therefore, the internal structures of the penis of the three Turkish species, Ena nogellii (Roth), Ena menkhorsti Hausdorf and Bank, sp. n. and Ena dazimonensis, sp. n., and two other Ena species of which preserved material was available, *Ena concolor* (Westerlund, 1887) and Ena monticola (Roth, 1856), have been examined (figures 8-12). All examined species are characterized by an imperforate penial papilla and actually belong to Ena. Besides these species, Ena subtilis (Rossmässler, 1837) and Ena elongata (Kobelt, 1877) have been referred to *Ena* based on shell characters (Bank and Menkhorst, 1992).

Schileyko (1984) included *Ena* and several genera which are characterized by numerous small papillae on the inside of the penial wall in the subfamily Eninae Woodward, 1903. The inside of the penial wall of *Ena* is more or less smooth or is sculptured with indistinct longitudinal ridges. Besides, two strong ridges or a V-shaped structure can be developed in the proximal section of the penis (figures 8–12). The numerous small papillae on the inside of the penial wall are a synapomorphy of the other genera included in the Eninae by Schileyko (1984). This group has to be called Chondrulini Wenz, 1923 (Hausdorf, 1994) and belongs to the Eninae Woodward, 1903 *sensu lato* (Bank and Neubert, 1998; Hausdorf, 1999).

Ena is similar to several genera which were included in the Pseudonapaeinae Schileyko, 1978 by Schileyko (1984). This group includes various Buliminidae with a short flagellum and with an imperforate penial papilla or without a penial papilla. No autapomorphy of this group is known and therefore it is questionable whether it is monophyletic. There is no reason to exclude *Ena* from this provisional group. Therefore, Pseudonapaeinae Schileyko, 1978 is a synonym of Enini Woodward, 1903, Eninae Woodward, 1903 (see also Bank and Neubert, 1998; Hausdorf, 1999).

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