Zitteliana 97, 2023, 53–88 | DOI 10.3897/zitteliana.97.115682

SNSB Bayerische Staatssammlung für Paläontologie und Geologie

ZITTELIANA
An International Journal of Paleontology and Geobiology

# The Early Pleistocene freshwater mollusks of the Denizli Basin (Turkey): a new long-lived lake fauna at the crossroads of Pontocaspian and Aegean-Anatolian realms

Thomas A. Neubauer[1,2], Frank P. Wesselingh[2,3]

1 *SNSB – Bavarian State Collection for Palaeontology and Geology, Richard-Wagner-Straße 10, 80333 Munich, Germany*
2 *Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, Netherlands*
3 *Department of Earth Sciences, Utrecht University, Princetonlaan 8a, 3584 CB Utrecht, Netherlands*

*https://zoobank.org/933EC356-F21C-45AF-9CFA-563E64D27953*

Corresponding author: Thomas A. Neubauer (neubauer@snsb.de)

Academic editor: A. Nützel ♦ **Received** 14 November 2023 ♦ **Accepted** 16 November 2023 ♦ **Published** 12 December 2023

## Abstract

We describe here a newly discovered, diverse fossil fauna of freshwater gastropods and bivalves from the Denizli Basin in SW Turkey. The material was collected from the Kolankaya Formation, for which latest chronostratigraphic and magnetostratigraphic data indicate an Early Pleistocene age, which is much younger than previously assumed for the fossil-bearing strata of the Denizli Basin. The fauna consists of at least 27 species (25 gastropods, 2 bivalves) and includes a new genus, *Harzhauseria* **gen. nov.**, and 6 new species within the Hydrobiidae: *Falsipyrgula*? *coronata* **sp. nov.**, *Graecoanatolica*? *alcicekorum* **sp. nov.**, *Harzhauseria schizopleura* **gen. et sp. nov.**, *Iraklimelania minutissima* **sp. nov.**, *Iraklimelania submediocarinata* **sp. nov.**, and *Xestopyrguloides*? *sagitta* **sp. nov.** Additionally, we define lectotypes for *Staja orientalis* (Bukowski, 1896) and *Valvata orientalis* Fischer, 1866, as well as a neotype for *Theodoxus percarinatus* (Oppenheim, 1919). Nine of the recovered species (33.3%) are only known from the Denizli Basin. Almost half of the fauna (44.7%) is endemic to the Aegean–Anatolian region, with biogeographical affinities to the Pliocene–Early Pleistocene faunas of Rhodes, Kos, and mainland Greece, as well as the Çameli and Eşen Basin in Turkey. On the genus level, the fauna also contains several typical Pontocaspian elements. The composition points toward a typical long-lived lake environment with oligohaline conditions.

## Zusammenfassung

Wir beschreiben hier eine neu entdeckte, diverse fossile Fauna von Süßwassergastropoden und -Bivalven aus dem Denizli-Becken im Südwesten der Türkei. Das Material stammt aus der Kolankaya-Formation, für die neueste chronostratigraphische und magnetostratigraphische Daten auf ein frühpleistozänes Alter hindeuten, das viel jünger ist als bisher für die fossilführenden Schichten des Denizli-Beckens angenommen. Die Fauna besteht aus mindestens 27 Arten (25 Gastropoden, 2 Bivalven) und umfasst eine neue Gattung, *Harzhauseria* **gen. nov.**, und 6 neue Arten innerhalb der Hydrobiidae: *Falsipyrgula*? *coronata* **sp. nov.**, *Graecoanatolica*? *alcicekorum* **sp. nov.**, *Harzhauseria schizopleura* **gen. et sp. nov.**, *Iraklimelania minutissima* **sp. nov.**, *Iraklimelania submediocarinata* **sp. nov.**, und *Xestopyrguloides*? *sagitta* **sp. nov.** Zusätzlich definieren wir Lektotypen für *Staja orientalis* (Bukowski, 1896) und *Valvata orientalis* Fischer, 1866, sowie einen Neotypus für *Theodoxus percarinatus* (Oppenheim, 1919). Neun der gefundenen Arten (33,3%) sind nur aus dem Denizli-Becken bekannt. Fast die Hälfte der Fauna (44,7%) ist endemisch für die ägäisch-anatolische Region, mit biogeografischen Verbindungen zu den pliozänen und frühpleistozänen Faunen von Rhodos, Kos und dem griechischen Festland sowie dem Çameli- und Eşen-Becken in der Türkei. Auf der Gattungsebene enthält die Fauna auch einige typische pontokaspische Elemente. Die Zusammensetzung deutet auf das Milieu eines typischen Langzeitsees mit oligohalinen Bedingungen hin.

Copyright *Thomas A. Neubauer & Frank P. Wesselingh.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

PENSOFT

## Keywords

Taxonomy, biogeography, Pontocaspian biota, Anatolia, Quaternary

## Introduction

The late Neogene to Quaternary non-marine mollusk faunas of Anatolia have attracted scientists since the 19th century. Early geological and geographical expeditions by Spratt and Forbes (1847) and Fischer (1866) yielded the first species records, already from a series of different basins and faunas. The first milestone work was published by Oppenheim (1919), who described numerous species from various basins and time horizons all over western Anatolia. The species inventory of the region grew further through contributions by Bukowski (1930), Taner (1974a, 1974b, 1980, 1983), Becker-Platen and Kuiper (1979, Schütt and Kavusan (1984), Schütt (1985b, 1991, 1992, 1994, 1997), Kapan Yesilyurt and Taner (2002), Wesselingh et al. (2008), Wesselingh and Alçiçek (2010), Vasilyan et al. (2014), van den Hoek Ostende et al. (2015), Alçiçek et al. (2017), Büyükmeriç and Wesselingh (2018), and Rausch et al. (2019). These contributions witness a heterogeneous species composition across different basins and time intervals, with a high degree of endemic developments. The earlier paleontological studies were put into context by the stratigraphical, tectonic, and paleoenvironmental studies of the 21st century (Becker-Platen 1970; Bering 1971; Becker-Platen et al. 1975, 1977; Alçiçek et al. 2005, 2007, 2013, 2015, 2019; Alçiçek 2007, 2010), which provide an important baseline to unravel the evolution and paleobiogeography of the Anatolian mollusks faunas.

Partly related faunas of similar age were detected especially in Greece. As for Turkish faunas, a wealth of contributions was published on Late Miocene to Early Pleistocene (and partly related) faunas of mainland Greece (Fuchs 1877; Neumayr 1880a; Oppenheim 1890, 1891; Papp 1947, 1953, 1955, 1979, 1980; Kühn 1951, 1963; Papp and Psarianos 1955; Schütt 1976, 1985a, 1986, 1988; Kaouras and Velitzelos 1985; Schütt et al. 1985; Rust 1997; Esu and Girotti 2015, 2020), the Aegean islands (Neumayr 1880b; Bukowski 1892, 1893, 1896; Schütt and Besenecker 1973; Willmann 1977, 1980, 1981, 1982, 1985; Schütt and Velitzelos 1991) and the Marmara Sea region (Hoernes 1876; Calvert and Neumayr 1880; Neumayr 1883; Gillet et al. 1978; Taner 1982, 1997; Rückert-Ülkümen et al. 2006).

Of all Anatolian faunas, the Denizli Basin contains probably the most diverse species inventory, which is partly owed to its long stratigraphic record (Figs 1, 2; Alçiçek et al. 2007, 2015; Wesselingh et al. 2008). Since the first description of a species by Fischer (1866), 43 species and another 13 subspecies (22 bivalves, 33 freshwater gastropods, 1 land snail) have been described from the Denizli Basin (not including species that have been reported from the basin but were first described elsewhere). Already Oppenheim (1919) recognized two different faunas with completely different species compositions and ecological implications, a "lower, more lacustrine type" and an "upper brackish type". The younger, brackish fauna was studied in detail by Wesselingh et al. (2008). It contains elements typical of Pleistocene to modern Pontocaspian faunas, such as bivalves of the subfamily Lymnocardiinae.

The ages of the two faunas have a long history of debate. For the older fauna, age estimates range from Middle Miocene or Sarmatian (Oppenheim 1919) to Maeotian (Taner 1975, 2001). The younger, Pontocaspian-type fauna was assumed to be Pontian by Oppenheim (1919) and Taner (1975, 2001) and Messinian by Wesselingh et al. (2008), respectively. Taner (1975) referred both faunas to the "Lower Pliocene" but she correlated it with the Maeotian/Pontian strata of the Paratethys.

Because of the presumed latest Miocene age, the younger fauna was previously considered to be among the oldest Pontocaspian-type faunas, serving as potential source of origin for Pliocene to Quaternary species lineages (Wesselingh et al. 2008). Latest chronostratigraphic and magnetostratigraphic data, however, indicate a much younger, Early Pleistocene age for both fossil-bearing deposits (S. Lazarev, pers. comm.). More precisely, the older ("Kolankaya I") fauna is classified as Gelasian (> ~1.8 Ma), the younger ("Kolankaya II") one as Calabrian (< ~1.8 Ma). These new ages call for a revised assessment of biogeographic relationships.

In contrast to the well-studied Kolankaya II fauna, a modern assessment of the older Kolankaya I is largely missing. Here we report a newly collected fauna from the southern margin of the Denizli Basin. We provide a comprehensive taxonomic study, along with paleoecological and paleobiogeographical interpretations.

## Geological setting

The Denizli Basin in SW Turkey is a 70 × 50 km graben-type basin trending WNW–ESE (Alçiçek et al. 2007, 2015; Figs 1, 2). The Neogene–Quaternary basin infill is bordered by the Paleozoic–Mesozoic metamorphic rocks of the Menderes Massif in the southwest and northwest and Lycian nappes in the eastern part, both of which form the bedrock of the basin. In the northwest, the basin is split into two subbasins by an intrabasinal high known as Buldan Horst (Alçiçek et al. 2007, 2015; and references therein). The study area is located in the SW subbasin.

The Neogene–Quaternary infill, referred to as the Denizli Group, attains a thickness of up to 1300 m and consists of a complex succession of alluvial, fluvial, and lacustrine deposits. Following the stratigraphic and paleo-

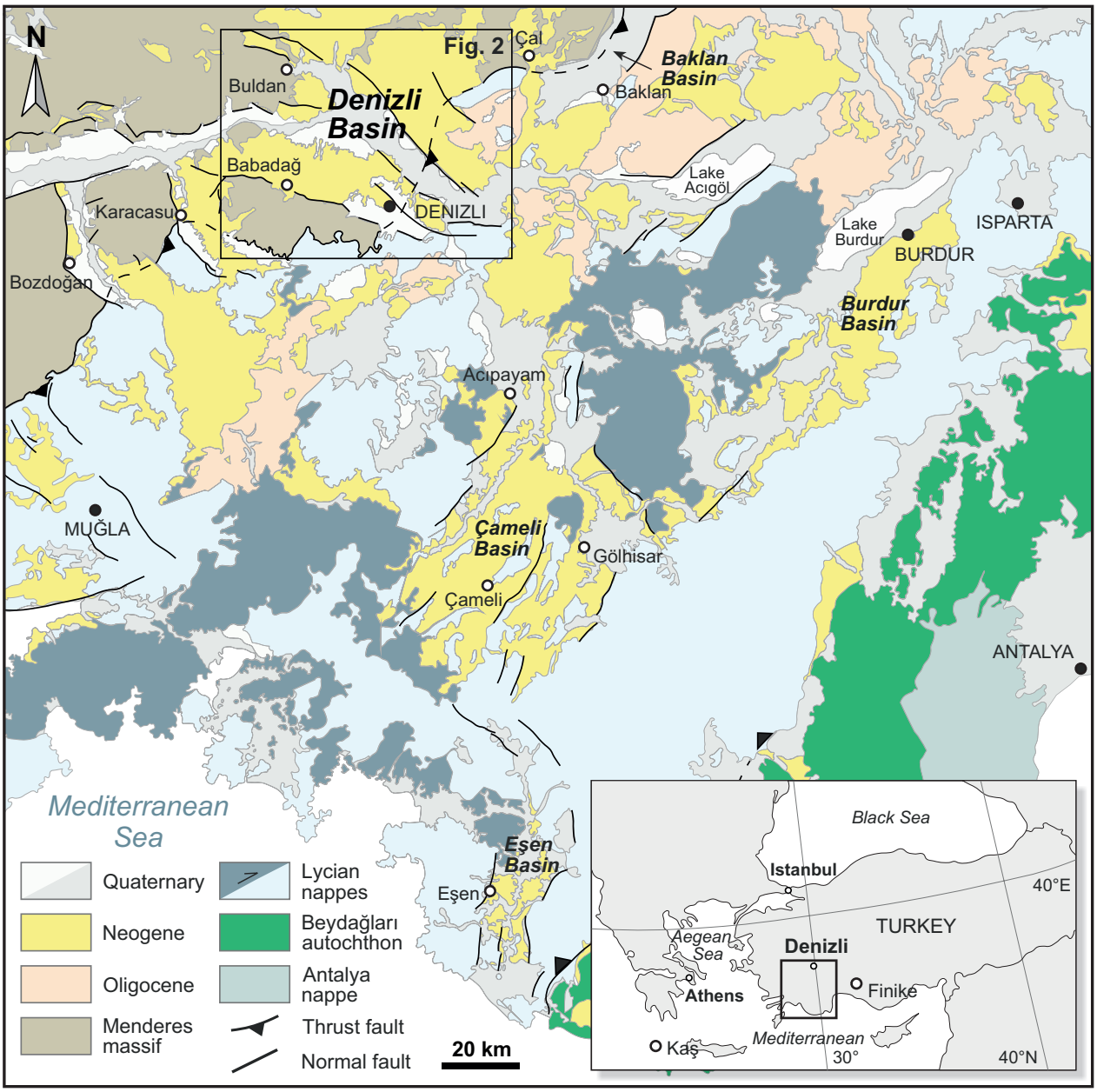


**Figure 1.** Geographical and geological overview of the study area in SW Turkey (modified from Alçiçek et al. 2015).

environmental studies of Alçiçek et al. (2007, 2015), four formations are recognized: 1) the Kızılburun Formation, unconformably overlying the bedrock, covers up to 450 m thick alluvial-fan to river deposits and represents a wetland type environment with small lakes, rivers, and mires; 2) the Sazak Formation, which gains a thickness of 300 m, comprises marls, claystones, mudstones, siltstones, limestones, dolostones, as well as gypsum and halite deposits in the upper part, and corresponds to the development of a marginal to shallow and finally saline lake; 3) the Kolankaya Formation, containing the here described mollusk fauna, reaches a thickness of up to 500 m and overlies conformably the Sazak Formation and unconformably metamorphic bedrock in the northern part of the basin, respectively. It represents a balanced-filled, shallow to deep-water lake; 4) the up to 150 m thick Tosunlar Formation, which rests unconformably on the Kolankaya Formation, consists of alluvial-fan and fluvial deposits.

The stratigraphic ages of the formations are currently subject of revision with radiometric age-constrained paleomagnetic approaches (S. Lazarev, pers. comm.). The new age estimates strongly deviate from earlier age estimates that were poorly constrained and show that the Kolankaya Formation is of a Pleistocene age rather than a Neogene age. The new age data also imply that the ages of the Sazak and Kızılburun formations will need re-evaluation. The older Kolankaya I fauna subject of this paper is very likely to be of a Gelasian age with an upper limit for this fauna of approximately 1.8 Ma (S. Lazarev, pers. comm.).

## Material and methods

Mollusks representing the Kolankaya I fauna were collected in three shell rich levels in the Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of

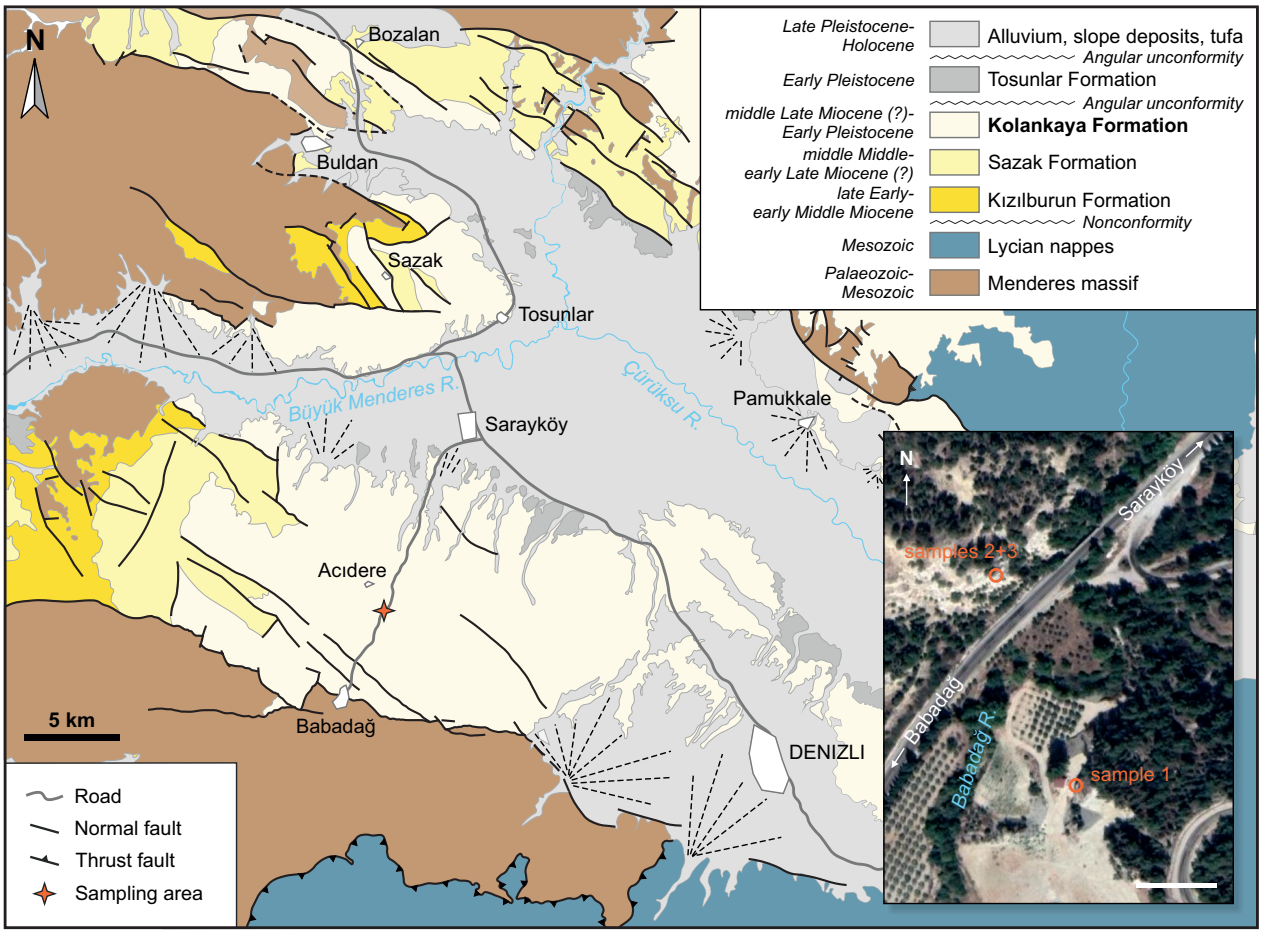


**Figure 2.** Geology of the Denizli Basin with indication of the sampling area (modified from Alçiçek et al. 2015). The insert shows the sampling locations in the Babadağ river valley along the Babadağ-Sarayköy road. Underlying satellite image © Google Maps 2023, CNES/Airbus, Maxar Technologies.

Babadağ. Sample 1 was taken from a small wall-cut behind a shed on the east side of the valley, from an interval with olive brown parallel-stratified siltstones and the scree zone around (37°50'40.3"N, 28°52'53.3"E, WGS84). Here, larger specimens were hand-picked and a few hundred grams of sediment was sampled and washed over a 0.5 mm sieve. Sample 2 was obtained at the top of a small cliff on the west side of the road (37°50'44.5"N, 28°52'51.3"E), at the contact between brown sandy siltstones and white limestones on top. About 3 kg of sediment was obtained and washed over 0.5 mm. Sample 3 refers to hand-picked material from scree deposits within a few meters radius of sample 2. The three samples were taken from the upper part of the lower Kolankaya Formation, below a major lithological transition toward a gravel interval that marks the transition to the overlying Kolankaya II interval (S. Lazarev, unpublished data). The stratigraphic levels of the bulk samples correspond to approximately 200 m (sample 1) and 230 m (sample 2) from the base of the Kolankaya Formation, respectively (S. Lazarev, pers. comm. 11/2023).

Preservation of shells varies, ranging from specimens with excellently preserved shell surface, protoconch sculpture, and even color patterns to fragmentary or abraded individuals. Especially larger specimens and those collected from the surface typically show signs of abrasion and ornament obliteration.

Photos were taken with a Keyence VHX-7000 digital microscope at SNSB-BSPG and a Leica M165C stacking microscope at Naturalis. Scanning electron microscopy photographs were taken with a ZEISS LEO-1430 VP with 20 kV at the Bavarian State Collection for Zoology, Munich (SNSB-ZSM) and a Tescan Vega\\xmu with 5 kV at the Department of Palaeontology at Friedrich-Alexander-Universität Erlangen-Nürnberg. For that purpose, specimens were sputter coated with gold with a Quorum Q150R S at BSPG and a Polaron SC510 at ZSM. Photos were edited with Adobe Photoshop CC, figures were arranged with CorelDRAW Graphics Suite X8.

For gastropods, dimensions are given as shell height × width and were measured based on frontal views with specimens arranged vertically along their axis (as illustrated on the figures). To calculate the proportion of the last whorl, the whorl's height was measured at the shell axis. For the dreissenid bivalves (all of which are fragmented), length is measured with the dorsal margin horizontally placed, height is measured perpendicularly, and the semidiameter is the shell width measured when the shell is put on a horizontal surface.

The material is stored at Naturalis Biodiversity Center (coll. no. RGM 962606–962621, 962689–962704, 1310375–1310377, 1310796–1310799, 1310837–1310861, 1365347–1365352) and the Bavarian State

Collection for Palaeontology and Geology (coll. no. SNSB-BSPG 2023 XII 1–24).

We aimed to compare our material with that of Oppenheim (1919), who described many species from the Denizli Basin. However, the material could be found neither in the Museum für Naturkunde Berlin (M. Aberhan, pers. comm. 09/2022), where Oppenheim himself originally deposited the specimens, nor in the Hebrew University of Jerusalem (R. Rabinovich, H.K. Mienis, pers. comm. 11/2022), which contains large parts of Oppenheim's collection. We contacted several other institutions in Europe for further information (Natural History Museum Vienna, Muséum national d'Histoire naturelle in Paris, Natural History Museum London, Moravské zemské muzeum in Brno, Masaryk University in Brno), but no hint on the whereabouts of the type material could be obtained. Hence, we have to assume it got lost, perhaps in the course of the relocation of the Berlin collection during and after World War II (Neumann et al. 2018).

Material from Pliocene to Pleistocene strata of Rhodes (Bukowski 1893, 1896) stored at the Department of Geology at the University of Vienna (IGUW) and of mainland Greece (Fuchs 1877) housed at the Geological-Paleontological Department of the Natural History Museum (NHMW) was studied for comparison. An updated stratigraphy of the relevant deposits on Rhodes was recently published by Schneider et al. (2023).

## Systematic paleontology

We follow the higher classification scheme of Bouchet et al. (2017) for Gastropoda and Carter et al. (2011) for Bivalvia. Synonymy/chresonymy lists include first descriptions, records where a taxon was illustrated or discussed in detail, as well as references to Wenz' (1923–1930) fossil catalogue (which may list further mentions of taxa in question).

**Class Gastropoda Cuvier, 1795**
**Subclass Neritimorpha Golikov & Starobogatov, 1975**
**Order Cycloneritida Frýda, 1998 emend. Bouchet et al. 2017**
**Superfamily Neritoidea Rafinesque, 1815**
**Family Neritidae Rafinesque, 1815**
**Subfamily Neritininae Poey, 1852**

### Genus *Theodoxus* Montfort, 1810

**Type species.** *Theodoxus lutetianus* Montfort, 1810 [unnecessary substitute name for *Theodoxus fluviatilis* (Linnaeus, 1758)]; by original designation.

### *Theodoxus percarinatus* (Oppenheim, 1919), comb. nov.

Fig. 3A–T

*1919 *Neritina percarinata* sp. nov. – Oppenheim: 128–129, pl. 9, fig. 7.

**Material.** Sample 1: c. 500 specimens (RGM 1310838) and 1 specimen (SNSB-BSPG 2023 XII 1); sample 2: 1 specimen tentatively attributed to the species (RGM 962606), 1 specimen (RGM 962607), 1 specimen (RGM 1310797), 123 specimens (RGM 1310839), 2 fragments and fragmented opercula (RGM 1310840), 1 specimen (SNSB-BSPG 2023 XII 2); sample 3: 53 specimens (RGM 1310841).

**Neotype.** Oppenheim's type material could not be found despite considerable efforts and is presumably lost (see Material and Methods section). To ensure nomenclatural stability and link the name to a type specimen, we herewith designate a neotype. The original type locality includes two localities, Giralan near Pamukkale and Bozalan near Buldan ("Abstieg nach Giralan.—Bosalan bei Bulladan.") in the Denizli Basin (Fig. 1). No material from those localities is available to us, but considering the geographic vicinity of the newly collected material as well as the distinct morphological features, there can be no doubt that our material represents the same species as the one described by Oppenheim (1919). We select as neotype the specimen illustrated on Fig. 3I–L, which comes from sample 2 (RGM 962607).

**Description.** Globular neritid with short, flattened spire and up to 3.3 whorls. Characteristic keel is observed in part of the material. In well preserved, keeled specimens narrow, distinct keel develops early in ontogeny. In first whorl it aligns with suture, but as shell growth becomes slightly more abapically oriented, keel emerges more clearly and separates whorl top and whorl flank. Expression and extent of keel varies, it may appear and disappear within 0.2 whorls or range until last whorl; however, no specimen is found with keel covering entire shell. Strength of keel very variable, ranging from robust and well delimited to almost obsolete. In much of the material the keel is worn. Aperture broadly semicircular with broad, smooth callus that is weakly thickened especially in its center (see lateral views). Coloration variable, including fully black, white with dark stripes, irregular mix of dark and white, white blotches arranged in spiral bands or entirely white.

**Dimensions.** 6.64 × 7.76 mm (neotype, RGM 962607; Fig. 1I–L), 10.66 × 10.51 mm (RGM 1310797; Fig. 1A–D), 6.72 × 7.24 mm (SNSB-BSPG 2023 XII 1; Fig. 1M–P).

**Remarks.** The species has not been treated in the literature since the original description. It was neither included in the Fossilium Catalogus by Wenz (1930), perhaps because he considered this form not to be a freshwater taxon, nor was it listed by Taner (1974a, 1975). The combination with the genus *Theodoxus* appears for the first time in Alçiçek (2010), but without discussion. Here, we formalize the classification and re-describe the species.

The diagnostic character of this species is its name-giving thin keel at the transition between whorl top and flank, which distinguishes the species from most others. A similarly keeled species is *Theodoxus carinatus* (Fuchs, 1877) from the Lower Pleistocene (Calabrian) of Livonates (mainland Greece). It differs in the flattened whorl flanks, the weakly raised spire, the broader keel and the color pattern consisting of wavy axial lines.

In addition to the majority of keeled specimens of *Theodoxus percarinatus*, shells occur that lack the

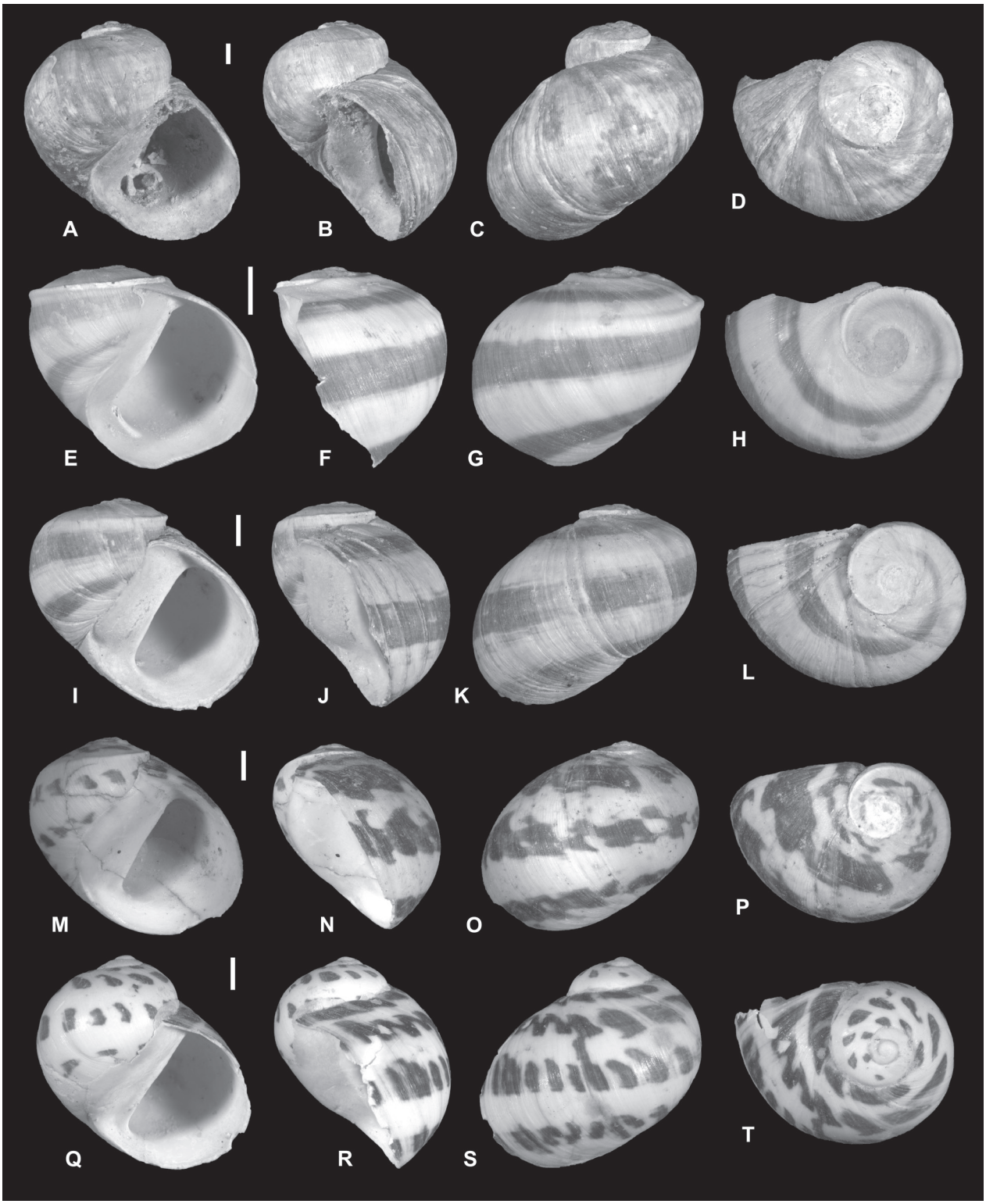


**Figure 3.** Neritidae of the Kolankaya I fauna. **A–D.** *Theodoxus percarinatus* (Oppenheim, 1919), RGM 1310797, sample 2. **E–H**. *T. percarinatus*, SNSB-BSPG 2023 XII 2, sample 2. **I–L.** *T. percarinatus*, Neotype, RGM 962607, sample 2. **M–P.** *T. percarinatus*, SNSB-BSPG 2023 XII 1, sample 1. **Q–T.** *T.* cf. *percarinatus*, RGM 962606, sample 2. Scale bars: 1 mm.

keel entirely and have a slightly more elevated spire (Fig. 3Q–T). In terms of size, general shape, and color patterns these specimens fall well within the range of *T. percarinatus*. Many *Theodoxus* species are known to have highly variable shells (Sands et al. 2020), which complicates a taxonomic decision about the status of these specimens. Apparent intermediate specimens occur in our material, but the worn nature of much of the material, the small numbers of specimens, and the general variability of the genus preclude confirmation whether it concerns untypically unkeeled representatives of *T. percarinatus* or constitute a separate, rare, and potentially new species.

**Distribution.** Only known from the Denizli Basin.

### *Theodoxus* aff. *pilidei* (Tournouër, 1879)

Fig. 4A–H

**Material.** 2 specimens (RGM 962608, RGM 1310796), 2 specimens and 1 fragment (RGM 1310842), 1 specimen (SNSB-BSPG 2023 XII 3); all from sample 2.

**Dimensions.** 1.97 × 2.69 mm (RGM 962608; Fig. 4A–D, H), 3.66 × 3.88 mm (RGM 1310796; Fig. 4E–G).

**Remarks.** Our material contains two moderately preserved specimens that exhibit a high variability in spire height and angulation. The low-spired morphotype (Fig. 4A–D, H) resembles *Theodoxus pilidei* (Tournouër, 1879), originally described from Pliocene or Lower Pleistocene strata of the Dacian Basin (Wenz 1942; Pană et al. 1981; Pană 2003; Papaianopol and Marinescu 2003), in terms of the general ovoid shell shape with depressed spire and the strong, papery lamellae. The illustrations of Pană et al. (1981) show quite some variability in the morphology of *T. pilidei*, including the expression of sculpture, which can be weak or nearly absent in some specimens. However, our material differs from that species particularly in the presence of a distinct angulation, which results in a nearly flat, apical plane. Specimens with elevated spire even show two angulations separated by a concave whorl flank (Fig. 4E–G). From the little material we have available it is difficult to judge the species' range of variability as well as make a taxonomic assignment. The distinct angulation present in our material, however, makes an affiliation with *T. pilidei* unlikely.

Another similar species is *Theodoxus boteani* (Porumbaru, 1881), which has a similar type of sculpture but more globular shells (Pană 2003). The extant, allegedly subterranean *Theodoxus gloeri* Odabaşi & Arslan, 2015 from Eskişehir region (Turkey), which also exhibits papery lamellae, differs in a slightly higher spire and the absence of an angulation (Odabaşi and Arslan 2015; Sands et al. 2020). Possibly our material signifies a new species.

## Subclass Caenogastropoda Cox, 1960
## Order unassigned
## Superfamily Cerithioidea Fleming, 1822
## Family Melanopsidae H. Adams & A. Adams, 1854

### Genus *Esperiana* Bourguignat, 1877

**Type species.** *Melanopsis esperi* Férussac, 1823; by original designation.

### *Esperiana esperi* (Férussac, 1823)

Fig. 5A–F

*1823 *Melanopsis Esperi*, nobis – Férussac: 160.
1974a *Melanopsis* (*Melanopsis*) cf. *bergeroni* Stefanescu – Taner: 116, pl. 9, figs 16–21.
2018 *Esperiana esperi* (Férussac, 1823) – Neubauer et al.: 89. fig. 17N.
2012 *Esperiana esperi* (Férussac, 1823) – Welter-Schultes: 35, unnumbered textfig.
2019 *Esperiana* (*Esperiana*) *esperi* (A. Férussac, 1823) – Glöer: 83, textfig. 83.

**Material.** Sample 1: 3 specimens (RGM 962691–962693), 10 specimens (SNSB-BSPG 2023 XII 4), ca. 300 specimens (RGM 1310843); sample 3: 13 specimens (RGM 1310844), 1 specimen (RGM 1365348).

**Dimensions.** 16.25 × 7.78 mm (RGM 962691; Fig. 5A–C), 14.44 × 7.47 mm (RGM 962692; Fig. 5D, E).

**Remarks.** The present material matches well the extant *Esperiana esperi* concerning the elongate, smooth shell with adpressed whorls, lanceolate aperture with thickened inner lip and the slight concavity between base of the last whorl and base of the aperture (Welter-Schultes 2012; Glöer 2019). Even the color pattern, consisting of dissected

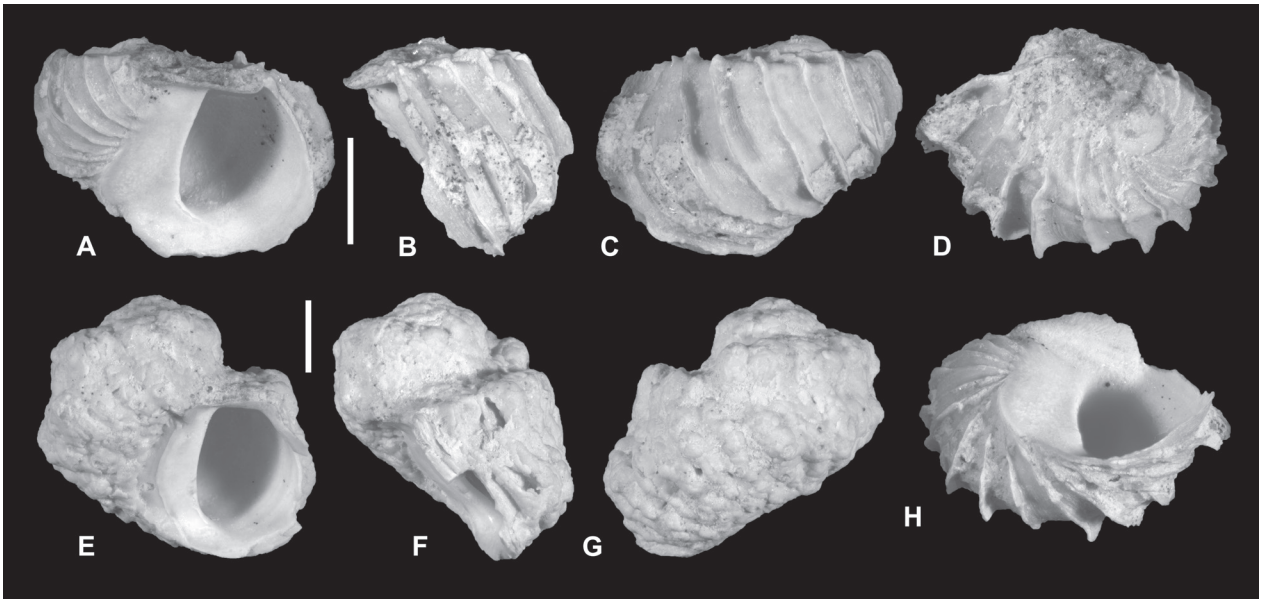


**Figure 4.** Neritidae of the Kolankaya I fauna. **A–D, H**. *Theodoxus* aff. *pilidei* (Tournouër, 1879), RGM 962608, sample 2. **E–G**. *T.* aff. *pilidei*, RGM 1310796, sample 2. Scale bars: 1 mm.

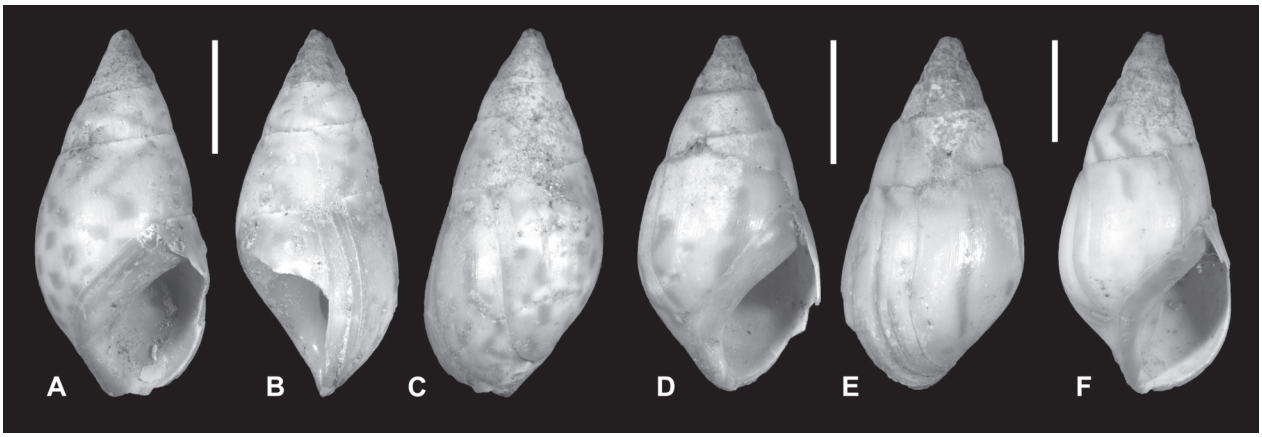


**Figure 5.** Melanopsidae of the Kolankaya I fauna. **A–C.** *Esperiana esperi* (Férussac, 1823), RGM 962691, sample 1. **D, E.** *E. esperi*, RGM 962692, sample 1. **F.** *E. esperi*, RGM 962693, sample 1. Scale bars: 5 mm.

zigzag lines to a chess-like arrangement of orange spots, and the corroded apex are typical of the modern species.

Shape, apertural characteristics and color pattern are also found in the Plio-Pleistocene species *Melanopsis bergeroni* Stefanescu, 1896 from the Dacian Basin (Romania) (Stefanescu 1896; Pană et al. 1981; Pană 2003). The same is true for *Melanopsis esperioides* Stefanescu, 1896 from the same region, which seems to be only slightly more slender and larger on average than *M. bergeroni* (Stefanescu 1896). It might well be that both species range within the morphological variability of *E. esperi*, but a final verdict on their status requires comparison with topotypic material from the Dacian Basin. In case of synonymy, the subgenus *Melanopsis* (*Calodiona*) Stefanescu, 1896, of which *M. bergeroni* is the type species, would become a synonym of *Esperiana*.

The specimens from the Denizli Basin studied by Taner (1974a) and identified as *M.* cf. *bergeroni* falls well into the range of *E. esperi* and considered conspecific herein.

**Distribution.** Today in central to southeastern Europe (western Black Sea region to Hungary, Slovakia, Austria, and Slovenia) and northwestern Anatolia (Welter-Schultes 2012; Glöer 2019). Also found in Pleistocene strata of the North Caspian Basin (Neubauer et al. 2018).

## Superfamily Truncatelloidea Gray, 1840
## Family Hydrobiidae Stimpson, 1865
## Subfamily Caspiinae B. Dybowski, 1913

### Genus *Graecoanatolica* Radoman, 1973b

**Type species.** *Hydrobia vegorriticola* Schütt, 1962; by original designation.

### *Graecoanatolica alcicekorum* sp. nov.

https://zoobank.org/DF386B7C-64EC-4328-B6C6-8DBC765BB6E0
Fig. 6A–E

**Etymology.** Named in honor of Hülya and M. Cihat Alçiçek, esteemed Turkish geologists with long research background in the Denizli Basin, for their continuing support and friendship.

**Holotype.** RGM 962617 (Fig. 6A–E). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

**Additional material.** None (holotype only).

**Diagnosis.** Slender, weakly ovoid shell with slightly tapered last whorl, adnate whorls with thin suture, faint subsutural concavity in late ontogeny, sinuate outer lip, and sigmoidal growth lines.

**Description.** Slender, ovoid hydrobiid shell, with 4.75 whorls. Protoconch consisting of c. 1 whorl, low domed with broad nucleus, weakly, finely-meshed malleate surface; sculpture fades out toward P/T transition; transition indicated by growth stop and onset of growth lines. Whorls moderately convex in early ontogeny; penultimate whorl exhibits nearly straight-sided upper whorl half and regularly convex lower half; last whorl, portion below suture weakly concave, producing weak constriction and slightly irregularly convex whorl profile. Last whorl attains 60% of shell height. Base ~45°, straight-sided. Aperture drop-shaped, tightly coiled, leaving no umbilicus; peristome not thickened or notably expanded; outer lip distinctly sigmoidal in lateral view. Growth lines sigmoidal, with opisthocyrt upper half and slightly weaker, prosocyrt lower half.

**Dimensions.** 2.21 × 0.97 mm (holotype, RGM 962617; Fig. 6A–E).

**Remarks.** The species' shell shape and size, the protoconch size, the subsutural concavity, the ovoid aperture with thin, sinuate peristome, and the sigmoidal growth lines are characteristics typical of extant members of the genus *Graecoanatolica*. The co-occurring species of *Iraklimelania* share many of these attributes, but they both have more slender shells with relatively smaller last whorls and larger protoconchs (1.2 whorls compared to 1 whorl).

The only fossil species of the genus was previously reported as *G. denizliensis* (Taner, 1974a) by Wesselingh et al. (2008) from the overlying "*Didacna* Beds" (= Kolankaya II fauna). The specimens, however, differ from

true "*Hydrobia*" *denizliensis* in the much smaller, ovoid shell with strongly convex whorls. The original species described by Taner is a large hydrobiid (7 mm) with moderately convex whorls and elongated aperture. The species of Wesselingh et al. (2008), which is currently without a name but fits well in the genus *Graecoanatolica*, differs from the new species in the slightly broader shell, the more convex whorls, and the presence of a narrow umbilicus.

*Graecoanatolica alcicekorum* sp. nov. resembles several extant representatives of the genus. Shells of the North Macedonian *Graecoanatolica macedonica* Radoman & Stankovič, 1979 and the Greek *G. vegorriticola* (Schütt, 1962) are similarly slender, but whorls have a regularly convex profile. The Turkish *G. dinarica* Kebapçı, Koca & Yıldırım, 2012 has a shell with highly convex whorls, a slightly irregularly shaped last whorl and a smaller aperture (Kebapçı et al. 2012). *Graecoanatolica lacustristurca* Radoman, 1973b (the type species) and *G. tenuis* Radoman, 1973b, both also described from Turkey, have conical shells with broad, blunt apex and a narrow umbilicus (Kebapçı et al. 2012).

The genus was recently placed in Caspiinae by Delicado et al. (2023) based on a comprehensive phylogenetic analysis.

**Distribution.** So far only known from the Early Pleistocene of the Denizli Basin.

### *Graecoanatolica*? sp.

Fig. 6F–I

**Material.** 1 specimen (RGM 1365349) from sample 1.

**Remarks.** At first glance, this shell reminds of *Iraklimelania minutissima* sp. nov. (see below) in terms of the very small, slender shell with convex whorls. However, the protoconch of *Graecoanatolica*? sp. is higher, whorls are more regularly convex, the aperture is oblique in lateral view, and the umbilicus is clearly visible. In all these characteristics it closely resembles extant *Graecoanatolica dinarica* Kebapçı, Koca & Yıldırım, 2012, for which we have studied topotypical material from İncirlipınar in Afyonkarahisar region. That species differs from *Graecoanatolica*? sp. in the larger size, the comparatively larger apex, the faster whorl expansion rate, and the often irregular growth (Kebapçı et al. 2012). Yet, the growth lines of *Graecoanatolica*? sp. are nearly orthocline, which has not been observed in any *Graecoanatolica* species, which is why we only tentatively associate the species with this genus.

## Genus *Iraklimelania* Willmann, 1981

**Type species.** *Iraklimelania levis* Willmann, 1981; by original designation.

**Remarks.** The revised attribution of *Iraklimelania*, originally tentatively placed in "Micromelaniidae" by Willmann (1981), to Caspiinae is based on two pillars. First, the protoconch sculpture, with the malleate surface bearing faint spiral striae and a thickened terminal portion, reminds of species of Caspiinae (Anistratenko et al. 2021). Extant Pontocaspian members are typically characterized by an increasing sculpture intensity toward the end and

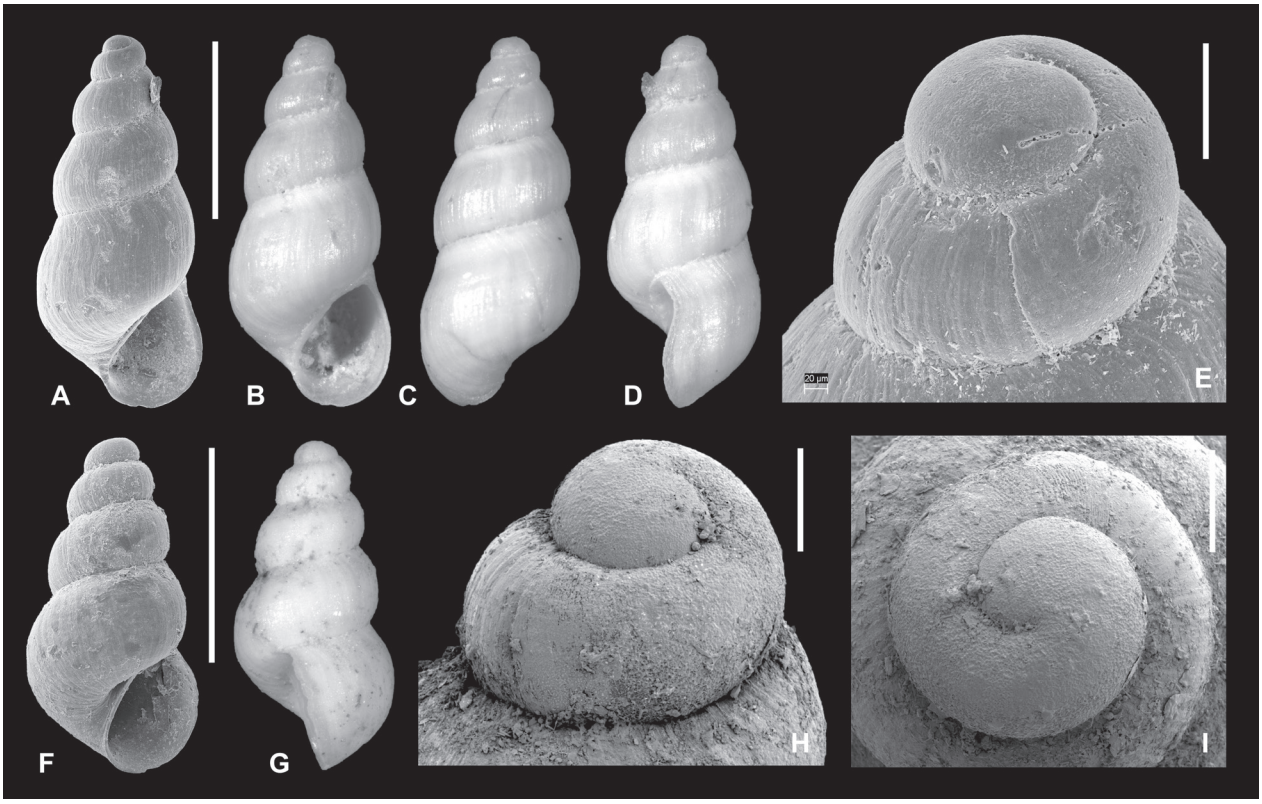


**Figure 6.** Caspiinae (Hydrobiidae) of the Kolankaya I fauna. **A–E.** *Graecoanatolica alcicekorum* sp. nov., holotype, RGM 962617, sample 2. **F–I.** *Graecoanatolica*? sp., RGM 1365349, sample 1. Scale bars: 1 mm (**1–D, F, G**); 100 µm (**E, H, I**).

the upper whorl half of the protoconch, as well as sculpture-free triangle at the P/T boundary (Anistratenko et al. 2021), which is missing though in the Turkish material. Second, the close morphological similarity to species of *Graecoanatolica*, recently placed in Caspiinae as well, supports a classification in that subfamily.

### *Iraklimelania minutissima* sp. nov.

https://zoobank.org/90224404-5C1A-443C-B219-D83B2A467FF4

**Etymology.** Referring to the exceptionally small shell size.

**Holotype.** RGM 962617 (Fig. 7A–E). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

**Additional material.** One juvenile or subadult form (SNSB-BSPG 2023 XII 5; Fig. 7F–J) from sample 2.

**Diagnosis.** Very small, slender hydrobiid with highly convex and slowly growing whorls that show weak subsutural concavity in late ontogeny, small aperture with weak bulge at columella, and sigmoidal growth lines.

**Description.** Exceptionally small, slender hydrobiid shell, with slightly less than 5 whorls that slowly expand in width and height. Protoconch consisting of c. 1.2 whorls; low domed with broad nucleus, malleate surface, with initially tiny mesh-size, which becomes coarser toward P/T

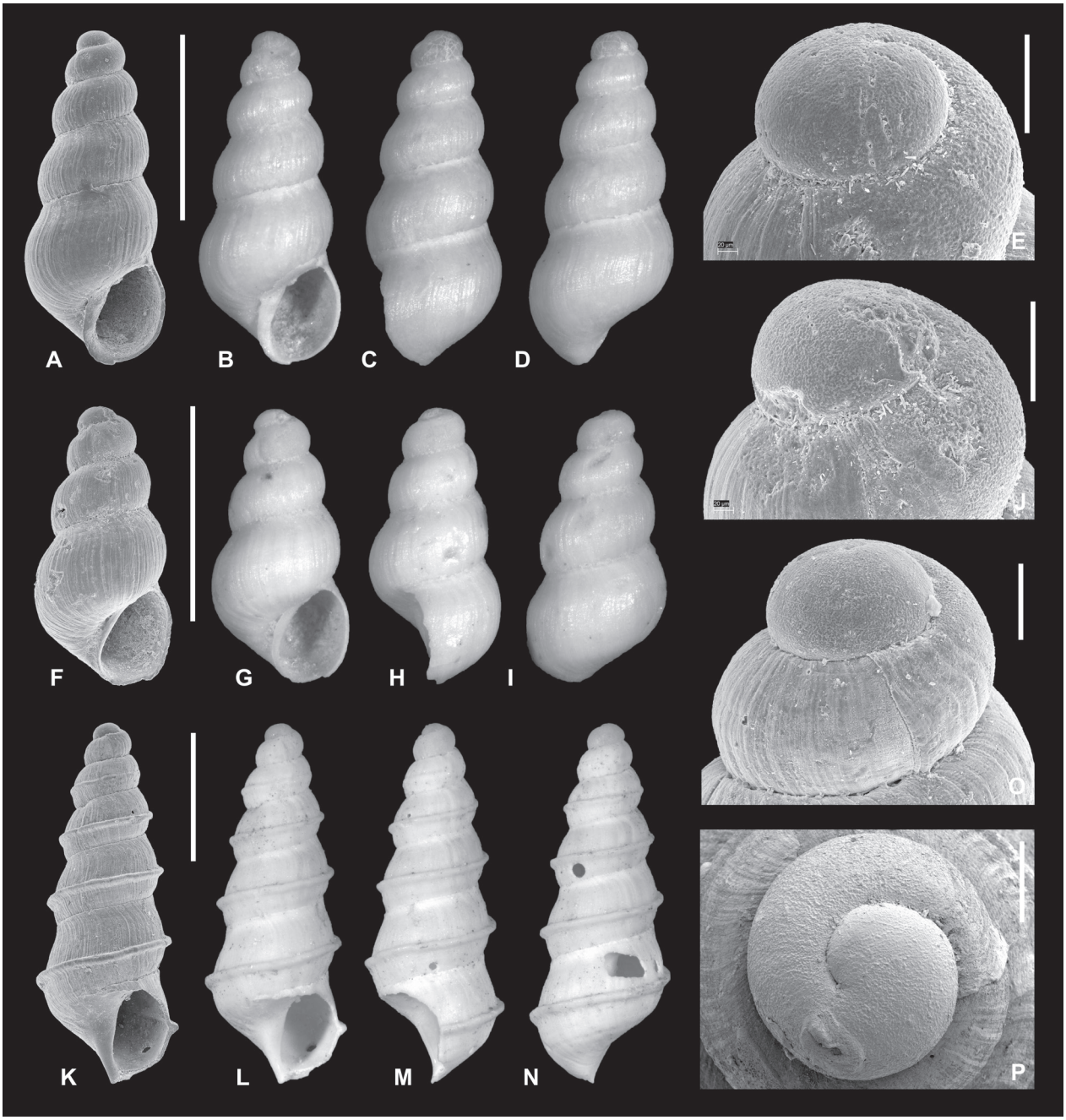


**Figure 7.** Caspiinae (Hydrobiidae) of the Kolankaya I fauna. **A–E.** *Iraklimelania minutissima* sp. nov., holotype, RGM 962618, sample 2. **F–J.** *Iraklimelania minutissima* sp. nov., juvenile or subadult form, SNSB-BSPG 2023 XII 5, sample 2. **K–P.** *Iraklimelania submediocarinata* sp. nov., holotype, RGM 962689, sample 1. Scale bars: 1 mm (**A–D, F–I, K–N**); 100 µm (**E, J, O, P**).

transition; P/T transition indicated by growth stop and onset of growth lines. Whorls highly convex throughout ontogeny; in last two whorls, faint concavity forms below suture. Last whorl attains c. 53% of total shell height. Base ~45°, straight-sided. Aperture small, elliptical; weak bulge occurs at columella. Inner lip covers sheet-like base of penultimate whorl, slightly expanded across columella, leaving very narrow umbilicus; outer lip not preserved. Growth lines distinct, sigmoidal, with opisthocyrt upper half and prosocyrt lower half.

**Dimensions.** 1.93 × 0.83 mm (holotype, RGM 962618; Fig. 7A–E).

**Remarks.** We attribute the new species to the genus *Iraklimelania* based on the following characters matching the type species, *I. levis* Willmann, 1981, from the Lower Pleistocene Irakli Formation of Kos Island: the small size; the small, simple aperture, having a slight bulge at the columella; the highly convex whorls, characterized by a narrow, faint constriction below the suture ("weak, concave sulcus" of Willmann 1981); the sigmoidal growth lines; the faint spiral striae. Our species can be distinguished by the even smaller size, the exceptionally slender shape and the narrower subsutural constriction. The only other species known for that genus, ?*Iraklimelania coa* Willmann, 1981 from the Lower Pleistocene Tafı Formation of Kos, differs in the conical shell and the presence of a blunt keel near the lower suture.

In addition to the holotype, a juvenile or subadult specimen is considered to belong to the new species (Fig. 7F–J). In that shell, the sigmoidality of the growth lines is not yet fully expressed, but the other features fit well to the holotype.

**Distribution.** So far only known from the Early Pleistocene of the Denizli Basin.

### *Iraklimelania submediocarinata* sp. nov.

https://zoobank.org/21403AD8-AA28-49B9-972F-AA7CECA9C827

**Etymology.** Named with respect to the keel below the whorl center.

**Holotype.** RGM 962689 (Fig. 7K–P). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 1 (37°50'40.3"N, 28°52'53.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

**Additional material.** None (holotype only).

**Diagnosis.** Small, slender hydrobiid with distinct, blunt keel below whorl center, slowly growing whorls that show weak subsutural concavity in late ontogeny, small aperture, and sigmoidal growth lines.

**Description.** Small, slender hydrobiid shell, with 6 whorls that slowly expand in width and height. Protoconch consisting of c. 1.2 whorls; low domed with broad nucleus, finely-meshed malleate surface with 6–7 widely, but more or less regularly, spaced, weak spiral striae; terminal phase thickened, devoid of surface sculpture; P/T transition indicated by growth stop and onset of growth lines. Distinct, blunt, relatively broad keel develops on about 2nd teleoconch whorl; becomes quickly more pronounced toward 3rd whorl; originally almost in whorl center, keel becomes successively shifted toward lower suture; on last whorl, it is placed between lower third and upper two thirds of whorl height. Keel leaves weak furrow inside shell, at least on last whorl (Fig. 7K). Disregarding keel, whorls are regularly convex in early whorls, but convexity decreases during ontogeny; whorl portion above keel in last whorl almost straight-sided, with faint concavity below upper suture. Last whorl attains c. 49% of total shell height. Base ~45°, grading from straight-sided upper part into concave neck. Aperture not preserved, but whorl cross-section suggests small, elliptical shape. Growth lines distinct, sigmoidal, with opisthocyrt upper half (above keel) and weakly prosocline lower half (below keel).

**Dimensions.** 2.83 × 1.13 mm (holotype, RGM 962689; Fig. 7K–P).

**Remarks.** As for the previous species, we consider this one to belong in *Iraklimelania*. It matches both *I. minutissima* sp. nov. and the type species in terms of the small, slender shell with convex whorls and narrow subsutural concavity, the small aperture with slight bulge and the sigmoidal growth lines. The main difference to both species is the blunt keel below the center of the whorls. This feature reminds of ?*Iraklimelania coa*, which differs however in the distinctly conical shell with nearly straight-sided whorls.

**Distribution.** So far only known from the Early Pleistocene of the Denizli Basin.

## Subfamily Hydrobiinae Stimpson, 1865

## Genus *Ecrobia* Stimpson, 1865

**Type species.** *Turbo minutus* Totten, 1834 [= *Ecrobia truncata* (Vanatta, 1924)]; by original designation.

### *Ecrobia* sp.

Fig. 8A–F, Q

**Material.** 1 specimen (RGM 962612), 4 specimens (RGM 1310850), 1 specimen SNSB-BSPG 2023 XII 6); all from sample 2.

**Dimensions.** 5.54 × 3.55 mm (RGM 962612; Fig. 8A–C, Q), 4.61 × 3.01 mm (SNSB-BSPG 2023 XII 6, Fig. 8D–F).

**Remarks.** The shape of the shell and the aperture and the type of growth lines are typical of the genus *Ecrobia*. The protoconch includes ~1.1 whorls and appears to be smooth (the preservation of the apex is, however, rather poor). The P/T boundary is marked by the onset of growth lines. Shape-wise our specimens fall well into the morphological range of extant *E. grimmi* (Clessin in Dybowski, 1887) from the Caspian Sea, but it also resembles stout forms of the widespread European *E. ventrosa* (Montagu, 1803) and the Black Sea/eastern Mediterranean species *E. maritima* (Milaschewitsch, 1916). Only, our material is exceptionally large for *Ecrobia* and has a slightly thickened aperture, which is untypical as well. It might well represent

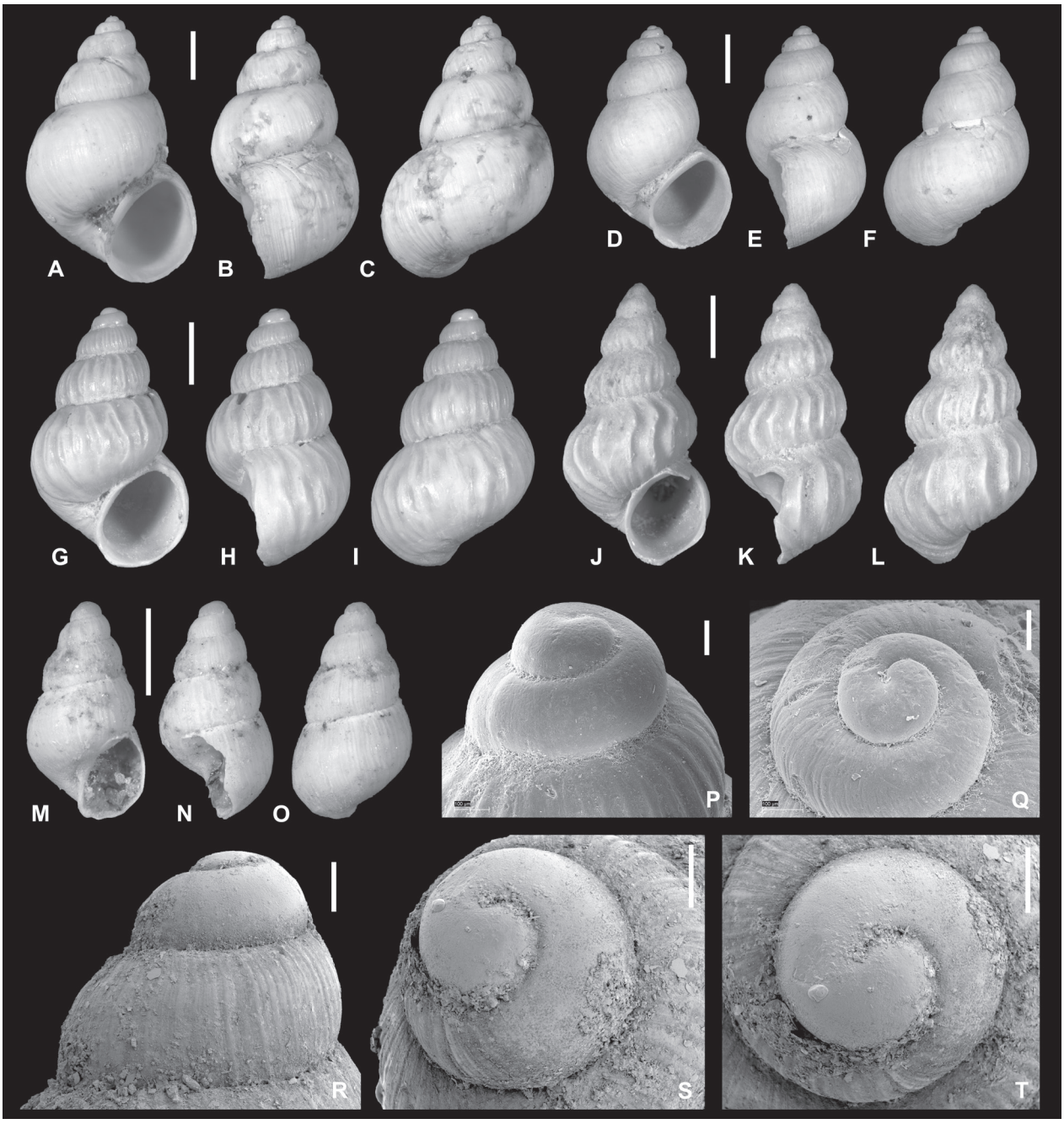


**Figure 8.** Hydrobiinae (Hydrobiidae) of the Kolankaya I fauna. **A–C, Q.** *Ecrobia* sp. RGM 962612, sample 2. **D–F.** *Ecrobia* sp. SNSB-BSPG 2023 XII 6, sample 2. **G–I.** P. *Harzhauseria schizopleura* gen. et sp. nov., holotype, RGM 962613, sample 2. **J–L.** *Harzhauseria schizopleura* gen. et sp. nov., paratype, RGM 962614, sample 2. **M–O, R–T.** Hydrobiinae sp. indet., RGM 1365350, sample 1. Scale bars: 1 mm (**A–O**); 100 µm (**P–T**).

an undescribed species, but since *Ecrobia* species are known to be extremely variable (Kantor and Sysoev 2006; Neubauer et al. 2018; Vandendorpe et al. 2019) and we have only limited material available for comparison, we refrain from introducing a new species.

### Genus *Harzhauseria* gen. nov.

https://zoobank.org/C9177CC8-F0D6-4C9C-9032-3A33BF833F25

**Type species.** *Harzhauseria schizopleura* gen. et sp. nov.; designated herewith.

**Etymology.** Named in honor of Mathias Harzhauser for his many contributions on fossil Mollusca, pan-Tethyan biogeography, and a long friendship.

**Diagnosis.** As for the type species (so far only the type species is known).

**Description.** As for the type species.

**Remarks.** The shell shape, convex whorls, and round, large aperture remind of species of *Ecrobia*, such as the co-occurring *Ecrobia* sp. The presence of ribs, however, makes the species unique and clearly distinguishes it from any other known species or genus of Hydrobiinae (or other Hydrobiidae for that matter).

### *Harzhauseria schizopleura* gen. et sp. nov.

https://zoobank.org/86156305-C9F6-41C3-BDD0-459193B1346E

**Etymology.** Derived from the Ancient Greek syllables σχίζω (skhízō) and πλευρόν (pleurón), referring to the extraordinary sculpture, occasionally showing diverging ribs.

**Holotype.** RGM 962613 (Fig. 8G–I, P). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

**Paratypes.** RGM 962614, SNSB-BSPG 2023 XII 7, SNSB-BSPG 2023 XII 8; all from the type locality and stratum.

**Additional material.** Sample 1: 1 specimen with traces of intense growth lines rather than distinct ribs (SNSB-BSPG 2023 XII 9); sample 2: 6 nearly complete specimens, lacking aperture or last whorl, plus 13 fragments (RGM 1310851), 1 specimen with fragmented aperture and 2 fragments (SNSB-BSPG 2023 XII 10).

**Diagnosis.** Small hydrobiine, conical, slender to slightly broader shell, with highly convex whorls that bear conspicuous irregular (straight to wavy, partly interfingering) ribs and large elliptical aperture.

**Description.** Shell conical, slender to slightly broader, with 5 highly convex whorls. Protoconch smooth, consisting of c. 1.25 regularly coiled whorls; P/T transition marked by distinct growth stop. Numerous, weak, regularly shaped axial ribs develop on first teleoconch whorl. Ribs soon become irregular, variably spanning full whorl height or only parts, partly interfingering with each other (Fig. 8G–I) or they become sigmoidal (Fig. 8J–L). Distance and intensity of ribs also varies across specimens. Sometimes, rib tops are abraded, creating illusion of two ribs merging near upper and lower suture, leaving narrow concavity in between. Last whorl attains 60–64% (n = 2) of total shell height. Base ~45°, straight-sided. Aperture relatively large, well-rounded, elliptical; peristome weakly and equally thickened; umbilicus narrow. Growth lines faint.

**Dimensions.** 3.50 × 2.23 mm (holotype, RGM 962613; Fig. 8G–I, P); 3.69 × 1.96 mm (paratype, RGM 962612; Fig. 8J–L).

**Remarks.** There is considerable morphological variability in the little material available to us. This concerns both shell shape and the expression of the ribs. However, it is well known that species of Hydrobiinae, such as the (probably related) genus *Ecrobia*, are morphologically highly variable, which often complicates establishing species boundaries (e.g., Wesselingh et al. 2019; Andreeva et al. 2022).

**Distribution.** So far only known from the Early Pleistocene of the Denizli Basin.

### Hydrobiinae sp. indet.

Fig. 8M–O, R–T

**Material.** 1 specimen (RGM 1365350) from sample 1.

**Dimensions.** 2.52 × 1.37 mm.

**Remarks.** A single specimen is available, characterized by a small, white, conical shell with convex whorls, simple aperture, and distinct, orthocline growth lines. The protoconch is low domed, forming a bulbous cap of ~1.2 whorls, and apparently smooth, but this might be a result of the moderate preservation. The available features suggest placement in Hydrobiinae, but at present an attribution to genus or species cannot be made.

## Subfamily Pyrgulinae Brusina, 1882

### Genus *Laevicaspia* Dybowski & Grochmalicki, 1917

**Type species.** *Rissoa caspia* Eichwald, 1838; by subsequent designation (Logvinenko and Starobogatov 1969).

### *Laevicaspia* sp.

Fig. 9A–C

**Material.** 1 specimen (RGM 962609) from sample 2.

**Dimensions.** 8.21 × 4.10 mm.

**Remarks.** The size and shape of the shell and the oblique, large, and slightly thickened aperture leaving a narrow umbilicus are characteristic of the Pontocaspian genus *Laevicaspia*. The species reminds of the Quaternary–extant species *L. lincta* (Milaschewitsch, 1908) from the Black Sea. That species is known for its high variability, which has led previous authors to introduce numerous species names (Wesselingh et al. 2019). The Denizli specimens differ from that species by a slightly broader shell with convex, spruce-like whorl profile. *Laevicaspia lincta* has mostly straight-sided whorls, sometimes convex ones; only some specimens approach this type of morphology [see lectotype illustrated by Kantor and Sysoev (2006: pl. 45, fig. D) as well as the holotype of *Pyrgula iljinae* Golikov & Starobogatov, 1966, now considered a synonym of *L. lincta* in Kantor and Sysoev (2006: pl. 49, fig. D)]. Also, the broad shell shape is approached by the holotype of the synonym *Pyrgula* (*Laevicaspia*) *milachevitchi* Golikov & Starobogatov, 1966 depicted in Kantor and Sysoev (2006: pl. 45, fig. C).

Another similar species is *Prososthenia sublaevis* Oppenheim, 1919, described from "Laodicäa", an ancient city 6 km north of Denizli. It differs in the flattened whorls and

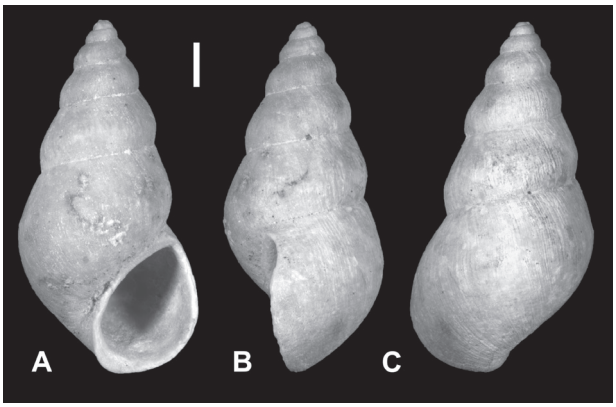


**Figure 9.** Pyrgulinae (Hydrobiidae) of the Kolankaya I fauna. **A–C.** *Laevicaspia* sp., RGM 962609, sample 2. Scale bar: 1 mm.

the presence of a weak subsutural band. *Prososthenia gregaria* (Fuchs, 1877) from the Early Pleistocene of mainland Greece is more slender and has low-convex whorls (see also Esu and Girotti 2020, fig. 9A–F).

Potentially our specimen represents an undescribed species, but given the limited material availability and the high morphological variability of related taxa, we do not introduce a new name.

### Genus *Prososthenia* Neumayr, 1869

**Type species.** *Prososthenia schwartzi* Neumayr, 1869; by subsequent designation (Herbich and Neumayr 1875).

### *Prososthenia* cf. *sturanyi communis* Willmann, 1981

Fig. 10A–J

cf. 1981 *Prososthenia sturanyi communis* ssp. nov. – Willmann: 160, pl. 6, figs 10, 11 (cum syn.).

**Material.** 1 specimen (RGM 962615), 7 specimens, 2 apertural fragments, and 2 apical fragments (RGM 1310852), 1 specimen (SNSB-BSPG 2023 XII 11); all from sample 2.

**Type locality.** Valley between Vokasia and Sefto valley, c. 3.5 km SW of Kos, Kos Island, Greece; lower Kos Formation, Lower Pleistocene.

**Description.** Shell elongate, ovoid, with 5 whorls that decrease in convexity. Early whorls regularly convex; penultimate to last whorl weakly convex to flattened in whorl center; last whorl occasionally has faint concavity below faintly expressed subsutural bulge; suture moderately incised. Base weakly convex to straight-sided. Aperture typically drop-shaped, relatively broad, only weakly inclined; slightly offset in fully grown specimen; peristome weakly and equally thickened, faintly expanded; umbilicus very narrow. Growth lines rather weak, weakly prosocline in upper half to nearly orthocline in lower half, crossed by faint spiral furrows. Protoconch consisting of ~0.9 whorls, with broad nucleus, covered by fine-meshed malleate sculpture.

**Dimensions.** 2.86 × 1.33 mm (RGM 962615; Fig. 10A–E), 2.77 × 1.20 mm (SNSB-BSPG 2023 XII 11; Fig. 10F–J).

**Remarks.** *Prososthenia sturanyi* encompasses shells with highly variable shapes and sizes (Willmann 1981). Slender specimens of *P. s. communis* from Kos Island match the Denizli material in terms of general shape, the flattened whorl flanks, the presence of a weak subsutural band, and faint spiral furrows, as well as the shape of the aperture (compare Willmann 1981, pl. 6, fig. 11). Yet, the Kos specimens are slightly larger and the apex appears to be smaller. Considering the otherwise close similarity, the generally great variability of the species, and the similar age and geographic vicinity, we tentatively refer the Denizli material to *Prososthenia sturanyi communis*.

*Prososthenia sturanyi sturanyi* (Bukowski, 1896) from Plio–Pleistocene formations of Rhodes has a stouter shell with a shorter spire (Willmann 1981). *Prososthenia gregaria* (Fuchs, 1877) from the Early Pleistocene of mainland Greece is much larger and has a slender, elongate shell with regularly, low-convex whorls. A particularly similar species is *Prososthenia eburnea* Brusina, 1897 from Middle Miocene (Langhian) strata of Miočić, Croatia, regarding the decreasing degree of whorl convexity through ontogeny. The species is, however, much larger and more regularly ovoid. The malleate protoconch (Fig. 10E), prosocline-orthocline growth lines, and the presence of spiral furrows also agree with a placement in the genus *Prososthenia* (compare Neubauer et al. 2020).

The taxon is also surprisingly similar to "*Caspia*" *laevigata* Jekelius, 1944 (p. 123–124, pl. 45, figs 9, 10) from the Early Pannonian (Early Tortonian) of Soceni in Romania. That species has a similarly slender, ovoid shell with straight-sided whorls, an angulation on the last whorl toward the straight base, and a slender ovoid aperture. It differs in the early whorls being also nearly straight-sided, where the Denizli species has convex whorls. Furthermore, there seems to be no umbilicus in the Romanian species. On a side note, despite the superficial similarity, it is questionable whether that species is a member of the genus *Caspia* and the Caspiinae. Shells of that group are characterized by a broad and rounded, dome-like protoconch. The Romanian species rather suggests a placement in Pyrgulinae, perhaps even *Prososthenia*. If, however, the species was transferred to *Prososthenia*, the species name *Prososthenia laevigata* Volkova, 1953 would be become a secondary homonym.

**Distribution.** Late Pliocene to Early Pleistocene (Phoka, Sefto, and Kos formations) of Kos Island (Willmann 1981) and, tentatively, Early Pleistocene of the Denizli Basin (this study).

### Genus *Xestopyrguloides* Willmann, 1981

**Type species.** *Xestopyrguloides neumayri* Willmann, 1981; by original designation.

### *Xestopyrguloides*? *sagitta* sp. nov.

https://zoobank.org/F8829057-B9CB-4F19-B7E4-29AF916C0FCB

**Etymology.** After the Latin sagitta meaning "arrow", referring to the slender, pointy shape reminding of an arrowhead (noun in apposition).

**Holotype.** RGM 962616 (Fig. 10K–Q). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

**Paratype.** SNSB-BSPG 2023 XII 12, specimen lacking aperture and apex; from type locality and stratum.

**Additional material.** 1 almost complete specimens and 5 fragments (RGM 1310853), 1 apertural fragment and 1 apical fragment (SNSB-BSPG 2023 XII 13); all from sample 2.

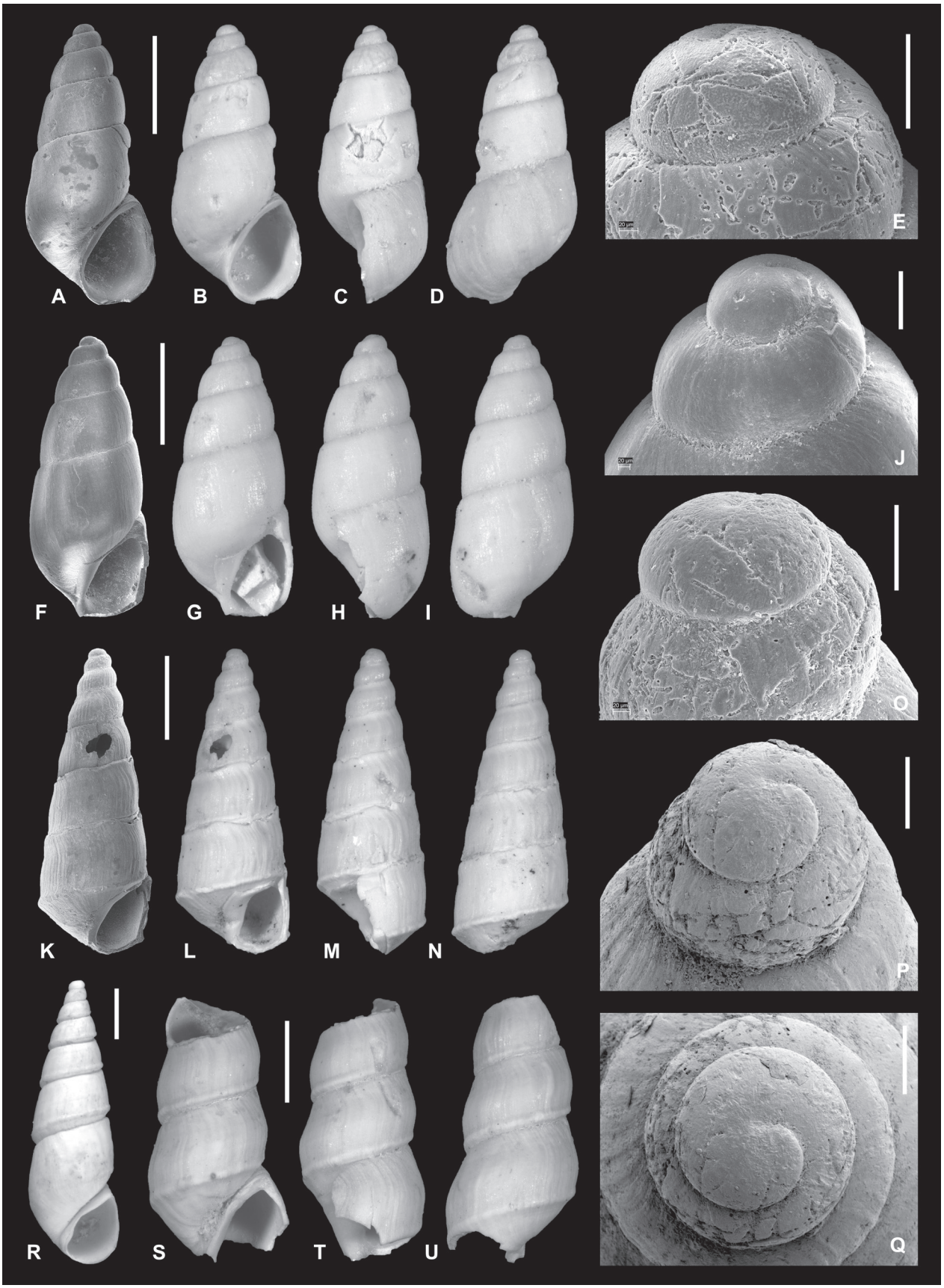


**Figure 10.** Pyrgulinae (Hydrobiidae) of the Kolankaya I fauna. **A–E.** *Prososthenia* cf. *sturanyi communis* Willmann, 1981, RGM 962615, sample 2. **F–J.** *P.* cf. *sturanyi communis*, SNSB-BSPG 2023 XII 11, sample 2. **K–Q.** *Xestopyrguloides*? *sagitta* sp. nov., holotype, RGM 962616, sample 2. **R**. *Xestopyrguloides*? *heldreichii* (Fuchs, 1870), lectotype (designated by Willmann 1981), NHMW 1878 XX 28, Megara, Pliocene. **S–U**. *Xestopyrguloides*? sp., RGM 1365347, sample 2. Scale bars: 1 mm (**A–D, F–I, K–N, R–T**); 100 µm (**E, J, O–Q**).

**Diagnosis.** Very slender, weakly ovoid pyrguline shell characterized by small last whorl, small aperture, narrow but distinct basal keel, and whorl convexity decreasing through ontogeny.

**Description.** Shell slender, elongate, faintly ovoid, almost conical, consists of about 7 whorls. Protoconch low domed, no sculpture discernible (perhaps because of poor preservation; Fig. 10O–Q); P/T boundary not visible. Initial teleoconch whorls are convex, but convexity decreases rapidly around 3rd to 4th whorl. Following whorls are straight-sided or nearly so, with only faint convexity remaining in center of whorls. Whorls bear thin keel directly at lower suture. Keel produces slight swelling at upper suture of following whorl where it overgrows keel. Onset of keel in ontogeny uncertain due to near full overlap; keel visible in parts on at least last four whorls, matching approximately change in convexity. Last whorl relatively small, attaining 43% of shell height. Keel there produces sharp angle toward straight-sided shallow base (~55° to shell axis). Aperture not full preserved, but appears to be narrow ovoid. Inner lip covers umbilicus. Growth lines opisthocyrt, but more distinctly in upper half of whorls.

**Dimensions.** 3.65 × 1.37 mm (holotype, RGM 962616; Fig. 10K–Q).

**Remarks.** Only two other *Xestopyrguloides* have been described so far: the type species *X. neumayri* (Willmann, 1981) from the Early Pleistocene of Kos Island and *X.*? *heldreichii* (Fuchs, 1877) from the Pliocene of Megara, whereas the second species is only tentatively referred to the genus (Willmann 1981, p. 202–203, textfig. 67). Both species have elongated shells with straight whorl flanks and distinct keel close to lower suture (or sometimes directly above it). Below the keel occurs a marked constriction toward the suture, which results in a weakly spruce-like appearance. *Xestopyrguloides*? *heldreichii* has in addition a slightly thickened peristome, especially at the inner lip. The lectotype designated by Willmann (1981, p. 203; NHMW 1878 XX 28) is illustrated on Fig. 10R.

The straight-sided whorls and keel at the lower suture are also present in *Xestopyrguloides sagitta* sp. nov. The aperture is, however, much smaller and the base is more shallow than in the other species of that genus, which is why we only tentatively allocate the Turkish species there.

A *Xestopyrguloides* sp. was mentioned by Schütt and Kavusan (1984) from supposedly Miocene deposits of the area around Harmancık but not illustrated. Judging from the brief description, referring to a rather stout form with lower height and a sharp keel right above the suture, it is a different species than the one we describe herein.

The new species also reminds of representatives of the genus *Falsipyrgula* Radoman, 1973a, many of which have a keel near the lower suture as well (Schütt and Yildirim 1999). The type species, *Falsipyrgula pfeiferi* (Weber, 1927), also shares the slender shape and the straight whorl flanks (Radoman 1973a). On average, however, *Falsipyrgula* species are broader and have larger and broadly ovoid apertures.

The placement in Pyrgulinae is preliminary and based on the comparison with Pontocaspian *Turricaspia* and *Laevicaspia*, with which *Xestopyrguloides*? *sagitta* sp. nov. shares the elongate, multi-whorled shell and the flattened, often smooth or faintly ornamented protoconch (Neubauer et al. 2018; T.A.N., pers. obs.).

**Distribution.** So far only known from the Early Pleistocene of the Denizli Basin.

### *Xestopyrguloides*? sp.

Fig. 10S–U

**Material.** 1 fragment (RGM 1365347) from sample 2.

**Remarks.** A second species is tentatively referred to the genus *Xestopyrguloides*. A single incomplete shell is available, containing the last 2.5 whorls and the upper part of the aperture. The shell is similarly elongate as *Xestopyrguloides*? *sagitta* sp. nov. and also bears a narrow basal keel, as well as the same type of growth lines. However, the shell is larger, the whorls are moderately convex, and the aperture is larger and drop-shaped. The basal keel and shape of the aperture, as well as the size, would also fit to the Greek *X. neumayri* and *Xestopyrguloides*? *heldreichii* (Fig. 10R), but both species have straight-sided whorls.

## The *Staja–Falsipyrgula* species complex

**Remarks.** The enormous morphological variability of the Denizli specimens, as well as other material from Turkey and Greece assigned to the genus *Staja* (e.g., Willmann 1982), makes a systematic classification incredibly difficult. This concerns variation in shell shape, size, and presence and expression of sculpture, which – if our assessment is correct – varies even within single species. The keeled representatives remind of and are considered to belong in the Pyrgulinae genus *Falsipyrgula*, while the smooth morphotypes are classically assigned to *Staja*, a genus that is originally described from the Late Miocene of the Pannonian Basin.

A full revision of the Greek–Turkish *Staja–Falsipyrgula* species complex is beyond the scope of this study. We follow the literature for the genus classifications of the known species, yet being aware of the unresolved genus concepts. A new species is placed in *Falsipyrgula* due to the close similarities to extant congeners.

## Genus *Staja* Brusina, 1897

**Type species.** *Staja adiaphora* Brusina, 1897; by subsequent designation (Cossmann 1898).

### *Staja lycica* (Oppenheim, 1919)

Fig. 11A–I, S, T

*1919 *Fluminicola* (*Gillia*) *lycica* sp. nov. – Oppenheim: 117–119, pl. 5, fig. 2, 2a.

1923 *Amnicola* (*Staja*) *lycica* (Oppenheim) – Wenz: 2086.

1982 *Pseudamnicola* (*Staja*) *lycica* (Oppenheim 1919) – Willmann: 313–314.

? 2008 *Pseudamnicola orientalis* (Bukowski, 1895) – Wesselingh et al.: 865, fig. 5(8a–c).

**Material.** Sample 1: 21 specimens and 5 fragments (RGM 1310854), 1 specimen (RGM 1365351), 2 specimens (SNSB-BSPG 2023 XII 14); sample 2: 1 specimen (RGM 962619), 1 specimen (SNSB-BSPG 2023 XII 15).

**Type locality.** Tlos (an ancient city in Muğla Province near Seydikemer), Turkey; probably Eşen Formation (Kocaçay Member), Zanclean, Lower Pliocene.

**Description.** Ovoid, slender to slightly broader shell with up to 5 moderately convex whorls. Protoconch low-domed, consisting of c. 1.2 apparently smooth whorls; P/T boundary marked by growth rim and onset of growth lines. Last whorl attains 79–82% (n = 3) of total height. Aperture oblique, ovoid to almost elliptical, weakly inclined in lateral view. Inner lip touches base of penultimate whorl but weakly detaches in some specimens near adapical tip and base, leaving very narrow umbilicus; latter occasionally opens into narrow canal that runs along inner lip toward base and is demarcated by weak fasciole. Shell surface smooth except for numerous faint spiral furrows detected in well-preserved specimens.

**Dimensions.** 6.08 × 4.24 mm (Fig. 11A–C, S; RGM 962619), 3.90 × 2.76 mm (SNSB-BSPG 2023 XII 15; Fig. 11D, T), 4.41 × 2.83 (Fig. 11G–I; RGM 1365351).

**Remarks.** Here, we combine a variety of morphologies under the name *Staja lycica*. This includes a comparatively large, broad morphotype with highly convex whorls (Fig. 11A–C, S; RGM 962619), which matches

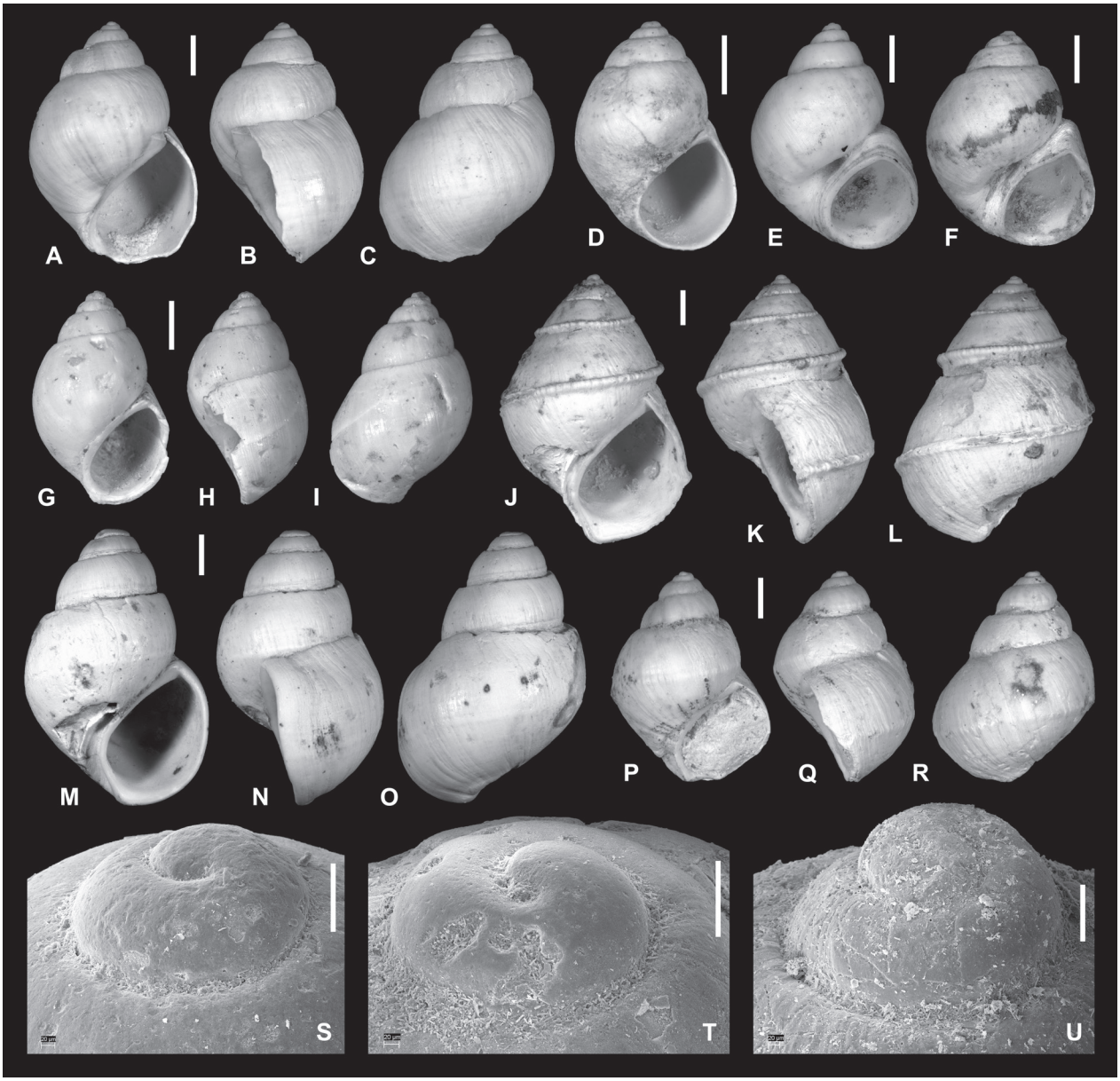


**Figure 11.** The *Staja–Falsipyrgula* species complex of the Kolankaya I fauna. **A–C.** S. *Staja lycica* (Oppenheim, 1919), RGM 962619, sample 2. **D, T.** *S. lycica*, SNSB-BSPG 2023 XII 15, sample 2. **E.** *Staja orientalis* (Bukowski, 1896), lectotype (designated herein), IGUW 1895 XII/45, between Profilia and Istrios, Rhodes, Greece, Istrios Formation (Pliocene). **F.** *S. orientalis*, paralectotype, IGUW 1895 XII/46, same locality and stratum. **G–I.** *S. lycica*, RGM 1365351, sample 1. **J–L, U.** *Staja*? *cibyratica* (Spratt & Forbes, 1847), RGM 962621, sample 2. **M–O.** *S.*? *cibyratica*, RGM 962620, sample 2. **P–R**. *S.*? *cibyratica*, SNSB-BSPG 2023 XII 16, sample 2. Scale bars: 1 mm (**A–R**); 100 µm (**S–U**).

the features illustrated by Oppenheim (1919). Also the overall size, the faint spiral furrows indicated by Oppenheim, as well as the slightly inclined aperture fit well. The very weak detachment of the aperture from the base of the last whorl and the "layered peristome" referred to by Oppenheim and shown in his illustrations match a morphotype that is more slender and smaller but otherwise fits the original description and illustration and cannot be reasonably distinguished (Fig. 11G–I). Since Oppenheim's type material seems to be lost, topotypic material from the Eşen Basin is needed to clarify the identity and variability of this species.

*Staja orientalis* (Bukowski, 1896) from the Pliocene Istrios Formation of Rhodes differs from *S. lycica* in the even broader shape, larger size, and presence of an umbilicus (Fig. 11E, F). However, some specimens of *S. orientalis* from Attica (mainland Greece) illustrated by Willmann (1982, fig. 3i–l) closely resemble *S. lycica*. Willmann (1982) even hypothesized that both species might be synonymous. A thorough revision of the *Staja lycica–orientalis* species group is required to settle these uncertainties. To fix the identity of *S. orientalis*, we hereby designate the specimen illustrated by Bukowski (1896, pl. 10, fig. 1) as the lectotype (IGUW 1895 XII/45; Fig. 11F).

The specimen from the Kolankaya II fauna of the upper Kolankaya Formation attributed to *S. orientalis* by Wesselingh et al. (2008) rather range within *S. lycica*; they even show the slightly detached aperture as mentioned by Oppenheim.

**Distribution.** So far only known from the type locality in the Eşen Basin (Oppenheim 1919), which is of Late Pliocene age according to (Alçiçek et al. 2019), and the Early Pleistocene of the Denizli Basin (this study).

### *Staja*? *cibyratica* (Spratt & Forbes, 1847)

Fig. 11J–R, T

*1847 *Paludina Cibyratica* – Spratt and Forbes: 177, textfig. b.
1928 *Viviparus cibyraticus* (Forbes) – Wenz: 2304.
? 1982 *Pseudamnicola* (*Staja*?) *cibyratica* (Forbes 1847) – Willmann: 315–318, textfigs 6, 7, 9g–h.

**Material.** Sample 2: 1 specimen (RGM 962620), 1 specimen (RGM 962621), 23 mostly poorly preserved specimens (RGM 1310855), 35 mostly poorly preserved specimens and a few fragments (RGM 1310856), 1 specimen (SNSB-BSPG 2023 XII 16); sample 3: 10 mostly poorly preserved specimens (RGM 1310857), 4 mostly poorly preserved specimens and 1 fragment (SNSB-BSPG 2023 XII 17).

**Type locality.** Between Altınyayla (former Dirmil) and the ancient city Kibyra ("between Tremeely and Cibyra"), Çameli Basin, Burdur, Turkey; Çameli Formation (Değne Member), Upper Pliocene; and Minare, Eşen Basin, Muğla; Eşen Formation (Kocaçay Member), Lower Pliocene.

**Description.** Large, bulky shell with up to 5.5 whorls. Apex raised, but top of protoconch depressed; protoconch consists of c. 1.2 whorls without discernible sculpture; P/T boundary marked by growth rim and onset of growth lines. Teleoconch whorls moderately convex to almost straight-sided; latter type creates nearly perfectly conical profile. Teleoconch bears keel close to or directly at lower suture. Expression of keel highly variable, ranging from distinct, blunt crest, typically with irregular surface (such as fused nodules), to almost absent, only with faint trace. Additionally, numerous fine spiral furrows cover well-preserved specimens. Last whorl attains 75–80% (n = 3) of total shell height; final portion occasionally grows stronger in adapical direction, creating slightly irregular shape and "raises" keel above whorl base (Fig. 11J–L). Base steep and straight-sided or weakly convex and passing into concavity toward neck. Aperture ovoid, pointed adapically, weakly inclined in lateral view. Peristome thin or occasionally thickened, with adnate inner lip. Umbilicus narrow, opens into narrow canal that runs along inner lip toward base, bordered by distinct, sharp fasciole.

**Dimensions.** 7.79 × 5.57 mm (RGM 962621; Fig. 11J–L, U), 11.02 × 7.28 mm (RGM 962620; Fig. 11M–O), 5.20 × 3.96 mm (SNSB-BSPG 2023 XII 16; Fig. 11P–R).

**Remarks.** This species covers a great variety of shell shapes and sizes, which complicates establishing species boundaries. The morphological variability is even larger when including Willmann's (1982) material from the Çameli Basin, which shows much thicker, bulkier shells with a thickened peristome and a keel that is blunt or entirely absent. Our specimens correspond more to the original, but rather poor illustrations by Spratt and Forbes (1847) showing shells bearing a slender keel and a thin peristome. Regarding size, the nearly conical spire, and the laterally oblique aperture, as well as the presence of a fasciole, our specimens correspond well to Willmann's.

The systematic placement of this species has proven difficult in the past. Because of its relatively large size and bulky morphology it was originally attributed to viviparids (Neumayr 1880b; Wenz 1923). Neumayr (1880b, footnote on p. 266) stated that he could not distinguish the species from juveniles of *Viviparus vukotinovicii* (Frauenfeld, 1862) ["die ich von jungen Exemplaren von *Viv. Vukotinovici* [sic] Frfld. aus Slavonien nicht unterscheiden kann"].

The species is classified in *Staja* following the opinion of Willmann (1982), but shell shape and keel remind of the genus *Falsipyrgula*, also in comparison with the co-occurring *F.* cf. *sieversi* and *F.*? *coronata* sp. nov. (see below). As stated above, the species complex and genus classifications therein may need reconsideration after a thorough revision.

**Distribution.** Known from several localities with Pliocene strata in the Çameli and Eşen basins (Spratt and Forbes 1847; Willmann 1982) and the Early Pleistocene of the Denizli Basin (this study).

### *Falsipyrgula*? *coronata* sp. nov.

https://zoobank.org/B3E4BA51-6674-436A-8F43-A3EF5A686A56

**Etymology.** The species epithet means "crowned" in Latin and refers to the beaded keel.

**Holotype.** RGM 1310837 (Fig. 12A–C). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

**Paratypes.** RGM 962611 (Fig. 12J–L) from sample 2; SNSB-BSPG 2023 XII 18 (Fig. 12D–F, T) from sample 2; SNSB-BSPG 2023 XII 19 (Fig. 12I) from sample 3.

**Additional material.** Sample 2: 1 specimen (RGM 1310377), 27 partly incomplete specimens and 10 fragments (RGM 1310858); sample 3: 4 specimens and 2 fragments (RGM 1310859).

**Diagnosis.** Conical pyrguline shell characterized by central to subcentral, typically beaded keel, topped by shallow, straight-sided subsutural whorl profile, convex portion below keel, grading into straight-sided base, thin peristome, and narrow umbilicus.

**Description.** Moderately sized conical shell with up to 6 whorls. Protoconch poorly preserved in all studied specimens; surface and P/T boundary unknown. Already on approximately first to second teleoconch whorl a central to subcentral keel appears, which increases continuously in strength through ontogeny. Also in cases with early keel placed at whorl center, keel becomes distinctly subcentral in later ontogeny. Keel typically bears nodules (Fig. 12D–F), which are sometimes not visible, probably due to abrasion (Fig. 12A–C, I–L). Whorl portions above and below keel straight-sided. Last whorl attains ~68–71% (n = 3) of total shell height; passes over weak convexity into moderately steep (~45°), straight-sided base. Aperture broadly ovoid, with rather thin peristome and adnate inner lip; umbilicus narrow.

**Dimensions.** 7.82 × 5.26 mm (holotype, RGM 1310837; Fig. 12A–C), 10.02 × 6.35 mm (paratype, RGM 962611; Fig. 12J–L), 6.73 × 3.78 mm (paratype, SNSB-BSPG 2023 XII 19; Fig. 12I), 4.05 × 2.84 mm (paratype, juvenile, SNSB-BSPG 2023 XII 18; Fig. 12D–F, T).

**Remarks.** As for other members in the *Staja–Falsipyrgula* species complex, the shell of this species exhibits a certain degree of variability. Occasionally, species with a more slender shell (Fig. 12I) or a narrower, non-beaded keel (Fig. 12J–L) are observed. The latter feature may, however, be the result of poor preservation, in many cases shell surfaces and sculptural elements are abraded. Common to all specimens is the conical shell, the comparatively shallow and straight-sided whorl profile above the keel, the thin and edgy peristome, and the narrow umbilicus. These features distinguish *Falsipyrgula*? *coronata* sp. nov. from similar species of *Falsipyrgula*, including the co-occurring *F.* cf. *sieversi*. The latter species shares the beaded keel, which is, however, consistently weaker and slightly lower positioned on the whorl, but the shell is ovoid, smaller, and has a stronger inclined, regularly ovoid aperture. Extant *Falsipyrgula* species have a lower positioned keel or multiple keels or otherwise differ in shape (Schütt and Yildirim 1999).

*Prososthenia attica* Fuchs, 1877 sensu Schütt and Besenecker (1973, pl. 1, fig. 7) from the Late Miocene (?) of Chios resembles *F.*? *coronata* in terms of overall shell shape and presence of a subcentral keel, but the last whorl is tapered and the whorl profile above the keel is convex. Original *P. attica* from the Pliocene of Megara is more elongate and has only a week keel near the whorl base (Fuchs 1877) and is probably a different species as the Chios specimens.

**Distribution.** Known only from the Early Pleistocene of the Denizli Basin.

### *Falsipyrgula* cf. *sieversi* (Boettger, 1881)

Fig. 12G, H, M–R, U

cf. *1881 *Hydrobia Sieversi* Bttg. sp. nov. – Boettger: 246–247, pl. 9, fig. 23.

cf. 2014 *Falsipyrgula sieversi* (Boettger, 1881) – Vasilyan et al: 297, fig. 2k.

cf. 2016 *Pyrgula* (?) *sieversi* (O. Boettger, 1881) – Vinarski and Kantor: 242–243.

cf. 2018 *Hydrobia sieversi* O. Boettger, 1881 – Sitnikova et al.: 74, 75, fig. 4j [as *Falsipyrgula* in the discussion].

**Material.** Sample 2: 1 specimen (RGM 962610), 1 specimen (RGM 1310376), 27 partly incomplete specimens and fragments (RGM 1310861), 1 specimen (SNSB-BSPG 2023 XII 20); sample 3: 1 specimen (RGM 1310375).

**Type locality.** Bank deposits of the Araks River near Nakhichevan' Town, Azerbaijan (approximately 39°10'30"N, 45°21'41"E); extant.

**Description.** Small, ovoid hydrobiid with 5 whorls. Protoconch consists of ~1 whorl, without discernible sculpture but clear P/T boundary (Fig. 12U). First teleoconch whorl smooth, soon weak, beaded keel with round, equally spaced nodules appears slightly below whorl center. Nodules increase slightly in intensity throughout ontogeny and form keel-like appearance on last whorl. Whorl profile weakly convex above nodules, convex below them, grading into weakly convex base. Last whorl attains ~70–76% (n = 3) of total shell height. Aperture ovoid, strongly inclined, faintly detached, leaving narrow umbilicus. Peristome continuous, not thickened or expanded, but weakly intensified abapical growth in final ontogeny typical of hydrobiids exposes shell layers at adapical tip.

**Dimensions.** 4.66 × 2.97 mm (RGM 962610; Fig. 12M–O, U), 3.54 × 2.43 mm (RGM 1310376; Fig. 12G, H), 3.60 × 2.56 mm (SNSB-BSPG 2023 XII 20; Fig. 12P–R).

**Remarks.** The available material shows high similarities and is perhaps conspecific with the extant *Falsipyrgula sieversi* (Boettger, 1881) from the Aras river in Nakhchivan (Azerbaijan). Sitnikova et al. (2018) recently studied and illustrated the holotype, which matches our specimens in terms of shell shape, size, whorl convexity, the position of the keel, the slightly convex base, and the shape and tilt of the aperture. The only difference is that the keel is not beaded as in the Denizli specimens. However, Sitnikova et al. (2018) also reported keel-less, fossil specimens of that species, confirming the variability of this trait in the *Staja–Falsipyrgula* species complex. Shells

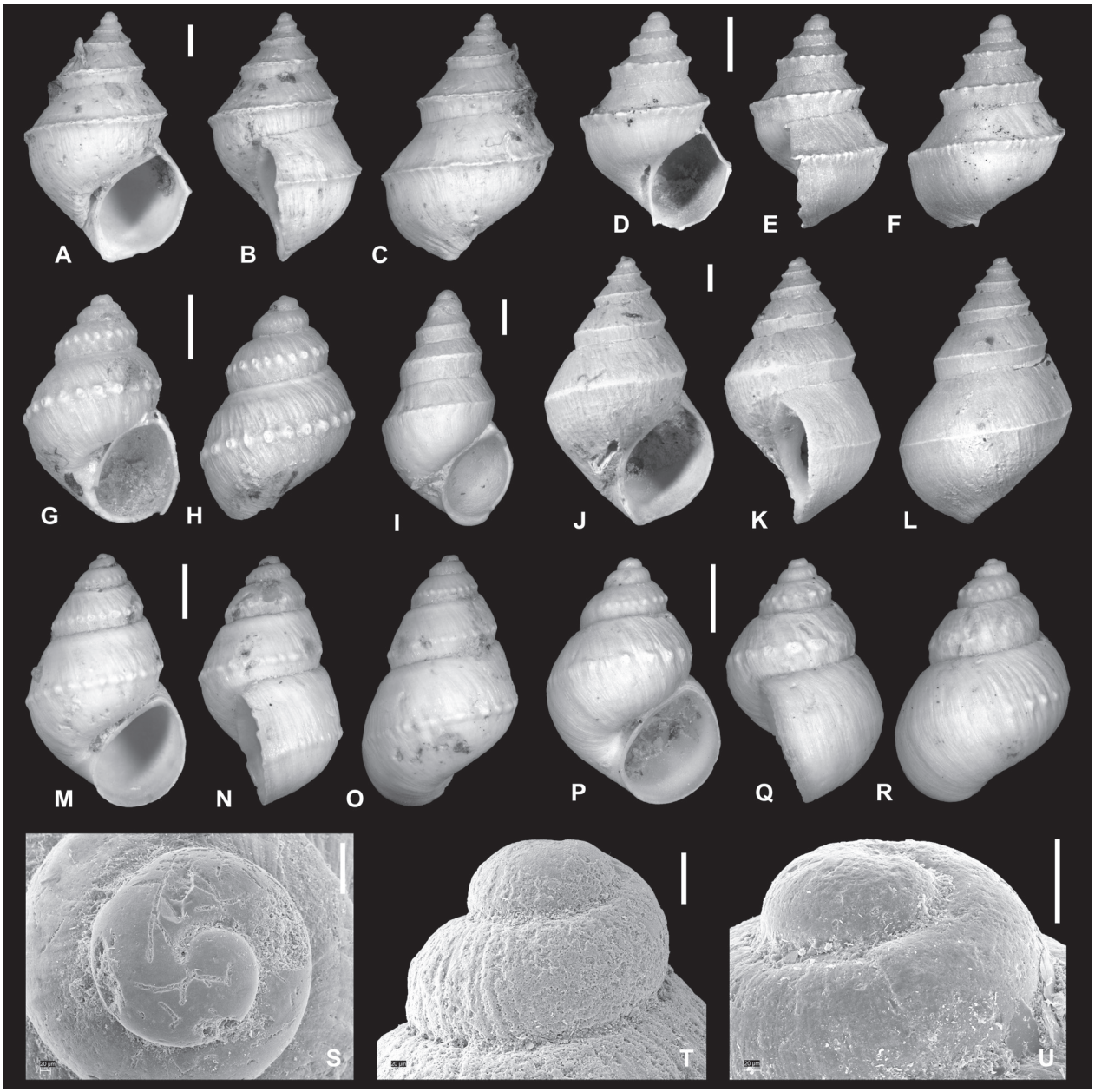


**Figure 12.** The *Staja–Falsipyrgula* species complex of the Kolankaya I fauna. **A–C.** *Falsipyrgula*? *coronata* sp. nov., holotype, RGM 1310837, sample 2. **D–F, T.** *F.*? *coronata* sp. nov., SNSB-BSPG 2023 XII 18, sample 2. **G, H.** *Falsipyrgula* cf. *sieversi* (Boettger, 1881), RGM 1310376, sample 2. **I.** *F.*? *coronata* sp. nov., SNSB-BSPG 2023 XII 19, sample 3. **J–L.** *F.*? *coronata* sp. nov., RGM 962611, sample 2. **M–O, U.** *F.* cf. *sieversi*, RGM 962610, sample 2. **P–R.** *F.* cf. *sieversi*, SNSB-BSPG 2023 XII 20, sample 2. **S.** *F.*? *coronata* sp. nov., RGM 1310377, sample 2. Scale bars: 1 mm (**A–R**); 100 µm (**S–U**).

reported from the Early Pleistocene of the Pasinler Basin are considerably broader, nearly conical, and bear the keel at the base of the whorl (Vasilyan et al. 2014).

Other similar species include *F. osmana* (Bukowski, 1930) from the Quaternary of Burdur and *Kirelia carinata* Radoman, 1973b (classified as *Falsipyrgula* by Schütt and Yildirim 1999), both of which differs in the stronger, continuous keel and the slightly more elongate shell (Schütt and Yildirim 1999).

**Distribution.** *Falsipyrgula sieversi* is known living and from Quaternary strata in Nakhchivan (Azerbaijan) (Sitnikova et al. 2018), the Early Pleistocene of Armenia (Tesakov et al. 2019), and the Pasinler Basin (Vasilyan et al. 2014).

## Subfamily indet.

## Hydrobiidae sp. indet.

Fig. 13A–C

**Material.** 1 shell (RGM 1310799) from sample 2.

**Dimensions.** 4.25 × 2.56 mm.

**Remarks.** The single specimen from Denizli closely resembles the extant *Radomaniola caputlacus* (Schütt & Şeşen, 1993), originally described as a species of *Orientalina* from eastern Anatolia. Both share the conical shape with weakly convex whorls and the simple ovate aperture. However, *Radomaniola caputlacus* is with 2.2 mm shell

height (Schütt and Şeşen 1993) only about half the size of the Denizli shell. Larger species (up to 4 mm) of that genus are known from the Balkan Pensinula, where it is considerably more diverse, but these species differ clearly from the Denizli shell (Delicado and Hauffe 2022).

Another similar species is the fossil *Bithynia giralanensis* Oppenheim, 1919 (pl. 10, fig. 1), described from the Denizli Basin. However, that species is much larger (10 × 8 mm) at about the same number of whorls and bears a weak subsutural band; also, the shell is slightly broader and has a shallower base. Given these features, classification in the genus *Bithynia* is unlikely. Considering the poor preservation of Oppenheim's material as cast and the apparent loss of the type material (see Introduction), the name *Bithynia giralanensis* Oppenheim, 1919 should be considered a nomen dubium.

Yet another similar species is *Bania urosevici* (Pavlović, 1931) from the middle Miocene of Serbia in terms of general shape, the angulation, and the tilt of the aperture (Neubauer et al. 2020). The Denizli shell is, however, much larger (height of *B. urosevici* ~1.8 mm). Moreover, no *Bania* species is known until now from Turkey or deposits younger than Tortonian. The shell similarity may rather be due to convergence.

Finally, the species shares similarities with species of Shadiniinae, e.g., *Persipyrgula saboori* (Glöer & Pešić, 2009), which has a similar size, number of whorls, and shell shape, but more rounded whorls and a larger aperture (Delicado et al. 2016).

Given the poor preservation of our material and the overall difficulty of assigning fossil hydrobiids with few morphological characteristics to genera and even subfamilies, we refrain from a tentative placement in any of the abovementioned taxa.

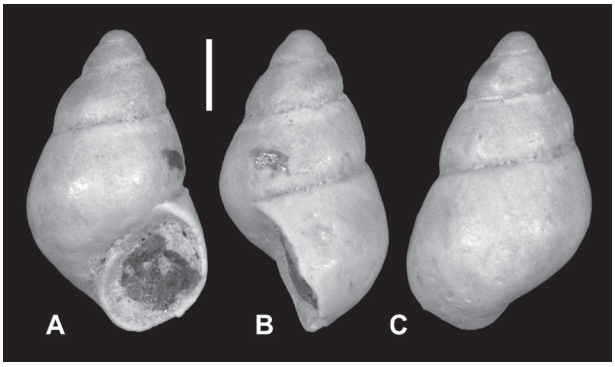


**Figure 13.** Hydrobiidae of the Kolankaya I fauna. **A–C.** Hydrobiidae sp. indet., RGM 1310799, sample 2. Scale bar: 1 mm.

## Subclass Heterobranchia Burmeister, 1837
## Informal group "Lower Heterobranchia" sensu Bouchet et al. 2017
## Superfamily Valvatoidea Gray, 1840
## Family Valvatidae Gray, 1840

### Genus *Valvata* Müller, 1773

**Type species.** *Valvata cristata* Müller, 1774; by subsequent monotypy.

### *Valvata piscinalis* (Müller, 1774)

Fig. 14A–D

*1774 *Nerita piscinalis* – Müller: 172.
1928 *Valvata* (*Cincinna*) *piscinalis piscinalis* (Müller) – Wenz: 2443–2445.
2002 *Valvata* (*Cincinna*) *piscinalis piscinalis* (O. F. Müller 1774) – Glöer: 190–191, textfig. 2019.
2012 *Valvata piscinalis* (Müller, 1774) – Welter-Schultes: 44, unnumbered textfig.
2019 *Valvata* (*Cincinna*) *piscinalis piscinalis* (O. F. Müller, 1774) – Glöer: 204–205, textfig. 256.

**Material.** 1 specimen (RGM 962694) from sample 3.

**Dimensions.** 6.25 × 6.15 mm.

**Remarks.** This well-known extant species is a typical representative of Quaternary freshwater mollusk faunas. It is known for its morphological variability, especially concerning the outline shape, ranging from nearly conical to broadly ovoid, being a result of an inflated penultimate whorl (Glöer 2002, 2019; Welter-Schultes 2012). The apex is depressed, the aperture is nearly circular and the umbilicus is wide. All these features match well the Turkish specimen, which also shows an expanded penultimate whorl. Only, it is slightly larger than the average extant members of the species (up to 4.5 mm high and 5 mm broad; Glöer 2019).

The material also resembles the depressed morphotype of the extant *Valvata lilljeborgi* Westerlund, 1897 in terms of the inflated penultimate whorl. That species comprises a broader range of morphologies, also including unusually high-spired forms (Vinarski et al. 2013). The species is today restricted to cold-temperate regions of the Baltic Sea Basin, the Dnieper Basin, and Western Siberia (Vinarski et al. 2013; Glöer 2019). Considering the above, we consider an identification with the more common *V. piscinalis* more likely.

**Distribution.** Today present throughout the Palearctic, also introduced to North America (Welter-Schultes 2012; Glöer 2019). Common in Upper Miocene to Pleistocene deposits across Europe (Wenz 1923).

### *Valvata* sp. 1

Fig. 14E–L, U–W

**Material.** Sample 1: 1 specimen (RGM 1365352), 1 specimen (SNSB-BSPG 2023 XII 21); sample 2: 1 specimen (RGM 962695), 1 specimen (SNSB-BSPG 2023 XII 22).

**Dimensions.** 1.60 × 2.48 mm (RGM 962695; Fig. 14I–L, W), 1.48 × 2.18 mm (RGM 1365352; Fig. 14E–H, U, V).

**Remarks.** This species is characterized by a small, low-trochiform shell with relatively large, nearly circular aperture, slightly raised, bulbous apex, wide umbilicus, and moderately distinct growth lines. The protoconch bears the typical valvatid pattern, with numerous distinct spiral ridges crossed by weaker axial, u-shaped ridges, creating a wavy impression (Fig. 14U, V).

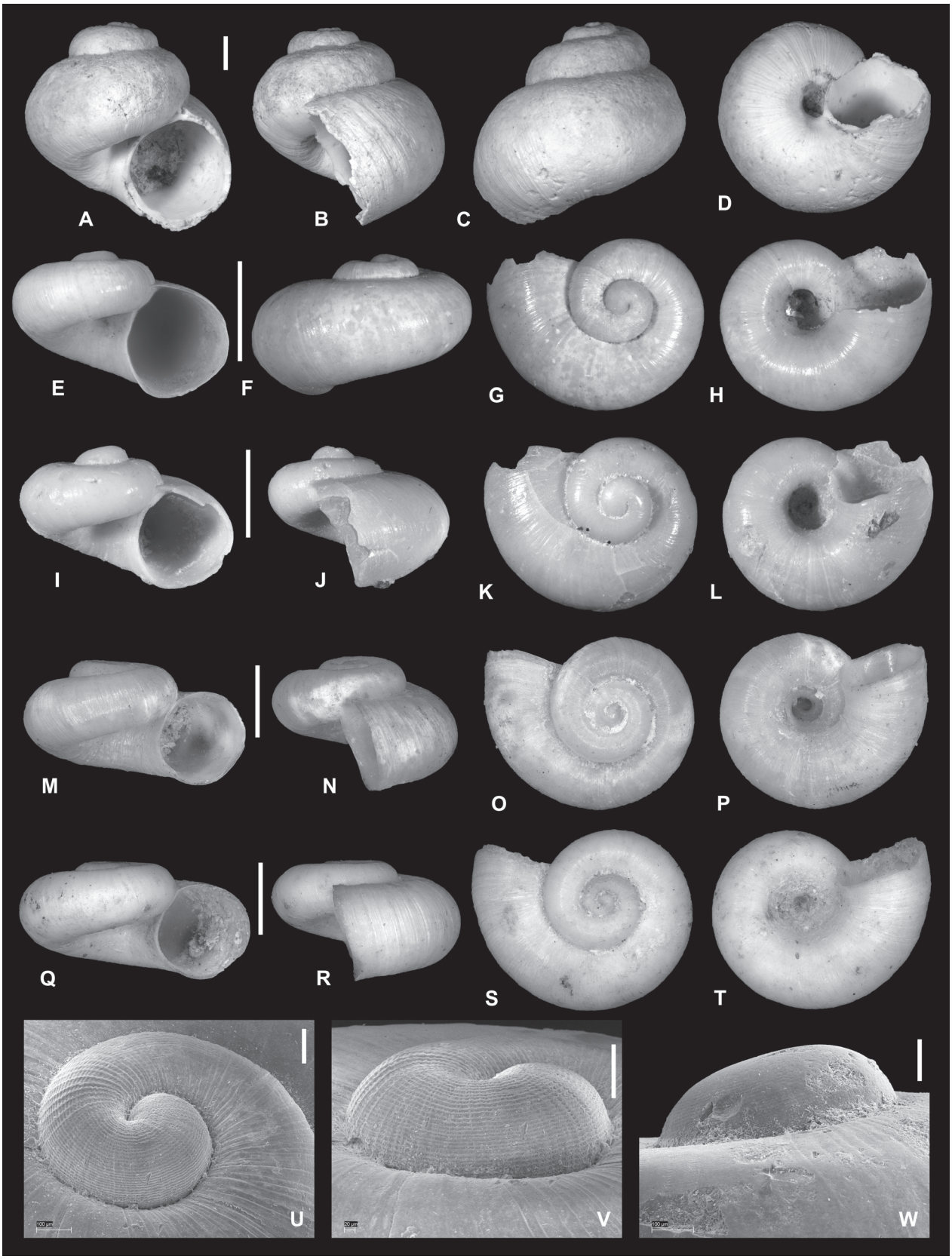


**Figure 14.** Valvatidae of the Kolankaya I fauna. **A–D.** *Valvata piscinalis* (Müller, 1774), RGM 962694, sample 3. **E–H, U, V.** *Valvata* sp. 1, RGM 1365352, sample 1. **I–L, W.** *Valvata* sp. 1, RGM 962695, sample 2. **M–P**. *Valvata gregaria* Bukowski, 1896, lectotype (designated by Willmann 1981), IGUW 1895 XII/25, Skiadhi Monastery, Rhodes, Greece, Istrios Formation (Pliocene). **Q–T.** *Valvata gregaria* Bukowski, 1896, paralectotype, IGUW 1895 XII/26, same locality and stratum. Scale bars: 1 mm (**A–T**); 100 µm (**U–W**).

The material closely resembles the Pliocene *Valvata gregaria* Bukowski, 1896 (p. 25–28, pl. 8, figs 7, 8) from Rhodes in terms of the shell size and shape, the relatively large aperture, and low number of whorls (see also Willmann 1981, p. 77, textfig. 25). However, the lectotype and paralectotype of that species (designated by Willmann 1981) show a depressed and unevenly coiled spire (Fig. 14M–T), while the Denizli specimens has a bulbous, almost pointy apex and a slightly more ovoid aperture.

Given the low amount of specimens available for comparison and assessing morphological variability, the perhaps not fully adult state of the specimens, as well as the low number of features, we do not describe a new species, although we could not detect any extant or late Cenozoic species that matches our material.

### *Valvata* sp. 2

Fig. 15A–D, H

**Material.** 1 specimen (RGM 962690) from sample 1.

**Dimensions.** 4.60 × 4.97 mm.

**Remarks.** Only a single specimen for that species is available. It closely resembles *V. monachorum* Bukowski, 1896 from the Pliocene Istrios Formation of Rhodes, which Willmann (1981) considered (together with *V. aberrans* Bukowski, 1896) as a synonym of *V. skhiadica* (Fig. 15I–P). Our specimen matches this species regarding the conical, high-spired but apically flattened shell with the typical, adapically flattened whorls and the moderately wide umbilicus. However, the Turkish specimen bears distinct riblets, has a more pronounced convexity at the transition between whorl flank and base, and the base is straight-sided. In addition, our material is stratigraphically younger by several million years.

Another similar species is *Valvata hellenica* Tournouër in Fischer, 1877 from Rhodes (Fischer 1877, p. 55), probably from the Lower Pleistocene Kritika Formation (Willmann 1981, p. 133, pl. 3, figs 8–17). Willmann (1981) included a great variety of morphologies under that name and it is unlikely that all belong to the same species. The morphotype from the Lower Pleistocene Tafi Formation of Kos illustrated by Willmann (1981, pl. 3, fig. 9) resembles our specimen regarding the general shape, but like *V. skhiadica* above Tournouër's species has a more depressed spire (see also Bandel 2010, pl. 4, figs 49–51).

*Valvata orientalis* Fischer, 1866, which was also found in the Denizli Basin (Fischer 1866), has a similarly bulbous apex but a higher spire and a relatively smaller aperture. We illustrate for comparison the syntype of that species from Quaternary strata at Lake Buldur stored at Muséum national d'Histoire naturelle (MNHN.F.B41478; Fig. 15E–G). The syntype from Denizli could not be located at MNHN and might be lost (J.-M. Pacaud, pers. comm. 12/2022). To settle the taxonomic status of *Valvata orientalis* we hereby designate the illustrated specimen as lectotype.

### *Valvata* sp. 3

Fig. 15Q–T

**Material.** 1 specimen (RGM 962697) from sample 2.

**Dimensions.** 2.79 × 2.92 mm.

**Remarks.** As for the previous species, this one is only known from a single specimen. It is characterized by a relatively small, globular shell with short apex and bulbous, regularly convex body whorl. The aperture is broken but appears to be nearly circular, the umbilicus is wide and the shell surface bears distinct orthocline growth lines. The protoconch is about half a whorl, weakly heterostrophic and bears weak signs of an originally spiral sculpture. The transition to the teleoconch is marked by a broad, shallow furrow and the onset of regular coiling.

The spherical shape with short apex and distinct growth lines reminds of the extant *Valvata montenegrina* Glöer & Pešić, 2008 from Lake Skadar and Podgorica (Montenegro). The Balkan species is, however, much larger (6–7 mm high, 6.2–6.8 mm wide; Glöer 2019) and slightly less broad than the Turkish specimen. Our specimen also reminds of juvenile *V. piscinalis*, but the shape is too conical and the umbilicus to wide with a too long straight upper flank. Given the generally large variability of *Valvata piscinalis* we cannot exclude the option that the specimen belongs to that species, but we consider it unlikely. The Turkish Quaternary species *Valvata orientalis* Fischer, 1866 (see above) shares the broad shape but has a higher apex and a relatively smaller aperture (Fig. 15E–G).

Although we could not find any species with which this one can be identified, we refrain from introducing a new name because of the low amount of material available, the incompleteness of the shell, and the small number of distinct morphological features.

## Infraclass Euthyneura Spengel, 1881
## Superorder Hygrophila Férussac, 1822
## Superfamily Lymnaeoidea Rafinesque, 1815
## Family Lymnaeidae Rafinesque, 1815
## Subfamily Amphipepleinae Pini, 1877

### Genus *Corymbina* Bukowski, 1892

**Type species.** *Corymbina rhodensis* Bukowski, 1892; by subsequent designation (Wenz 1923).

### *Corymbina elegans* (Cantraine, 1841)

Fig. 16A–C

* 1841 *Ad.*[*elina*] *elegans*. Nob. – Cantraine: 156, pl. 5, fig. 12, 12a.
1847 *Limneus Adelina* – Spratt and Forbes: 177, textfig. a.
? 1877 *Lymnaeus Adelinae* [sic] Forbes [sic] – Fuchs: 5, pl. 1, fig. 4.
? 1877 *Lymnaeus Adelinae* [sic] Cantr. – Fuchs: 37, pl. 4, figs 1–6.
1923 *Radix* (*Adelinella*) *elegans* (Cantraine) – Wenz: 1319–1320.

1973 *Radix* (*Adelinella*) *elegans* (Cantraine) – Schütt and Besenecker: 16, pl. 1, figs 19, 20.
1981 *Corymbina elegans* (Cantraine) – Willmann: pl. 13, figs 18–20.
? 2022 *Corymbina elegans* (Cantraine, 1841) – Neubauer: fig. 6.7k, l.

**Material.** 1 juvenile specimen (RGM 962696) from sample 2.

**Type locality.** Italy; no further details known—Cantraine wrote: "Je ne connais cette espèce qu'à l'état fossile, le seul individu que je possède m'a été donnée par mon ami M. Rossi de Livourne, qui a'en connaissait pas exactement la provenarco." [I only know this species in the fossil state, the only individual I have was given to me by my friend

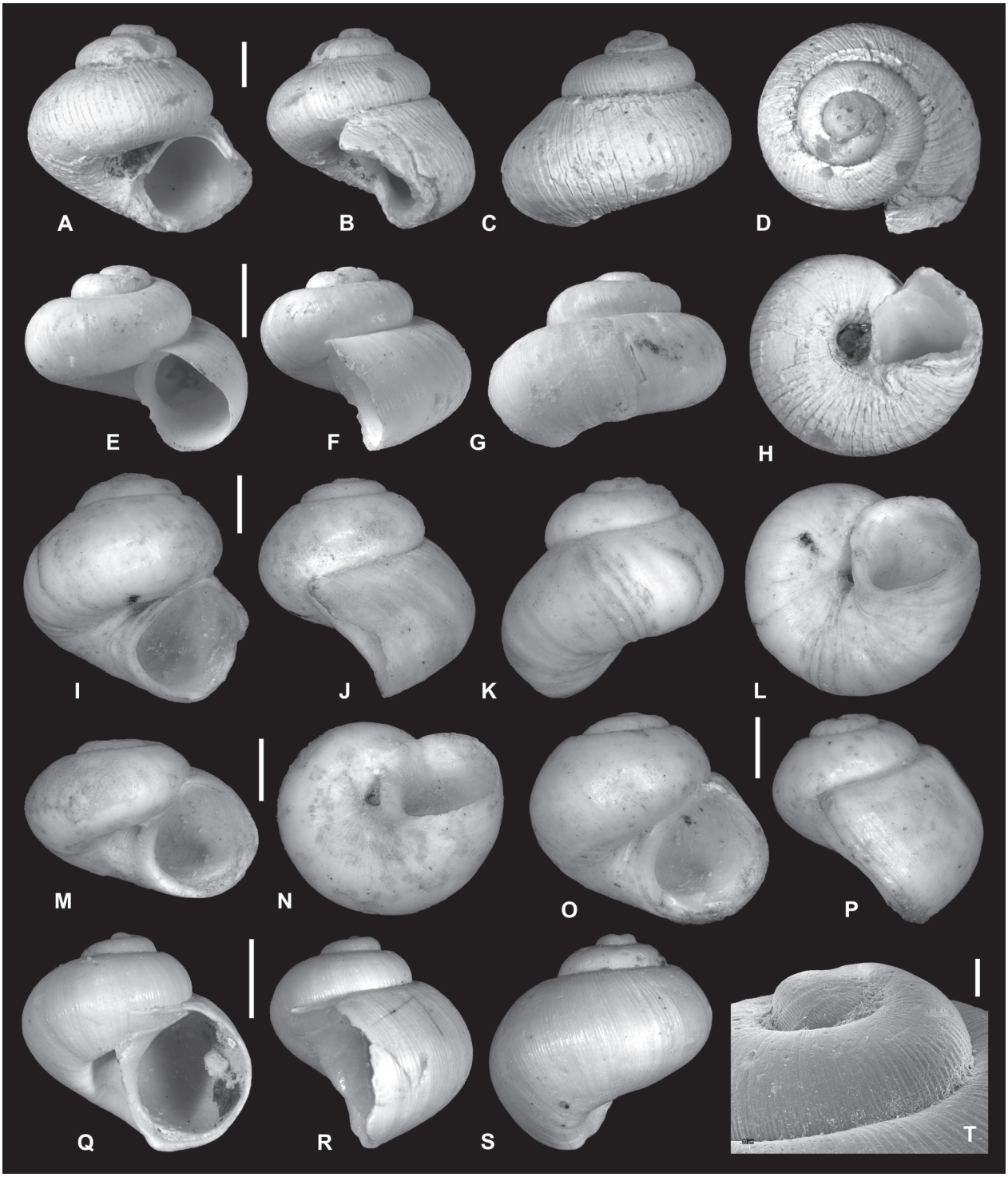


**Figure 15.** Valvatidae of the Kolankaya I fauna. **A–D, H.** *Valvata* sp. 2, RGM 962690, sample 1. **E–G.** *Valvata orientalis* Fischer, 1866, lectotype (designated herein), MNHN.F.B41478, Lake Buldur, Quaternary. **I–L.** *Valvata skhiadica* Bukowski, 1896, lectotype of *V. monachorum* Bukowski, 1896 (designated by Willmann 1981), IGUW 1895 XII/30, Skiadhi Monastery, Rhodes, Greece, Istrios Formation (Pliocene). **M–P.** *V. skhiadica*, lectotype (designated by Willmann 1981), IGUW 1895 XII/27, same locality and stratum. **Q–T.** *Valvata* sp. 3, RGM 962697, sample 2. Scale bars: 1 mm (**A–S**); 100 µm (**T**).

Mr. Rossi from Livorno, who didn't know exactly where it came from.].

**Description.** Shell comprises protoconch and about 0.75 teleoconch whorls. Initial part of protoconch smooth, followed by quarter whorl bearing faint riblets. P/T boundary not clearly visible, but probably coincides with weak angulation and onset of growth lines. Soon distinct, sharp ribs develop, which soon become broader and bulgier, leading to an irregular, wavy surface. Aperture fragmented, parts of outer lip missing; originally apparently elliptical. Umbilicus narrow.

**Remarks.** Spratt and Forbes (1847) mentioned the name *Limneus* [sic] *adelina* along with an illustration, making the name available. However, they clearly referred it to be the same species as *Adelina elegans* Cantraine, 1841, rendering *Lymnaea adelina* a junior objective synonym of *Corymbina elegans*. The specimen they illustrated has a much larger aperture, but the species has an extremely variable shell (see also Willmann 1981).

*Corymbina bicarinata* (Fuchs, 1877) from the Early Pleistocene of Livanates (Phthiotis, Greece) has a *Radix*-like appearance, with broad ovoid, attached aperture, an angulated last whorl, slender ribs, and small, pointy spire (Neubauer 2023b). Specimens from the same deposits identified by Fuchs (1877) as *L. adelinae* [= *C. elegans*] differ considerably from the phenotypes shown by Cantraine (1841), Spratt and Forbes (1847), and Willmann (1981). They rather resemble *C. bicarinata*, yet with a keel at the angulation. More data on the variability of both species is needed to disentangle their taxonomy and synonymies. We tentatively associate our single juvenile specimen with *C. elegans* given the general match in shell shape and sculpture as well as the known stratigraphic and geographic distribution of the species.

The Late Miocene *Corymbina rhodensis* Bukowski, 1892 is smaller and has a more slender shell, often with reduced sculpture (Willmann 1981). In both *C. elegans* and *C. rhodensis* specimens occur with the last whorl partly or entirely uncoiled (Willmann 1981). *Corymbina aegaea* (Oppenheim, 1919) from Upper Miocene (?) deposits near Harmancık (NW Turkey) has a more elongated shell (Schütt and Kavusan 1984). The Early Sarmatian (Serravallian, Middle Miocene) *Corymbina coronata* (Marinescu, 1992) from Romania differs from *C. elegans* in the more angulated body whorl and the ribs being reduced to elongated knobs at the uppermost whorl portion.

*Corymbina rhodensis senestris* İnal, 1975 from supposedly Pliocene sediments at Gürleyik SE Afyonkarahisar (c. 170 km ENE Denizli) shows a similar type of sculpture, but it is a rare case of a sinistral representative (İnal 1975). It is questionable, however, if it represents a distinct species or simply an aberrant morphotype of an existing species.

**Distribution.** *Corymbina elegans* has been reported from the Pliocene of the Denizli, Eşen, and Çameli basins in Turkey (Spratt and Forbes 1847; Oppenheim 1919; Wenz 1923), the Early Pliocene of central Italy (Esu and Girotti 2018), and the Pliocene–Pleistocene of Greece (Wenz 1923; Schütt and Besenecker 1973; Gillet et al. 1979). Records from the Late Miocene (Chios Island; Schütt and Besenecker 1973) are probably based on an outdated stratigraphy.

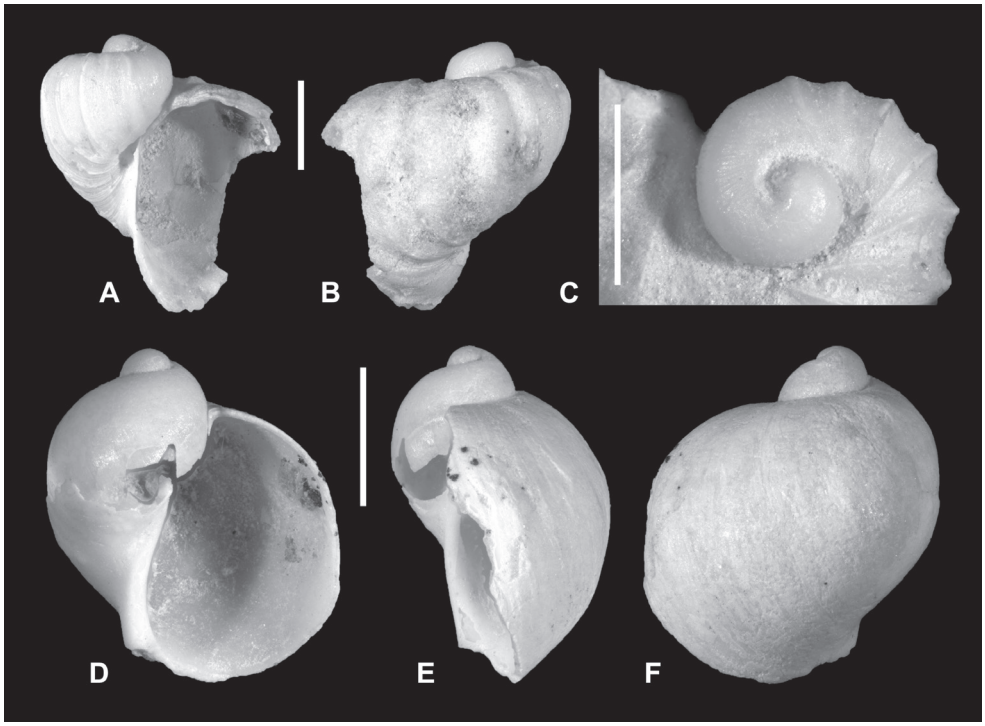


**Figure 16.** Lymnaeidae of the Kolankaya I fauna. **A–C.** *Corymbina elegans* (Cantraine, 1841), RGM 962696, sample 2. **D–F.** *Radix* sp., RGM 1310798, sample 2. Scale bars: 1 mm.

### Genus *Radix* Montfort, 1810

**Type species.** *Radix auriculatus* Montfort, 1810 [unnecessary substitute name for *Radix auricularia* (Linnaeus, 1758)]; by original designation.

#### *Radix* sp.

Fig. 16D–F

**Material.** 1 juvenile specimen (RGM 1310798) from sample 2.

**Remarks.** The single available specimen contains about 2 whorls, with a small, bulbous protoconch and a large, inflated, and convex body whorl. The aperture is broad and semi-circular. Although a more precise identification is not possible, these features suggest a classification in the genus *Radix*.

## Class Bivalvia Linnaeus, 1758
## Infraclass Heteroconchia Gray, 1854
## Order Cardiida Férussac, 1822
## Superfamily Dreissenoidea Gray, 1840
## Family Dreissenidae Gray, 1840
## Subfamily Dreisseninae Gray, 1840

### Genus *Dreissena* Van Beneden, 1835

**Type species.** *Mytulus* [sic] *polymorphus* Pallas, 1771; by monotypy.

**Remarks.** The dreissenid material at hand is very much broken and displays huge variability in shape and ornamentation. We have found it nearly impossible to distinguish species within the material. Our distinction of two morphotypes below will require confirmation by further designated collecting of entire specimens and populations in the region.

#### *Dreissena kairanderensis* (Oppenheim, 1919)

Fig. 17A–J

*1919 *Congeria* (?) *kairanderensis* sp. nov. – Oppenheim: 126–127, pl. 6, fig. 11.

? 1919 *Dreissensia* (?) *phrygica* sp. nov. – Oppenheim: 124–125, pl. 6, figs 1–3.

? 1919 *Dreissensia* (?) *hierapolitana* sp. nov. – Oppenheim: 127–128, pl. 6, fig. 12.

**Material.** Sample 2: 5 valves (RGM 962698–962702), c. 690 valves (RGM 1310845), 2 valves (SNSB-BSPG 2023 XII 23); sample 3: 28 valves (RGM 1310846).

**Type locality.** "Kairandere zwischen Bosalan und Bulladan" [Kairandere between Bozalan and Buldan], Denizli Basin, Turkey.

**Description.** Variably shaped *Dreissena* with outlines ranging from mytiliform to flat, wide, and broad with apparent intermediate shapes. Dorsal margin usually curved but in some specimens can be straight. Ventral margin slightly curved, lacks byssate inflection. Semidiameter located toward ventral margin in adult stages. External ornamentation remarkably variable. Most specimens contain some sort of fanning out (axial) ribs. Number, shape, and length of these ribs highly variable; smooth specimens also occur. Typically 1–3 ribs develop almost immediately below umbo; often most prominent rib located at dorsal margin forms distinct dorsal angle. Ribs can fade within short distance or run entire shell length. Irregular small secondary ribs occur in some specimens. Hinge plate variable in strength. Plane of symmetry appears to be flat.

**Dimensions.** All material is broken, but measurements from cracked specimens in the field gave maximum dimensions of approximately 25 × 21 × 9.5 mm (width × height × semidiameter) for adult valves.

**Remarks.** Our material concerns a hugely variably shaped species for which additional study is required to determine whether it is a single species or consists of multiple species. Our juvenile and broken adult material does not enable making such a distinction. The flat plane of symmetry, the lack of a byssate inflexion on the shells exterior, and the relative prominence of the posterodorsal ridge in many of the specimens makes a close relationship with the *Dreissena polymorpha* Pallas, 1771 species group possible.

The species differs from the co-occurring *Dreissena* sp. 1 particularly in the shifting position of the semidiameter through ontogeny, which runs with an almost straight line 45° from the umbo toward the posterior margin, and the generally more curved shell. *Dreissena phrygica* Oppenheim, 1919 and *D. hierapolitana* Oppenheim, 1919, both also described from the Denizli Basin, seem to differ from *Dreissena kairanderensis* mostly in size, shell curvature, and/or the presence of additional keels. Given the variability we observe in our material, these names probably only signify morphological varieties of a single, polymorphic species. However, further studies are required to verify their taxonomic status. The same applies to other Denizli dreissenids, i.e., *Dreissena lycophila* Oppenheim, 1919, *Dreissena filifera* Andrusov, 1893, sensu Taner, 1974b, *Congeria prekairenderensis* Taner, 1974b, and *C. spathulata minor* Taner, 1974b [non *Congeria minor* Fuchs, 1877], all of which require investigation.

**Distribution.** Endemic to the Denizli Basin.

#### *Dreissena* sp. 1

Fig. 17K–N

**Material.** Sample 2: 2 valves (RGM 962703, 962704), 49 valves (RGM 1310847), 2 valves (SNSB-BSPG 2023 XII 24); sample 3: 6 valves (RGM 1310848).

**Description.** Shell large, wide, and distinctly flat. Exterior smooth, apart from fine growth lines. Dorsal margin long, almost straight, with robust but rounded posterodorsal angle. Through ontogeny, semidiameter shifts with al-

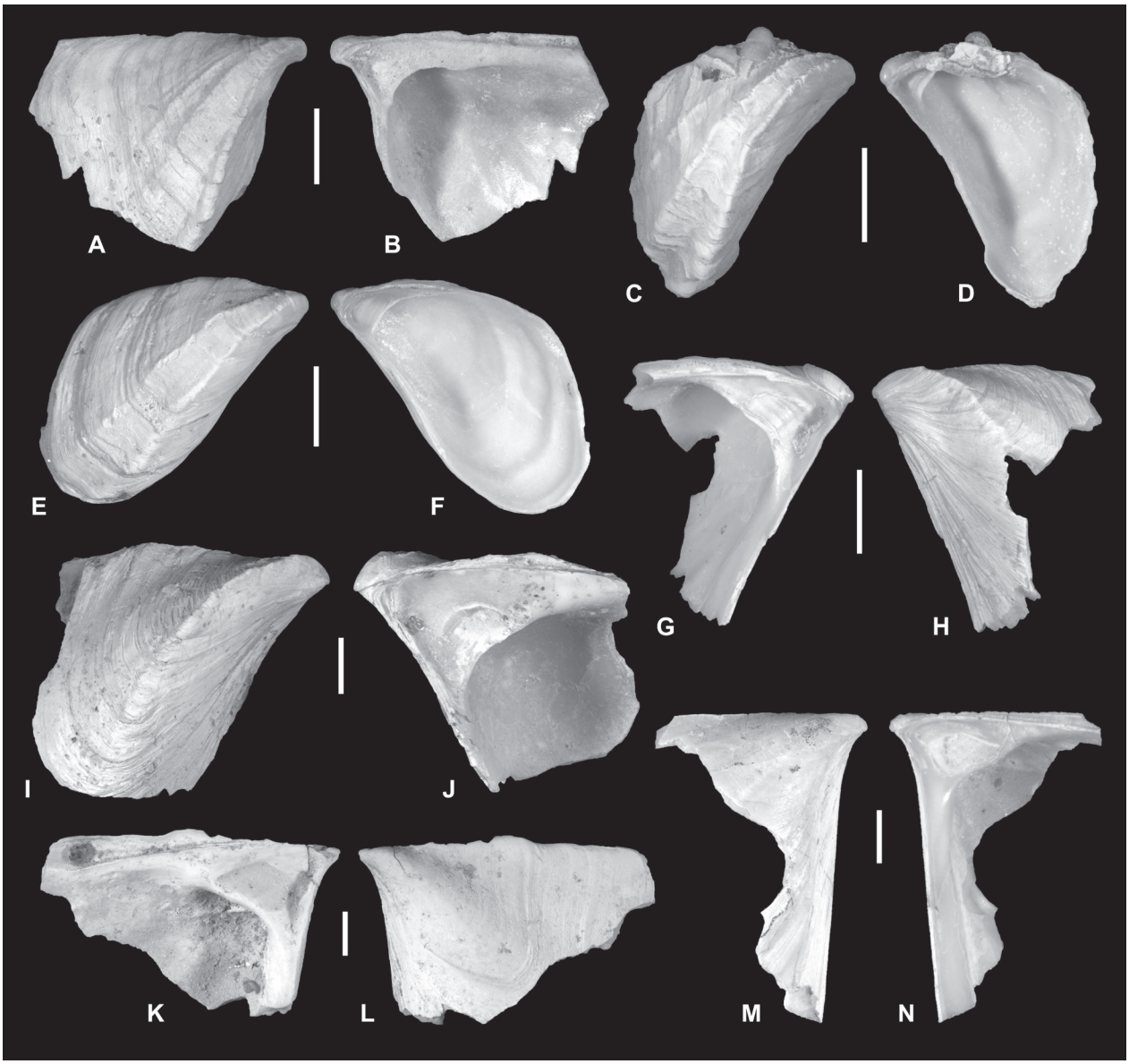


**Figure 17.** Dreissenidae of the Kolankaya I fauna. A, B. *Dreissena kairanderensis* (Oppenheim, 1919), RGM 962699, sample 2. **C, D.** *D. kairanderensis*, RGM 962701, sample 2. **E, F.** *D. kairanderensis*, RGM 962702, sample 2. **G, H.** *D. kairanderensis*, RGM 962700, sample 2. **I, J.** *D. kairanderensis*, RGM 962698, sample 2. **K, L.** *Dreissena* sp. 1, RGM 962703, sample 2. **M, N.** *Dreissena* sp. 1, RGM 962704, sample 2. Scale bar: 2 mm.

most straight line 45° from umbo toward posterior margin (which is broken in all specimens). In some specimens, slight byssal inflection may be developed on ventral margin, which is otherwise almost straight. Plane of symmetry between valves appears to be not entirely flat. Hinge plate robust, wide, and flat.

**Dimensions.** Length c. 20 mm (all material is broken).

**Remarks.** The smooth appearance and the presence of a very slight byssate inflection are characters that may point to a relationship with the Pontocaspian *Dreissena rostriformis* Deshayes, 1838 species group (Wesselingh et al. 2019). However, the very wide nature of specimens is unknown from this group and resembles superficially *Congeria* species.

**Distribution.** *Dreissena* sp. 1 is only known from the Lower Pleistocene Kolankaya Formation of the Denizli Basin.

## Discussion

The Kolankaya I fauna described here contains 27 species (25 gastropods, two bivalves) in six families (Table 1). Six species and one genus (all among Hydrobiidae) are new to science. The composition, including endemic species, many hydrobiids, melanopsids, and comparatively few pulmonate species, is typical of a long-lived lake, which fits to previous reconstructions of the paleoenvironment of Lake Denizli (Alçiçek et al. 2007, 2015). Similar compositions featuring neritids, melanopsids, hydrobiids, pulmonates, and dreissenids are known from other long-lived lake faunas from late Cenozoic strata of Europe (e.g., Neubauer et al. 2013, 2016, 2020).

The fauna containing *Ecrobia*, *Dreissena*, *Theodoxus*, and Pyrgulinae/Caspiinae is typical of a Pontocas-

**Table 1.** Species inventory of the here described fauna, with indication of family attribution, samples, and status as endemic (to the Denizli Basin and the Aegean-Anatolian region, respectively). The Aegean-Anatolian region follows here the definition by Neubauer et al. (2015) based on Pliocene faunas.

| Species | Family | Sample 1 | Sample 2 | Sample 3 | Denizli endemic | Aegean-Anatolian endemic |
|---|---|---|---|---|---|---|
| *Theodoxus percarinatus* (Oppenheim, 1919) | Neritidae | x | x | x | x | x |
| *Theodoxus* aff. *pilidei* (Tournouër, 1879) | Neritidae | | x | | | |
| *Esperiana esperi* (Férussac, 1823) | Melanopsidae | x | | x | | |
| *Graecoanatolica alcicekorum* sp. nov. | Hydrobiidae | | x | | x | x |
| *Graecoanatolica*? sp. | Hydrobiidae | x | | | | |
| *Iraklimelania minutissima* sp. nov. | Hydrobiidae | | x | | x | x |
| *Iraklimelania submediocarinata* sp. nov. | Hydrobiidae | x | | | x | x |
| *Ecrobia* sp. | Hydrobiidae | | x | | | |
| *Harzhauseria schizopleura* gen. et sp. nov. | Hydrobiidae | x | x | | x | x |
| Hydrobiinae sp. indet. | Hydrobiidae | x | | | | |
| *Laevicaspia* sp. | Hydrobiidae | | x | | | |
| *Prososthenia* cf. *sturanyi communis* Willmann, 1981 | Hydrobiidae | | x | | | x |
| *Xestopyrguloides*? *sagitta* sp. nov. | Hydrobiidae | | x | | x | x |
| *Xestopyrguloides*? sp. | Hydrobiidae | | x | | | |
| *Staja lycica* (Oppenheim, 1919) | Hydrobiidae | x | x | | | x |
| *Staja*? *cibyratica* (Spratt & Forbes, 1847) | Hydrobiidae | | x | x | | x |
| *Falsipyrgula*? *coronata* sp. nov. | Hydrobiidae | | x | x | x | x |
| *Falsipyrgula* cf. *sieversi* (Boettger, 1881) | Hydrobiidae | | x | x | | |
| Hydrobiidae sp. indet. | Hydrobiidae | | x | | | |
| *Valvata piscinalis* (Müller, 1774) | Valvatidae | | | x | | |
| *Valvata* sp. 1 | Valvatidae | x | x | | | |
| *Valvata* sp. 2 | Valvatidae | x | | | | |
| *Valvata* sp. 3 | Valvatidae | | x | | | |
| *Corymbina elegans* (Cantraine, 1841) | Lymnaeidae | | x | | | |
| *Radix* sp. | Lymnaeidae | | x | | | |
| *Dreissena kairanderensis* (Oppenheim, 1919) | Dreissenidae | | x | x | x | x |
| *Dreissena* sp. 1 | Dreissenidae | | x | x | x | x |

pian-type assemblage (Wesselingh et al. 2019). Pyrgulinae and Caspiinae are adapted to a wide range of salinities, from freshwater to mesohaline, but typically are dominant in oligohaline and lower mesohaline Pontocaspian faunas (Anistratenko 2008; Anistratenko et al. 2021). *Ecrobia* is distinctly euryhaline. Modern representatives are found under low oligohaline conditions (<1 psu for *E. maritima*; Kevrekidis and Wilke 2005), but usually occur at higher salinities. *Dreissena* and *Theodoxus* are typically found at oligohaline as well as freshwater conditions, while *Graecoanatolica*, *Falsipyrgula*, *Esperiana*, *Valvata*, and *Radix* are typical for freshwater settings, but many species do tolerate oligohaline conditions (e.g., Yildirim et al. 2006; Kebapçı et al. 2012; Verbrugge et al. 2012; van de Velde et al. 2019, 2020; Karatayev and Burlakova 2022).

The taxonomic composition of the fauna, with rare pulmonate gastropods and without clear freshwater indicators such as unionid and sphaeriid bivalves, suggests an oligohaline setting.

Comparing different sampling localities (here considering bulk samples 1 and 2 only), there is a certain degree of variation in the species compositions. Samples 1 and 2 share a number of taxonomic groups, i.e., Neritidae, Caspiinae, Hydrobiinae, Pyrgulinae, and Valvatidae, but Dreissenidae and Lymnaeidae are missing in sample 1, while sample 2 lacks Melanopsidae (in the surrounding scree deposits they have been found however). Also missing in sample 1 is the ecological indicator *Ecrobia*, but that sample contains the assumed sister taxon *Harzhauseria* gen. nov., which supposedly lived under similar environmental conditions. Hence, we assume that the observed compositional differences are only partly owed to variation in the local ecological conditions. Differences in stratigraphic position of the sampling levels and/or sampling/preservation bias probably played additional roles.

Biogeographically, the fauna is typical of the Aegean–Anatolian region, which has been a hotspot for freshwater mollusk diversity since the Neogene (Neubauer et al. 2015; Neubauer 2023a). Many of the here recovered genera are typical or even endemic to this region. *Theodoxus*, *Esperiana*, *Falsipyrgula*, *Valvata*, *Radix*, and *Dreissena* are widespread genera of little biogeographic significance but are also documented from extant Anatolian freshwater faunas (Radoman 1973a, 1973b; Yildirim 1999, 2004; Yildirim et al. 2006; Kebapçı et al. 2012; Karatayev and Burlakova 2022). *Graecoanatolica* and the fossil genera *Iraklimelania* and *Xestopyrguloides* are endemic to the Aegean–Anatolian region (Willmann 1981; Kebapçı et al. 2012). The fossil, enigmatic genus *Corymbina* is commonly found in Pliocene–Pleistocene deposits of many Greek and Turk-

ish freshwater environments, but it also occurs in Italy and Romania (Marinescu 1992; Esu and Girotti 2018).

As mentioned above, the Denizli fauna also contains several elements typical of Pontocaspian assemblages, such as *Theodoxus*, *Ecrobia*, *Laevicaspia*, and *Dreissena* (Wesselingh et al. 2019). Although most of them are widespread genera today, they have a long evolutionary history in the Pontocaspian realm (Andrusov 1897; Roshka 1973; Babak 1983; Anistratenko and Gozhik 1995; Neubauer et al. 2018; Wesselingh et al. 2019). Also *Esperiana* has been found in Pleistocene strata of the Caspian Sea (Neubauer et al. 2018). The current assignment of the genera *Graecoanatolica* and *Iraklimelania* to Caspiinae, a typical Pontocaspian group (Anistratenko et al. 2021), also contributes to the biogeographical affinity to that realm.

On the species level, the fauna is characterized by a moderate degree of endemism – a third of all species (33.3%), including all new species, is endemic to the Denizli Basin. Almost half of the fauna (44.7%, if cf.-records are considered) is restricted to the Aegean–Anatolian region, with three species (11.1%) being shared with the Eşen Basin and two with the Çameli Basin (7.4%). Although only 1–2 species (*Prososthenia* cf. *sturanyi communis*, *Corymbina elegans*) are shared with Pliocene–Early Pleistocene Greek faunas, the similarities observed between several Denizli species (*Theodoxus percarinatus*, *Iraklimelania minutissima*, *I. submediocarinata*, *Xestopyrguloides*? *sagitta*, *Xestopyrguloides*? sp., *Staja lycica*, *Valvata* sp. 1, *Valvata* sp. 2) and those from Kos, Rhodes, and mainland Greece (Fuchs 1877; Willmann 1981; Esu and Girotti 2015) suggest they are closely related lineages.

Three species (11.1%) are still among the living European fauna, including two widely distributed species (*Esperiana esperi*, *Valvata piscinalis*) (Welter-Schultes 2012; Glöer 2019) and, if our identification proves correct, a species nowadays restricted to the Caucasus region (*Falsipyrgula sieversi*) (Sitnikova et al. 2018). *Corymbina elegans* has been documented from various Pliocene–Pleistocene sites in Greece, Turkey, and Italy (Spratt and Forbes 1847; Oppenheim 1919; Wenz 1923; Schütt and Besenecker 1973; Esu and Girotti 2018, 2020). *Theodoxus* aff. *pilidei* has similarities with a species from the Pliocene–Early Pleistocene of Romania and possibly the Late Miocene–Early Pliocene (?) of Kosovo (Wenz 1942; Atanacković 1959; Papaianopol and Marinescu 2003), but it is potentially an unrelated, new species.

## Acknowledgments

We are grateful to Martin Aberhan (Museum für Naturkunde Berlin), Mathias Harzhauser and Oleg Mandic (NHMW), Bernhard Grasemann, Michael Wagreich and Christian Stocker (IGUW), Rivka Rabinovich and Henk K. Mienis (Hebrew University of Jerusalem), Jean-Michel Pacaud and Lilian Cazes (MNHN Paris), Růžena Gregorová (Moravské zemské muzeum, Brno), Tomáš Turek (Masaryk University, Brno), and Jon Todd (Natural History Museum London) for information on type material, making the scientific collections under their care accessible to us and/or providing photographs. Ruud Bank (University of Groningen) kindly supplied missing literature. Diana Delicado (Justus Liebig University Giessen) shared ideas on the systematic placement of the unidentified hydrobiid. Roland Melzer (SNSB-ZSM) provided access to the SEM and supported during sputter coating and image acquisition. Ümit Kebapçı (Mehmet Akif Ersoy University, Burdur) sent specimens of extant Turkish species for comparison. Alexander Nützel (SNSB-BSPG) kindly helped with additional SEM photographs. We are deeply indebted to Hülya and M. Cihat Alçiçek (Pamukkale University, Denizli) for their continued support of all our Denizli work in the past decade. Further field support was delivered by Lea Rausch (Petrostrat), Sergei Lazarev (Université de Fribourg), and Wout Krijgsman (Utrecht University). The fieldwork was carried out in the frame of the PRIDE project ("Pontocaspian biodiversity Rise and Demise", 2015–2019), which was funded by European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie Action (grant agreement No. 642973). Mathias Harzhauser (NHMW) and Vitaliy V. Anistratenko (National Academy of Sciences of Ukraine) are thanked for constructive and incredibly fast reviews.

## References

Adams H, Adams A (1853–1858) The genera of Recent Mollusca arranged according to their organizations. Van Voorst, London, 2 vol. of text (661 pp.), 1 vol. of plates. https://doi.org/10.5962/bhl.title.4772

Alçiçek H (2010) Stratigraphic correlation of the Neogene basins in southwestern Anatolia: Regional palaeogeographical, palaeoclimatic and tectonic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 291: 297–318. https://doi.org/10.1016/j.palaeo.2010.03.002

Alçiçek H, Varol B, Özkul M (2007) Sedimentary facies, depositional environments and palaeogeographic evolution of the Neogene Denizli Basin, SW Anatolia, Turkey. Sedimentary Geology 202: 596–637. https://doi.org/10.1016/j.sedgeo.2007.06.002

Alçiçek H, Wesselingh FP, Alçiçek MC (2015) Paleoenvironmental evolution of the late Pliocene-early Pleistocene fluvio-deltaic sequence of the Denizli Basin (SW Turkey). Palaeogeography, Palaeoclimatology, Palaeoecology 437: 98–116. https://doi.org/10.1016/j.palaeo.2015.06.019

Alçiçek H, Wesselingh FP, Alçiçek MC, Jiménez-Moreno G, Feijen FJ, van den Hoek Ostende LW, Mayda S, Tesakov AS (2017) A multiproxy study of the early Pleistocene paleoenvironmental and paleoclimatic conditions of an anastomosed fluvial sequence from the Çameli Basin (SW Anatolia, Turkey). Palaeogeography, Palaeoclimatology, Palaeoecology 467: 232–252. https://doi.org/10.1016/j.palaeo.2016.08.019

Alçiçek MC (2007) Tectonic development of an orogen-top rift recorded by its terrestrial sedimentation pattern: The Neogene Eşen Basin of southwestern Anatolia, Turkey. Sedimentary Geology 200: 117–140. https://doi.org/10.1016/j.sedgeo.2007.04.003

Alçiçek MC, Kazanci N, Özkul M (2005) Multiple rifting pulses and sedimentation pattern in the Cameli Basin, southwestern Anatolia, Turkey. Sedimentary Geology 173: 409–431. https://doi.org/10.1016/j.sedgeo.2003.12.012

Alçiçek MC, Mayda S, Titov VV (2013) Lower Pleistocene stratigraphy of the Burdur Basin of SW Anatolia. Comptes Rendus Palevol 12: 1–11. https://doi.org/10.1016/j.crpv.2012.09.005

Alçiçek MC, Mayda S, ten Veen JH, Boulton SJ, Neubauer TA, Alçiçek H, Tesakov AS, Saraç G, Hakyemez HY, Göktas F, Murray AM, Titov VV, Jiménez-Moreno G, Büyükmeriç Y, Wesselingh FP, Bouchal JM, Demirel FA, Kaya TT, Halaçlar K, Bilgin M, van den Hoek Ostende LW (2019) Reconciling the stratigraphy and depositional history of the Lycian orogen-top basins, SW Anatolia. Palaeobiodiversity and Palaeoenvironments 99: 551–570. https://doi.org/10.1007/s12549-019-00394-3

Andreeva SI, Kijashko PV, Sitnikova TYa, Vinarski MV (2022) A review of the Ponto-Caspian genus *Caspiohydrobia* (Mollusca: Gastropoda: Hydrobiidae). Zoosystematica Rossica 31: 304–328. https://doi.org/10.31610/zsr/2022.31.2.304

Andrusov N (1893) Zamechanyya o semeystve Dreissensidae. Zapiski Novorossijskago Obshchestva Estestvoispytatelej 18: 69–94.

Anistratenko VV (2008) Evolutionary trends and relationships in hydrobiids (Mollusca, Caenogastropoda) of the Azov-Black Sea Basin in the light of their comparative morphology and paleozoogeography. Zoosystematics and Evolution 84: 129–142. https://doi.org/10.1002/zoos.200800001

Anistratenko VV, Gozhik PF (1995) Mollyuski semeystv Neritidae, Viviparidae, Lithoglyphidae i Pyrgulidae (Gastropoda, Pectinibranchia) iz kimmeriyskikh otlozheniy Abkhazii. Vestnik Zoologii 1: 3–13.

Anistratenko VV, Neubauer TA, Anistratenko OY, Kijashko PV, Wesselingh FP (2021) A revision of the Pontocaspian gastropods of the subfamily Caspiinae (Caenogastropoda: Hydrobiidae). Zootaxa 4933: 151–197. https://doi.org/10.11646/zootaxa.4933.2.1

Babak EV (1983) Pliotsenovyye i chetvertichnyye dreyssenidy Evskinskogo basseyna. Trudy Paleontologicheskogo Instituta 204: 1–104. http://www.geokniga.org/books/14107

Bandel K (2010) Valvatiform Gastropoda (Heterostropha and Caenogastropoda) from the Paratethys Basin compared to living relatives, with description of several new genera and species. Freiberger Forschungshefte: Paläontologie, Stratigraphie, Fazies C 536: 91–155.

Becker-Platen JD (1970) Lithostratigraphische Untersuchungen im Känozoikum Südwest-Anatoliens (Türkei). Beihefte zum Geologischen Jahrbuch 97: 1–244.

Becker-Platen JD, Kuiper JGJ (1979) Sphaeriiden (Mollusca, Lamellibranchia) aus dem Känozoikum der Türkei. Geologisches Jahrbuch B 33: 159–185.

Becker-Platen JD, Sickenberg O, Tobien H (1975) Die Gliederung der känozoischen Sedimente der Türkei nach Vertebraten-Faunengruppen. Sickenberg O (Ed.). Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie (Känozoikum und Braunkohlen der Türkei, 17.) 15: 19–100.

Becker-Platen JD, Benda L, Steffens P (1977) Litho- und biostratigraphische Deutung radiometrischer Altersbestimmungen aus dem Jungtertiär der Türkei (Känozoikum und Braunkohlen der Türkei, 18). Geologisches Jahrbuch B25: 139–167.

Bering D (1971) Lithostratigraphie, tektonische Entwicklung und Seengeschichte der neogenen und quartären intramontanen Becken der Pisidischen Seenregion (Südanatolien). (Känozoikum und Braunkohlen der Türkei 5.). Beihefte zum Geologischen Jahrbuch 101: 1–151.

Boettger O (1881) Sechstes Verzeichniss transkaukasischer, armenischer und nordpersischer Mollusken. Jahrbücher der Deutschen Malakozoologischen Gesellschaft 8: 167–261. https://www.biodiversitylibrary.org/page/16287147

Bouchet P, Rocroi J-P, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61: 1–526. https://doi.org/10.4002/040.061.0201

Bourguignat JR (1877) Descriptions de deux nouveaux genres algériens, suivies d'une classification des familles et des genres de mollusques terrestres et fluviatiles du système européen. Bulletin de la Société des Sciences Physiques et Naturelles de Toulouse 3: 49–101. http://www.animalbase.uni-goettingen.de/zooweb/servlet/AnimalBase/home/digireference?id=43

Brusina S (1882) Le Pyrgulinae dell'Europa orientale. Bollettino della Società Malacologica Italiana 7: 229–292. https://www.biodiversitylibrary.org/page/39283992

Brusina S (1897) Gragja za neogensku malakološku faunu Dalmacije, Hrvatske i Slavonije uz neke vrste iz Bosne i Hercegovine i Srbije. Djela Jugoslavenske akademije znanosti i umjetnosti 18: 1–43. http://archive.org/stream/djelajugoslaven03umjegoog#page/n6/mode/2up

Bukowski G (1930) Bemerkungen über die Binnenablagerungen in der Umgebung des Buldur Giöl in Kleinasien. Annales Societatis Geologorum Poloniae 6: 73–90.

Bukowski G von (1892) Notiz über die Molluskenfauna der levantinischen Bildungen der Insel Rhodus. Anzeiger der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe 29: 247–250.

Bukowski G von (1893) Die levantinische Molluskenfauna der Insel Rhodus, I. Theil. Denkschriften der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 60: 265–306. https://www.biodiversitylibrary.org/page/7217409

Bukowski G von (1896) Die levantinische Molluskenfauna der Insel Rhodus, II. Theil. Schluss. Denkschriften der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 63: 1–70. https://www.biodiversitylibrary.org/page/55502326

Burmeister H (1837) Handbuch der Naturgeschichte, vol. 2. Zoologie. Enslin, Berlin, xii + 369–858.

Büyükmeriç Y, Wesselingh FP (2018) New cockles (Bivalvia: Cardiidae: Lymnocardiinae) from Late Pleistocene Lake Karapinar (Turkey): Discovery of a Pontocaspian refuge? Quaternary International 465: 37–45. https://doi.org/10.1016/j.quaint.2016.03.018

Calvert F, Neumayr M (1880) Die jungen Ablagerungen am Hellespont. Denkschriften der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 40: 357–378. https://www.biodiversitylibrary.org/page/33417035

Cantraine F (1841) Malacologie méditerranéenne et littorale, ou description des mollusques qui vivent dans la Méditerranée ou sur le continent de l'Italie, ainsi que des coquilles qui se trouvent dans les terrains tertiaires italiens, avec des observations sur leur anatomie, leurs moeurs, leur analogie et leur gisement. Ouvrage servant de faune malacologique italienne et de complément à la Conchiologia fossile subapennina de Brocchi. Nouveaux Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles 13: 1–173. http://www.digizeitschriften.de/dms/img/?PPN=PPN129323640_0013&DMDID=dmdlog24

Carter JG, Altaba CR, Anderson LC, Araujo R, Biakov AS, Bogan AE, Campbell DC, Campbell M, Chen J-H, Cope JCW, Delvene G, Dijkstra HH, Fang Z-J, Gardner RN, Gavrilova VA, Goncharova IA, Harries PJ, Hartman JH, Hautmann M, Hoeh WR, Hylleberg J, Jiang B-Y, Johnston P, Kirkendale L, Kleemann K, Koppka J, Kříž J, Machado D, Malchus N, Márquez-Aliaga A, Masse J-P, McRoberts CA, Middelfart PU, Mitchell S, Nevesskaja LA, Özer S, Pojeta Jr J, Polubotko IV, Pons JM, Popov S, Sánchez T, Sartori AF, Scott RW, Sey II, Signorelli JH, Silantiev VV, Skelton PW, Steuber T, Waterhouse JB, Wingard GL, Yancey T (2011) A synoptical classification of the Bivalvia (Mollusca). Paleontological Contributions 4: 1–47.

Cossmann M (1898) Paléoconchologie. Revue critique de paléozoologie 2: 42–63. https://www.biodiversitylibrary.org/page/14497773

Cox LR (1960) Thoughts on the classification of the Gastropoda. Proceedings of the Malacological Society of London 33: 239–261.

Cuvier G (1795) Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. Magasin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts 2: 433–449. https://www.biodiversitylibrary.org/page/6736775

Delicado D, Hauffe T (2022) Shell features and anatomy of the springsnail genus *Radomaniola* (Caenogastropoda: Hydrobiidae) show a different pace and mode of evolution over five million years. Zoological Journal of the Linnean Society 196: 393–441. https://doi.org/10.1093/zoolinnean/zlab121

Delicado D, Pesic V, Glöer P (2016) Unraveling a new lineage of Hydrobiidae genera (Caenogastropoda: Truncatelloidea) from the Ponto-Caspian region. European Journal of Taxonomy 208: 1–29. https://doi.org/10.5852/ejt.2016.208

Delicado D, Hauffe T, Wilke T (2023) Fifth mass extinction event triggered the diversification of the largest family of freshwater gastropods (Caenogastropoda: Truncatelloidea: Hydrobiidae). Cladistics. https://doi.org/10.1111/cla.12558

Deshayes GP (1838) Description des coquilles fossiles recueillies en Crimée par M. de Verneuil, et observations générales à leur sujet. Mémoirs de la Société Géologique de France, première série 3: 37–69. https://www.biodiversitylibrary.org/page/42370331

Dybowski B (1913) Ueber Kaspische Schnecken aus der Abteilung Turricaspiinae subfam. nova, zum Vergleich mit den Turribaicalinae subfam. nova. Bulletin de l'Académie Impériale des Sciences de St.-Pétersbourg, sixième série 7: 905–906. https://www.biodiversitylibrary.org/page/4183344

Dybowski B, Grochmalicki J (1917) Studien über die turmförmigen Schnecken des Baikalsees und des Kaspimeeres (Turribaicalinae – Turricaspiinae). Abhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 9: 1–55. https://www.biodiversitylibrary.org/page/5550074

Dybowski W (1887–1888) Die Gasteropoden-Fauna des Kaspischen Meeres. Nach der Sammlung des Akademikers Dr. K. E. v. Baer. Malakozoologische Blätter (Neue Folge) 10: 1–64 [(issue 1, 1887)], 65–79 [(issue 2, 1888)], pl. 1–3 [(issue 3, 1888)]. https://www.biodiversitylibrary.org/page/35483241

Eichwald E (1838) Faunae Caspii Maris primitiae. Bulletin de la Société Impériale des Naturalistes de Moscou 11: 125–174. https://www.biodiversitylibrary.org/page/41342125

Esu D, Girotti O (2015) The late Early Pleistocene non-marine molluscan fauna from the Synania Formation (Achaia, Greece), with description of nine new species. Archiv für Molluskenkunde 144: 65–81. https://doi.org/10.1127/arch.moll/1869-0963/144/065-081

Esu D, Girotti O (2018) *Valvata mathiasi* n. sp. (Gastropoda: Heterobranchia: Valvatidae) from the Lower Pliocene of the Val di Pesa (Tuscany, Central Italy). Archiv für Molluskenkunde 147: 49–54. https://doi.org/10.1127/arch.moll/147/049-054

Esu D, Girotti O (2020) Updating a late Early – Middle Pleistocene non-marine molluscan fauna from Achaia (Greece). Systematics and palaeoecological remarks. Bollettino Malacologico 56: 59–83.

Férussac AEJPJF [d'Audebard de] (1821–1822) Tableaux systématiques des animaux mollusques classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; suivis d'un prodrome général pour tous les mollusques terrestres ou fluviatiles, vivants ou fossiles. Bertrand, Sowerby, Paris, Londres, xlvii + 110 pp. https://www.biodiversitylibrary.org/page/11057234

Férussac AEJPJF [d'Audebard de] (1823) Monographie des espèces vivantes et fossiles du genre mélanopside, *Melanopsis*, et observations géologiques à leur sujet. Mémoires de la Société d'Histoire Naturelle de Paris 1: 132–164. https://www.biodiversitylibrary.org/page/3555191.

Fischer P (1866) Faune tertiaire lacustre. In: de Tchihatcheff P, d'Archiac A, Fischer P, de Verneuil É (Eds) Asie mineure: description physique de cette contrée. Paléontologie. L. Guérin et Cie, Paris, 327–351. https://reader.digitale-sammlungen.de/de/fs3/object/display/bsb10359048_00367.html

Fischer P (1877) Paléontologie des terrains tertiaires de l'île de Rhodes avec la collaboration de MM. Cotteau, Manzoni et Tournouër. Mémoirs de la Société Géologique de France, troisième série 1: 1–74.

Fleming J (1822) The philosophy of zoology, a general view of the structure, functions and classification of animals, 2. Constable & Co., Edinburgh, 618 pp. https://www.biodiversitylibrary.org/page/28230157

Frauenfeld G von (1862) Ueber ein neues Höhlen-*Carychium* (*Zospeum* Brg.) und zwei neue fossile Paludinen. Verhandlungen der zoologisch-botanischen Gesellschaft in Wien 12: 969–972. https://www.biodiversitylibrary.org/page/30333078

Frýda J (1998) Higher classification of the Paleozoic gastropods inferred from their early shell ontogeny. In: Bieler R, Mikkelsen PM (Eds) 13th International Malacological Congress, Abstracts. Unitas Malacologica, Washington, D.C., 108 pp.

Fuchs T (1877) Studien über die jüngeren Tertiärbildungen Griechenlands. Denkschriften der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 37: 1–42. https://www.biodiversitylibrary.org/page/7221662

Gillet S, Gramann F, Steffens P (1978) Neue biostratigraphische Ergebnisse aus dem brackischen Neogen an Dardanellen und Marmara-Meer (Türkei). Newsletter on Stratigraphy 7: 53–64. https://doi.org/10.1127/nos/7/1978/53

Gillet S, Sauvage J, Keraudren B (1979) Etude paléontologique du plio-pléistocéne de Locride et d'Eubée occidentale (Gréce centrale): Malacologie et palynologie. Annales Géologiques des Pays Helléniques 29: 554–580.

Glöer P (2002) Die Tierwelt Deutschlands, 73. Teil: Die Süßwassergastropoden Nord- und Mitteleuropas. Bestimmungsschlüssel, Lebensweise, Verbreitung. ConchBooks, Hackenheim, 327 pp.

Glöer P (2019) The Freshwater Gastropods of the West-Palaearctis. Volume I. Fresh- and brackish waters except spring and subterranean snails. Identification key, Anatomy, Ecology, Distribution. Privately published, 399 pp.

Glöer P, Pešić V (2008) The freshwater gastropods of Skadar Lake with the description of *Valvata montenegrina* n. sp. (Mollusca, Gastropoda, Valvatidae). In: Pavićević D, Perreau M (Eds) Advances in the studies of the fauna of the Balkan Peninsula. Papers dedicated to the memory of Guido Nonveiller. Institute for Nature Conservation of Serbia, Monograph 22: 341–348.

Glöer P, Pešić V (2009) New freshwater gastropod species of the Iran (Gastropoda: Stenothyridae, Bithyniidae, Hydrobiidae). Mollusca 27: 33–39.

Golikov AN, Starobogatov YaI (1966) Ponto-kaspiyskiye bryukhonogiye mollyuski v Azovo-Chernomorskom basseyne. Zoologicheskiy Zhurnal 45: 352–362.

Golikov AN, Starobogatov YaI (1975) Systematics of prosobranch gastropods. Malacologia 15: 185–232.

Gray JE (1840) A manual of the land and freshwater shells of the British Islands, with figures of each of the kinds. By William Turton, M.D. A new edition, thoroughly revised and much enlarged. Longman, Orme, Brown, Green, and Longmans, Paternoster Row, London, 324 pp. https://www.biodiversitylibrary.org/page/18243759

Gray JE (1854) A revision of the arrangement of the families of bivalve shells (Conchifera). The Annals and Magazine of Natural History, second series 13: 408–418. https://www.biodiversitylibrary.org/page/22193740

Herbich F, Neumayr M (1875) Beiträge zur Kenntniss fossiler Binnenfaunen. VII. Die Süsswasserablagerungen im südöstlichen Siebenbürgen. Jahrbuch der k. k. geologischen Reichsanstalt 25: 401–431. https://www.biodiversitylibrary.org/page/35708234

van den Hoek Ostende LW, Gardner JD, van Bennekom L, Alçiçek MC, Murray A, Wesselingh FP, Alçiçek H, Tesakov A (2015) Ericek, a new Pliocene vertebrate locality in the Çameli Basin (southwestern Anatolia, Turkey). Palaeobiodiversity and Palaeoenvironments 95: 305–320. https://doi.org/10.1007/s12549-015-0202-3

Hoernes R (1876) Ein Beitrag zur Kenntniss fossiler Binnenfaunen. (Süsswasserschichten unter den sarmatischen Ablagerungen am Marmorameere.). Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 74: 7–34. https://www.biodiversitylibrary.org/page/8772827

İnal A (1975) Description of two new Gastropod species and one sub-species from the lacustrine sediments of Neogene age Afyon, Turkey. Bulletin of the Geological Society of Turkey 18: 161–164.

Jekelius E (1944) Sarmat und Pont von Soceni (Banat). Memoriile Institutului geologic al României 5: 1–167.

Kantor YuI, Sysoev AV (2006) Morskiye i solonovatovodnyye bryukhonogiye mollyuski Rossii i sopredel'nykh stran: illyustrirovannyy katalog. KMK Scientific Press, Moscow, 372 pp. [+ 140 pls.]

Kaouras G, Velitzelos E (1985) Süsswassergastropoden von Ag. Thomas-Preveza, W. Griechenland. Revue de Paléobiologie 4: 59–63.

Kapan Yesilyurt S, Taner G (2002) Datca yarimadasinin gec pliyosen Pelecypoda ve Gastropoda faunasi ve stratigrafisi (Mugla-Güneybati Anadolu). MTA Dergisi 125: 89–120. http://www.mta.gov.tr/v2.0/daire-baskanliklari/bdt/kutuphane/mtadergi/125_6.pdf

Karatayev AY, Burlakova LE (2022) What we know and don't know about the invasive zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels. Hydrobiologia. https://doi.org/10.1007/s10750-022-04950-5

Kebapçı Ü, Bahadir Koca S, Yildirim MZ (2012) Revision of Graecoanatolica (Gastropoda: Hydrobiidae) species in Turkey. Turkish Journal of Zoology 36: 399–411. https://doi.org/10.3906/zoo-1011-10

Kühn O (1951) Süsswassermiozän von bosnischem Typus in Griechenland. Annales Géologiques des Pays Helléniques 3: 185–192.

Kühn O (1963) Das Süsswassermiozän von Attika. Praktika tis Akademias Athinon 38: 370–400.

Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentius Salvius, Holmiae, [iv +] 824 pp. https://www.biodiversitylibrary.org/page/726886.

Logvinenko BM, Starobogatov YI (1969) Mollusca. In: Birshtein YA, Vinogradov LG, Kondakov NN, Kuhn MS, Astakhova TV, Romanova NN (Eds) Atlas bespozvonochnykh Kaspiyskogo morya. Pishchevaya Promyshlennost (Vsesoyuznyi Nauchno-issledovatel'skii Institut Morskogo Rybnogo Khozyaistva i Okeanografii), Moskva, 412.

Marinescu F (1992) *Radix* (*Adelinella*) *coronatus* n. sp. (Mollusca, Gastropoda) dans le Sarmatien du Bassin de Borod. Romanian Journal of Paleontology 75: 9–10.

Milaschewitch KO (1916) Mollyuski Russkikh Morey. Tom 1. Mollyuski Chernago i Azovskago Morey. Imperatorskaya Akademiya Nauk, Zoologicheskiy Muzey, Petrograd, 312 pp. https://www.biodiversitylibrary.org/page/12116351

Montagu G (1803) Testacea Britannica, or natural history of British shells, marine, land, and fresh-water, including the most minute: systematically arranged and embellished with figures. White, London, 606 pp. https://www.biodiversitylibrary.org/page/24430071

Montfort PD de (1810) Conchyliologie systématique et classification méthodique de coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. Tome second. Schoell, Paris, 676 pp. https://www.biodiversitylibrary.org/page/11065017

Müller OF (1773–1774) Vermium terrestrium et fluviatilium historia, seu animalium Infusoriorum, Helminthicorum et Testaceorum non marinorum succincta historia. Heineck & Faber, Havniae et Lipsiae, xxxiii + 135, xxxvi + 214 pp. https://www.biodiversitylibrary.org/bibliography/46299

Neubauer TA (2023a) The fossil record of freshwater Gastropoda – a global review. Biological Reviews (early view). https://doi.org/10.1111/brv.13016

Neubauer TA (2023b [in press]) The fossil record of the Lymnaeidae – revisiting a 200-Myr-long story of success. In: Vinarski MV, Vázquez A (Eds) The Lymnaeidae. A handbook on their natural history and parasitological significance. Springer, Cham.

Neubauer TA, Mandic O, Harzhauser M (2016) The early Middle Miocene lacustrine gastropod fauna of Džepi, Bosnia and Herzegovina (Dinaride Lake System): high endemism in a small space. Bulletin of Geosciences 91: 271–296. https://doi.org/10.3140/bull.geosci.1584

Neubauer TA, Mandic O, Harzhauser M, Hrvatović H (2013) A new Miocene lacustrine mollusc fauna of the Dinaride Lake System and its palaeobiogeographic, palaeoecologic, and taxonomic implications. Palaeontology 56: 129–156. https://doi.org/10.1111/j.1475-4983.2012.01171.x

Neubauer TA, van de Velde S, Yanina T, Wesselingh FP (2018) A late Pleistocene gastropod fauna from the northern Caspian Sea with implications for Pontocaspian gastropod taxonomy. ZooKeys 770: 43–103. https://doi.org/10.3897/zookeys.770.25365

Neubauer TA, Mandic O, Jovanović G, Harzhauser M (2020) The Serbian Lake System: a stepping stone for freshwater molluscs in the middle Miocene. Papers in Palaeontology 6: 533–569. https://doi.org/10.1002/spp2.1308

Neubauer TA, Harzhauser M, Kroh A, Georgopoulou E, Mandic O (2015) A gastropod-based biogeographic scheme for the European Neogene freshwater systems. Earth-Science Reviews 143: 98–116. https://doi.org/10.1016/j.earscirev.2015.01.010

Neumann C, Schultka S, Witzmann F (2018) Berlin: The Palaeontological Collections of the Museum für Naturkunde Berlin. In: Beck LA, Joger U (Eds) Paleontological Collections of Germany, Austria and Switzerland. Natural History Collections. Springer, Cham, 39–56. https://doi.org/10.1007/978-3-319-77401-5_5

Neumayr M (1869) Beiträge zur Kenntniss fossiler Binnenfaunen. Jahrbuch der k. k. geologischen Reichsanstalt 19: 355–382. https://www.biodiversitylibrary.org/page/36221771

Neumayr M (1880a) Der geologische Bau des westlichen Mittel-Griechenland. Denkschriften der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 40: 91–128. https://www.biodiversitylibrary.org/page/33416754

Neumayr M (1880b) Über den geologischen Bau der Insel Kos und über die Gliederung der jungtertiären Binnenablagerungen des Archipels. Denkschriften der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften 40: 213–314. https://www.biodiversitylibrary.org/page/33416883

Neumayr M (1883) Ueber einige tertiäre Süsswasserschnecken aus dem Orient. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 1883: 37–44. https://www.biodiversitylibrary.org/page/44135315

Odabaşi DA, Arslan N (2015) Description of a new subterranean nerite: *Theodoxus gloeri* n. sp. with some data on the freshwater gastropod fauna of Balikdami Wetland (Sakarya River, Turkey). Ecologica Montenegrina 4: 327–333. https://doi.org/10.37828/em.2015.2.39

Oppenheim P (1890) Neue oder wenig gekannte Binnenschnecken des Neogen im Peloponnes und im südlichen Mittel-Griechenland. Zeitschrift der Deutschen Geologischen Gesellschaft 42: 588–592. https://www.biodiversitylibrary.org/page/9816790

Oppenheim P (1891) Beiträge zur Kenntniss des Neogen in Griechenland. Zeitschrift der Deutschen Geologischen Gesellschaft 43: 421–487. https://www.biodiversitylibrary.org/page/43539245.

Oppenheim P (1919) Das Neogen in Kleinasien. Zeitschrift der Deutschen Geologischen Gesellschaft 70: 1–210. https://www.biodiversitylibrary.org/page/43778447

Pallas PS (1771) Reise durch verschiedene Provinzen des Rußischen Reichs. Erster Theil. Kayserliche Academie der Wissenschaften, St. Petersburg, [xii +] 504 pp. http://resolver.sub.uni-goettingen.de/purl?PPN329913735

Pană I (2003) Les nannogastropodes. In: Papaianopol I, Marinescu F, Krstić N, Macalet R (Eds) Chronostratigraphie und Neostratotypen. Neogen der Zentrale Paratethys, Bd. X, Pl2. Romanien. Editura Academiei Române, Bucuresti, 296–349.

Pană I, Enache C, Andreescu I (1981) Fauna de moluste a depozitelor cu ligniti din Oltenia. Institutul de cercetări, inginerie tehnologică și proiectări miniere pentru lignit, Craiova, 276 pp.

Papaianopol I, Marinescu F (2003) Les gastropodes. In: Papaianopol I, Marinescu F, Krstić N, Macalet R (Eds) Chronostratigraphie und Neostratotypen. Neogen der Zentrale Paratethys, Bd. X, Pl2. Romanien. Editura Academiei Române, Bucuresti, 262–295.

Papp A (1947) Brack- und Süsswasserfaunen Griechenlands. 2. Brack- und Süsswasserarten von Kythera. Annales Géologiques des Pays Helléniques 1: 112–119.

Papp A (1953) Brack- und Süsswasserfaunen Griechenlands. IV. Süsswassermollusken aus dem Pliozän von Elis (Peloponnes). Annales Géologiques des Pays Helléniques 5: 107–113.

Papp A (1955) Brack- u. Süsswasserfaunen Griechenlands. V. Bemerkungen über Melanopsiden der Untergattung Melanosteira Oppenheim, 1891. Annales Géologiques des Pays Helléniques 6: 122–132.

Papp A (1979) Zur Kenntnis neogener Süßwasserfaunen in Attika (Griechenland). Annales Géologiques des Pays Helléniques 29: 664–678.

Papp A (1980) Die Molluskenfauna von Trilophos südlich von Thessaloniki (Griechenland) und ihre paläogeographische Bedeutung. Annales Géologiques des Pays Helléniques 30: 225–247.

Papp A, Psarianos P (1955) Über einige Süsswassergastropoden aus pliozänen Ablagerungen Griechenlands. Annales Géologiques des Pays Helléniques 6: 145–150.

Pavlović PS (1931) O fosilnoj fauni mekušaca iz Skopske Kotline. Glasnik Skopskog naucnog društva, Odeljenje prirodnih Nauka 9: 1–28.

Pini N (1877) Molluschi terrestri e d'acque dolce viventi nel territorio d'Esino. Bullettino della Società Malacologica Italiana 2: 67–205. https://www.biodiversitylibrary.org/page/39453441

Poey F (1852) Introduccion a los Ciclostomas con generalidades sobre los moluscos gastropodos y particularmente sobre los terrestres operculados. Memorias sobre la historia natural de la isla de Cuba 1: 77–96. https://www.biodiversitylibrary.org/page/2524896

Porumbaru RC (1881) Étude géologique des environs de Craiova, parcours Bucovatzu-Cretzesci. Première partie. Gauthier-Villars, Imprimeur-Libraire, Paris, 42 pp.

Radoman P (1973a) On the relations of some freshwater Mollusca of the Balkan Peninsula and Asia Minor. Basteria 37: 77–84.

Radoman P (1973b) New classification of fresh and brakish water Prosobranchia from the Balkans and Asia Minor. Prirodnjacki Muzej u Beogradu, Posebna Izdanja 32: 3–30.

Radoman P, Stankovič S (1979) Jedan novi predstavnik roda *Graecoanatolica* iz Dojranskog jezera. Glasnik Prirodnjatshkog Muzeja u Beogradu, Serija B, Bioloshke Nauke [Bulletin du Muséum d'Histoire Naturelle Belgrade, Série B] 33: 5–6.

Rafinesque CS (1815) Analyse de la nature ou tableau de l'univers et des corps organisés. Privately published by author, Palermo, 223 pp. http://gallica.bnf.fr/ark:/12148/bpt6k98061z

Rausch L, Alçiçek H, Vialet A, Boulbes N, Mayda S, Titov VV, Stoica M, Charbonnier S, Abels HA, Tesakov AS, Moigne A-M, Andrieu-Ponel V, De Franceschi D, Neubauer TA, Wesselingh FP, Alçiçek MC (2019) An integrated reconstruction of the early Pleistocene palaeoenvironment of *Homo erectus* in the Denizli Basin (SW Turkey). Geobios 57: 77–95. https://doi.org/10.1016/j.geobios.2019.10.003

Roshka VK (1973) Mollyuski meotisa severo-zapadnogo prichernomor'ya. Shtiintsa, Kishinev, 284 pp.

Rückert-Ülkümen N, Kowalke T, Matzke-Karasz R, Witt W, Yigitbas E (2006) Biostratigraphy of the Paratethyan Neogene at Yalova (Izmit-Province, NW-Turkey). Newsletter on Stratigraphy 42: 43–68. https://doi.org/10.1127/0078-0421/2006/0042-0043

Rust J (1997) Evolution, Systematik, Paläoökologie und stratigraphischer Nutzen neogener Süß- und Brackwasser-Gastropoden im Nord-Ägäis-Raum. Palaeontographica Abt. A 243: 37–180. https://doi.org/10.1127/pala/243/1997/37

Sands AF, Glöer P, Gürlek ME, Albrecht C, Neubauer TA (2020) A revision of the extant species of *Theodoxus* (Gastropoda, Neritidae) in Asia, with the description of three new species. Zoosystematics and Evolution 96: 25–66. https://doi.org/10.3897/zse.96.48312

Schneider S, Linse U, Stamatiadis P, Falkenberg J, Mutterlose J, Weich M (2023) First record of Pliocene (Zanclean to mid Piacenzian) marine deposits on Rhodes (Greece): implications for eastern Mediterranean palaeo(bio)geography. Palaeobiodiversity and Palaeoenvironments 103: 109–128. https://doi.org/10.1007/s12549-022-00533-3

Schütt H (1962) Neue Süßwasser-Prosobranchier Griechenlands. Archiv für Molluskenkunde 91: 157–166.

Schütt H (1976) Zur Molluskenfauna der unterpliozänen Süßwasserkalke von Attika. Archiv für Molluskenkunde 107: 35–61.

Schütt H (1985a) Die Mollusken des Vegorrites-Sees in Makedonien. Mitteilungen der Zoologischen Gesellschaft Braunau 4: 301–302.

Schütt H (1985b) Känozoische Landschnecken der Türkei. (Känozoikum und Braunkohlen der Türkei, Nr. 25). Archiv für Molluskenkunde 115: 179–223.

Schütt H (1986) Mollusken aus jungpliozänen Seesedimenten von Antirrion in Akarnanien. Symeonidis N, Theodorou G, Schütt H, Velitzelos E (Eds) Palaeontological and stratigraphical observations in the area of Achaia and Etoloakamania (W-Greece) 33, 329–365.

Schütt H (1988) Mollusken aus den tertiären Brackwasserschichten von Githion in Lakonia (Griechenland). Geologica et Palaeontologica 22: 145–155.

Schütt H (1991) Fossile Mollusken dreier anatolischer Ovas. Archiv für Molluskenkunde 120: 131–147. https://doi.org/10.1127/arch.moll/120/1991/131

Schütt H (1992) Der altpleistozäne Molluskenfundort Kurna bei Burdur in der Türkei. Mitteilungen der deutschen malakozoologischen Gesellschaft 49: 17–18.

Schütt H (1994) Neogene Mollusken aus den Tertiärbecken bei Afyon, Türkei. Geologica et Palaeontologica 28: 167–183.

Schütt H (1997) Altpleistozäne Mollusken im Becken von Pasinler bei Erzurum, Türkei. Geologica et Palaeontologica 31: 275–284.

Schütt H, Besenecker H (1973) Eine Molluskenfauna aus dem Neogen von Chios (Ägäis). Archiv für Molluskenkunde 103: 1–29.

Schütt H, Kavusan G (1984) Mollusken der miozänen Süßwasserablagerungen in der Umgebung von Harmancik bei Kütahya-Bursa in Nordwestanatolien. Archiv für Molluskenkunde 114: 217–229.

Schütt H, Velitzelos E (1991) Mollusken aus dem verkieselten Wald von Kerassia im Nordteil der Insel Euböa/Griechenland. Documenta naturae 67: 1–19.

Schütt H, Şeşen R (1993) *Pseudamnicola* species and other freshwater gastropoda (Mollusca, Gastropoda) from East Anatolia (Turkey, the Ukraine and the Lebanon. Basteria 57: 161–171.

Schütt H, Yildirim ZA (1999) A new freshwater snail from the Beysehir Lake in South-west Anatolia (Gastropoda: Prosobranchia: Hydrobioidea). Malakologische Abhandlungen 19: 243–246.

Schütt H, Velitzelos E, Kaouras G (1985) Die Quartärmollusken von Megalopolis (Griechenland). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 170: 183–204. https://doi.org/10.1127/njgpa/170/1985/183

Stimpson W (1865) Researches upon the Hydrobiinae and allied forms: chiefly made from materials in the Museum of the Smithsonian Institution. Smithsonian Miscellaneous Collections 7: 1–59. https://www.biodiversitylibrary.org/page/8817453

Sitnikova TYa, Peretolchina TE, Anistratenko VV, Anistratenko OY, Palatov DM (2018) Variability and taxonomy of South Caucasian freshwater snails of the genus *Shadinia* Akramowski, 1976 (Caenogastropoda: Hydrobiidae) based on new morphological and molecular data. Archiv für Molluskenkunde 147: 63–76. https://doi.org/10.1127/arch.moll/147/063-076

Spengel JW (1881) Die Geruchsorgane und das Nervensystem der Mollusken. Zeitschrift für wissenschaftliche Zoologie 35: 333–383.

Spratt TAB, Forbes E (1847) Travels in Lycia, Milyas, and the Cibyratis, in company with the late Rev. E. T. Daniell. 2 volumes. John van Voorst, Paternoster Row, London. [Volume 1:] http://reader.digitale-sammlungen.de/de/fs1/object/display/bsb10468250_00009.html [Volume 2:] http://reader.digitale-sammlungen.de/de/fs1/object/display/bsb10468251_00007.html

Stefanescu S (1896) Études sur les Terrains tertiaires de Roumanie. Contribution à l'étude des faunes sarmatique, pontique et levantine. Mémoirs de la Société Géologique de France, Mémoir 15. Paléontologique 6: 1–147.

Taner G (1974a) Denizli bölgesi Neojeninin paleontolojik ve stratigrafik etüdü. Bulletin of Mineral Research and Exploration Institute of Turkey (MTA) 82: 89–126.

Taner G (1974b) Denizli bölgesi Neojeninin paleontolojik ve stratigrafik etüdü. Bulletin of Mineral Research and Exploration Institute of Turkey (MTA) 83: 145–177.

Taner G (1975) Denizli bölgesi Neojeninin paleontolojik ve stratigrafik etüdü. Bulletin of Mineral Research and Exploration Institute of Turkey (MTA) 85: 45–66.

Taner G (1980) Das Neogen in der Umgebung Yalova. Communications de la Faculté des Sciences de l'Université d'Ankara, Série C1: Géologie 23: 1–19.

Taner G (1982) Die Molluskenfauna und pliozäne Stratigraphie der Halbinsel Gelibolu. Communications de la Faculté des Sciences de l'Université d'Ankara, Série C1: Géologie 25: 1–27.

Taner G (1983) Hamzaköy formasyonunun Çavda (Baküniyen) Bivalvleri, Gelibolu Yarımadası [Tschauda (Bakunian) Bivalves of Hamzakoy formation, Gelibolu Peninsula]. Bulletin of the Geological Society of Turkey 26: 59–64.

Taner G (1997) Das Pliozän des östlichen Dardanellen-Beckens, Türkei. Molluskenfauna und Stratigraphie. Annalen des Naturhistorischen Museums in Wien 98 A: 35–67. http://www.zobodat.at/pdf/ANNA_98A_0035-0067.pdf

Taner G (2001) Denizli Bölgesi Neojenine ait katların stratigrafik konumlarında yeni düzenleme [New arrangement of the stages at stratigraphic levels belonging to Neogene of Denizli Region]. 54th Geological Congress of Turkey, May 7–10, 2001, Ankara. Proceedings 54–79: 5.

Tesakov A, Simakova A, Frolov P, Sytchevskaya E, Syromyatnikova E, Foronova I, Shalaeva E, Trifonov V (2019) Early-Middle Pleistocene environmental and biotic transition in NW Armenia, southern Caucasus. Palaeontologia Electronica 22: 25A. https://doi.org/10.26879/916

Totten JG (1834) Description of some new Shells, belonging to the coast of New England. American Journal of Science and Arts 26: 366–369. https://www.biodiversitylibrary.org/page/15985663

Tournouër R (1879) Conchyliorum fluviatilium fossilium, quae in stratis tertiariis superioribus Rumaniae Dr. Gregorio Stefanesco collegit, novae species. Journal de Conchyliologie 27: 261–264. https://www.biodiversitylibrary.org/page/15928316

Vandendorpe J, van Baak CGC, Stelbrink B, Delicado D, Albrecht C, Wilke T (2019) Historical faunal exchange between the Pontocaspian Basin and North America. Ecology and Evolution 9: 10816–10827. https://doi.org/10.1002/ece3.5602

Vasilyan D, Schneider S, Bayraktutan MS, Sen S (2014) Early Pleistocene freshwater communities and rodents from the Pasinler Basin (Erzurum Province, north-eastern Turkey). Turkish Journal of Earth Sciences 23: 293–307. https://doi.org/10.3906/yer-1307-16

Vanatta EG (1924) Descriptions of four new American shells. Proceedings of the Academy of Natural Sciences of Philadelphia 76: 25–27.

Van Beneden P-J (1835) Mémoire sur le *Dreissena*, nouveau genre de la famille des Mytilacées, avec l'anatomie et la description de deux espèces. Annales des sciences naturelles : Zoologie et biologie animale, Seconde Série 3: 193–213. https://www.biodiversitylibrary.org/page/36071717

van de Velde S, Yanina TA, Neubauer TA, Wesselingh FP (2020) The Late Pleistocene mollusk fauna of Selitrennoye (Astrakhan province, Russia): A natural baseline for endemic Caspian Sea faunas. Journal of Great Lakes Research 46: 1227–1239. https://doi.org/10.1016/j.jglr.2019.04.001

van de Velde S, Jorissen EL, Neubauer TA, Radan S, Pavel AB, Stoica M, van Baak CGC, Martínez Gandara A, Popa L, de Stigter H, Abels HA, Krijgsman W, Wesselingh FP (2019) A conservation palaeobiological approach to assess faunal response of threatened biota under natural and anthropogenic environmental change. Biogeosciences 16: 2423–2442. https://doi.org/10.5194/bg-16-2423-2019

Verbrugge LNH, Schipper AM, Huijbregts MAJ, Van der Velde G, Leuven RSEW (2012) Sensitivity of native and non-native mollusc species to changing river water temperature and salinity. Biological Invasions 14: 1187–1199. https://doi.org/10.1007/s10530-011-0148-y

Vinarski MV, Kantor YI (2016) Analytical catalogue of fresh and brackish water molluscs of Russia and adjacent countries. A.N. Severtsov Institute of Ecology and Evolution of RAS, Moscow, 544 pp.

Vinarski MV, Nekhaev IO, Glöer P, Proschwitz T von (2013) Type materials of freshwater gastropod species described by C.A. Westerlund and accepted in current malacological taxonomy: a taxonomic and nomenclatorial study. Ruthenica 23: 79–108. http://www.ruthenica.com/documents/VOL23_Vinarski_et_al_79-108_standard.pdf

Volkova NS (1953) Fauna nizhney chasti verkhnego sarmata okrestnostey g. Armavira. Trudy VSEGEI. Paleontologiya i stratigrafiya 1953: 52–76. https://doi.org/10.1021/cr60161a900

Weber A (1927) Eine neue *Pyrgula*. – *Pyrgula pfeiferi*. m. Zoologischer Anzeiger 70: 313–314.

Welter-Schultes FW (2012) European non-marine molluscs, a guide for species identification. Planet Poster Editions, Göttingen, 679 pp.

Wenz W (1923–1930) Fossilium Catalogus I: Animalia. Gastropoda extramarina tertiaria. Diener C (I–V), Pompeckj JF (VIII–X) (Eds) W. Junk, Berlin, 1–352 (1923), II: 353–736 (1923), III: 737–1068 (1923), IV: 1069–1420 (1923), V: 1421–1734 (1923), VI: 1735–1862 (1923), VII: 1863–2230 (1926), VIII: 2231–2502 (1928), IX: 2503–2886 (1929), X: 2887–3014 (1929), XI: 3015–3387 (1930). https://www.biodiversitylibrary.org/page/40593222 [(vol. I–VI)].

Wenz W (1942) Die Mollusken des Pliozäns der rumänischen Erdöl-Gebiete als Leitversteinerungen für die Aufschluß-Arbeiten. Senckenbergiana 24: 1–293.

Wesselingh FP, Alçiçek H (2010) A new cardiid bivalve from the Pliocene Baklan Basin (Turkey) and the origin of modern Ponto-Caspian taxa. Palaeontology 53: 711–719. https://doi.org/10.1111/j.1475-4983.2010.00958.x

Wesselingh FP, Alçiçek H, Magyar I (2008) A Late Miocene Paratethyan mollusc fauna from the Denizli Basin (southwestern Anatolia, Turkey) and its regional palaeobiogeographic implications. Geobios 41: 861–879. https://doi.org/10.1016/j.geobios.2008.07.003

Wesselingh FP, Neubauer TA, Anistratenko VV, Vinarski MV, Yanina T, ter Poorten JJ, Kijashko PV, Albrecht C, Anistratenko OY, D'Hont A, Frolov P, Martínez Gándara A, Gittenberger A, Gogaladze A, Karpinsky M, Lattuada M, Popa L, Sands AF, van de Velde S, Vandendorpe J, Wilke T (2019) Mollusc species from the Pontocaspian region – an expert opinion list. ZooKeys 827: 31–124. https://doi.org/10.3897/zookeys.827.31365

Westerlund CA (1897) Synopsis molluscorum extramarinorum Scandinaviae (Sueciae, Norvegiae, Daniae & Fenniae). Acta Societatis pro Fauna et Flora Fennica 13: 1–238. https://www.biodiversitylibrary.org/page/5589865

Willmann R (1977) Biostratigraphie mit limnischen Mollusken am Beispiel des Neogens von Kos (Griechenland). Meyniana 29: 71–79.

Willmann R (1980) Die neogenen Süßwassergastropoden von Chersonisos (Kreta). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 159: 273–295.

Willmann R (1981) Evolution, Systematik und stratigraphische Bedeutung der neogenen Süßwassergastropoden von Rhodos und Kos/Ägäis. Palaeontographica Abt. A 174: 10–235.

Willmann R (1982) Biostratigraphisch wichtige Süßwassergastropoden (Prosobranchia, Hydrobiidae) aus dem Neogen des Ägäis-Raumes. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 162: 304–331.

Willmann R (1985) Responses of the Plio-Pleistocene freshwater gastropods of Kos (Greece, Aegean Sea) to environmental changes. In: Bayer U, Seilacher A (Eds) Sedimentary and Evolutionary Cycles. Springer-Verlag, Berlin, 295–321. https://doi.org/10.1007/BFb0009847

Yildirim MZ (1999) Türkiye Prosobranchia (Gastropoda: Mollusca) türleri ve zoocoðrafik yayýlýslarý. 1. Tatlý ve acý sular. Turkish Journal of Zoology 23: 877–900.

Yildirim MZ (2004) The Gastropods of Lake Egirdir. Turkish Journal of Zoology 28: 97–102.

Yildirim MZ, Koca SB, Kebapçı Ü (2006) Supplement to the Prosobranchia (Mollusca: Gastropoda) Fauna of Fresh and Brackish Waters of Turkey. Turkish Journal of Zoology 30: 197–204.

# Supplementary material 1

## Complete list of specimens, with indication of inventory numbers and samples

Authors: Thomas A. Neubauer, Frank P. Wesselingh

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zitteliana.97.115682.suppl1