A Late Miocene Paratethyan mollusc fauna from the Denizli Basin (southwestern Anatolia, Turkey) and its regional palaeobiogeographic implications

Frank P. Wesselingh, Hülya Alçiçek, Imre Magyar

Disponible en ligne sur ScienceDirect www.sciencedirect.com

Elsevier Masson France EM|consulte www.em-consulte.com

GEOBIOS

Geobios 41 (2008) 861–879

Original article

A Late Miocene Paratethyan mollusc fauna from the Denizli Basin (southwestern Anatolia, Turkey) and its regional palaeobiogeographic implications☆

Une faune de mollusques paratéthysienne du Miocène tardif du bassin de Denizli (Anatolie du sud-ouest, Turquie) et ses implications paléobiogéographiques régionales

Frank P. Wesselingh [a,*], Hülya Alçiçek [b], Imre Magyar [c]

[a] *Naturalis, PO Box 9517, 2300 RA, Leiden, The Netherlands*
[b] *Pamukkale University, Faculty of Engineering, Department of Geological Engineering, Kınıklı, 20070, Denizli, Turkey*
[c] *MOL Plc., Október 23. u. 18, 1117 Budapest, Hungary*

Received 7 September 2007; accepted 4 July 2008
Available online 26 September 2008

Abstract

We report on a Late Miocene mollusc fauna from a single locality in the Denizli Basin in southwestern Turkey that is composed of ten presumably euryhaline species and three freshwater species. The fauna is remarkably distinct from faunas of the adjacent Late Miocene Aegean and Euxinian Basins, and has elements in common with the modern Caspian Sea fauna in the form of *Didacna* species. The suggested age of the fauna (Late Miocene) would extend the stratigraphic range of the lymnocardiid genus *Didacna* (hitherto Calabrian-Extant) considerably. The palaeobiogeographic significance of the Denizli fauna is discussed.

Résumé

Dans cet article, nous décrivons une faune locale de mollusques du Miocène tardif du bassin de Denizli (sud-ouest de la Turquie). Cette faune est composée de dix espèces probablement euryhalines et trois espèces d'eau douce. Elle est distincte de celle des bassins miocènes supérieurs adjacents (Égée et Euxinien) et contient des éléments (espèces de *Didacna*) en commun avec la faune Caspienne moderne. L'âge probable de cette faune (Miocène supérieur) prolonge considérablement la répartition stratigraphique du genre lymnocardiidé *Didacna* (Calabrien-Récent). La signification paléobiogéographique de la faune de Denizli est discutée.

Keywords: Turkey; Neogene; Paratethys; Mollusca; *Didacna*

Mots clés : Turquie ; Néogène ; Paratethys ; Mollusca ; *Didacna*

1. Introduction

From the Oligocene onward, spectacular radiations of euryhaline molluscs occurred in Central and Eastern Europe, of which the present-day Caspian Sea fauna is a relic. In a succession of basins, including the Late Miocene Pannonian Basin, the latest Miocene-Pliocene Euxinian and Aegean Basins and the Pliocene-Extant Caspian Sea Basin (Fig. 1),

☆ Corresponding editor: Serge Legendre.
* Corresponding author.
E-mail address: wesselingh@naturalis.nnm.nl (F.P. Wesselingh).

0016-6995/$ – see front matter
doi:10.1016/j.geobios.2008.07.003

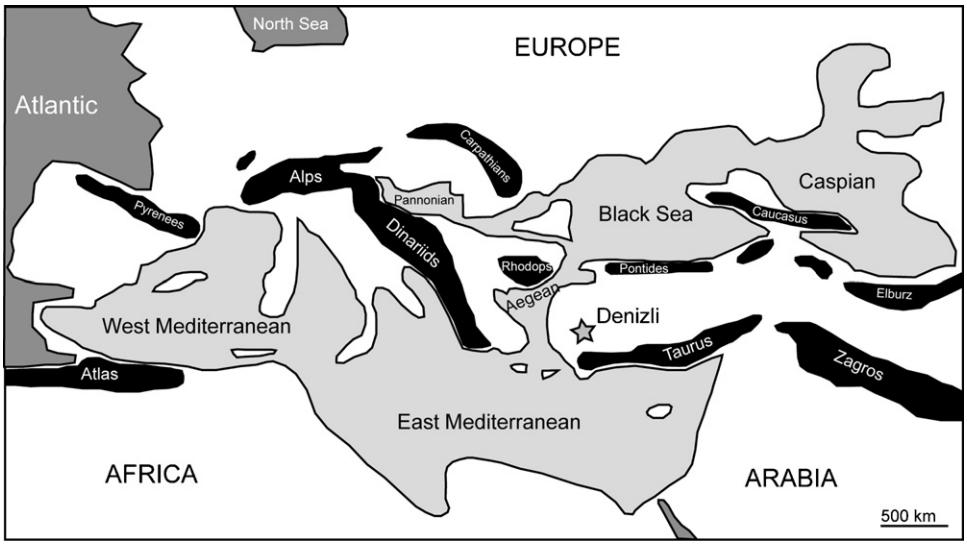

Fig. 1. Paratethyan sedimentary basins and the location of the Denizli Basin. Simplified from Popov et al. (2006).

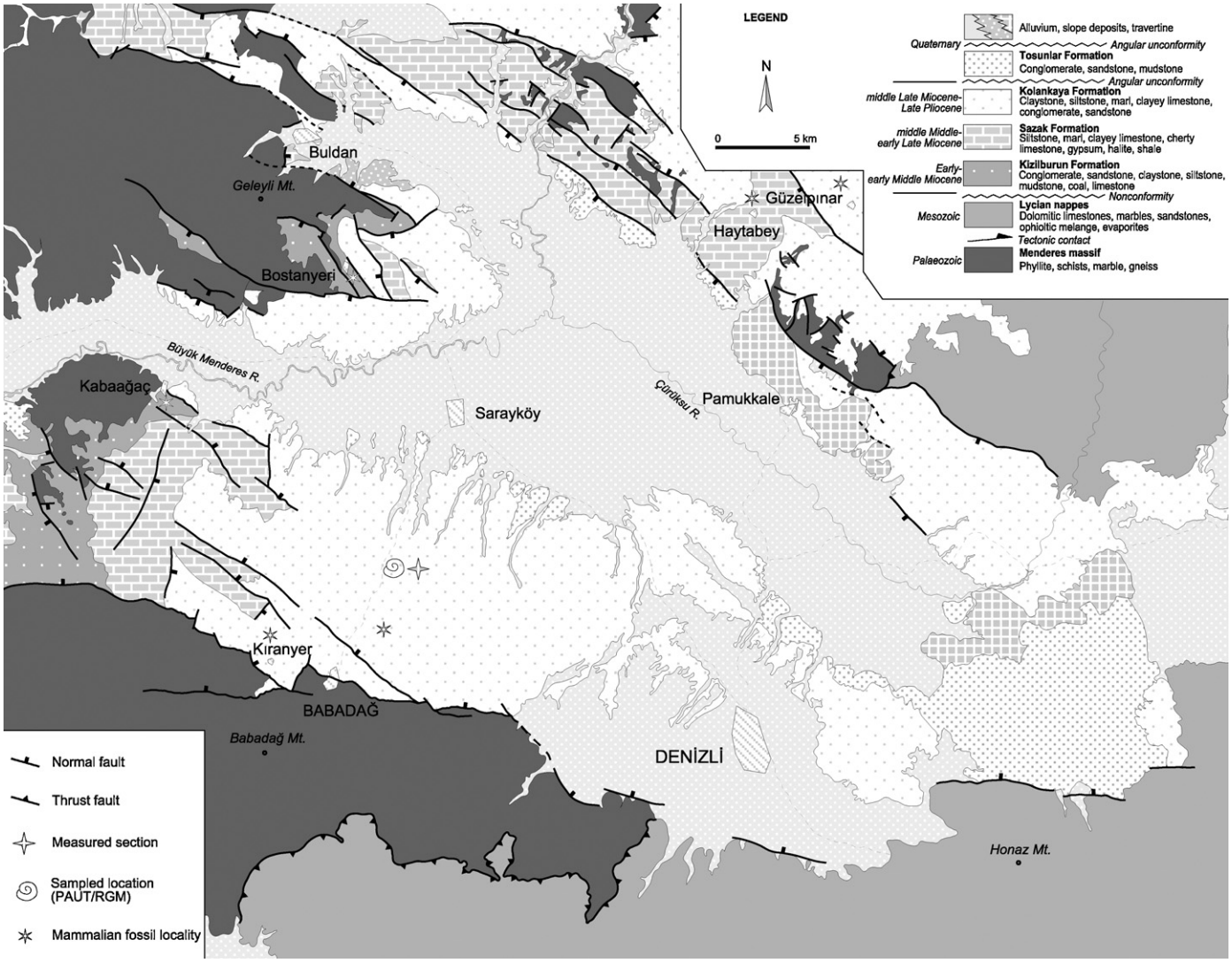

Fig. 2. Simplified geological map of the Denizli Basin, modified from Yalçınlar (1983), Sun (1990), Saraç (2003), Kaymakçı (2006), Konak and Göktaş (in press).

radiations occurred in mollusc groups such as Dreissenidae, Lymnocardiidae and Hydrobioidae. Several of the basins experienced repeated radiations of anomalohaline faunas (such as the Pliocene Aktschagylian and Quaternary Caspian Sea both in the Caspian Basin). On a number of occasions, freshening occurred in the final stages of these lakes, giving rise to a number of independent radiations of Unionoidea and Viviparidae (Neumayr and Paul, 1875; Brusina, 1902; Wenz, 1942; Pana et al., 1981; Lubenescu and Zazuleas, 1985; Papaianopol et al., 2003; Wesselingh, 2007). The so-called Paratethyan mollusc faunas are characterised by their morphological exuberance, high diversity and endemicity. The most abundant mollusk families of the Paratethyan faunas are dreissenid and lymnocardiid bivalves and hydrobioid, melanopsid, viviparid and neritid gastropods. The temporal continuity and direction of evolution and distribution of Paratethyan species and genera are subject of scientific debate (Popov et al., 2006).

In this paper we report on a previously poorly known Paratethyan-like mollusc fauna from the Denizli Basin in southwestern Anatolia (Turkey, Fig. 2). Several of the species of the fauna resemble modern Caspian taxa, but at the same time the fauna shares some similarities with Miocene Aegean faunas. There appears to be very little resemblance with Late Miocene-Pliocene faunas from the Euxinian Basin that should have been in a stratigraphic and geographic intermediate position between the Caspian and Denizli faunas. Aim of this work is to characterize the fauna from the Denizli Basin and to investigate the relationship of that fauna with those from adjacent Paratethyan Basins.

The Neogene Denizli Basin is a WNW-ESE trending depression of approximately 75 km long and 50 km wide located in western Anatolia (Fig. 2). To the west it is connected through the Büyük-Menderes Graben to the Aegean Sea region, but during the Neogene connections with other inland basins in southwestern Turkey also existed (Westaway et al., 2005; Koçyiğit, 2005; Kaymakçı, 2006). The basin is developed in a basement of metamorphic rocks. The basin-fill succession documents a complex Miocene to Quaternary history (Alçiçek et al., 2007: Fig. 3). Fossiliferous marls, sandstones and conglomerates containing an abundant endemic brackish water fauna dominated by lymnocardiid, hydrobioid, dreissenid and neritid species are widely outcropping in the Denizli Basin (Oppenheim, 1918; Nebert, 1958; Taner, 1974a, 1974b). The

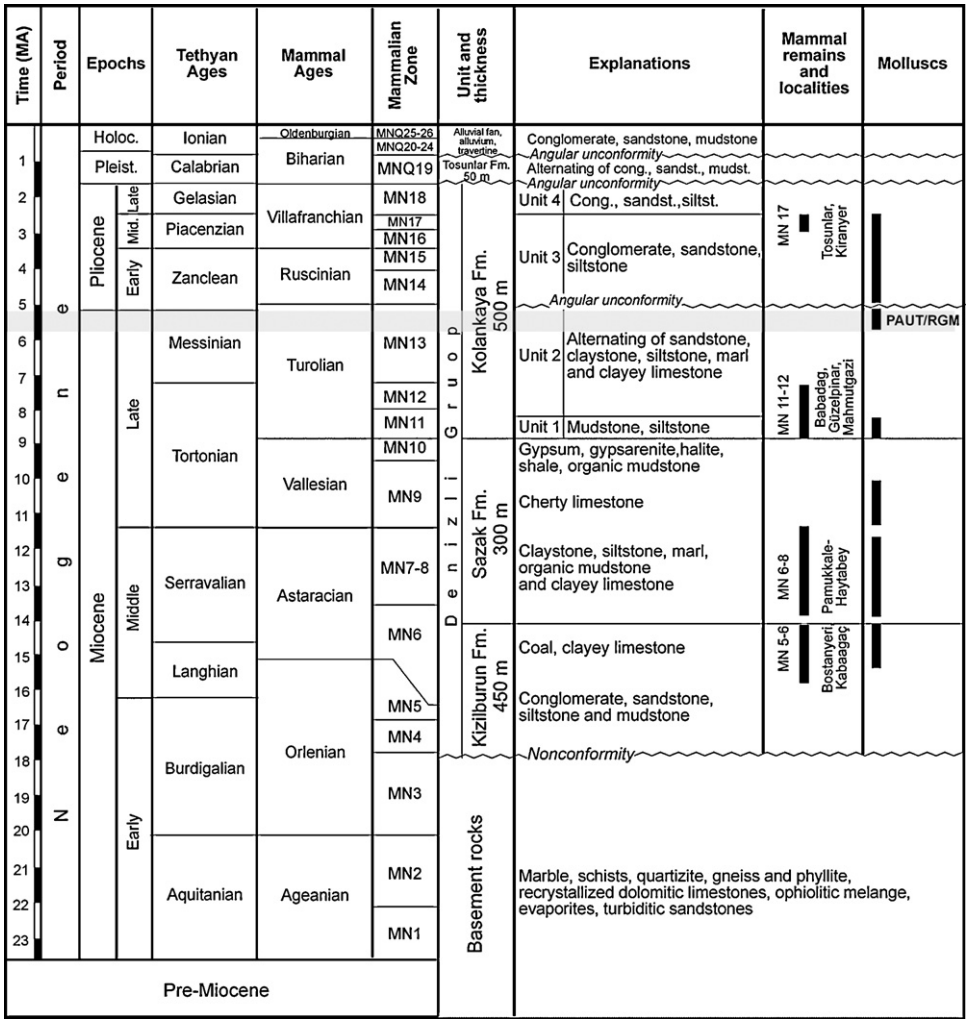

Fig. 3. Stratigraphic framework for the units discussed (adapted from Alçiçek et al., 2007).

Neogene-Quaternary fill of the Denizli Basin comprises some 1300 m of siliciclastic deposits, carbonates and minor evaporite intercalations. The deposits unconformably overlie the metamorphic basement and are subdivided into three lithostratigraphical units that form the Denizli Group (Şimşek, 1984; Sun, 1990; Alçiçek et al., 2007). These three lithostratigraphic units are the Early – early Middle Miocene Kızılburun Formation, the Middle – early Late Miocene Sazak Formation and the Late Miocene – Late Pliocene Kolankaya Formation (Figs. 3 and 4).

The fossil fauna reported herein is from the Kolankaya Formation (Fig. 4). That formation conformably overlies the Middle to early Late Miocene Sazak Formation and in the northern basin margin it overlies directly metamorphic basement rocks. The Kolankaya Formation is maximally 500 m thick and is subdivided in four subunits (Fig. 4, Alçiçek et al., 2007):

- *Unit 1*: a 100 m thick unit of alternating laminated mudstone-siltstone and marls. The deposits are interpreted to reflect low energy conditions in shallow standing bodies of lake water. The presence of desiccation cracks is indicative for the ephemeral (shallow) nature of the lake. Oxygen isotope ratios are negative, indicating the lakes to be composed of freshwater or only marginally brackish waters (Alçiçek et al., 2007);
- *Unit 2*: a 200 m thick unit composed of laminated marl-claystone, sandstone and clayey limestone and black shales containing the invertebrate faunas reported herein. Mammal remains from this unit found in Babadağ, Güzelpınar and Mahmutgazi (Fig. 2) are assigned to MN 11-12 biozone (late Tortonian: Sickenberg and Tobien, 1971; Saraç, 2003). This unit represents anomalohaline open lacustrine settings as is witnessed by sedimentary and oxygen isotope evidence (Alçiçek et al., 2007). The studied sample is from the top of this unit that was deposited under gradually shallowing settings;
- *Unit 3*: a 120 m thick unit of thinly bedded, well-sorted coarse – to very fine-grained sandstones and ripple cross – laminated sandstones followed by planar cross-stratified conglomerates and sandstones, ripple cross-laminated sandstones and massive sandstones. Some layers contain abundant molluscs, ostracods as well as mammal fossils. The molluscs were interpreted to represent a freshwater environment of a Late Pliocene age (Nebert, 1958; Taner, 1974a, 1974b, 1975). Mammal remains from the upper part of this unit from the Tosunlar and Kıranyer areas are represent the Late Piacenzian-Early Gelasian biozone MN17 (Yalçınlar, 1983; Kaymakçı, 2006). The shoreface and foreshore deposits of this unit represent wave-dominated settings in a freshwater lake;
- *Unit 4*: an 80 m thick unit of cross-stratified, poorly sorted subangular conglomerates, sandstone and mudstone alternations with few mudstone-dominated layers. This unit represents fluvial to alluvial fan depositional settings.

The mollusc fauna reported herein is obtained from an outcrop 7 km northeast of Babadağ village, *ca.* 15 km west of Denizli (Fig. 2). The outcrop is located on the right side of the Babadağ-Denizli road (37°49′56.15″N; 28°51′33.46″E).

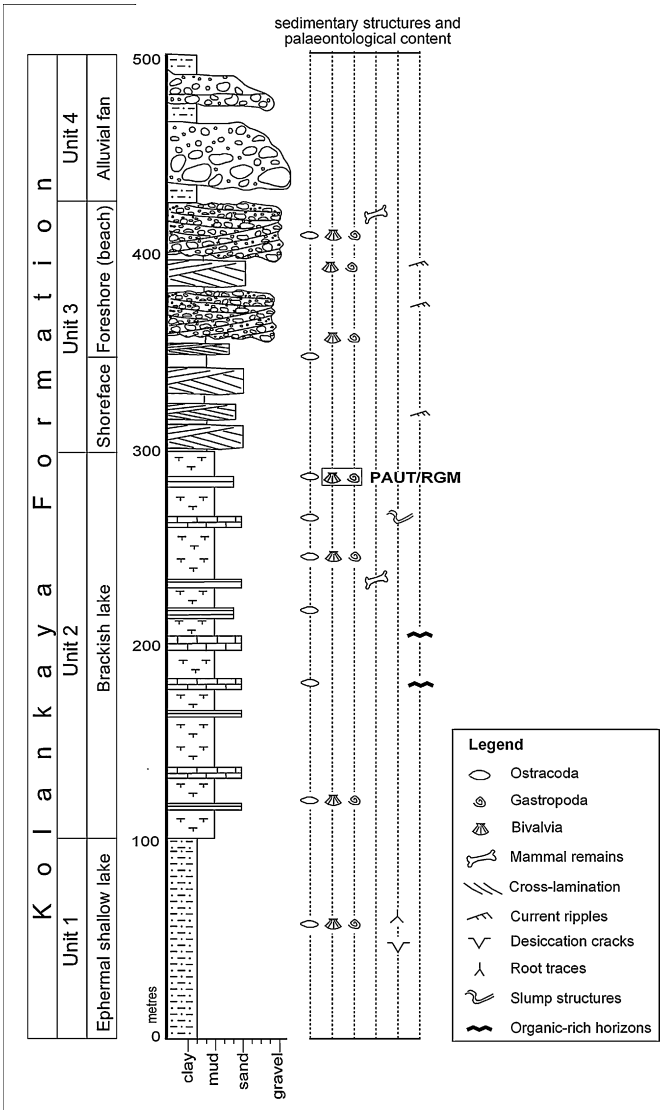

Fig. 4. Stratigraphy of the Kolankaya Formation, locating the studied fossil assemblage (PAUT/RGM).

2. Systematic palaeontology

The material is housed in the Pamukkale University (Denizli, Turkey, samples indicated by PAUT) and in the National Museum of Natural History, Leiden, the Netherlands (samples indicated as RGM).

Abbreviations: *H*: Height; Hap: Height of aperture (measured from the attachment of the outerlip to the preceding whorl); LV: left valve; n.n.: no number; RV: right valve; SD: semidiameter; *W*: Width. All dimensions in millimeter.

Class GASTROPODA
Family NERITIDAE

Genus ***Theodoxus*** Montfort, 1810

Type species: *Theodoxus luteianus* Montfort, 1810 (= *Nerita fluviatilis* Linnaeus, 1758).

Theodoxus bukowskii (Oppenheim, 1918)

Fig. 5(5–7)

1918. *Neritina bukowskii* - Oppenheim, p. 150, Pl. 10, Figs. 5–13.

1974a. *Theodoxus (Calvertia) depressus* - Taner, p. 91, Pl. 1, Figs. 1–5; Pl. ç1, Figs. 1, 1a.

1974a. *Theodoxus (Calvertia) karakovensis* - Taner, p. 91, Pl. 1, Figs. 6–17; Pl. ç1, Figs. 2 and 3.

1974a. *Theodoxus (Calvertia) karakovensis strictus* - Taner, p. 92, Pl. 2, Figs. 1–8; Pl. ç1, Figs. 4, 5, 7.

1974a. *Theodoxus (Neritaea) bukorspkii* [sic] (Oppenheim) - Taner, p. 93, Pl. 2, Figs. 9–13, Pl. ç2, Figs. 1, 2.

Material: 206 specimens.

Description: This is an ovate to slightly shouldered *Theodoxus* with a variable colour pattern of spiral line elements. The apical area of the shells is invariably decollate. The whorl profile of the penultimate whorl is convex, but a subsutural platform, delimited by a rounded and poorly defined shoulder, gains in prominence on the body whorl, giving the species a shouldered outline of variable strength. Rarely, shells are efface, but usually they have spirally arranged dark colour bands. These bands can be thin or thick, they can split into thinner bands and new bands can be added during growth. Usually two to seven bands are found, but up to 18 have been observed on specimens. The aperture is semicircular. The apertural plane is approximately 45° inclined in respect to the columellar axis. The innerlip is greatly expanding over the umbilical area and the innerlip callus is thickened. The innerlip lacks grooves or denticles. We did not find any opercula in the material.

Dimensions: PAUT n.n.: *H* 9.8, *W* 10.8, Hap 8.7; RGM 550.135: *H* 9.2, *W* 9.6, Hap 8.3; PAUT n.n.: *H* 6.3, *W* 6.6, Hap 5.4.

Remarks: A remarkably similar colour pattern appears in some Lake Pannon *Theodoxus* species such as *Theodoxus vetranici* (Brusina, 1902) and *T. radmanesti* (Fuchs, 1870). These species usually have 4–10 black spiral lines on a white background (Jekelius, 1944; Bartha, 1971; Bandel, 2001). According to Bandel (2001), this colour pattern is only one of the many variations that these forms display, and he expressed his doubts about the ''traditional'' species-level distinction between these two, and many other, Lake Pannon taxa. In contrast, Müller (1990) carefully compared the type specimens of *T. vetranici* and *T. radmanesti* and found that the former has a flat or slightly hollowed callus, whereas the latter has a smooth convex callus with an indented margin. In any case, both forms have a higher whorl profile and, most importantly, lack the shouldered habitus of *T. bukowskii*. *Theodoxus depressus* and *T. karakovensis* described by Taner (1974a) from the Denizli Basin fall within the range of morphological variation of the studied sample of *T. bukowskii*.

Family HYDROBIIDAE

Genus ***Pseudamnicola*** Paulucci, 1878

Type species: *Pseudamnicola lucensis* Issel, 1866.

Pseudamnicola orientalis (Bukowski, 1895)

Fig. 5(8a–c)

1974a. *Pseudamnicola (Andrusesowiella)* cf. *kochi* (Brusina) - Taner, p. 109, Pl. 7, Figs. 6, 6a; Pl. ç8, Figs. 3, 3a.

1982. *Pseudamnicola (Staja) orientalis orientalis* (Bukowski) - Willmann, p. 305, Figs. 3a–h, 9.

1982. *Pseudamnicola (Staja) orientalis* spp. (Nominatform?) - Willmann, p. 309, Figs. 3i–l, 5, 9b.

Material: 177 specimens.

Description: Small, ovate, thick-shelled hydrobiid. The apex is slightly abraded in the studied material. The flat nucleus has a diameter of approximately 70 µm. The shell has a very slightly convex whorl profile and a shallowly impressed suture. The latter may be slightly pronounced by a low and rounded subsutural ridge. This ridge bounds a very narrow, rounded shoulder on the body whorl in part of the specimens. The shell is smooth apart from very fine slightly prosocline growth lines. Just before reaching the aperture, growth lines become orthocline and slightly irregular, tending even to very marginal opisthocline at the outerlip. The aperture is broadly drop-shaped. The margins are reinforced and robust. The parietal margin is adnate; a thin parietal callus adheres to the preceding whorl. The columellar margin is low, rounded and very slightly erect. The shell is imperforate.

Dimensions: PAUT n.n.: *H* 2.6, *W* 1.7, Hap 1.3, 4.3 whorls; RGM n.n.: *H* 2.55, *W* 1.6, Hap 1.2, 4.3 whorls.

Remarks: The *Pseudamnicola orientalis* group from Neogene deposits of the Aegean region has been reviewed by Willmann (1982), who attributed a late Middle to early Late Miocene age to these snails. Taner (1974a) described and illustrated three *Pseudamnicola*-like species (*P. elongata, P. e. inflata* and *P. truncus*) from the Denizli Basin that are more elongate and apparently have a thinner shell than *P. orientalis orientalis*. We did not find such forms in our material.

Genus ***Pyrgula*** Cristofori and Jan, 1832

Type species: *Turbo annulatus* Linnaeus, 1758.

?*Pyrgula* sp.

Fig. 5(9a, b)

Material: One specimen.

Description: Only one slightly worn specimen was found in the sample. The apical area is corroded, yet the flat nucleus was found to be very large (diameter approximately 170 µm). The shell is elongate conical and contains a rounded and subdued but slightly reinforced median spiral keel. The whorl profile is carinate. The suture is slightly impressed. A vague and low secondary spiral develops at the base of the whorl, and is visible at the body whorl but disappears before reaching the aperture. Irregular microscopic spiral grooves occur on later teleoconch whorls. Part of the orthocline to very slightly prosocyrth growth lines are developed as irregular groovelets. Also, numerous, low, very fine axial riblets occur, that are so low that they are not

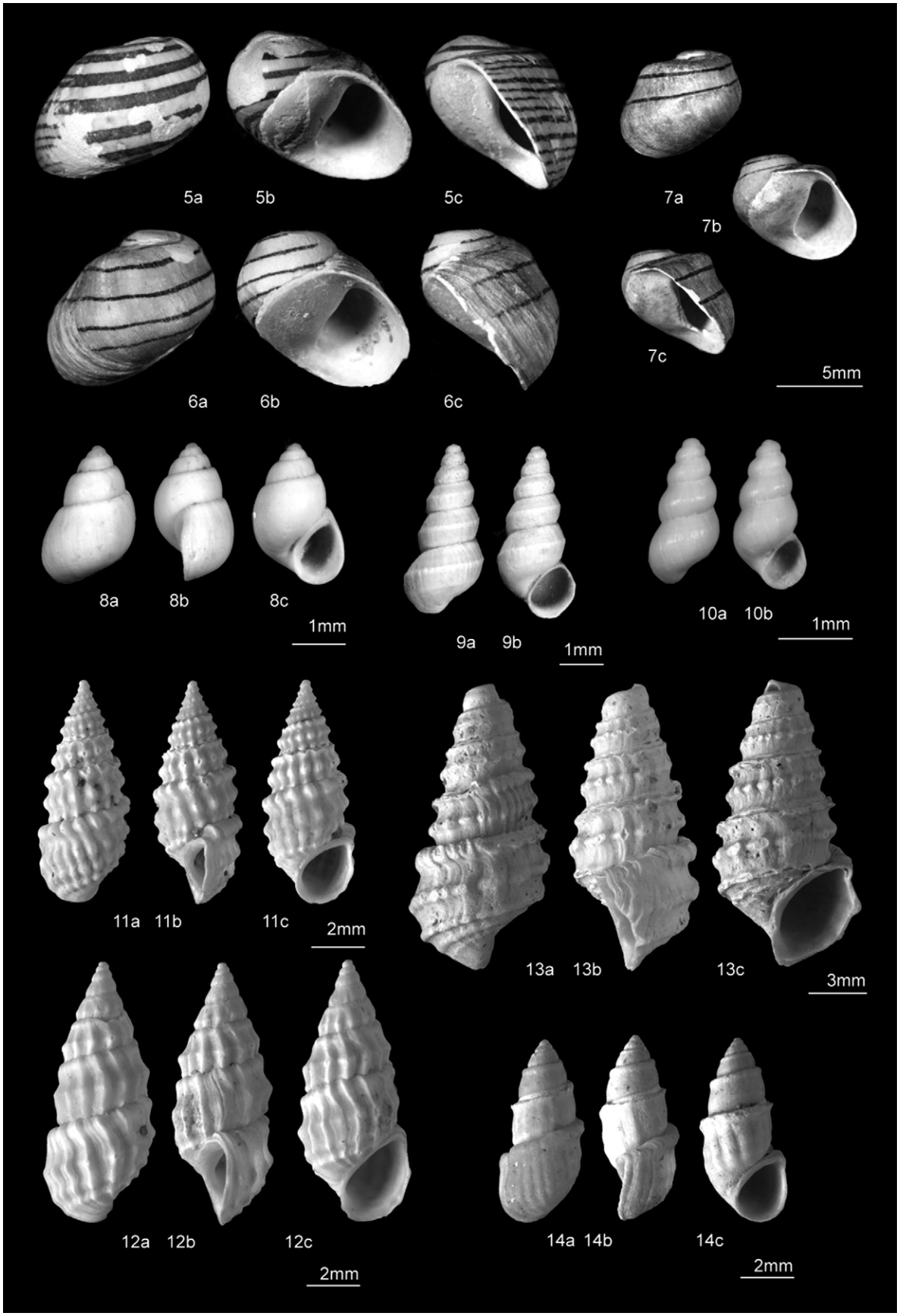

Fig. 5. **5–7**. *Theodoxus bukowskii* (Oppenheim, 1918), (5) PAUT n.n.: a: rear view; b: frontal view; c: side view; (6) RGM 550.135: a: rear view; b: frontal view; c: side view; (7) PAUT n.n.: a: rear view; b: side view; c: frontal view. **8**. *Pseudamnicola orientalis* (Bukowski, 1895), PAUT n.n.: a: rear view; b: side view; c: frontal

visible under small magnifications. Where they cross the median keel, very low and irregular, small knobs may be present. The semicircular aperture is adnate along the parietal margin. The columellar margin is very slightly erect. The basal and outer lips are thin. The shell has an extremely shallow, rimate umbilicus.

Dimensions: RGM 550.139: *H* 3.9, *W* 1.75, Hap 1.3, 6.1 whorls.

Remarks: The attribution of this snail to the genus *Pyrgula* is questionable. The general hydrobiiform outline with the spiral keel resembles *Pyrgula* species known from Neogene and Quaternary deposits of southeastern Europe and western Asia, but Taner (1974a: Pl. ç9, Figs. 1–4) illustrates specimens here attributed to *Micromelania phrygica* (Oppenheim, 1918), with juvenile stages closely resembling the specimen described here. However, similar *Pyrgula*-like juvenile stages were not encountered in the abundant material of *Micromelania* treated below. The taxonomic status of ?*Pyrgula* sp. therefore remains enigmatic.

Genus ***Graecoanatolica*** Radoman, 1973

Type species: *Graecoanatolica lacustristurca* Radoman, 1973.

Graecoanatolica cf. *denizliensis* (Taner, 1974a)

Fig. 5(10a, b)

1974a. *Hydrobia denizliensis* - Taner, p. 97, Pl. 4, Figs. 4–9; Pl. ç3, Figs. 3, 3a.

Material: Two specimens.

Description: A small hydrobiiform snail that is superficially smooth. The slightly inclined nucleus has a diameter of about 90 µm. No differentiation within the protoconch or between the protoconch and teleoconch shell could be observed. The whorl profile is at first subrounded with a somewhat impressed suture, but becomes progressively somewhat flatter. The shell has numerous microscopic orthocline to slightly wavy, prosocline growth lines that can be expressed as very low axial riblets. Irregular microscopic spiral groovelets are found on later teleoconch whorls. The aperture is subovate. The parietal margin is attached. A very shallow, rimate umbilicus is present.

Dimensions: RGM 550.140: *H* 2.05, *W* 1.0, Hap 6.5, 4.1 whorls.

Remarks: The identity of this species is doubtful. Various recent *Graecoanatolica* species are known from Turkey (Yıldırım, 2004) that have all very few distinct shell morphological characters, and for the moment we cannot exclude a possible attribution of this species to one of the recent species.

Genus ***Micromelania*** Brusina, 1874

Type species: *Micromelania cerithiopsis* Brusina, 1874.

Micromelania phrygica (Oppenheim, 1918)

Fig. 5(11–14)

1918. *Prososthenia phrygica* - Oppenheim, p. 148, Pl. 10, Figs. 3, 3a.

?1918. *Prososthenia sublaevis* - Oppenheim, p. 150, Pl. 10, Figs. 4, 4a.

1974a. *Prososthenia phrygica* Oppenheim - Taner, p. 101, Pl. 5, Figs. 1–3; Pl. ç5, Figs. 1, 1a.

1974a. *Prososthenia phrygica cincta* - Taner, p. 102, Pl. 5, Figs. 4–7; Pl. ç5, Figs. 2, 2a.

1974a. *Prososthenia phrygica elongata* - Taner, p. 102, Pl. 5, Figs. 8–10; Pl. ç5, Figs. 3, 3a.

1974a. *Prososthenia phrygica gracilis* - Taner, p. 103, Pl. 5, Figs. 11–18; Pl. ç6, Figs. 1 and 2.

1974a. *Prososthenia phrygica spinosa* - Taner, p. 104, Pl. 6, Figs. 1–3; Pl. ç6, Figs. 3, 3a.

1974a. *Prososthenia cincta* Neumayr - Taner, p. 105, Pl. 6, Figs. 4, 4a; Pl. ç6, Figs. 4, 4a.

?1974a. *Prososthenia cincta raricostata* - Taner, p. 106, Pl. 6, Figs. 5–7; Pl. ç7, Figs. 1, 1a.

?1974a. *Prososthenia sublaevis* Oppenheim - Taner, p. 106, Pl. 6, Figs. 8–19; Pl. ç7, Figs. 2 and 3.

1974a. *Pyrgula erentözi* - Taner, p. 112, Pl. 8, Figs. 4–12; Pl. ç9, Figs. 5, 5.

1974a. *Pyrgula turris* - Taner, p. 31, Pl. 9, Figs. 1–4.

Material: *ca.* 990 specimens.

Description: This is an extremely variably shaped, thick-shelled, rissoiniform to cerithiform, variably sized species. All specimens have in common their tendency to develop a rimate shoulder on later teleoconch whorls, the presence of spiral and axial ribs, often with profuse knobs on the intersections, an aperture whose long axis is strongly inclined in respect with the columellar axis, an apertural plane being opisthocline and an imperforate shell. Four morphs are described in more detail to deal with the range of morphological variation, but all kind of intermediates were found between these morphs.

Morph 1 (PAUT n.n., Fig. 5(11)) has an elongate-ovate fusiform shell with well-developed, blunt tubercles. The corroded nucleus is flat and has an approximate diameter of 100 µm. At about 1.1 whorls, a very delicate axial line might mark the protoconch-teleoconch boundary. Soon thereafter a spiral keel develops at half the whorl height that migrates to about one third of the whorl height on the subsequent whorl, to become located on the middle on later whorls again. On the second teleoconch whorl a subsutural ridge develops that bounds a narrow but characteristic shoulder. From the fourth whorl onwards a lower spiral develops at the base of the whorl and a fourth, thinner spiral is located below on the body whorl. The shell is ornamented with broad axial ribs that produce massive and prominent tubercles on the intersections with the spirals. Sixteen axial ribs are counted on the penultimate whorl. Most of the ribs are located at regular distances but some variation occurs. Ribs are in general orthocline. The four spirals are thinner downward on the body whorl, as are the tubercles on

view. **9**. ?*Pyrgula* sp. RGM 550.139: a: rear view: b; frontal view. **10**. *Graecoanatolica* cf. *denizliensis* Taner, 1974a, RGM 550.140: a: rear view; b: frontal view. **11–14**. *Micromelania phrygica* (Oppenheim, 1918), (11) PAUT n.n.: a: rear view; b: side view; c: frontal view; (12) RGM 550.142: a: rear view; b: frontal view; (13) PAUT n.n.: a: rear view; b: side view; c: frontal view; (14) RGM 550.143: a: rear view; b: frontal view. All materials (also other molluscs) from the Babadağ locality (level BA14), Kolankaya Formation, Late Miocene, unless stated otherwise.

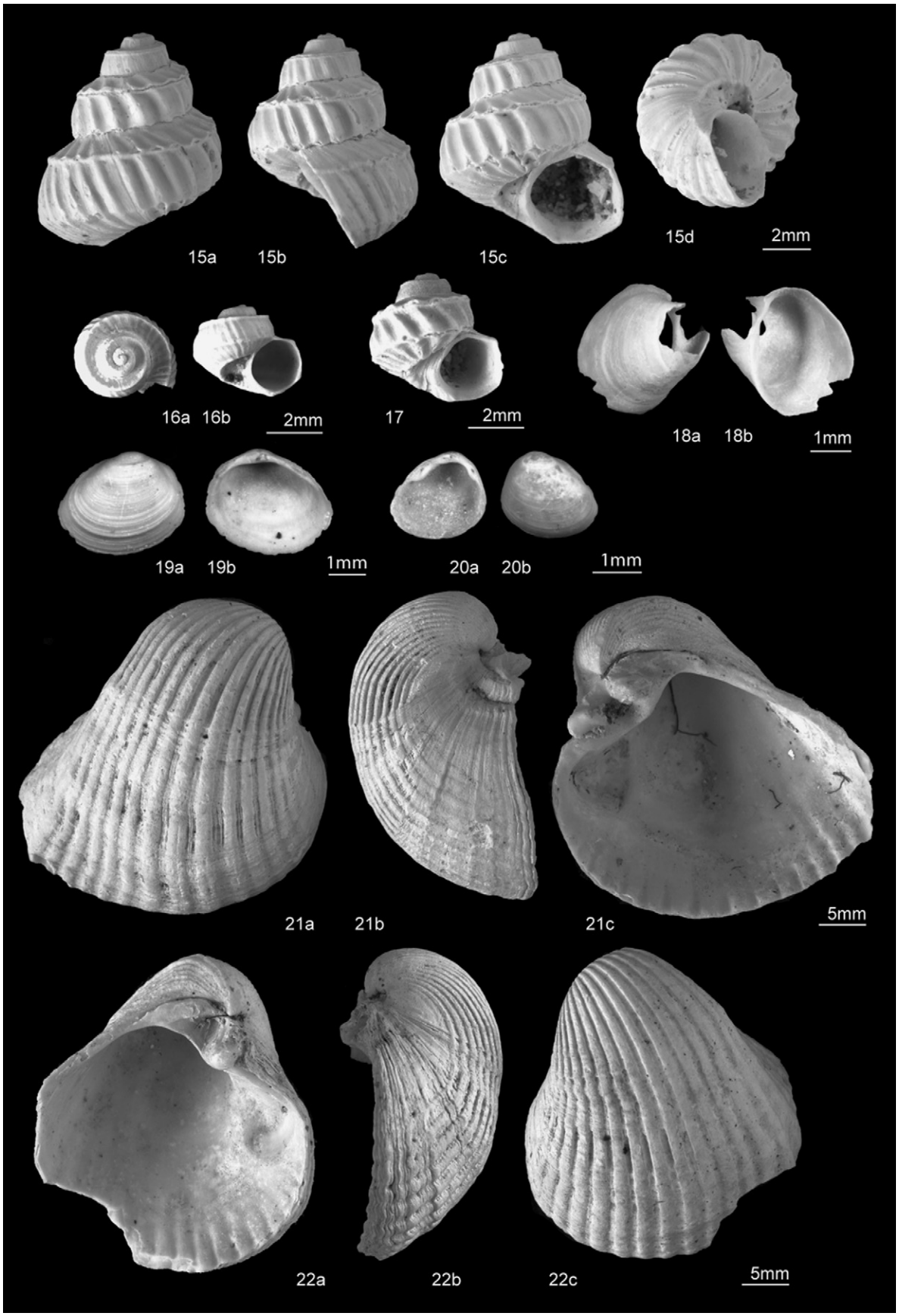

Fig. 6. **15–17**. *Valvata cincta* Taner, 1974a, (15) RGM 550.145: a: rear view; b: side view; c: frontal view; d: umbilical view; (16) RGM 550.146: a: apical view; b: frontal view; (17) PAUT n.n., frontal view. **18**. *Radix* cf. *ampla* (Hartmann, 1821), RGM 550.148: a: rear view; b: frontal view. **19**. *Sphaerium* sp., RGM 550.149,

them. Very fine growth lines occur that have the same orientation as the axial ribs. The aperture is ovate. The long axis is inclined about 40° in respect with the columellar axis. The leftmost part of the columellar margin is to the left of the shell's axis. The innerlip is broadly adnate. The upper part is slightly constricted and runs into an abaxially located notch that corresponds to the shoulder. The apertural plane is slightly opisthocline. The shell is imperforate.

The development of teleoconch ornament on morph 2 (RGM 550.142, Fig. 5(12)) starts at the third whorl. Here, a very low, rounded median spiral keel with increasingly low and rounded knobs develops. The subsequent whorl, a very low subsutural rib develops, bounding a narrow and poorly defined shoulder. Two basal spirals are added at the body whorl. Axial ribs are thin compared to morph 1, and prosocyrth. At intersections with the spirals they develop thinner and slightly more pointed tubercles. There are 14 such ribs on the penultimate whorl.

Morph 3 (PAUT n.n., Fig. 5(13)) is the largest of the forms and resembles a cerithoidean snail. However, the early teleoconch whorls are nearly identical to those of the other specimens. The apical area in this specimen (and in other such large specimens) is lacking. A central spiral rib exists that bears very marked, slightly irregularly spaced knobs. The knobs are often eroded giving them a circular flat surface. An upper and a basal keel develop on later whorls. The upper keel bounds an increasing pronounced shoulder. A fourth spiral appears on the base of the body whorl. Nineteen knobs located at slightly irregular distances were counted on the penultimate whorl.

The first three whorls of morph 4 (RGM 550.143, Fig. 5(14)) are smooth. At the fourth whorl a very prominent upper keel develops, bounding a distinct but narrow horizontal shoulder. Only on the last two whorls very broad and low axial and spiral ribs develop that give the shell a slightly irregular, superficially smooth appearance. The plane of aperture is more distinctly opisthocline than in the previous morphs, as are the growth lines. The outerlip, when viewed from the side, has a '7' form.

Dimensions: PAUT n.n.: *H* 9.3, *W* 3.8, Hap 2.7, 8.3 whorls; RGM 550.142: *H* 10.8, *W* 4.05, Hap 4.7, 7.6 whorls; RGM 550.143: *H* 7.65, *W* 3.5, Hap 2.85, *ca.* 7 whorls; PAUT n.n.: $H > 15.5$, *W* 8.4, Hap > 5.3 (apex missing).

Remarks: The presence of intermediates between the four described morphs indicates that we deal with a single variable species. The nine *Prososthenia* species described by Taner (1974a) all fall within the range of morphological variation. The very large, rather thin-shelled third morph may have resulted from parasitic infestation. This is known to produce unusually large and rather thin-shelled specimens in *Hydrobia* species (Gorbushin, 1997). Taner (1974a: Pl. ç9, Figs. 1–4) showed specimens with a pyrguliform early teleoconch grading into a typical *Micromelania phrygica* shell in later teleoconch whorls. Such specimens where not observed in the studied material, and as the single specimen attributed to ?*Pyrgula* is more elongate, we consider them as two distinct species for the moment.

Family VALVATIDAE
Genus ***Valvata*** Müller, 1774
Type species: *Valvata cristata* Müller, 1774.

Valvata cincta Taner, 1974a
Fig. 6(15–17)
1974a. *Valvata costata cinctus* - Taner, p. 97, Pl. 4, Figs. 1–3; Pl. ç3, Figs. 2, 2a.

Material: 51 specimens.

Description: This is a remarkably large, thick-shelled, viviparifom, highly ornate *Valvata* species. The nucleus is rather convex and has a diameter of approximately 180 µm. The top of the first 1.3 whorls is coiled more or less in plane, and descends rapidly afterward. At *ca.* 1.0 whorls, a keel develops that bounds a flat and broad subsutural ramp above that gives the species a distinctly shouldered outline. Growth lines are numerous, fine and prosocline. Regularly recurring robust axial ribs are also prosocline. At the intersections of these ribs and the spiral keel, elongated hollow knobs develop. Between the intersections the keel is slightly curved downward, pronouncing the ornate character of the shell. On the body whorl 19–21 axial ribs are present. A second, less pronounced keel, develops at the lower suture, and becomes visible at the body whorl. A third keel on the base of the body whorl acts as the umbilical ridge that bounds the deep umbilicus. The aperture is semicircular, with an evenly rounded innerlip. The parietal wall is adnate. The columellar lip is slightly bent outward. The outerlip can be slightly expanding and thickened in some specimens.

Dimensions: PAUT n.n.: *H* 9.6, *W* 8.4, Hap 4.9, 4.7 whorls; RGM 550.145: *H* 9.6, *W* 8.3, Hap 4.6, 5.0 whorls.

Remarks: This is an unusually ornate and highly characteristic *Valvata* species. Only two species described by Oppenheim (*Valvata (Aegaea) viviparifomis* Oppenheim, 1891 and *V. (A.) philippsoni* Oppenheim, 1891) from unnamed beds at Kumari near Aegion (Greece) share similarities with the Denizli species. The former has the strongly developed axial ribs in common, but lacks the spiral elements (including a shoulder). *V. (A.) philippsoni* is spirally ornamented, but lacks the axial ribs typical of *V. costata*. However, all three species could be closely related. We suspect that the species described by Taner (1974a) as *V. costatus s.s.* might be a *Viviparus*.

Family LYMNAEIDAE
Genus ***Radix*** Montfort, 1810
Type species: *Radix auricularia* (Linnaeus, 1758).

Radix cf. *ampla* (Hartmann, 1821)
Fig. 6(18a, b)
?1974a. *Radix (Adelinella) phrygovata* (Oppenheim) - Taner, p. 116, Pl. 10, Figs. 1–4.

Material: One specimen.

RV: a: exterior; b: interior. **20**. *Pisidium crassissimum* Oppenheim, 1918, PAUT n.n., LV: a; interior: b; exterior. **21–22**. *Didacna phrygica* (Oppenheim, 1918), (21) RGM 550.152, RV: a: exterior; b: anterior view; c: interior; (22) PAUT n.n., LV: a: exterior; b: anterior; c: interior.

Description: Only the damaged body whorl of a single specimen was found. The fragment shows a thin shell that has a conspicuously enlarged, auriculate aperture. The ovate aperture is broadly adnate. The innerlip callus is slightly folded over the columellar area and the shell is imperforate.

Dimensions: RGM 550.148: *W ca.* 3.2, $H > 3.1$.

Remarks: The very high position of the upper part of the outerlip resembles that of *Radix ampla* that nowadays lives from Middle Europe to Siberia (Glöer, 2002). The incompleteness of our specimen does not allow a specific identification, nor are we certain whether it is conspecific with *Radix phrygovata* reported by Taner (1974a) from the Denizli Basin.

Class BIVALVIA
Family SPHAERIIDAE
Genus ***Sphaerium*** Scopoli, 1777
Type species: *Tellina cornea* Linnaeus, 1758.

Sphaerium sp.
Fig. 6(19)

Material: Five valves.

Description: Ovate to nut-shaped, inflate *Sphaerium*. The umbo is located at *ca.* one third from the truncate anterior margin. The ventral margin is broadly rounded; the posterior end is slightly tapering. The shell has one or two prominent concentric ribs on the juvenile stages ($W < 1.5$ mm). Otherwise the shell yields fine commarginal growth lines and low irregular ridges. The RV has a thin triangular bifid cardinal tooth. A thin, rather deep, narrowly triangular resilifer lies in front of the cardinal, and in front thereof a thin and elongate triangular small cardinal tooth is present. The lateral teeth are short but erect. Only a single damaged apical LV fragment was present in the material. The cardinal area contains a small shallow socket bounded by a thin, erect arched wall. The superficially impressed adductors are semilunate; a pallial line was not observed.

Dimensions: RGM 550.149: *H* 2.75, *W* 3.4.

Genus ***Pisidium*** Pfeiffer, 1821
Type species: *Pisidium amnicum* (Müller, 1774).

Pisidium crassissimum Oppenheim, 1918
Fig. 6(20)

1918. *Pisidium crassissimum* - Oppenheim, p. 146, Pl. 10, Figs. 2, 2a.

1974b. *Pisidium crassissimum* Oppenheim - Taner, p. 147, Pl. 11, Figs. 6–11; Pl. ç12, Figs. 1, 1a.

Material: Seven valves.

Description: Small, very thick-shelled globose *Pisidium*. The high shell has an oblique subtrigonal outline. The rounded umbo, which is slightly shouldered, is located at about one quarter from the anterior margin. A rounded posterior is present. The anterior margin is truncate, the ventral margin broadly rounded. The shell is ornamented with fine concentric growth lines. The cardinal part of the hinge area is worn in all specimens. The RV hinge plate is wide and robust. Two small triangular cardinal teeth meet at their top under an angle of about 70°. Before the cardinals a shallow resilifer is present. The base of the central part of the hinge plate is horizontal, and is lowered staircase wise laterally. The RV lateral hinge area is prominently expanding and contains a short, very robust lateral tooth flanked on its upper dorsal side by an equally short but deep depression. The LV cardinal teeth are small and worn in the studied material. The lateral teeth are also short, erect and robust. The small adductors are semilunate.

Dimensions: PAUT n.n.: *H* 1.8, *W* 2.05.

Family LYMNOCARDIIDAE
Genus ***Didacna*** Eichwald, 1838
Type species: *Didacna trigonoides* (Pallas, 1771).

Discussion: Various *Pseudocardita* species have been described from Neogene deposits of the Denizli Basin by Oppenheim (1918) and Taner (1974b). We suspect that most of these can be attributed to one of the three species recognised below. In that case, much of the profuse morphological variation illustrated by Taner (1974b) of *Didacna* and *Pseudocardita* either represents stratigraphic forms or ecophenotypic variation, or both. Study on stratigraphically collected material is needed to further improve the systematic understanding of the *Didacna* group of the Denizli Basin. *Pseudocardita* is attributed here to *Didacna* based on the general habitus, the presence of a posterior keel on juvenile stages, the general architecture of the hinge and in particular the posterior truncation of the hinge plate. The origin of the Quaternary-Recent *Didacna* and its relationship to other lymnocardiid genera has been long debated and are still poorly understood. According to Taktakishivili (1987), there are three opinions as to the origin of *Didacna*:

- *Didacna* originated in the Euxinian Basin during the Early Pleistocene and migrated from there into the Caspian Sea. This view gains support from the fossil record of earliest Pleistocene Euxinian cardiids (*Digressodacna* or *Tschaudia*) with a morphology closely resembling *Didacna*. These possible ancestors, in turn, eventually derived from Late Miocene forms, probably *Pseudocatillus*. In this scenario, *Didacna* would be a late member of a Late Miocene radiation;
- *Didacna* originated in the Caspian Basin from one of the Apsheronian (Early Pleistocene) cardiids, probably from *Didacnoides didacnoides* (Andrussov, 1923) and invaded the Euxinian Basin only later. The Apsheronian cardiids are often – although not exclusively – considered descendants of Aktschagylian ancestors, which are in turn all derived from *Cerastoderma dombra*, a Mediterranean immigrant (Danukalova, 1996). In this scenario, *Didacna* is a product of a Pliocene to Recent radiation, and has nothing to do with the Miocene Lymnocardiinae;
- *Didacna* is polyphyletic, some species having an Euxinian origin and others a Caspian origin.

In a recent review on the systematics and evolution of Lymnocardiinae, Nevesskaja et al. (2001) favoured the second scenario. They indicated a relatively sudden appearance of *Didacna* in the Caspian faunas during the Quaternary, and postulated a derivation from one of the endemic species of the

widespread (marginal) marine genus *Cerastoderma* (through *Didacnoides didacnoides*) instead of descending from one of the many Paratethyan genera present in the Euxinian and Aktschagylian lakes during the Pliocene. We find it difficult to envisage a sudden development of the *Cerastoderma* type of hinge, with well-developed lateral teeth, into the *Didacna* type of hinge, lacking such teeth. Therefore, the extension of the fossil record of *Didacna* reported herein appears entirely reasonable. However, we cannot see any direct geographic link between the Denizli area in southwestern Turkey and the Caspian Sea Basin, and a large time interval comprising the Pliocene separates these faunas as well.

A possible phylogenetic link between the Miocene Anatolian *Didacna* early referred to as ''*Pseudocardita*'' by various authors, and the recent Caspian *Didacna* can be the Late Miocene to earliest Pleistocene *Pontalmyra,* widespread (in different time intervals) in the Pannonian, Dacian, Aegean, Mediterranean, Euxinian, and Caspian basins. Nevesskaja et al. (1986, 1997) assigned *Pontalmyra* to the tribe Pseudocarditini; later they assigned *Pseudocardita,* although with a question mark, to the tribe Pontalmyrini (Nevesskaja et al., 2001). The close systematic placement of the two genera should reflect an opinion about close relationship. A comparison of the Denizli cardiids with *Pontalmyra,* however, is complicated due to the uncertain status of the latter genus; it is probably polyphyletic (Taktakishvili, 1987). Although Taktakishvili (1987) excludes the possibility of a direct phylogenetic link between *Pontalmyra* and *Didacna,* some earlier authors favoured this idea (e.g. Ebersin, 1962). Investigating and comparing the shell structure and ontogenetic development of the sculpture in *Didacna*, *Pontalmyra*, and *Didacnoides*, Popov (1977) concluded that these genera are similar to such an extent that it was impossible to decide which of the two latter could have been the direct ancestor of *Didacna*.

Finally, it is possible that the cardiids from Denizli are only mere convergent with *Didacna*. However, both the posterior ridge in juvenile specimens as well as the hinge characteristics (such as the posterior truncation of the hinge plate) of the Denizli lymnocardiids and Caspian *Didacna* are very similar. A cladistic analysis of the entire lymnocardiid family would be needed to assess the robustness of these characters, which is beyond the aims of the present study. In order to refute or demonstrate convergence, additional study of (yet unavailable) stratigraphic precursors of the Denizli specimens described might also be helpful.

Didacna phrygica (Oppenheim, 1918)
Figs. 6(21, 22) and 7(23)

1918. *Cardium (Pseudocardita) phrygicum* - Oppenheim, p. 140, Pl. 5, Fig. 5a, b; Pl. 6, Fig. 8.

1918. *Cardium (Pseudocardita) laodicaeense* - Oppenheim, p. 141 (*pars*), Pl. 11, Fig. 3 (*non* Figs. 1, 2, 4).

1974b. *Didacna (Pontalmyra) convexa* - Taner, p. 153 (*pars*), Pl. 13, Figs. 3, 3a (*non* Figs. 1 and 2); Pl. ç12, Figs. 3, 3a.

1974b. *Didacna (Pontalmyra) rostriformis* - Taner, p. 155 (*pars*), Pl. 14, Figs. 1, 1a, 3, 4 (*non* Figs. 2, 2a); Pl. ç13, Figs. 2, 2a.

1974b. *Pseudocardita bukowskii* Oppenheim - Taner, p. 160, Pl. 16, Figs. 3–6a; Pl. 17, Figs. 1–8; Pl. ç14, Figs. 2, 2a; Pl. ç15, Fig. 1.

1974b. *Pseudocardita chamaeformis* Oppenheim - Taner, p. 162, Pl. 18, Figs. 2 and 3.

?1974b. *Pseudocardita gibbosa* - Taner, p. 163, Pl. 18, Figs. 4–7; Pl. ç15, Figs. 2, 2a.

1974b. *Pseudocardita phrygicum* Oppenheim - Taner, p. 167, Pl. 21, Figs. 6 and 8; Pl. ç17, Figs. 1, 1b.

1974b. *Pseudocardita* sp. - Taner, p. 167, Pl. 21, Figs. 4 and 5; Pl. ç17, Figs. 1, 1b.

Material: 131 valves.

Description: The shell is incurved and extremely inflated. The left valve appears to be slightly less inflate than the right valve, but differences are subtle, and morphological variation in our material is large. The shells are relatively high and are thickened along the anterior side, and the hinge region is very thick as well. The lower half of the posterior margin can be produced, and is in general thinner shelled. Juvenile stages ($H < 5$ mm) are wider, have a well-developed posterodorsal keel, and resemble in general the outline of unrelated *Parvicardium* species. The shell has 17–21 ribs on the central portion. All ribs are already discernable in the juvenile stages, apart from those at the posterior and anterior ends that may develop on adult stages. The ribs are regular, well defined. They have a sub-quadrangular cross-section, and are separated by equally deep and sub-quadrangular interspaces. On larger (adult) specimens, the ribs may broaden and become lower, but they remain well defined all over the shell. Wear of the shells results in deepening of the interspaces between the ribs, making the ribs even more pronounced. Occasionally, a slight depression may develop in the centre of the rib in adult stages. Commarginal growth lines are common, very often densely spaced. Concentric growth stops (possibly year rings) are well developed at decreasing distances. There are five to seven on adult valves. A widened rib forms the posterodorsal keel. The keel becomes subdued in adult stages. The posterior ramp contains six to seven low, broad, poorly defined ribs. At the anterodorsal margin ribs become low and poorly defined as well. The anterior cardinal of the RV as well as the anterior cardinal and receiving furrow of the LV are very strongly developed and located at the shell edge, and produce visible structures on the shell's exterior. The hinge of the RV contains two very prominent cardinal teeth. In subadult specimens the anterior cardinal is much smaller than the posterior, but in adult specimens both are of about equal dimensions. The anterior cardinal is an upstanding pillar with a triangular cross section (subadult) and becomes a broad knob in larger specimens. The posterior cardinal is a massive, broad-based and slightly pointed feature. In between, a deep, but poorly defined resilifer is present. The base of the hinge plate has a strong upward retraction behind the posterior cardinal tooth, forming an arch. Lateral teeth are lacking. In the hinge of the LV, a cardinal tooth is located on the anterior side. This cardinal develops from a broad erect area with a central depression on top in subadult stages to a massive, rounded knob in adult specimens. The posterodorsal margin is straight, and much longer than the

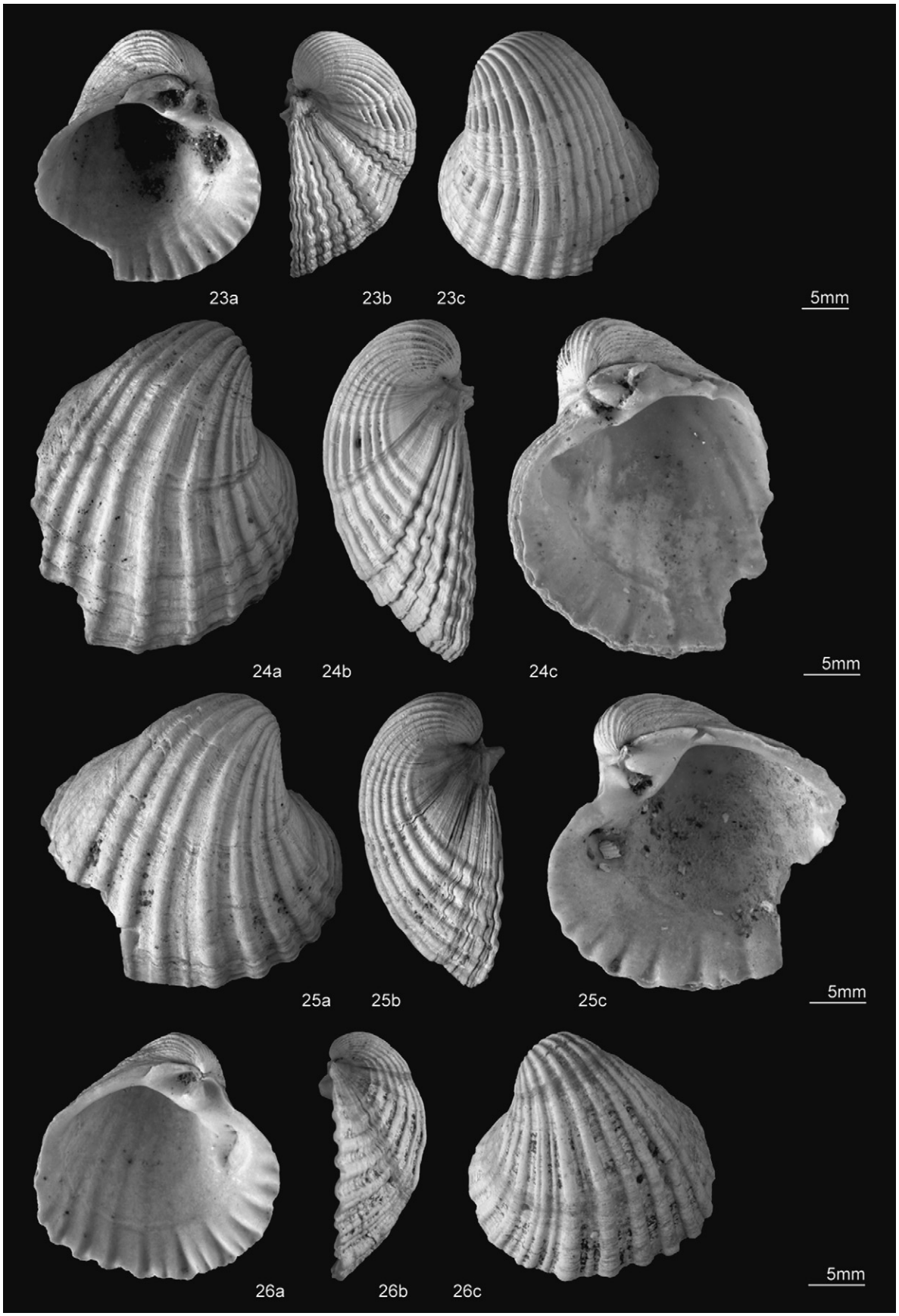

Fig. 7. **23**. *Didacna phrygica* (Oppenheim, 1918), RGM 550.153, LV: a: interior; b: anterior view; c: exterior. **24–26**. *Didacna laodicaeense* (Oppenheim, 1918), (24) PAUT n.n., RV: a: exterior; b: anterior; c: interior; (25) RGM 550.155, RV: a: exterior; b: anterior; c: interior; (26) RGM 550.156, LV: a: interior; b: anterior; c: exterior.

anterodorsal margin. The ribs extend on the interior of the lower margin. The irregular ovate anterior adductor scar is deeply embedded and located below the anterior cardinal tooth. The broad drop-formed posterior adductor scar is poorly defined. The pallial line runs oblique, it is located further into the shell at the anterior side, and is entire.

Dimensions: PAUT n.n.: *H* 32, *W* 34, SD 19; RGM 550.152: *H* 34, SD 18.5; RGM 550.153: *H* 27, SD 15; PAUT n.n: *H* 26, *W* 25, SD 14.5; PAUT n.n: *H* 20, *W* 19, SD 13.

Remarks: The Denizli *Pseudocardita*'s (here attributed to *Didacna*), published by Oppenheim (1918) and Taner (1974b), shows a wide variability in shell shape and ornamentation. In our sample, only two well recognizable forms of the very inflate *Didacna* were found (there are a further two flatter species, see below) that also yield a wide variation of ribbing types and show distinct changes in general outline, ribbing and hinge characteristics during ontogeny.

Didacna laodicaeense (Oppenheim, 1918)
Figs. 7(24–26) and 8(27)

1918. *Cardium (Pseudocardita) laodicaeense* - Oppenheim, p. 141 (*pars*), Pl. 11, Figs. 1, 2, 4 (*non* Fig. 3).

1918. *Cardium (Pseudocardita) phillippsoni* - Oppenheim, p. 143 (*pars*), Pl. 11, Figs. 5, 5c (*non* Pl. 6, Fig. 9, 9a).

1974b. *Didacna (Pontalmyra) rostriformis* - Taner, 155 (*pars*), p. 155, Pl. 14, Figs. 2, 2a (*non* Figs. 1, 1a, 3, 4, Pl. ç13, Figs. 2, 2a).

?1974b. *Pseudocardita denizliensis* Oppenheim - Taner, p. 161, Pl. 18, Figs. 1, 1a.

1974b. *Pseudocardita laodicaeense laodicaeense* Oppenheim - Taner, p. 164, Pl. 19, Figs. 1–8; Pl. ç15, Figs. 3, 3a.

?1974b. *Pseudocardita laodicaeense intermedius* - Taner, p. 165, Pl. 20, Figs. 1–4; Pl. ç16, Figs. 1, 1a.

?1974b. *Pseudocardita laodicaeense intercostata* - Taner, p. 166, Pl. 20, Figs. 5 and 6.

Material: 162 valves.

Description: Intermediate-sized, inflate and incurved, robust lymnocardiid with 14–18 narrow and well defined primary ribs that are separated by interspaces that are twice as wide. The shell has a subtrigonate outline and appears aequivalve. The shells are relatively high; they are slightly thickened along the posterior side. All ribs are already discernable on the juvenile stages, apart for those at the posterior and anterior ends that may develop on adult stages. The ribs are regular and well defined. They have a sub-quadrangular cross-section, and are separated by sub-quadrangular interspaces that are about twice as broad as the ribs. Very thin and low secondary ribs may develop between the primaries. The 2–4 anterior-most ribs are more closely spaced and slightly lower. At the posterior end, three or four very thin and low ribs are present that are very delicate compared to the robust ribs on the central part of the shell. Commarginal growth lines are common, very often densely spaced. Nine to twelve well-defined growth stops (possibly year rings) are present at decreasing distances. A posterior ridge coinciding with one of the ribs is not particularly well developed. The posteroventral portion of the shell is broken off in all adult specimens. The anterior cardinal of the RV as well as the anterior cardinal or socket of the LV are very strongly developed and located at the shell edge and produce visible structures on the shell's exterior. The hinge of the RV contains two very prominent cardinal teeth, the anterior is smaller than the posterior. The posterior cardinal tooth grades into a platform on the dorsal side, which has a sharp upper nymph that is truncate posteriorly. In between a deep, but poorly defined resilifer is present. The base of the hinge plate is strongly curved upward behind the posterior cardinal tooth, forming an arch. Lateral teeth are lacking. In the hinge of the LV the cardinal tooth is located between two depressions, the posterior/upper of which is the most prominent. Growth lines indicate that the posterodorsal margin is straight and much longer than the anterodorsal margin. The ribs extend on the interior of the lower margin. The subquadrate anterior adductor scar is embedded and located below the anterior cardinal tooth. The posterior adductor scar is lacking in adult specimens. The pallial line is located deeply into the shell. The posterior part, including a possible sinus, is lacking in the material.

Dimensions: RGM 550.155: *H* 32, SD 15.5; PAUT n.n.: *H* 30.5, SD 14; RGM 550.156: *H* 30, SD 13.5; PAUT n.n.: *H* 30.5, SD 15. Posterior end in all specimens broken, precluding measurement of shell *W*.

Remarks: This species is less inflate than *Didacna phrygica*. It furthermore differs from that species by the fewer ribs with broad interspaces, the more central location of the cardinal tooth in the LV and the thinner shell that is only slightly thickened on the anterior margin.

Didacna elongata Taner, 1974b
Fig. 8(28, 29)

1974b. *Didacna (Pontalmyra) elongata* - Taner, p. 153 (*pars*), Pl. 13, Figs. 4 and 5; Pl. ç13, Fig. 1, 1a.

1974b. *Didacna (Pontalmyra) tosunlari* - Taner, p. 156 (*pars*), Pl. 15, Figs. 1, 1a (*non* Figs. 2–5, Pl. ç13, Figs. 2, 2a); ?Pl. ç14, Figs. 1, 1a.

Material: Three valves.

Description: Intermediate-large subtrigonal solid but not overtly thick shell. Umbones prosogyrate located about one sixth from the anterior margin. Shell with 17–19 low radial ribs that fade on the posterior and anterior margins. The ribs have a more or less quadrangular cross-section; the interspaces are 0.5–1.5 times as wide. A posterior ridge is absent. The species has a narrow lunule. The shells are markedly thickened on the anterior half. Lateral teeth are lacking. The LV hinge has a prominent triangular cardinal that is flanked anteriorly by a well-defined inverted C-shaped, sharp but low wall that is part of the shell's exterior. A broadly triangular, somewhat inclined socket is located in front of the cardinal tooth. The upper margin of the socket is formed by a prominent but non-erect, subhorizontal nymph. The RV hinge has a broadly elongate, oblique-subhorizontal cardinal tooth with a triangular socket in front. The socket is bounded by a low but sharp, C-shaped wall in front that forms part of the shell's exterior. The posterodorsal side of the cardinal tooth grades into a sort of broad and characteristic cardinal platform. The dorsal side of

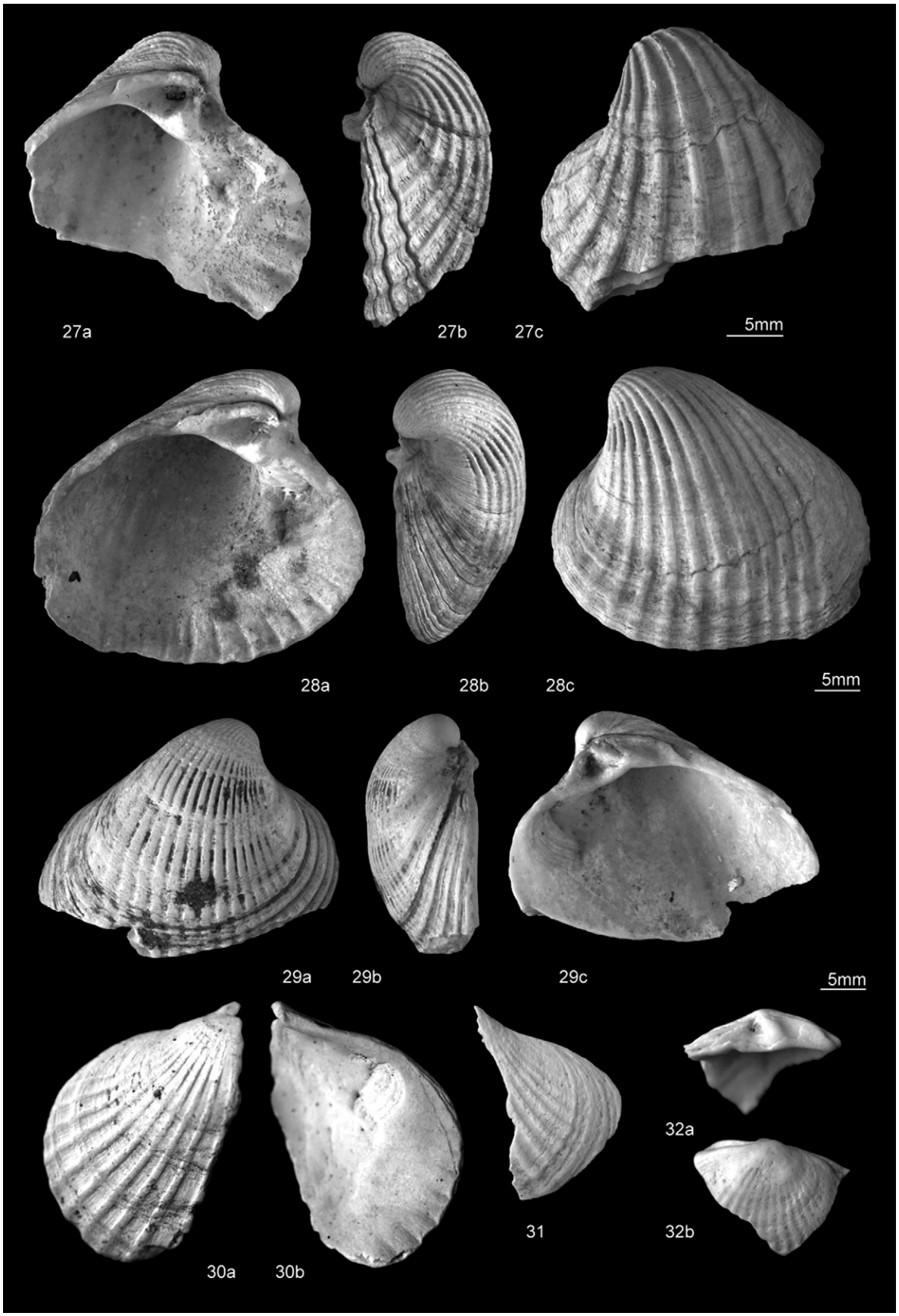

Fig. 8. **27**. *Didacna laodicaeense* (Oppenheim, 1918), PAUT n.n., LV: a: interior; b: anterior; c: exterior. **28, 29**. *Didacna elongata* Taner, 1974b, (28) RGM 550.158, LV: a: interior; b: anterior; c: exterior; (29) PAUT n.n., RV: a: exterior; b: anterior; c: interior. **30–32**. *Didacna* sp. (30) RGM 550.160, fragment RV: a: exterior; b: interior; (31) PAUT n.n., fragment RV exterior; (32) RGM 550.161, fragment RV: a: exterior; b: interior.

this platform forms the lunule. At the posterodorsal side, this platform is truncate. The semilunate anterior adductor scar is deeply impressed. The posterior adductor scar is also semilunate, but very shallowly impressed. The pallial line is hardly preserved in the studied material, but appears to run oblique from the anterior adductor scar downwards posteriorly. The pallial line in the area below the anterior adductor scar is completely worn in the material precluding the documentation of possible pallial sinus. Ribs extend into the shells interior margin.

Dimensions: RGM 550.158 (LV): *H* 34, *W* 39, SD 15; PAUT n.n. (damaged RV): $H > 29$, *W ca.* 36, SD 1.3.

Remarks: This species lacks the thick shells and incurved nature of both previously described *Didacna* species, but their hinge architecture is broadly similar.

Didacna sp.

Fig. 8(30–32)

Material: 89 valves and fragments.

Description: Only abraded fragments of this species were recovered in the studied sample. This comprises a large ($H > 45$ mm), flat but robuste species. From the fragments a large, rather high shell with a rounded posterior margin, a depressed umbonal region and a slightly tapering anterior margin is deduced. A low, poorly defined posterior ridge is present on juvenile stages that has a subtrigonal to subtrapezoid outline. From a single top fragment, the presence of c. 22 radial ribs is estimated. The ribs are low and rectangular in cross-section. Interspaces on adult fragments are typically 1.5–2 times as wide, but ribs can be slightly irregularly positioned and become thinner and closer spaced at the posterior end. All apical fragments are extremely worn, complicating the assessment of the hinge. The RV contains a low rounded cardinal that is about 60° inclined in respect with the L axis. In front lies a low, broadly triangular resilifer. A short nymph appears to be present in front of the resilifer, but that area is extremely worn and damaged in the specimens. To the posterior side, the RV cardinal grades through a very shallow depression into a marked posterior platform, the top of which forms an apparent narrow lunule. The LV has a broad and flat hinge platform with a robust cardinal tooth located slightly anteriorly from the apex that grades backward into a flat lateral platform. Behind the cardinal an embedded triangular to drop-shaped socket exists that is inclined *ca.* 60° in respect with the length axis. Other hinge characters were not observable due to wear, as were the internal characters such as the adductor scars and the pallial line. Thin grooves, corresponding to ribs, were found in the shells exterior at the posteroventral-margin.

Remarks: The flat nature of this species, with the low and relatively broad hinge platform, distinguishes it from other Denizli lymnocardiids. The cardinal tooth are well developed in ?*Didacna* sp., unlike the dentition in the extant Caspian and Black Sea *Adacna* species that has a broadly similar shell outline. The reminiscence of the outline of ?*Didacna* sp. and, e.g., that of the extant *Adacna laeviuscula* (Eichwald, 1829), may indicate convergence.

3. Discussion

3.1. Diversity

The Denizli fauna is predominantly composed of endemic (Paratethyan) long-lived lake taxa typical of brackish waters. The morphological variation within endemic long-lived lake species is often very large and usually leads to oversplitting (Müller et al., 1999).

Furthermore, the presence of successive stratigraphic morphs also complicates the systematic treatment of such faunas. As a result, we are not able to indicate exactly how many species were present in the Denizli Basin during the Late Miocene, but we know that a number of species were not present in our studied sample. These include *Neritina denisluensis* (see Oppenheim, 1918), *Theodoxus karakovensis*, *Viviparus* sp. and a number of hydrobioid species documented by Taner (1974a), '*Hydrobia acuta*' (Oppenheim, 1918: p. 147), *Corbicula, Unio* s.l. and *Dreissena* spp. (see Taner, 1974b), and additional lymnocardiid taxa, such as *Avicardium denizliensis* (Taner, 1974b).

3.2. Ecology and depositional environment

The studied sample contains only a few, rare species that are normally restricted to freshwater (*Radix* cf. *ampla*, *Sphaerium* sp., *Pisidium crassissimum*), although alleged brackish occurrences of similar taxa have been recorded from Lake Pannon deposits (Müller et al., 1999). The majority of the fauna either has uncertain but possibly brackish salinity preferences (*Theodoxus bukowskii*, *Valvata cincta*, the hydrobioid snails), or are almost certainly brackish Paratethyan endemics (*Didacna* spp.). These latter two groups of taxa numerically dominate the studied fauna. The predominance of Paratethyan endemics and the lack of ordinary (marginal) marine mollusc species, with the possible exception of a juvenile cardiid (illustrated by Oppenheim, 1918: Pl. 6, Fig. 9 as *Cardium* (*Pseudocardita*) cf. *phillippsoni* indicate that the Denizli fauna should be considered as genuine Paratethyan, and does not represent a marine incursion fauna, as suggested by Westaway et al. (2005). It is very likely that the Denizli fauna lived in an enclosed brackish sea, whose salinity was maintained by oppressive evaporation, alike the modern Caspian Sea. The studied sample possibly consists of an admixture of shells from three depositional settings. The before mentioned freshwater taxa were possibly washed in from adjacent rivers, streams or coastal swamps or reworked from such deposits during transgression. The extremely abraded *Didacna* sp. likely represents extensive reworking in a shore zone, either during transgression or as a result of a general living mode in the shore zone. *Theodoxus bukowskii* may also have been an inhabitant of this shore zone. Most taxa (*Valvata cincta*, the hydrobioids, *Didacna* spp. other than *D.* sp.) are in general reasonably well preserved, although some wear does occur. The shells are commonly slightly dissolved. The apparent lack of bivalve pairs, however, does indicate physical disturbance. This may have resulted from dislodging by burrowers in the shell's

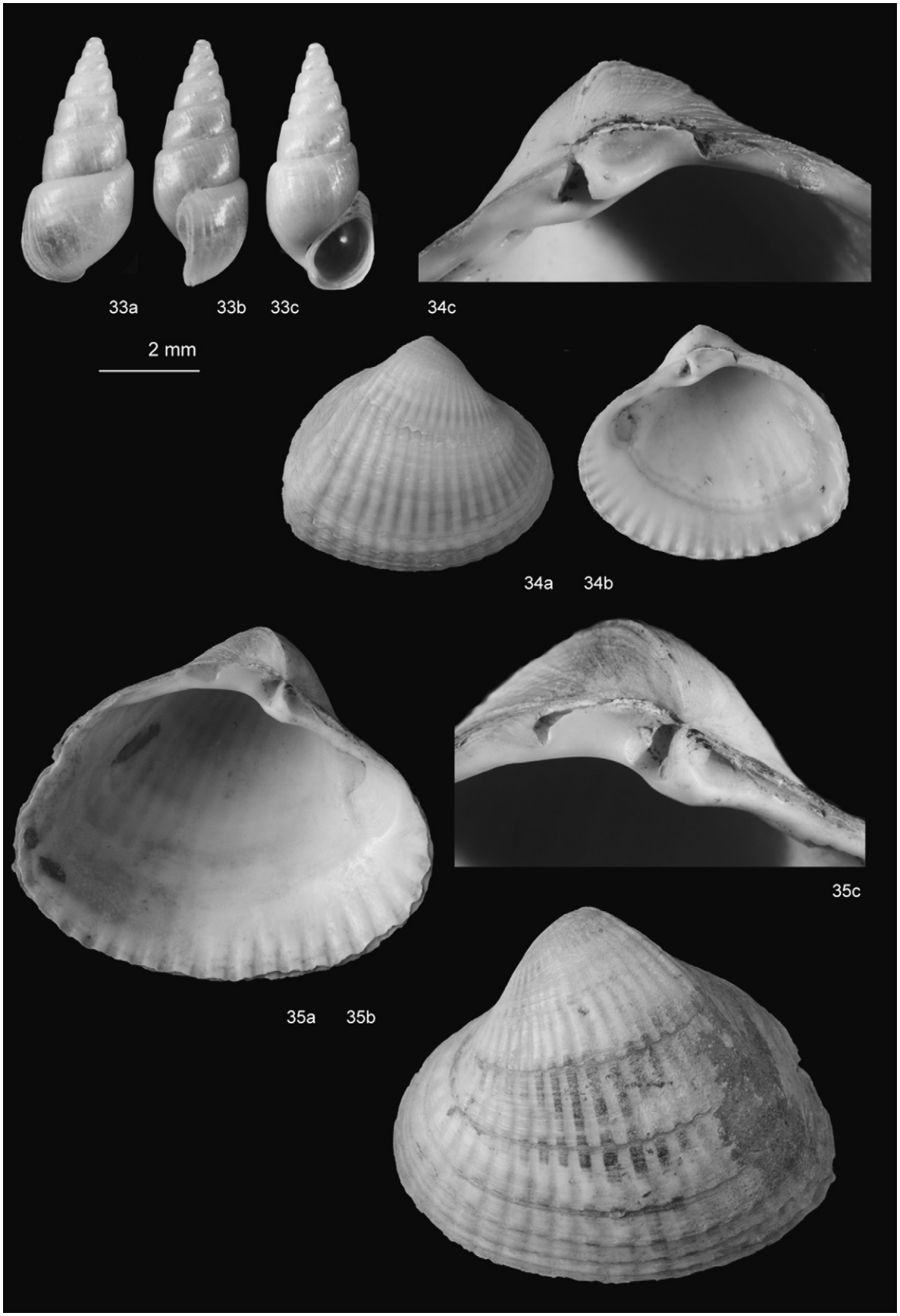

Fig. 9. **33**. *Micromelania* aff. *lincta* Milachewich, 1908, RGM n.n., unnamed Holocene beds, Caspian Sea east of Kura delta (Azerbaijan): a: rear view; b: side view; c: frontal view. **34, 35**. *Didacna trigonoides* (Pallas, 1771), unnamed Holocene beds, Caspian Sea east of Kura delta (Azerbaijan), (34) RGM n.n, RV: a: exterior; b: interior; c: detail hinge; (35) RGM n.n, LV: a: exterior; b: interior; c: detail hinge.

habitats or tumbling in waves or currents. The fauna might thus represent depths between the storm and fair-weather wave base that should have been comparatively shallow in the sheltered Denizli Basin at the time.

3.3. Age

The Denizli fauna is most likely of a Late Miocene age. However, the exact correlation with the small mammal bearing horizons within the Kolankaya Formation (that are of a Tortonian age) is uncertain. Only a single potential age diagnostic mollusc species (*Pseudamnicola orientalis*, indicative of a Late Miocene age: Willmann, 1982) was found matching the age estimate of Westaway et al. (2005) based on the presence of large regional erosional unconformities above the fossiliferous intervals attributed to the Messinian Mediterranean lowstand. As mentioned before, the Denizli fauna is not a Mediterranean fauna, and therefore cannot be correlated with Mediterranean events directly without independent time constraints.

3.4. Biogeographic signature of the Denizli fauna and implications for Paratethyan palaeobiogeography

The Denizli fauna is remarkable in its biogeographic signature. On the one hand, it contains taxa (presumably) related to Neogene and Quaternary species from the Aegean region, such as *Neritina bukowskii*, *Valvata cincta, Graecoanatolica* cf. *denizliensis* and *Pseudamnicola orientalis*. On the other hand, *Micromelania phrygica* and especially *Didacna* species morphologically resemble modern Caspian Sea taxa (Fig. 9(33–35)).

A Late Miocene age and geographic location of the Denizli Basin are difficult to match with a close Caspian affinity of the fauna. *Didacna* species were absent in Lake Aktschagyl, a Late Pliocene precursor of the Caspian Sea (Danukalova, 1996). *Didacna* is also unknown from the Pliocene Euxinian Basin that should have been the logical stepping-stone in space and time between the Denizli and Caspian faunas.

We were unable to check the record of *Avicardium* by Taner (1974b) from Denizli. *Avicardium* is an alleged exclusive Aktschagylian genus (Nevesskaja et al., 2001). Other alleged Aktschagylian taxa have been reported before from the southeastern shores of the Dardanelles in western Turkey (Taner, 1982). The species *Aktschagylia subcaspia* and *A. karabugasica* (belonging to an Aktschagylian mactraid radiation: Danukalova, 1996) were reported from two localities. Furthermore, a record of *Potamidus caspius* was made from a third locality by Taner (1982). If Taner's identifications are correct, it supports the possibility of a connection between the Caspian Basin and southwestern Turkey bypassing the Euxinian (Black Sea) Basin as described earlier by Nevesskaja et al. (2001) based on suggestions by Starobogatov (1970) and Chepalyga (1995). However, this connection, which should have postdated the Denizli faunas described in this paper, apparently did not allow extension of the modern Caspian type of *Didacna* and possibly the thick-shelled *Micromelania* species found in Denizli into the precursor of the Caspian Sea, Lake Aktschagyl.

Improvement of the exact age of the Denizli fauna is required in order to assess its potential connection with Messinian Lagomare faunas that occupied brackish and saline basins at the end of the Messinian throughout the Mediterranean (Orszag-Sperber, 2006; Esu, 2007). In the few hundreds of thousands of years that the Lagomare existed, a shift towards endemic forms may have occurred in gastropods in various basins of the Mediterranean. Lagomare bivalve species had in general a more widespread distribution, and are considered to be of Paratethyan (Euxinian) origin (Esu and Girotti, 1989; Esu, 2007) but are remarkably different from the possibly time-equivalent Denizli lymnocardiid species.

4. Conclusions

A Paratethyan mollusc fauna from the Denizli Basin (southwestern Turkey) of a probable Late Miocene age is discussed, containing the hitherto oldest record of the lymnocardiid bivalve genus *Didacna* (represented by four species). These species indicate a close biogeographic affinity between the Denizli fauna and the Quaternary-modern Caspian Sea fauna. However, the presence of large Paratethyan faunas in the Euxinian Basin during the Pliocene, that forms an intermediate stage (geographical as well as stratigraphical) between the Denizli and Caspian faunas, but that lacks these mollusc taxa, is difficult to reconcile with a close relationship as suggested by the fauna.

Acknowledgements

This study was supported by the Scientific and technical Research Council of Turkey (TÜBITAK: research grant ÇAYDAG 104Y156) and the Scientific Research Fund of the Pamukkale University (BAP: research grant 2008KKP066). We thank Tom Meijer and Wim Maassen (Naturalis, Leiden, The Netherlands) for additional information on the taxonomy of Anatolian *Valvata* and hydrobioids. We thank Didier Merle and an unnamed reviewer for their constructive and helpful comments that improved the manuscript.

References

Alçiçek, H., Varol, B., Özkul, M., 2007. Sedimentary facies, depositional environments and palaeogeographic evolution of the Neogene Denizli Basin of SW Anatolia, Turkey. Sedimentary Geology 202, 596–637.

Andrussov, N.I., 1923. Apsheronian Stage. Trudy Geolicestago Komiteta, new serie 110, 1–294.

Bandel, K., 2001. The history of *Theodoxus* and *Neritina* connected with description and systematic evaluation of related Neritimorpha (Gastropoda). Mitteilungen aus dem Geologisch-Paläontologischen Institut Universität Hamburg 85, 65–164.

Bartha, F., 1971. A magyarországi pannon biosztratigráfiai vizsgálata. In: Góczán, F., Benk, F. (Eds.), A magyarországi pannonkori képzdmények kutatásai. Akadémiai Kiadó, Budapest, pp. 9–172 (in Hungarian).

Brusina, S., 1874. Prilozi paleontologiji hrvatskoj ili kopnene i slatkovodne terciarne izkopine Dalmacije, Hrvatske i Slavonije [Fossil non-marine

molluscs from Dalmatia, Croatia and Slavonia]. Rad Jugoslavenske akademije znanosti i umjetnosti 28, 1–109 (in Serbo-Croatian).

Brusina, S., 1902. Iconographia molluscorum fossilium in tellure Tertiaria (Hungariae, Croatiae, Slavoniae, Dalmatiae, Bosniae, Herzegovinae, Serbiae et Bulgariae inventorum). Atlas II. Plates 30. Agram, Zagreb.

Bukowski, G.V., 1895. Die levantinische Molluskenfauna der Insel Rhodus (II. Teil, Schluss). Anzeiger der kaiserlichen Akademie der Wissenschaften, mathematisch naturwissenschaftliche Classe 32, 55–56.

Chepalyga, A.L., 1995. East Paratethys-Tethys marine connections along Euphrat passage during Neogene. Romanian Journal of Stratigraphy 76, 149–150.

Cristofori, G. de Jan, G., 1832. Catalogus in IV sectiones divisus rerum naturalium in Museo extantium Josephi de Cristofori et Georgii Jan. Section II. Conchyliologa. Carmignani, Parma.

Danukalova, G., 1996. Bivalves and Aktschagylian stratigraphy. Trudy Paleontologicheskogo Instituta Rossia Akademii Nauk 265, 1–132 (in Russian).

Ebersin, A.G., 1962. Brackish-water cardiids from the Pliocene of the USSR, Part 4, the genus *Didacna* Eichwald. Trudy Paleontologicheskogo Instituta Akademii Nauk 91, 1–179.

Eichwald, E., 1829. Zoologia specialis, quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum et Poloniae in specie, in usum lectionum publicarum in Universitate Caesarea Vilnensi. Volume 1. Josephi Zawadski, Vilnae.

Eichwald, E., 1838. Faunae Caspic maris primitiae. Bulletin de la Sociéte Impériale des Naturalistes de Moscou 2, 125–174.

Esu, D., 2007. Latest Messinian ''Lago-Mare'' Lymnocardiinae from Italy: close relations with the Pontian fauna from the Dacic Basin. Geobios 40, 291–302.

Esu, D., Girotti, O., 1989. Late Miocene and Early Pliocene continental and oligohaline molluscan faunas of Italy. Bolletino della Societa Paleontologica Italiana 28, 253–263.

Fuchs, T., 1870. Beiträge zur Kenntniss fossiler Binnenfaunen 3: Die Fauna der Congerienschichten von Radmanest im Banate. Jahrbuch der Geologische Reichsanstalt in Wien 20, 343–364.

Glöer, P., 2002. Mollusca I. Süsswasser gastropoden Nord- und Mitteleuropas. Bestimmungsschlüssel, Lebensweise, Verbreitung. 2. neubearbeitete Auflage. Conchbook, Hackenheim.

Gorbushin, A.M., 1997. Field evidence of trematode-induced gigantism in *Hydrobia* spp. (Gastropoda: Prosobranchia). Journal of Marine Biological Association of the United Kingdom 77, 785–800.

Hartmann, W., 1821. System der Erd- und Flusschnecken der Schweiz: mit vergleichender Aufzählung aller auch in den benachbarten Ländern, Deutschland. Frankreich und Italien sich vorfindenden Arten. Neue Alpina 1, 194–268.

Issel, A., 1866. Dei molluschi raccolti nella provincia de Pisa. Memorie della Società Italiana di Scienze Naturali 2, 1–36.

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

Kaymakçı, N., 2006. Kinematic development and paleostress analysis of the Denizli Basin (Western Turkey): Implications of spatial variation of relative paleostress magnitudes and orientations. Journal of Asian Earth Sciences 27, 207–222.

Koçyiğit, A., 2005. The Denizli Graben-horst system and the eastern limit of western Anatolian continental extension: basin-fill, structure, deformational mode, throw amount and episodic evolutionary history, SW Turkey. Geodinamica Acta 18, 167–208.

Konak, N., Göktaş, F., in press. Geological maps of Turkey in 1:100,000 scale: Denizli M21 sheet. Publication of Mineral Research and Exploration Directorate of Turkey.(MTA).

Linnaeus, C., 1758. Systema Naturæ per Regni tria Naturæ, Secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Laurentii Salvii, Stockholm (Holmiae).

Lubenescu, V., Zazuleas, D., 1985. Viviparidae du Basin dacique. Geologic al Romaniei 32, 77–136.

Milachewich, K.O., 1908. Mollyuski, sobrannye S.A. Spisok vidov mollyuskov, sobrannykh S.H. Zernovym v 1908 g. v severo-zapadnoi chasti Chernogo morya [List of mollusk species collected by S. A. Zernov in 1908 in the northwestern part of the Black Sea] Ezhegodnik Zoologicheskogo Museya Akademii Nauk 14, 145–166 (in Russian).

Montfort, D. de, 1810. Conchyliologie systématique et classification de coquilles : coquilles univalves, cloisonnées. F. Schoell, Paris.

Müller, O.F., 1774. Vermium terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum, et testaceorum, non marnorum succinta historia. Havniae, Copenhague.

Müller, P., 1990. Revised and other species of malacofauna from Tihany (Fehérpart) in Hungary. In: Stevanovic, P.M., Nevesskaja, L.A., Marinescu, Fl., Sokac, A., Jámbor, Á. (Eds.), Chronostratigraphie und Neostratotypen. Neogen der Westlichen (''Zentrale'') Paratethys VIII, Pl1, Pontien. JAZU and SANU, Zagreb-Beograd, pp. 558–581.

Müller, P., Geary, D.H., Magyar, I., 1999. The endemic molluscs of the Late Miocene Lake Pannon: their origin, evolution, and family level taxonomy. Lethaia 32, 47–60.

Nebert, K., 1958. Denizli Pliosen Teressübati ve bunların Batı Anadolu tatlı su Neojen stratigrafisi için ehemmiyeti [The Pliocene deposits of Denizli and their significance for the stratigraphy of the west Anatolian freshwater Neogene]. Bulletin Mineral Research and Exploration Institute Turkey (MTA). MTA Bulletin 51, 7–18 (in Turkish).

Neumayr, M., Paul, C.M., 1875. Die Congerien- und Paludinenschichten Slavoniens und deren Faunen. Ein Beitrag zur Descendenz-Theorie. Abhandlungen der kaiserlich-königlichen Geologischen Reichsanstalt 7, 1–111.

Nevesskaja, L.A., Gontcharova, I.A., Iljina, L.B., Paramonova, N.P., Popov, S.V., Babak, E.V., Bagdasarian, K.G., Voronina, A.A., 1986. History of the Neogene molluscs of Paratethys. Trudy Paleontologicheskogo Instituta Akademii Nauk SSR 220, 1–208.

Nevesskaja, L.A., Paramonova, S.V., Babak, E.V., 1997. Atlas of the Pliocene bivalves of southwestern Eurasia. Trudy Paleontologicheskogo Instituta Akademii Nauk SSR 269, 1–267.

Nevesskaja, L.A., Paramonova, N.P., Popov, S.G., 2001. History of Lymnocardiinae (Bivalvia, Cardiidae). Paleontological Journal 35, S147–S217.

Oppenheim, P., 1891. Beiträge zur Kenntnis des Neogen in Griechenland. Zeitschrift Deutsche Geologische Gesellschaft 43, 421–487.

Oppenheim, P., 1918. Das Neogen in Kleinasien. Zeitschrift Deutsche Geologische Gesellschaft 70, 1–210.

Orszag-Sperber, F., 2006. Changing perspectives in the concept of ''Lago-Mare'' in Mediterranean Late Miocene evolution. Sedimentary Geology 188/189, 259–277.

Pallas, P.S., 1771. Reise durch verschiedene Provinzen des Russischen Reichs, 1. Kaiserlichen Academie der Wissenschaften, St. Petersburg.

Pana, I., Enache, C., Andreescu, I., 1981. Fauna de moluste a depozitelor cu ligniti din Oltenia [Mollusc fauna from the lignite-bearing deposits of Oltenia]. Institutul de Cercetari, Inginerie Tehnologica si Proiecari Miniere pentru Lignit. Craiova 1–276 (in Rumanian).

Papaianopol, I., Marinescu, F., Krstic, N., Macalet, R. (Eds.), 2003. Chronostratigraphie und Neostratotypen. Neogen der Zentrale Paratethys X, Romanien. Editura Academiei Romane, Bucharest.

Paulucci, M., 1878. Matériaux pour servir à l'étude de la faune malacologique, terrestre et fluviatile de l'Italie et de ses îles. Unnamed publisher, Paris.

Pfeiffer, C., 1821. Naturgeschichte deutscher Land- und Süsswasser-Mollusken. Unnamed publisher, Weimar.

Popov, S.V., 1977. The shell structure and system of the cardiids. Transactions of the Paleontological Institute. Academy of Sciences of the USSR 153, 1–124.

Popov, S.V., Shchreba, I.G., Ilyina, L.B., Nevesskaya, L.A., Paramonova, N.P., Khondkarian, S.O., Magyar, I., 2006. Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. Palaeogeography, Palaeoclimatology, Palaeoecology 238, 91–106.

Radoman, P., 1973. New classification of fresh and brackish water Prosobranchia from the Balkans and Asia Minor. Prirodnjacki Musej u Beogradu 32, 1–30.

Saraç, G., 2003. Türkiye Omurgalı Fosil Yatakları [Vertebrate Fossil Localities of Turkey]. Mineral Research and Exploration Institute of Turkey (MTA) Report 10609. Ankara, Turkey. (in Turkish, unpublished report).

Scopoli, J.A., 1777. Introductio ad historiam naturalem sistems genera lapidum, plantarum et animalium hactenus Detecta, caracteribus essentialibus

donata, in tribus divisa, subinde ad leges naturae. Wolfgangum Gerle, Prague.

Sickenberg, O., Tobien, H., 1971. New Neogene and Lower Quaternary vertebrate faunas in Turkey. Newsletter Stratigraphy 1, 51–61.

Şimşek, Ş., 1984. Denizli-Kızıldere-Tekkehamam-Tosunlar-Buldan-Yenice alanının jeolojisi ve jeotermal enerji olanakları [Geology and geothermal energy potential of the Denizli-Kızıldere-Tekkehamam-Tosunlar-Buldan-Yenice area]. Mineral Research and Exploration Institute of Turkey (MTA) Report 7846. (in Turkish, unpublished report).

Starobogatov, Y.I., 1970. Fauna mollyuskov i zoogeographicheskoe rajonirovanie kontinental'nykh vodoemov zemnogo shara [Molluscan fauna and zoogeographical differentiation of Earth's continental water bodies]. Akademiya Nauk SSR, Zoologicheskij Institut, Leningrad (in Russian).

Sun, S., 1990. Denizli-Uşak arasının jeolojisi ve linyit olanakları [Geology and lignite potential of the Denizli-Uşak area]. Mineral Research and Exploration Institute of Turkey (MTA), Scientific Report 9985. (in Turkish, unpublished report).

Taner, G., 1974a. Denizli bölgesi Neojen'inin paleontolojik ve stratigrafik etüdü [Palaeontological and stratigraphical investigation of the Neogene Denizli area]. Bulletin of Mineral Research and Exploration Institute of Turkey (MTA) 82, 89–126 (in Turkish).

Taner, G., 1974b. Denizli bölgesi Neojen'inin paleontolojik ve stratigrafik etüdü [Palaeontological and stratigraphical investigation of the Neogene Denizli area]. Bulletin of Mineral Research and Exploration Institute of Turkey (MTA) 83, 145–177 (in Turkish).

Taner, G., 1975. Denizli bölgesi Neojen'inin paleontolojik ve stratigrafik etüdü [Palaeontological and stratigraphical investigation of the Neogene Denizli area]. Bulletin of Mineral Research and Exploration Institute of Turkey (MTA) 85, 45–66 (in Turkish).

Taner, G., 1982. Die Molluskenfauna und pliozane Stratigraphie des Halbinsel Gelibolu. Communications de la Faculté des Sciences de l'université d'Ankara, Série C. Géologie 25, 1–27.

Taktakishvili, I.G., 1987. Sistematika i filogeniia Pliotsenovikh kardiid paratetisa [Systematics and phylogeny of the Pliocene cardiids of the Parathys]. Metsniereba, Tbilisi. (in Russian).

Wenz, W., 1942. Die Mollusken des Pliozäns der rumänischen Erdöl-Gebiete. Senckenbergiana 24, 1–293.

Wesselingh, F.P., 2007. Long-lived lake molluscs as island faunas: a bivalve perspective. In: Renema, W. (Ed.), Biogeography, time and place: distributions, barriers and islands. Springer, Dordrecht, pp. 275–314.

Westaway, R., Guillou, H., Yurtmen, S., Demir, T., Scaillet, S., Rowbotham, G., 2005. Constraints on the timing and regional conditions at the start of the present phase of crustal extension in western Turkey, from observations in and around the Denizli region. Geodinamica Acta 18, 209–238.

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

Yalçınlar, İ., 1983. Türkiye'de Neojen ve Kuvaterner omurgalı arazileri ve jeomorfolojik karakterleri [Neogene and Quaternary Vertebrate Fields of Turkey and their Geomorphologic Characteristics]. Publication of Faculty of Literature, Istanbul Technical University 2741, 1–240. (in Turkish).

Yıldırım, M.Z., 2004. The gastropods of Lake Eğirdir. Turkish Journal of Zoology 28, 97–102.