

Early Pleistocene freshwater communities and rodents from the Pasinler Basin (Erzurum Province, north-eastern Turkey)

Davit VASILYAN^{1*}, Simon SCHNEIDER², M. Salih BAYRAKTUTAN³, Şevket ŞEN⁴

¹Department of Geosciences, Faculty of Science, University of Tübingen, Tübingen, Germany

²CASP, University of Cambridge, Cambridge, UK

³Civil Engineering Department, Faculty of Engineering, Atatürk University, Erzurum, Turkey

⁴Laboratory of Palaeontology Museum, CR2P-CNRS-UPMC, Paris, France

Received: 01.08.2013 • Accepted: 14.02.2014 • Published Online: 21.03.2014 • Printed: 18.04.2014

Abstract: An Early Pleistocene lacustrine faunal assemblage from Pasinler (Erzurum Province, north-eastern Turkey) is described, which encompasses 13 mollusc, 5 fish, 2 amphibian, 1 reptile, and 1 mammal species. The autochthonous freshwater mollusc fauna indicates shallow stagnant waters and a fine-sandy to muddy lake bottom, grown with submersed plants. The fish community (*Leuciscus* sp., *Rutilus* sp., *Chondrostoma* sp., *Leuciscinae* sp. 1 and 2, and *Capoeta* sp.) and autochthonous herpetofauna (*Latonia* sp. and *Natrix* sp.) provide evidence of a well-oxygenised palaeolake with rich periphyton and partially rocky to gravelly bottom. Moreover, the presence of the terrestrial snail *Caspicyclotus* cf. *akramowsii*, the peri- to semiaquatic *Latonia*, *Natrix*, and *Allophaiomys* cf. *pliocaenicus* reflects wet-shore habitats surrounding the lake. The specimens of *Latonia* sp. from Pasinler represent the youngest fossils of *Latonia* recorded from western Asia. Apparently, *Latonia* survived well into the Early Pleistocene in western Asia and southern Europe. Due to progressive cooling during the Late Pleistocene, however, the genus finally became extinct to the north of its present distribution area. The presence of the arvicolid *Allophaiomys* cf. *pliocaenicus* allows for dating the locality at ca. 1.0 to 1.55 Ma. The overlying alluvial sediments of the Pasinler Beds mark the onset of sedimentation of the Palaeo-Araks River into the basin and are Middle to Late Pleistocene in age.

Key words: Mollusca, Teleostei, Amphibia, Reptilia, Rodentia, palaeoecology, palaeogeography, Early Pleistocene, eastern Turkey

1. Introduction

The Pasinler-Horasan Basin is one of the major Cenozoic intramontane basins in eastern Anatolia. Geographically, the basin is situated close to the major regional drainage divide. The Pasinler-Horasan Basin itself is drained by the headwaters of the River Araks, which empties into the Caspian Sea. To the west, the Erzurum Basin, which is separated by the Palandöken-Sivishli Mountain Range from the Pasinler-Horasan Basin, is drained by the headwaters of the Euphrates (namely the Karasu River), while the region to the south, separated by the Palandöken-Shahveled Mountains, is part of the Tigris catchment area. The area to the north of the Pasinler-Horasan Basin drains into the Black Sea via the Çoruh River (Figure 1a).

Tilting and subsidence permitted the accumulation of sediments in the Pasinler Basin, which may reach a maximum thickness of several hundred metres. In early stages, the Pasinler-Horasan Basin formed a single entity, which was later divided into the western Pasinler and eastern Horasan subbasins. These subbasins are separated by a volcano-tectonic ridge, the Agmelek Dag, that formed

along the seismically active NE-striking Çobandede fault zone (the Horasan earthquake in October 1983 reached M 7.0) and defines the eastern margin of the Pasinler Subbasin. The western margin of the Pasinler Subbasin is formed by the NNE-striking Dumlu Fault Zone, and another volcano-tectonic ridge, the Palandöken Sivishli Mountain Range, which also acts as a watershed between the Araks and Euphrates drainage systems, separates the Pasinler Basin from the Erzurum Basin further to the west. Therefore, the western and eastern boundaries of the Pasinler Subbasin are defined by left lateral oblique slip normal faults, while its northern margin is formed by strike slip reverse component faults and the Kargapazari Basalt Plateau. The southern margin is defined by northward convex thrust planes, between pre-Upper Miocene sedimentary and volcanic units (Palandöken Volcanic and Shahveled Complex). According to Irrlitz (1972; tabs 8 and 9) and Huvaz (2009), the basement of the Pasinler-Horasan Basin is formed by Upper Cretaceous–Middle Eocene ultrabasites. The intrabasin succession consists of Upper Eocene to Oligocene flysch and molasse

* Correspondence: davit.vasilyan@ifg.uni-tuebingen.de

sediments, followed by alternating Miocene marine limestones, siliciclastics and volcanic deposits, and massive ?Miocene–Pliocene volcanic rocks. The final sedimentary infill comprises Pliocene to Pleistocene lacustrine deposits and extensive Pleistocene to Holocene fluvio-terrestrial siliciclastics that directly underlie much of the present-day valley floor (Collins et al., 2005, 2008) (Figure 1b). These 2 lithological units correspond to the Horasan Beds and Pasinler Beds of Irrlitz (1972), respectively. Subsequently, sedimentation in the Pasinler-Horasan Basin ceased and, today, the Holocene sediments are gradually being eroded and washed away by the Araks River (Irrlitz, 1972).

The Horasan Beds yielded fossil mollusc shells described as *Dreissena diluvii*, *Caspicyclotus armenicus*, *Pyrgula quimplex*, *Radix lessonae*, and *Gyraulus horasanensis* (Schütt, 1991). The Pasinler Beds, which have been sampled for the present study, are up to 300 m thick; they are exposed at several isolated spots along the northern basin margin (Irrlitz, 1972; pl. 8). A rich mollusc fauna from the Pasinler Beds collected from an outcrop near Yayladag revealed close affinities to mollusc faunas of Early Pleistocene age from adjacent regions; as a result, the Pasinler Beds were dated as Early Pleistocene (Schütt, 1997). The Yayladag locality also yielded remains of the steppe mammoth, *Mammuthus trogontherii* (Dayan, 1989). However, *M. trogontherii* is usually attributed to the Middle Pleistocene (Lister, 2005; Meller, 2010) and the elephant fossils may thus originate from younger sediments than the molluscs. In the south-eastern part of the basin, Ünay and De Bruijn (1988) collected a rodent association at 3 spots of a coal mine near Pekecik village, in “the Yolüstü Formation that unconformably overlies the Upper Miocene and older units, and that consists of conglomerates, sandstones, mudstones and marls” (Ünay

and De Bruijn, 1988: 445). The Yolüstü Formation seems to be a local equivalent of the Horasan Beds of Irrlitz (1972). The fauna consists of 3 vole species: *Clethrionomys* sp., *Mimomys pliocaenicus*, and *Borsodia* sp. Such association is typical for the latest Pliocene (MN17 zone), as the authors rightly suggested.

In the present study we conduct a first comprehensive documentation of the fossil fauna of the Pasinler Beds, including data on molluscs, fishes, amphibians, reptiles, and mammals. Furthermore, we provide a palaeoecological interpretation of the fossil ecosystem in and around Lake Pasinler. Finally, we also provide a relatively precise age estimate for the Pasinler Beds based on the small mammal assemblage.

2. Materials and methods

During the early 1990s, ca. 30 samples, each consisting of approximately 2–3 kg of sediment, were collected by one of the authors (MSB). These samples come from 2 sections. Section A (Pasinler A, Yayladag Site) is situated approximately 13 km to the east of Erzurum (Figure 1b), at the north-eastern slope of the Hasandag Volcanic Neck, right to the north of the town of Pasinler, close to the basin margin. The central part of the depositional sequence at Yayladag contains abundant greyish-green clays and bentonites, fine-grained volcanoclastics, and marls including the fossiliferous layers. At the top, the succession is cut by erosion and overlain by lavas and ignimbrites.

Section B (Pasinler B, Hamamderesi Site) is situated approximately 5 km to the north/north-west of Pasinler, close to the western margin of the Pasinler Basin (Figure 1b). The depositional sequence at Hamamderesi starts with the upper parts of the Pasinler Beds, with a sharp contact to the underlying volcanic rocks. The sequence

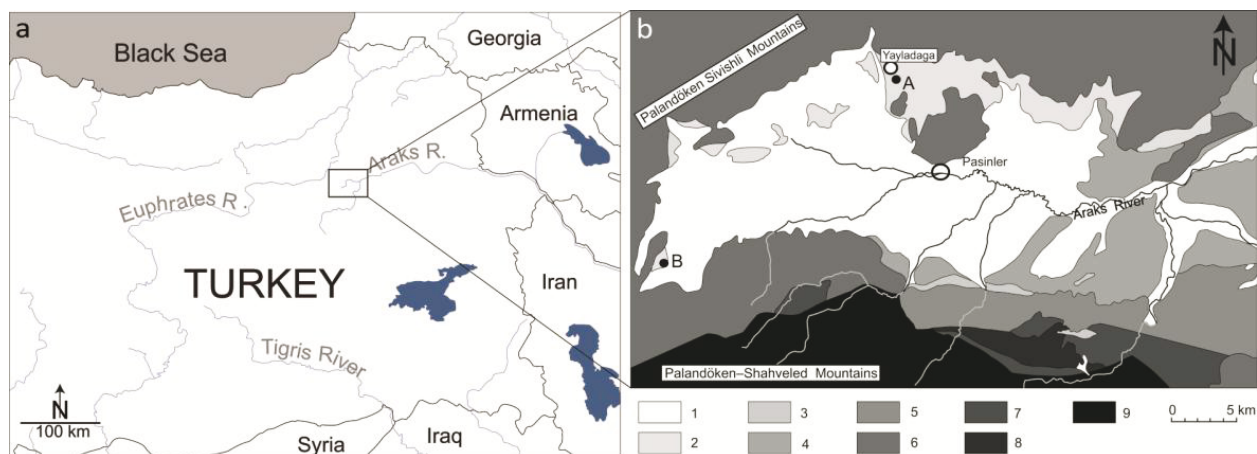


Figure 1. a) Geographical overview, indicating the position of the Pasinler-Horasan Basin (black frame). b) Geological map of the study area, modified from Irrlitz (1972). 1. Quaternary alluvio-fluvial sediments. 2. Pasinler Beds. 3. Upper volcanic rocks. 4. Emrekom Beds. 5. Pekecik Beds, forming the basement of the Pasinler-Horasan Basin. 6. Lower volcanic rocks. 7. Marine limestone. 8. “Molasse succession”. 9. Ultrabasites. The sampled sections, Pasinler-A and Pasinler-B, are indicated by black dots.

starts with volcanoclastics, overlain by layers of sand and silt, followed by 1) alternating clay, silt, and sand horizons; 2) dark-coloured clays intercalated with lignites and fine-grained conglomerates; 3) thick diatomite beds (50–60 m); 4) coarse volcanoclastics and lapilli; and finally 5) ignimbrite flows. The transition to the younger volcanics (Kargapazari basalts) at top is gradual.

The sediments were screen-washed down to a mesh width of 0.5 mm, and the dried residues were screened for fossils.

The sediments comprise fluvial, alluvial fan, and lacustrine deposits (see also Collins et al., 2008; figs. 2 and 4). Nine out of more than 30 samples (i.e. A2, A4, A5-1, A5-2, A13, A15, A18, A19, B12; see Table 1 and Figure 1b for details) yielded fossils. In the present study, we treat all samples as a single assemblage, since they were all collected from a single, relatively short-lived lithostratigraphic unit.

For scanning electron microscopy (SEM), the mollusc shells were sputter-coated with gold. Voucher material of the molluscs is provisionally stored at the Natural History Museum Vienna (NHMW), Austria. Vertebrate remains (fishes, amphibians, and reptiles) are provisionally deposited at the Institute of Geosciences, Tübingen University (GPIT). Small mammal remains are provisionally stored at the Museum National d'Histoire Naturelle, Paris, France (MNHN). The studied material will finally be transferred to Erzurum Museum, Turkey.

3. Systematic palaeontology

Mollusca

The mollusc fauna from Pasinler was described by Schütt (1997), who recorded 8 species of gastropods and 4 bivalve species. The new sample from level A18 has yielded an almost identical assemblage. It lacks 3 of the bivalve

Table 1. List of fossils from Pasinler. Numbers of specimens per sample and total numbers of specimens are given in the last 9 columns. Numbers in brackets correspond to opercula of gastropods.

Taxon		Samples										
		A2	A4	A5-1	A5-2	A13	A15	A18	A19	B12	Total	
Bivalvia	<i>Dreissena diluvii</i> (Abich, 1859)	-	-	-	-	-	-	3	-	-	3	
	<i>Cincinna piscinalis</i> (Müller, 1774)	-	-	-	4	-	-	151	-	2	157	
	<i>Caspicyclotus</i> cf. <i>akramowsii</i> Schütt, 1997	-	-	-	-	-	-	1	-	-	1	
	? <i>Pyrgorientalia shadini</i> (Akramowski, 1956)	-	-	-	-	-	-	8	-	-	8	
	<i>Falsipyrgula sieversi</i> (Boettger, 1881)	-	-	-	-	-	-	26	-	-	26	
	" <i>Pyrgula</i> " sp.	-	-	-	-	-	-	-	-	1	1	
	<i>Pseudamnicola</i> sp.	-	-	-	-	-	-	30	-	-	30	
	Bithyniidae sp. indet.	-	-	-	(1)	-	-	1 (1)	-	-	2	
	<i>Gyraulus horasanensis</i> Schütt, 1991	-	-	-	-	-	-	6	-	-	6	
	<i>Gyraulus</i> sp.	-	-	-	2	-	-	2	-	-	4	
Gastropoda	<i>Armiger crista</i> (Linnaeus, 1758)	-	-	-	-	-	-	2	-	-	2	
	<i>Radix</i> sp. A	-	-	-	-	-	-	39	-	-	39	
	<i>Radix</i> sp. B	-	-	-	-	-	-	6	-	-	6	
	<i>Chondrostoma</i> sp.	10	2	-	2	-	6	-	11	-	31	
	<i>Leuciscus</i> sp.	2	-	-	4	-	3	3	14	7	33	
	<i>Rutilus</i> sp.	1	7	-	-	3	5	4	6	-	26	
	Teleostei	<i>Capoeta</i> sp.	-	-	-	-	1	-	1	-	2	4
		Leuciscinae sp. 1	-	-	-	3	1	3	-	-	-	7
		Leuciscinae sp. 2	-	4	-	3	3	5	4	6	-	25
		Cyprinidae indet.	-	7	-	-	-	9	-	-	-	17
Amphibia	<i>Latonia</i> sp.	-	-	-	-	-	-	-	-	3	3	
	Reptilia	<i>Natrix</i> sp.	-	-	-	-	1	-	-	-	-	1
Colubridae indet.		-	-	-	1	-	-	-	-	1	2	
Mammalia	<i>Allophaiomys</i> cf. <i>pliocaenicus</i> Kormos, 1932	-	-	1	-	3	-	-	-	-	-	

species reported by Schütt (1997), but includes 3 additional gastropod species. Samples A5-2 and B12 produced only a few, relatively poorly preserved gastropods (see Table 1 for details). Below, we provide short remarks on those species present in the new samples, basic quantitative data, and a palaeoecological evaluation of the assemblage. Moreover,

the species have been documented by SEM and binocular microscope photographs (Figures 2a–2l, 3a, and 3b), since Schütt's (1997) illustrations are of limited quality.

Dreissena diluvii (Abich, 1859) (Figure 2g).—The median keel, which is characteristic for this species, emerges gradually during growth and thus cannot be

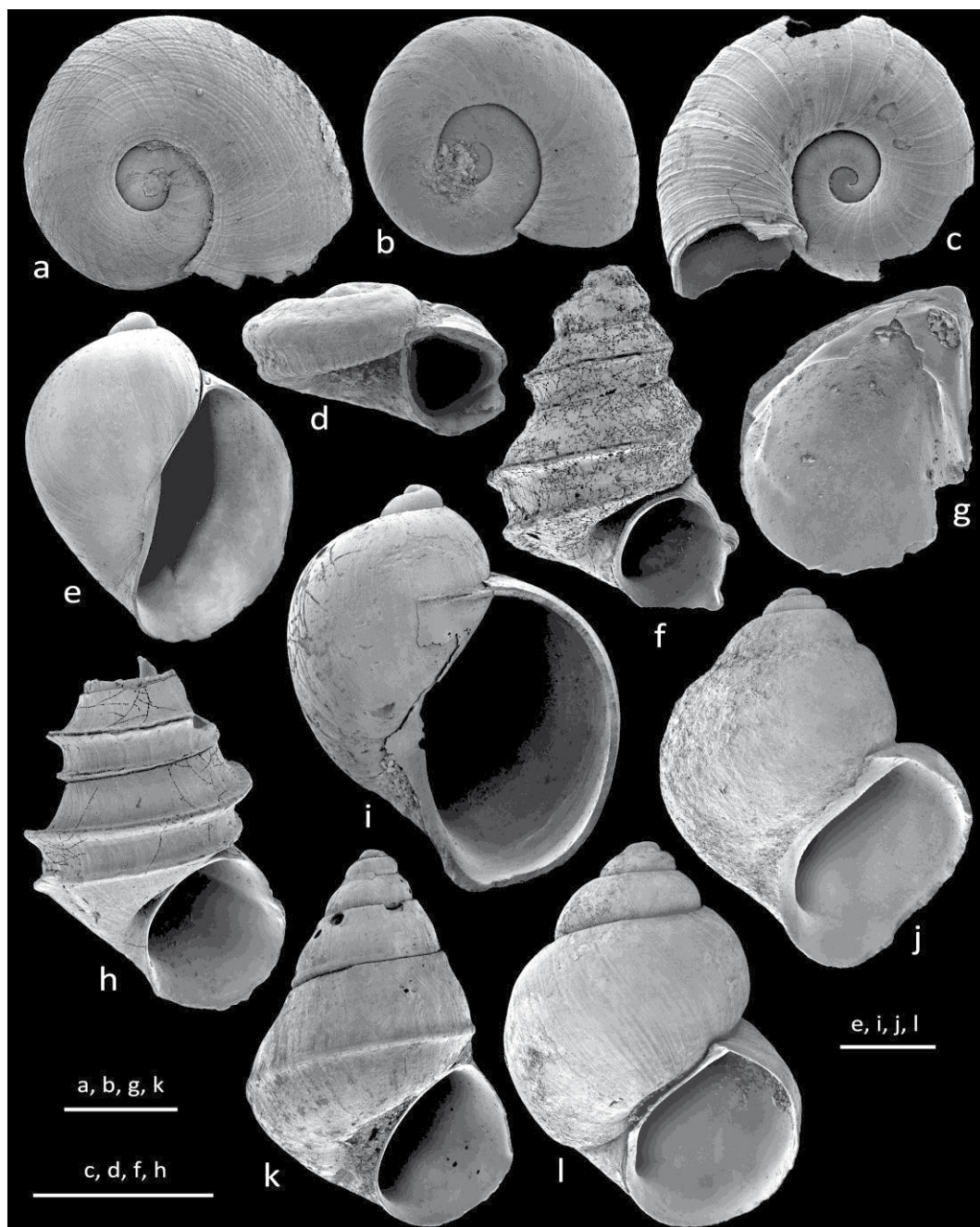


Figure 2. Mollusca from the Early Pleistocene of Pasinler; SEM pictures. **a)** *Gyraulus horasanensis* Schütt, 1991. **b)** *Gyraulus* sp. **c)** *Armiger crista* (Linnaeus, 1758). **d)** *Caspicyclotus* cf. *akramowsii* Schütt, 1997. **e)** *Radix* sp. **A.** **f, h)** *Pyrgula shadini* Akramowski, 1956. **g)** *Dreissena diluvii* (Abich, 1859). **i)** *Radix* sp. **B.** **j)** *Pseudamnicola* sp. **k)** *Falsipyrgula sieversi* (Boettger, 1881). **l)** Bithyniidae sp. indet. Scale bars = 1 mm.

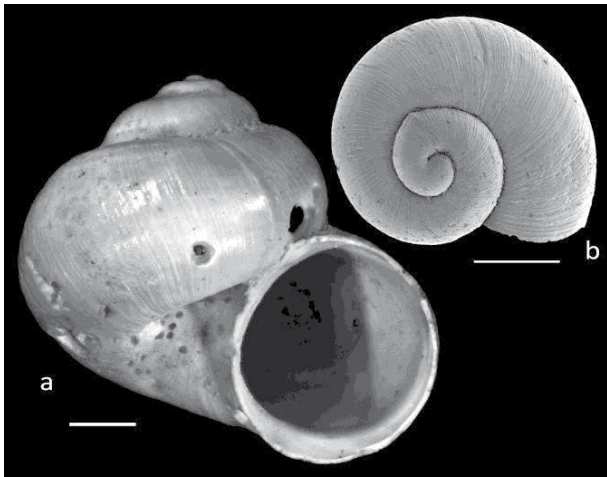


Figure 3. *Cincinna piscinalis* (O.F. Müller, 1774), the most abundant freshwater snail of the Early Pleistocene deposits at Pasinler. **a)** Adult specimen. **b)** Juvenile specimen; SEM picture. Scale bars = 1 mm.

observed in the broken juvenile shells from our samples. Determination is based on the typical specimens figured by Schütt (1997).

Cincinna piscinalis (Müller, 1774) (Figure 3).—This is the most abundant species of the A18 assemblage (55%). As outlined by Schütt (1997), the specimens from sample A18 display the typical morphology of the species. In the few individuals from the other samples, the spire is relatively low.

Caspicyclotus cf. *akramowsii* Schütt (1997) (Figure 2d).—The single juvenile shell from sample A18 and the holotype figured by Schütt (1997) are similar with regard to ornamentation. However, the juvenile specimen from Pasinler has a lower spire than the holotype, and assignment is thus tentative.

Pyrgula shadini Akramowski, 1956 (Figures 2f and 2h).—This species has been assigned to *Pyrgula* by Akramowski (1956) and Schütt (1997). Although seemingly typical and derived, the ornamentation of 2 sharp-crested keels is found as a convergent feature in several fairly distant groups of the Rissosoidea, e.g., in the much more elongate extant *Pyrgorientalia zilchi* (Schütt, 1964) from southern Anatolia and *Pyrgula annulata* (Linnaeus, 1758) from northern Italy and Croatia, the Pliocene *Pyrgula pagoda* Neumayr in Neumayr and Paul (1875) from Romania, or the recently described *Bacbotricula nhamaygachensis* Neubauer and Schneider, 2012 (in Neubauer et al., 2012) from the Palaeogene of Vietnam. Present-day systematics within the Rissosoidea are based predominantly on anatomy and molecular characters, rendering generic assignment of fossils species largely arbitrary. We thus retain the original combination of Akramowski (1956).

Falsipyrgula sieversi (Boettger, 1881) (Figure 2k).—Erected on a single, redeposited specimen described by Boettger (1881), this species was rediscovered from the Lower Pleistocene sediments of Byurakn (Gyullibulag) in north-western Armenia (Akramowski, 1956). Later it was also found at Pasinler (Schütt, 1997), where it is, at least in sample A18, 1 of 4 abundant species of the assemblage.

“Pyrgula” sp.—The single specimen from sample B12 is markedly corroded and the aperture is broken. However, whorl geometry and apical angle differ significantly from *Falsipyrgula sieversi*, indicating the presence of another Hydrobiidae species of *Pyrgula*-like shape at Pasinler.

Pseudammicola sp. (Figure 2j).—Schütt (1997) recorded this species in open nomenclature, since the taxonomy in this genus, both Recent and fossils, appeared largely unresolved. As can be inferred from the revision of *Pseudammicola* from Algeria and Tunisia by Glöer et al. (2010a), this genus likely has successfully radiated several times in different regions. Because palaeoecology is the main issue of the present study of molluscs, we refrain from extensive discussion of taxonomy and follow Schütt (1997), leaving the species in open nomenclature. Though unresolved with regard to taxonomy, this species is among the 4 abundant gastropod taxa in sample A18.

Bithyniidae sp. indet. (Figure 2l).—The single shell is stout, with a low spire and well-inflated, quickly escalating whorls, separated by a relatively deep suture. The 2 isolated opercula from samples A18 and sample A5-2 are relatively different in outline; the latter is much more oval. Whether the opercula belong to a single variable species or rather to 2 different ones has to be evaluated from larger samples. As demonstrated by Glöer and Pešič (2006) and Glöer et al. (2010b), the genera *Bithynia* and *Pseudobithynia* can only be distinguished based on soft part anatomy. Any fossil species of *Bithynia* morphology may thus belong to either of the genera, and generic assignment would be arbitrary.

Gyraulus horasanensis Schütt, 1991 (Figure 2a).—Originally described as a subspecies, the type material of *G. horasanensis* comes from the Pliocene Horasan Beds of the Pasinler Basin, which directly underlie the Pasinler Beds containing the fauna detailed herein (Schütt, 1997). The quickly escalating whorls and distinct spiral ornamentation are typical features of this species, which are well expressed also in our specimens.

Gyraulus sp. (Figure 2b).—Present in samples A18 and A5-2 with 2 specimens each, this species differs from the preceding in the much more slowly escalating whorls, more rounded whorl cross-section, less pronounced growth lines, and absence of spiral ornamentation. The aperture slightly overlaps the preceding whorl at ventral side. With regard to general morphology, the species closely resembles *Gyraulus rosmaessleri* (Auerswald, 1852).

Armiger crista (Linnaeus, 1758) (Figure 2c).—The

typical ornamentation of relatively closely spaced and moderately pronounced radial crests is clearly observable in the 2 specimens from Pasinler, leaving no doubts on specific assignment.

Radix sp. A (Figure 2e).—This species is characterised by a low spire and asymmetrical whorls with a marked abapical slope (rounded D-shaped in cross-section). Treated as *Radix ovata* (Draparnaud, 1805) by Schütt (1997), this species is now left in open nomenclature. Molecular genetics have confirmed the high degree of morphologic plasticity in *Radix* and raised doubts on the specific identity of European and Asian populations

(Bargues et al., 2001). We thus refrain from specific assignment of the 2 fossil *Radix* from Pasinler. *Radix* sp. A is the second-most abundant species of the Pasinler A18 assemblage.

Radix sp. B (Figure 2i).—This species differs from the much more abundant *Radix* sp. A in a slightly higher spire, more constantly rounded whorls (lack of abapical slope; sub-elliptical in cross-section), and deeper suture.

Class Actinopterygii Cope, 1887

Order Cypriniformes Bleeker, 1859

Family Cyprinidae Bonaparte, 1832

Subfamily Leuciscinae Howes, 1991

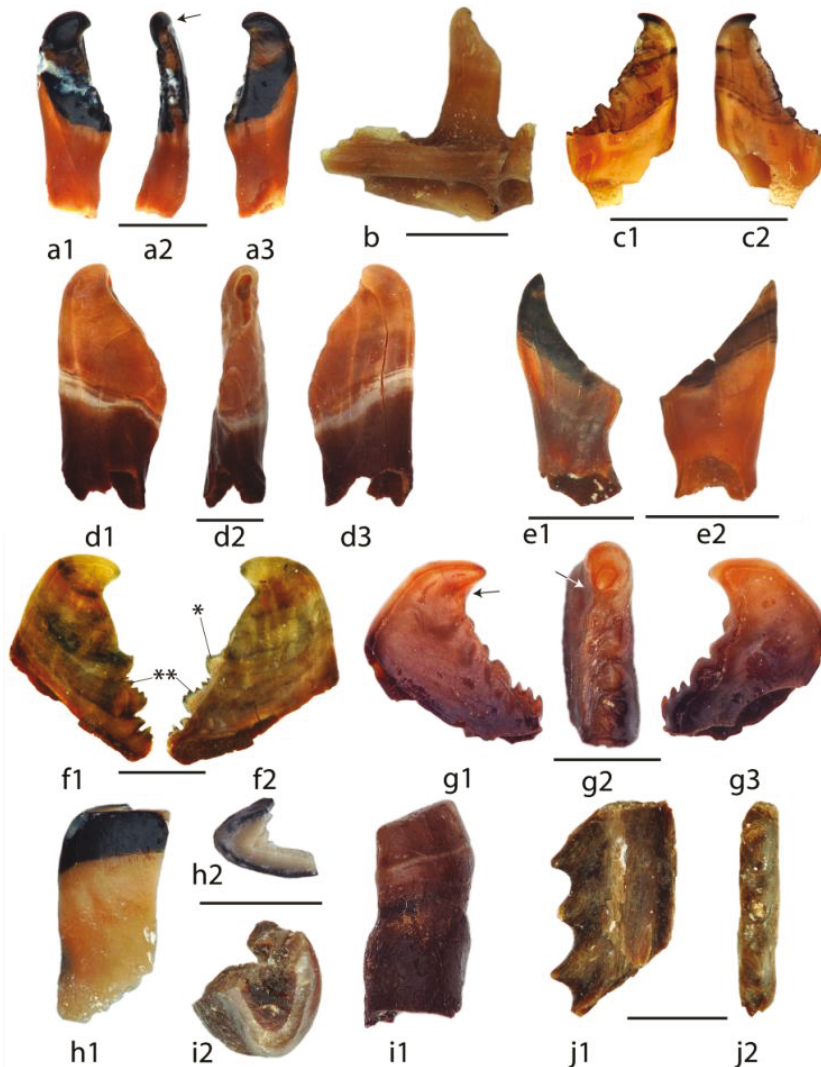


Figure 4. Fish remains from the Early Pleistocene of Pasinler. **a–c)** Pharyngeal teeth of *Leuciscus* sp. **a)** Pharyngeal tooth in (1) mesial, (2) anterior, and (3) distal views [PSL-A2.02]. **b)** Pharyngeal tooth attached to pharyngeal bone [PSL-A19.01]. **c)** Pharyngeal tooth in (1) mesial and (2) distal views [PSL-A2.02]. **d)** Pharyngeal tooth of *Rutilus* sp. in (1) mesial, (2) anterior, and (3) distal views [PSL-A15.03]. **e)** Pharyngeal tooth of *Chondrostoma* sp. [PSL-A2.01]. **f, g)** Pharyngeal teeth of Leuciscinae sp. 1 in (a1, b1) mesial, (a2) posterior, (b2) anterior, and (b3) distal views [PSL-A15.03, PSL-A5-2.02]. Asterisks indicate primary (*) and secondary (**) serrations. Arrows indicate concave surface below hook. **h–j)** *Capoeta* sp. **h, i)** Pharyngeal teeth in (1) mesial and (2) dorsal views [PSL-A13.05 and PSL-A18.02]. **j)** Fragment of serrated dorsal fin ray in (1) lateral and (2) posterior views. Scale bars = 1 mm.

Genus *Leuciscus* Cuvier, 1817

Leuciscus sp.

Figures 4a–4c.

Material: 33 pharyngeal teeth (see Table 1).

Description: Teeth elongate; characteristically strongly bent; occurring isolated (e.g., Figures 4a and 4c) as well as articulated to pharyngeal bone (Figure 4b). Crown high. Hook short, delicate, sharp. Hook and longitudinal axis of tooth meeting at right or slightly smaller angles. Teeth mesiodistally compressed. Tooth crown narrows dorsally. Grinding surface long and narrow, almost straight and smooth; edges marked, sharp (Figure 4c) to round (Figure 4a). Mesial edge of grinding surface bearing protuberances and small denticles.

Remarks: The teeth display common *Leuciscus* morphology. From distal view a concave surface is visible below the base of the hook (Figure 4a2). Some teeth show reduced protuberances and denticles, which are typical for aged specimens of *Leuciscus* (Obrhelová, 1971). The majority of the teeth have been found isolated and show resorption structures at around the base (Table 2), indicating that virtually all teeth are accumulated in the sediment due to resorption.

Genus *Rutilus* Rafinesque, 1820

Rutilus sp.

Figure 4d.

Material: 26 isolated pharyngeal teeth (see Table 1).

Description: Teeth compact, mesiodistally flattened, slightly curved in outline. Crown higher than tooth “foot”. Teeth broadest at base of crown, narrowing dorsoventrally. Anterior surface (anterior ridge) of crown rough, with small protuberances at its base. Grinding surface reduced, smooth, rounded to elongated, located below crown tip. Angle between grinding surface and longitudinal axis of tooth sharp. Tooth characterised by rounded to elongated, irregularly shaped, straight rather than concave grinding surface. Tooth tip without hook.

Remarks: The teeth are similar to those of *Rutilus* cf. *rutilus* described by Hierholzer and Mörs (2003; figs. 12d, 12e) and thus assigned to *Rutilus* sp. More than half of the teeth of *Rutilus* sp. display traces of resorption around the tooth base (Table 2).

Genus *Chondrostoma* Agassiz, 1832

Chondrostoma sp.

Figure 4e.

Material: 31 isolated pharyngeal teeth (see Table 1).

Description: Teeth straight, slender, laterally flattened. Crown elongated, without hook. Grinding surface well developed, corresponding to slightly to fairly concave anterior ridge of tooth. Grinding surface and dorsal ridge generally smooth, without protuberances and hooks. Posterior side of tooth straight or slightly convex. Tooth neck concave in some specimens (Figure 4e2). Angle between dorsal ridge and longitudinal axis of tooth sharp. Teeth showing traces of resorption.

Remarks: Straight, slender teeth with a concave, smooth grinding surface lacking protuberances and hooks, as described above, are characteristic of the genus *Chondrostoma* (Rutte, 1962). However, the teeth do not yield any taxonomically relevant characters for specific identification. The vast majority of the teeth of *Chondrostoma* sp. show traces of resorption near their bases (Table 2).

Leuciscinae sp. 1

Figures 4f–4g.

Material: 7 isolated pharyngeal teeth (see Table 1).

Description: Teeth crowns 1–2.5 mm long. Teeth mesiodistally compressed, narrowing dorsally; short, robust and pointed terminal hook and tooth longitudinal axis meeting at almost right angles. Concave surface present at base of hook; visible only from distal view (Figures 4f1 and 4f2). Grinding surface elongate and narrow. Lower portion of mesial edge of grinding surface displaying primary and secondary serrations (denticles). Primary serration

Table 2. Numbers and percentages of fish teeth with or without resorption traces listed for taxa (horizontal) and samples (vertical). r = resorptive. n/r = nonresorptive (rock samples with bones).

	A2		A4		A5-2		A13		A15		A18		A19		B12		Total		%	
	r	n/r	r	n/r	r	n/r	r	n/r	r	n/r	r	n/r	r	n/r	r	n/r	r	n/r	r	n/r
<i>Chondrostoma</i> sp.	4	6	2	-	2	-	-	-	3	3	-	-	11	-	-	-	22	9	71	29
<i>Leuciscus</i> sp.	-	2	-	-	4	-	-	-	2	1	-	3	12	2	3	4	21	12	64	36
<i>Rutilus</i> sp.	1	-	-	7	-	-	2	1	4	1	1	3	6	-	-	-	14	12	54	46
<i>Capoeta</i> sp.	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	1	1	50	50
<i>Leuciscinae</i> sp. 1	-	-	-	-	3	-	1	-	3	-	-	-	-	-	-	-	7	0	100	0
<i>Leuciscinae</i> sp. 2	-	-	1	3	3	-	-	3	-	5	1	3	-	6	-	-	5	20	20	80
Cyprinidae indet.	-	-	-	7	-	-	-	-	9	-	-	-	-	-	-	-	9	7	56	44
total	5	8	3	17	12	0	3	5	21	10	3	9	29	8	3	4	79	61		
%	38	62	15	85	100	0	38	63	68	32	25	75	78	22	43	57				

consisting of low, robust, conical denticles, located at lower portion of mesial edge of grinding surface. Secondary serration consisting of numerous small and sharp denticles, located at dorsal edges of primary denticles. Upper portion of mesial edge rounded, lacking protuberance. Distal edge of grinding surface not marked; small protuberances arranged near mesial edge of lower part; grinding surface fades out ventrally.

Comments: The 7 teeth are all represented by tooth-crowns only, showing resorption structures at their bases. A similar tooth morphology can be observed in several genera within the Leuciscinae, e.g., *Palaeoleuciscus*, *Pseudophoxinus*, *Delminichthys*, and *Leuciscus* (Obrhelová, 1971; Hierholzer and Mörs, 2003). Identification to genus and species level is only possible based on representative bone material.

Leuciscinae sp. 2

Material: 25 isolated pharyngeal teeth (see Table 1).

Comments: Teeth of both first and second rows present. Teeth compressed, robust, comparatively broad. Some specimens possessing hook with tip of variant length. Grinding surface strongly reduced or (usually) absent.

Remarks: Generally, pharyngeal teeth from the second tooth row do not have taxonomically significant characteristics as they are similar in morphology in numerous genera in the Leuciscinae.

Subfamily Barbinae Bleeker, 1859

Genus *Capoeta* Valenciennes, 1842

Capoeta sp.

Figures 4h–4j.

Material: 2 isolated pharyngeal teeth and 2 fragments of serrated dorsal fin rays.

Description and remarks: Fragmentary pharyngeal teeth oval or elongated-oval in cross-section. Teeth compact, relatively low. Rounded, plane grinding surface encompassing entire dorsal top of tooth; angle between grinding surface and longitudinal axis of tooth slightly oblique to straight. Edge of grinding surface smooth, without protuberances or hooks (Figures 4h and 4i).

Fragments of dorsal fin rays serrated, with small, sharp denticles at caudal edge of ray (Figure 4j). Denticles short, robust, slightly curved, directed posteroventrally; caudal tips dorsoventrally flattened. Distinct, rounded longitudinal ridge present on medial side of rays.

Cyprinidae indet.

Material: 17 isolated pharyngeal teeth (see Table 1).

Remarks: These teeth are fragmentary or do not show any taxonomically relevant features for identification below family level.

Class Amphibia Gray, 1825

Order Anura Rafinesque, 1815

Family Alytidae Fitzinger, 1843

Genus *Latonia* Meyer, 1843

Latonia sp.

Figures 5a and 5b.

Material: 2 fragments of frontoparietals, i.e. a posterior part and a small anterior fragment; 1 right ilium (see Table 1).

Description: Facies dorsalis of both fragments fused and sculptured with tubercles and pits with marked rim. Facies dorsalis 2 times narrower than widest part of bone. Occipital lamella long, thin. Median crest running from posterior margin of facies dorsalis to occipital margin. Paraoccipital processes and prootical lamella partially preserved. Surface between median crest and paraoccipital processes concave with numerous foramina of variable size. Rounded, U-shaped frontoparietal incrustation with lateral and posterior margins well delimited by a crest, visible in ventral view. Pars contacta broken.

Corpus ossi and posterior fragment of iliac shift preserved. Acetabulum small, triangular in outline in lateral view. Pars ascendens (distally broken) high, robust, rising obliquely upwards, with supraacetabular fossa. Pars descendens low, with narrow subacetabular groove, arranged directly under acetabular rim. Rim well marked. Knob-like, dorsally broken tuber superior present. Fragment of dorsal crest observable between tuber superior and iliac shaft. Groove in base of tuber superior visible in medial view. Oblique, dorsoventrally projecting ridge present.

Remarks: In contrast to the remains of fossil *Latonia* from Europe and from Pasinler, the extant *Latonia nigriventer* from Hula Lake (Israel) lacks sculpture on the frontoparietal (Biton et al., 2013). The specimens from Pasinler are thus compared in detail to those fossil species, which possess sculptured frontoparietal bones. These are 1) *Latonia gigantea* from Sansan [juvenile; Middle Miocene; SW France (Rage and Hossini, 2000; fig. 11)], Szentendre [late Middle Miocene; Hungary (Venczel, 2004)], Osztramos 1 [Earliest Pliocene; Hungary (Venczel, 2001; fig. 1a)], and Grytsev (Roček, 1994; fig. 7; plate 1, figs. 6 and 7); 2) *L. ragei* Hossini, 1993 from Oberdorf [late Early Miocene, Austria (Sanchíz, 1998; figs. 32 and 33)]; and 3) *Latonia* sp. from Pietrafitta [Early Pleistocene; Tuscany, Italy (Delfino, 2002)]. The frontoparietal fragments from Pasinler differ from those of all of these species in having a longer and wider occipital lamella, a narrower facies dorsalis, and a well-pronounced median crest. Frontoparietals of *L. seyfriedi* v. Meyer, 1843 and *L. vertaizoni* (Friant, 1944) have not been reported to date, and comparison with these species is thus impossible. Likely, the frontoparietals from Pasinler may belong to a new species of *Latonia*. However, since only 2 fragmentary bones are preserved and comparable data for *L. seyfriedi* and *L. vertaizoni* are lacking, the specific identity of the specimens from Pasinler remains elusive.

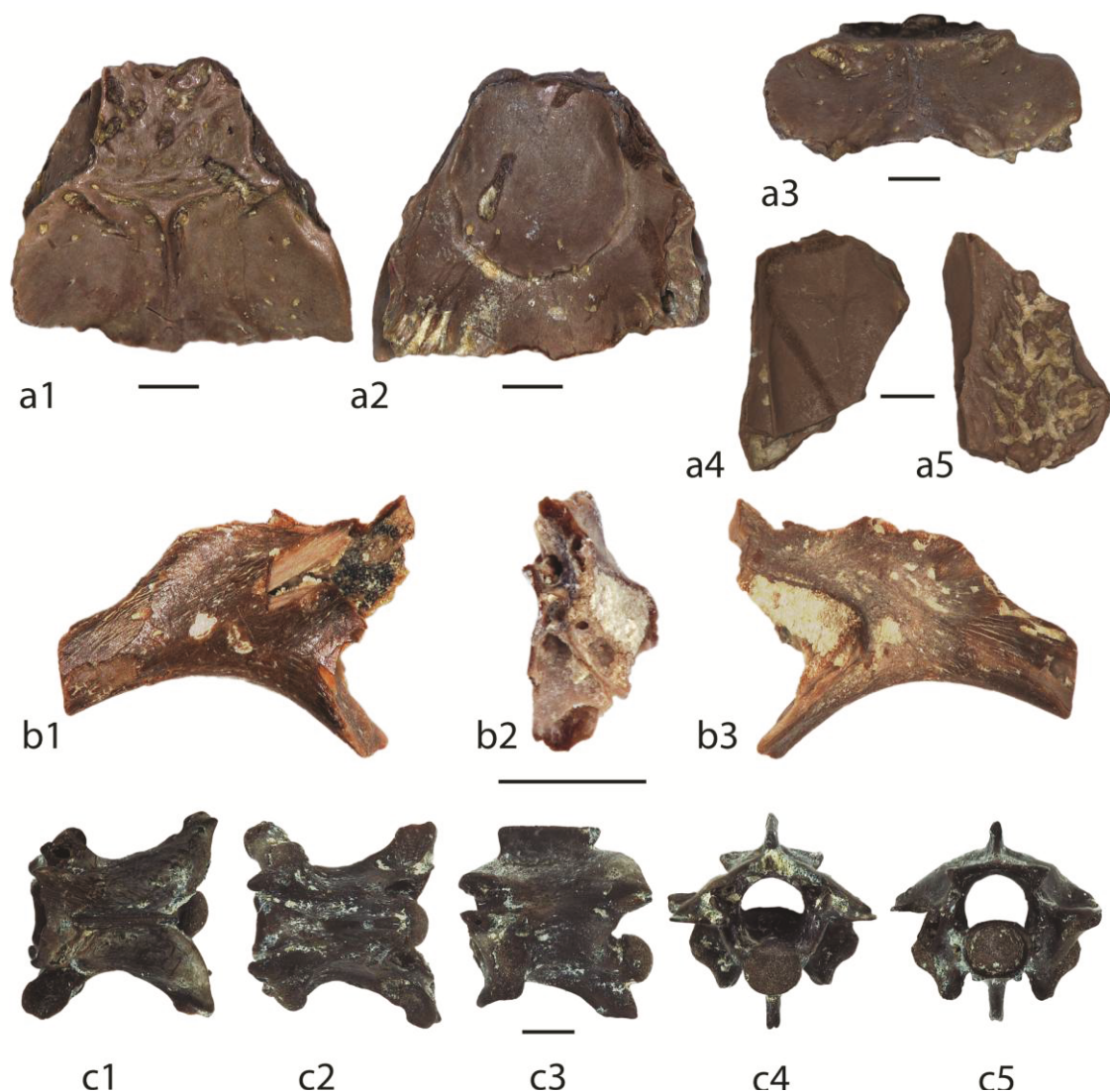


Figure 5. Amphibian and reptilian remains from the Early Pleistocene of Pasinler. **a, b)** *Latonia* sp. **a)** Fragments of frontoparietal portion of bone in (1) dorsal, (2) ventral, and (3) caudal views. Anterior portion of bone in (4) ventral and (5) dorsal views [PSL-A12.04]. **b)** Fragmentary ilium in (1) medial, (2) distal, and (3) lateral views [PSL-A12.05]. **c)** *Natrix* sp.; trunk vertebra in (1) dorsal, (2) ventral, (3) lateral, (4) posterior, and (5) anterior views [PSL-A13.04]. Scale bars = 1 mm.

Reptilia Laurenti, 1768
 Squamata Opperl, 1811
 Colubridae Opperl, 1811
 Natricinae Bonaparte, 1838
Natrix Laurenti, 1768
Natrix sp.

Figure 5c.

Material: A single trunk vertebra (see Table 1).

Description: Well-preserved, 3.8-mm-long, compact vertebra, belonging to a medium-sized snake. Centrum longer than wide. Neural arch weakly vaulted. Neural canal rounded in outline. Neural spine high, more than 2 times as long as high. Cranial margin inclined

anteriorly. Caudal margin inclined posteriorly, starting behind zygosphene, terminating at posterior edge of neural arc. Spine slightly longer than half-length of vertebra centrum. Dorsal edge of neural arc straight. Hypapophysis short, slightly sigmoid in shape, starting at middle part of centrum. Ventral edge of hypapophysis slightly oblique. Neural spine and hypapophysis thin. Two moderately deep, parallel subcentral grooves in vertebra centrum positioned lateral with regard to hypapophysis. Straight to faintly dorsally vaulted subcentral ridges prominent. Pre- and postzygapophyses distally pointed. Pre- and postzygapophyseal articular facets rounded, slightly elongated, connected by weakly developed

interzygapophyseal ridge. Paradiapophyses relatively large; subdivided into robust diapophyses and slender, pointed, anteroventrally directed parapophyses, which are longer than diapophyses. Paracotylar, lateral, postdiapophyseal, and subcentral foramina distinct. Condyle and cotyle rounded. Distinct subcotylar tubercles present on both ventrolateral margins of cotylar rim. Zygosphenal roof smooth, slightly convex in dorsal view, with several slopes.

Remarks: The vertebra is confidently assigned to the Natricinae based on the presence of sigmoid instead of straight hypapophyses, posteriorly vaulted (not depressed) neural arches, short parapophyseal processes, a long centrum, and strong subcentral ridges (Szyndlar, 1991). Several characters suggest that the vertebra from Pasinler is assignable to *Natrix*: the vertebral centrum is elongated, and the neural spine is high and has inclined anterior (cranial) and posterior (caudal) margins. Moreover, the subcentral ridges are marked, the hypapophysis is narrow, and the subcotylar tubercles are well-developed (Ivanov and Böhme, 2011).

Mammalia Linnaeus, 1758

Rodentia Bowdich, 1821

Arvicolidae Gray, 1821

The dental terminology for arvicolid cheek teeth follows Van der Meulen (1974). All measurements are given in millimetres.

Allophaiomys Kormos, 1932

Allophaiomys cf. *pliocaenicus* Kormos, 1932

Figure 6.

Material: Left M1 (L × W = 2.27 × 1.21; PSL5-1), left m1 (L = 2.43; W = 1.02; a = 1.01; b = 0.27; c = 0.13; A/L = 41; B/W = 27; C/W = 13; PSL13-1), left m2 (L × W = 1.50 × 0.88; PSL13-1), and right m3 (L × W = 1.49 × 0.80; PSL13-2). The specimens have been collected from 2 horizons (A5 and A13) along Section A. The size and general characteristics of the molars argue in favour of their belonging to the same species. The diagnostic characters of fossil arvicolids are mainly found on the m1. Consequently, only this molar will be described in detail and compared with those of other species.

Description: All molars rootless. More or less all reentrant angles filled with cement. Enamel interrupted in some salient angles, in particular on anterocone of M1, and on anterior loop and posterolophid of m1 (see Figure 6). Enamel thickness at anterior and posterior sides of triangles almost the same; enamel thinner than elsewhere at tips of reentrant angles.

Anterior loop of m1 small (AC2), broadly connected to T4–T5 complex. Confluence between T4 and T5 weak, because of deep, anteriorly curved BRA2. Enamel interrupted on AC2 and on both edges of posterolophid. Connection between anteroconid complex and T3 weak.

Remarks: The size of the teeth, number of triangles, pattern of the anteroconid complex on the m1, and

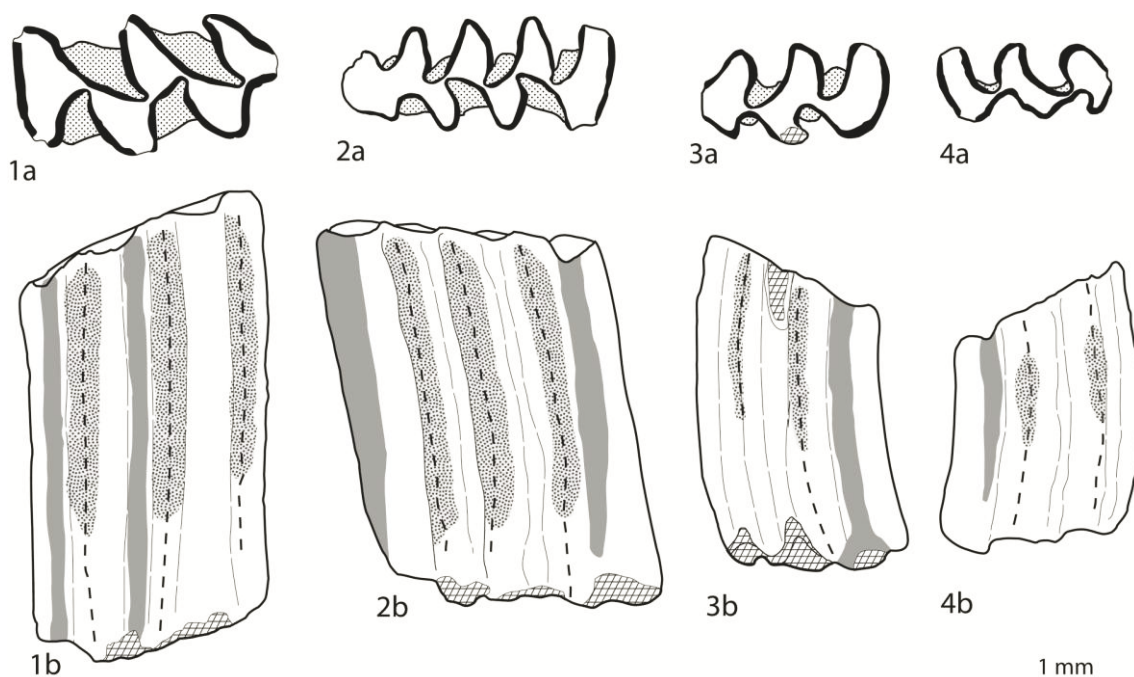


Figure 6. Schematic drawings of teeth of *Allophaiomys* cf. *pliocaenicus* from the Early Pleistocene of Pasinler. 1. Left M1 in (a) occlusal and (b) lingual views [PSL5-1]. 2. Left m1 in (a) occlusal and (b) labial views [PSL13-1]. 3. Left m2 in (a) occlusal and (b) labial views [PSL13-1]. 4. Right m3 in (a) occlusal and (b) labial views [PSL13-2]. Scale bar = 1 mm.

reentrant angles moderately filled with cement are the main characters that allow for the attribution of the vole from Pasinler to the genus *Allophaiomys*. The teeth of the species referred to the genus *Arvicola* Lacépède, 1799 are larger than in *Allophaiomys*, while the molars of *Microtus* Schrank, 1798 have more abundant cement in reentrant angles than in *Allophaiomys*, and they have a different anteroconid complex pattern.

The first lower molar from Pasinler is shorter (or in the lower size range) than those of several other species from their respective type localities, i.e. of *A. deucalion* Kretzoi, 1969 from Villany-5 (Hungary); *A. chalinei* Alcalde et al., 1981 from Cava Victoria (Spain); and *A. vandermeuleni* Agusti, 1991 from Barranco Conejos (Spain). However, the length of the m1 from Pasinler is close to the average values of *A. pliocaenicus* Kormos, 1932 from its type locality Betfia-2 (Van der Meulen, 1974) and of *A. nutiensis* Chaline, 1972 from Les Valerots (France; Chaline, 1972) and Monte Peglia-A (Italy; Van der Meulen, 1973).

Van der Meulen (1973, 1974) proposed several parameters to distinguish *Allophaiomys* species, and these parameters were commonly used in later studies. The main criteria are the length of the anteroconid complex (A), the width of the T4–T5 complex (W), the width of the neck between the anterior loop and the T4–T5 complex (B), and the width of the distance between the third buccal and lingual reentrant folds, respectively (C) (see Van der Meulen, 1974; fig. 2). The indices A/L and B/W of the m1 from Pasinler, which are the most discriminatory ones for species identification, are close to the average values of *A. pliocaenicus*, but smaller than those of the other species. In addition, the AC2 of *A. deucalion* is usually rounded, while it is rather angular distally in *A. pliocaenicus*, as it is in the m1 from Pasinler. In *A. deucalion* from Les Valerots, its type locality, the neck between the anterior loop (AC2) and the T4–T5 complex is clearly narrower than on the Pasinler m1. In summary, the general pattern of the m1 and the main discriminative indices evidence that the 4 vole teeth from Pasinler are better comparable to *A. pliocaenicus* than any other species.

However, the anteroconid complex in all *Allophaiomys* species displays large intrapopulation variation as observed by Chaline (1972), Terzea (1973), Rabeder (1981), Rekovets and Nadachowski (1995), and others. Rekovets and Nadachowski distinguished several morphotypes of the m1 pattern (from ancestral to derived: mimopliocaenicus, phaiomyoid, ratticepoid, arvaloid, pitymyoid, and nivaloid morphotypes), and the frequency of these morphotypes is used, together with size parameters and indices, to distinguish species. The pattern of the Pasinler m1 recalls the ratticepoid morphotype (Rekovets and Nadachowski, 1995; fig. 41). This morphotype is abundant in the populations referred to *A.*

pliocaenicus, in some cases accounting for more than 40% of the specimens, while it is less abundant in populations referred to *A. deucalion* (between 18% and 35%).

Allophaiomys occurred with several species all over Eurasia and in North America during the Early Pleistocene (Agusti, 1991; Repenning, 1992; Rekovets and Nadachowski, 1995; Mayhew, 2013). In Turkey, *Allophaiomys* was previously recorded from an outcrop at Hamamayagi (Samsun Province), which yielded a single m1 referred to *Allophaiomys deucalion* by Ünay and de Bruijn (1998). The locality was dated as “Latest Villanyian–Early Biharian”. Ünay (1988) referred a few specimens from Kürttepe (Aydın Province, West Anatolia) to *Allophaiomys* sp. or *Tibericola* sp. and she referred a rich collection from the coal mine of Dursunlu (Konya Province, Central Anatolia) to *A. nutiensis*. The Kürttepe locality is tentatively correlated to the latest Villanyian or early Biharian, while the Dursunlu section provided reversed polarities that were tentatively correlated to the reverse chron between the Jaramillo event and Brunhes chron, i.e. C1r.1r (Ünay, 1998), and this correlation implies an age ca. 0.9 Ma for the Dursunlu locality.

The Pasinler m1 is similar in size and A/L index to the m1 from Hamamayagi *A. cf. deucalion*, but differs from it in having less confluent T4–T5 triangles and narrower neck between the AC2 and T4–T5 complex. *Allophaiomys* or *Tibericola* sp. from Kürttepe is clearly larger than the Pasinler m1 and its anteroconid pattern is different in having narrow neck and elongated AC2. The species determination of the material from Dursunlu should be reconsidered. The m1s from Dursunlu are shorter than that of *A. nutiensis* from its type locality, Les Valerots (France; Chaline, 1972), and that of Monte Peglia and Chlum in Italy (Masini et al., 1998). It is a derived species in having lower B/W and C/W indices and differentiated enamel thickness between the anterior and posterior parts of triangles, although preserving some primitive features such as small size and strong confluence between T4–T5. In any case, the Dursunlu *Allophaiomys* is different from that of Pasinler in having narrow neck between AC2 and T4–T5, and strong confluence between these triangles.

Despite the great similarity of the Pasinler m1 with that of *A. pliocaenicus* from its type locality of Villany 5, and from many other Eurasian localities, the teeth from Pasinler are referred to *Allophaiomys cf. pliocaenicus* due to the large morphological variation of the m1 pattern in different species and the paucity of the Pasinler material.

Because of their large distribution in the northern hemisphere, the *Allophaiomys* species are an efficient biochronological tool. Recently, Mayhew (2013) discussed the stratigraphic distribution of Pleistocene arvicolids. The oldest representative of the genus, *Allophaiomys deucalion*, appears in the biozone MQR11 (2.0–2.1 Ma), while *A.*

plioaenicus appears in the biozone MQR9 (1.2–1.55 Ma) and becomes extinct at the end of the biozone MQR8 (1.0–1.2 Ma). Thus, the tentative determination of the Pasinler arvicolid as *A. cf. plioaenicus* suggests an Early Pleistocene age, between 1.0 and 1.55 Ma.

4. Palaeoecological and palaeogeographical implications

The Lower Pleistocene faunal assemblage from Pasinler is relatively diverse, comprising 22 taxa in total. In particular, the fauna consists of molluscs (13 taxa), fishes (6 taxa), amphibians (1 taxon), reptiles (1 taxon), and mammals (1 taxon). Since most of the genera and several of the species recorded from Pasinler persist until today, an actualistic approach to evaluate the palaeoecology of the beds is highly appropriate.

The discussion of mollusc palaeoecology is largely based on sample A18 (N = 276), since only 2 additional samples respectively yielded 7 (A5) and 3 (B12) specimens of gastropods. The mollusc shells are generally well preserved, showing shiny and glossy surfaces. Any signs of transport or reworking are lacking, and, with the exception of a single terrestrial *Caspicyclotus* specimen, the fauna is clearly autochthonous. Only 4 species account for 89% of the individuals in sample A18, i.e. *Cincinna piscinalis* (55%), *Radix* sp. A (14%), *Pseudamnicola* sp. (11%), and *Falsipyrgula sieversi* (9%). All other species occur with less than 10 specimens, accounting for less than 5% of the individuals. Nonetheless, the rare species may also provide valuable evidence for palaeoecology.

As already pointed out by Schütt (1997), the mollusc fauna is indicative of a well-oxygenated still-water habitat. There is sound evidence for such conditions from the most abundant species of the community, *Cincinna piscinalis*, which is typically living in sandy to muddy bottom sediment and has been found intolerant with regard to lowered oxygen content (Falkner, 1990; Glöer and Meier-Brook, 2003). Moreover, the German trivial name of this species, “Plötzenschnecke” (= roach snail), indicates the great importance of the snails as a food source for cyprinid fishes. As mentioned earlier, modern *Radix* from Anatolia have been found genetically different from European species (Bargues et al., 2001), leaving doubts on their specific identity. Nevertheless, the fossil *Radix* from Pasinler may have had ecological requirements similar to those of their modern counterparts and may have preferred shallow stagnant waters, usually with rich (partially) submersed vegetation (Falkner, 1990; Glöer and Meier-Brook, 2003). Most species of *Gyraulus* also prefer still waters with rich vegetation (Falkner, 1990; Glöer and Meier-Brook, 2003). One of the best indicators with regard to palaeoecology is the tiny planorbid *Armiger crista*, since it is today exclusively found in persistent, shallow, stagnant water bodies with densely growing plants (Falkner, 1990; Glöer and Meier-Brook, 2003).

Modern species of *Dreissena* are often highly adaptable to various ecologic conditions, but usually prefer moderately agitated waters with a constant supply of suspended organic matter. Typical specimens of the Pliocene–Pleistocene *Dreissena diluvii* are relatively large and heavy-shelled. Schütt (1997) suggested that the small size of the specimens from Pasinler is due to unfavourable conditions (environmental stunting). The stagnant, densely vegetated shallow waters of the Pasinler Lake certainly were not the preferred habitat of *D. diluvii*. Anyway, the small shells from Schütt’s (1997) and our samples probably just represent juvenile specimens.

The mollusc fauna from Pasinler is closely similar to that from the Lower Pleistocene of Vardaghbyur (also known as Gyulibulak) in western Armenia (Akramovski, 1956). Both faunas contain *Dreissena diluvii*, *Cincinna piscinalis*, *Pyrgula shadini*, *Falsipyrgula sieversi*, and *Radix* sp. A. However, the assemblage from Vardaghbyur is less diverse than that from Pasinler and several gastropod species are absent. In turn, *Pisidium subtruncatum altum*, which has been reported from Vardaghbyur (Akramovski, 1956), has not been found at Pasinler.

All fish remains can only be identified to the genus level, which renders palaeoecological interpretations highly difficult, since many fishes exhibit a wide ecological diversity within genera. The most common fish genera at Pasinler are *Chondrostoma*, *Leuciscus*, and *Rutilus*. All species of *Chondrostoma*, *Capoeta*, *Leuciscus*, and *Rutilus* inhabit fresh water bodies – fast and slow flowing streams and rivers, as well as lakes and springs. The mostly rheophile taxon, *Capoeta*, is restricted to water bodies rich in oxygen. Its pharyngeal teeth are typically adapted to malacophagy. Similar to *Chondrostoma*, *Capoeta* also obtains food by scraping periphyton from rocks (Bănărescu, 1999; Kottelat and Freyhof, 2007; Turan et al., 2008).

Cyprinid fishes are characterised by continuous, life-time pharyngeal tooth replacement, which occurs independent from environmental factors. Isolated teeth collected from sediment samples may be identified as replaced in vivo if they show resorption traces around their base (e.g., Figures 4c and 4h). In contrast, teeth without resorption traces, which are broken at the base and detached from the pharyngeal bone (Figure 4b), derive from skeletons that broke post mortem. Resorptive teeth in sediments may therefore be indicative of fish autecology (if not transported), whereas broken teeth and cranial and postcranial bones indicate accumulation of dead fishes and potential taphonomic alteration of the assemblage (Böhme, 2010).

Taking this into account, the ratios of resorptive versus broken teeth were calculated for different size classes (Table 2). *Capoeta* sp. is only represented by 2 pharyngeal teeth and thus was not statistically evaluated. As a first

result, teeth of different size classes are present, making evident that size sorting did not occur. With the exception of Leuciscinae sp. 2 (20%), all fish taxa are represented predominantly by pharyngeal teeth with resorption traces (*Chondrostoma* sp.: 71%, *Leuciscus* sp.: 64%, *Rutilus* sp.: 54%, Leuciscinae sp. 1: 100%, Cyprinidae indet.: 56%). Based on these numbers, it can be firmly stated that the fossil fish assemblage from Pasinler, comprising well-preserved pharyngeal teeth, which, to a large degree, show traces of resorption at their bases, is autochthonous.

Summing up the palaeoecological evidence, the Pasinler fossil community lived in a shallow, well-oxygenised lake. The mollusc community of Pasinler A18 is indicative of shallow, stagnant water less than 15 m deep. The fine-sandy to muddy bottom in this part of the lake obviously was densely grown with (submersed) plants, but well oxygenised in its uppermost layers, indicating oligotrophic to mesotrophic conditions. The vertebrate fauna also shows that the palaeolake environment was rich in oxygen and had a prolific periphyton, but additionally indicates areas with rocky or gravelly lake bottom. The presence of the terrestrial gastropod *Caspicyclotus* cf. *akramowsii* and the peri- to semiaquatic *Latonia* and *Natrix* reflects wet shore habitats surrounding the lake.

With the exception of *Latonia* and *Allophaiomys*, the fossil vertebrate assemblage from Pasinler resembles the present-day fauna of the area. Moreover, all vertebrate taxa found at Pasinler have also been reported from stratigraphically older localities (Böhme and Ilg, 2003). The occurrence of the alytid genus *Latonia* at Pasinler is of particular scientific interest. The genus had a wide geographic distribution from western (Spain) to eastern Europe (Southern Russia) and western Asia [Turkey (Delfino, 2002; Böhme and Ilg, 2003)]. Up to now, the eastern-most fossil record of *Latonia*, dated as Middle Miocene, was from Bağıçi (Ankara Province, west-central Turkey) (Böhme and Ilg, 2003). The youngest previous fossil record of *Latonia* from Asia was from the Mio-Pliocene boundary of western Turkey (locality Develiköy H 69) (Böhme and Ilg, 2003; Biton et al., 2013). *Latonia* was long deemed to have gone extinct during the Pleistocene (Delfino, 2002; Böhme and Ilg, 2003). Recently, Biton et al. (2013) attributed the extant *Discoglossus nigriventer*

Mendelssohn and Steinitz, 1943, which is endemic to the Hula Valley of northern Israel, to the “fossil” genus *Latonia*. However, extant and fossil representatives of *Latonia* differ significantly with regard to the ornamentation of the facies dorsalis. In all fossil species where the frontoparietal is preserved, the surface of the facies dorsalis is sculptured, whereas it is smooth in the extant “living fossil” *L. nigriventer*, which may be regarded as an apomorphic state of this character. As a result, the find of *Latonia* sp. from Pasinler represents the easternmost occurrence of *Latonia*, while outside Asia the youngest fossils of the genus have been reported from the Early Pleistocene (ca. 1.5 Ma) of Pietrafitta (Italy) (Sala and Masini, 2007). Apparently, *Latonia* went extinct to the north of its present distribution area during the Late Pleistocene. However, its extinction in the Mediterranean and Anatolia occurred much later than in central Europe.

Extant relatives of *Allophaiomys* are grouped in the genus *Microtus*. This group mainly lives in wet environments such as grassland, grassy marshland, and swamp areas along rivers and lakes. During the Early Pleistocene, *Allophaiomys* was widely distributed over all continents of the northern hemisphere. *Allophaiomys pliocaenicus* has been established as a biostratigraphic index species for the time interval between ca. 1.0 and 1.55 Ma. The presence of this vole species in the Pasinler Beds not only provides an age estimate for the sampled horizon, but also for the overlying fluvial sediments of the Palaeo-Araks tributaries. Consequently, the Pasinler-Horasan Basin became part of the Palaeo-Araks catchment area after the Early Pleistocene.

Acknowledgements

We would like to thank Madelaine Böhme (Tübingen) for constructive comments and support, Massimo Delfino (CITA) for bibliographic help, and Borja Sanchiz (Madrid) for useful advice. Thomas Neubauer (Vienna) assisted in the production of SEM photographs of molluscs. During preparation of the work, DV was supported by the Deutsche Forschungsgemeinschaft (DFG; project number BO 1550/14). The research of SS was mainly conducted during the term of a research fellowship granted by the Deutsche Forschungsgemeinschaft (DFG SCHN1264/1-1).

References

- Abich HOW (1859). Vergleichende geologische Grundzüge der kaukasischen, armenischen und nordpersischen Gebirge. Prodröm einer Geologie der kaukasischen Länder. Mem Acad Sci St.-Petersbourg Mat Phys 7: 358–534.
- Agusti J (1991). The *Allophaiomys* complex in southern Europe. *Geobios-Lyon* 25: 133–144.
- Akramovski NN (1956). Pleistocene freshwater mollusks of a sandpit in suburbs of Leninakan. *Izv An Arm Ssr Biol Agr* 9: 81–90.
- Alcalde G, Agustí J, Villata JF (1981). Un nuevo *Allophaiomys* (Arvicolidae, Rodentia, Mammalia) en el Pleistoceno Inferior del sur de España. *Acta Geol Hisp* 16: 203–205.

- Bănărescu P (1999). The Freshwater Fishes of Europe. Wiebelsheim: AULA-Verlag.
- Bargues MD, Vigo M, Horak P, Dvorak J, Patzner RA, Pointier JP, Jackiewicz M, Meier-Brook C, Mas-Coma S (2001). European Lymnaeidae (Mollusca: Gastropoda), intermediate hosts of trematodiasis, based on nuclear ribosomal DNA ITS-2 sequences. *Infect Genet Evol* 1: 85–107.
- Biton R, Geffen R, Vences E, Cohen O, Bailon S, Rabinovich R, Malka Y, Malka Y, Oron T, Boistel R et al. (2013) The rediscovered Hula painted frog is a living fossil. *Nat Commun* 4: 1–6.
- Bleeker P (1859). Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensis, Tasmanicis. *Neerlandense* 6: 1–276.
- Boettger O (1881). Diagnoses molluscorum novorum Transcaucasiae, Armeniae et Persiae. *Nachrbl Deut Malak Ges* 13: 117–129.
- Böhme M (2010). Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodela, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate. *Palaeont Z* 84: 3–41.
- Böhme M, Ilg A (2003). fosFARbase. Available at www.wahre-staerke.com.
- Chaline J (1972). Les rongeurs du Pleistocène moyen et supérieur de France. Paris: Cahiers de Paléontologie, Editions du Centre National de la Recherche Scientifique.
- Collins PEF, Rust DJ, Bayraktutan SM (2008). Geomorphological evidence for a changing tectonic regime, Pasinler Basin, Turkey. *J Geol Soc London* 165: 849–857.
- Collins PEF, Rust DJ, Bayraktutan SM, Turner SD (2005). Fluvial stratigraphy and palaeoenvironments in the Pasinler Basin, eastern Turkey. *Quatern Int* 140–141: 121–134.
- Cuvier G (1817). Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides 2: 1–532.
- Dayan E (1989). Über pleistozäne Elefanten-Funde im Umland von Erzurum in Ostanatolien. Ein Beitrag zur Fundgeschichte des *Elephas trogontherii* im Becken von Pasinler. *Stutt Beitr Natkd B* 147: 1–21.
- Delfino M (2002). Erpetofaune italiane del Neogene e del Quaternario. PhD, Università degli Studi di Modena e Reggio Emilia, Modena, Italy.
- Draparnaud JPR (1805). Histoire naturelle des mollusques terrestres et fluviatiles de la France. Paris: E. Colas.
- Falkner G (1990). Binnenmollusken. In Steinbach G, editor. Weichtiere. Europäische Meeres- und Binnenmollusken. Munich: Mosaik Verlag, pp. 112–275.
- Glöer P, Bouzid S, Boeters HD (2010a). Revision of the genera *Pseudamnicola* Paulucci 1878 and *Mercuria* Boeters 1971 from Algeria with particular emphasis on museum collections (Gastropoda: Prosobranchia: Hydrobiidae). *Archiv Molluskenkd* 139: 1–22.
- Glöer P, Falnioski A, Pešić V (2010b). The Bithyniidae of Greece (Gastropoda: Bithyniidae). *J Conch* 40: 179–187.
- Glöer P, Meier-Brook C (2003). Süßwassermollusken. Ein Bestimmungsschlüssel für die Bundesrepublik Deutschland. 13. Aufl. Hamburg: Deutscher Jugendbund für Naturbeobachtung.
- Glöer P, Pešić V (2006). On the identity of *Bithynia graeca* Westerlund, 1879 with the description of three new *Pseudobithynia* n. gen. species from Iran and Greece (Gastropoda: Bithyniidae). *Malak Abh* 24: 29–36.
- Hierholzer E, Thomas M (2003). Cypriniden-Schlundzähne (Osteichthyes: Teleostei) aus dem Tertiär von Hambach (Niederrheinische Bucht, NW-Deutschland). *Palaeontogr Abt A* 269: 1–38.
- Hossini S (1993). A new species of *Latonia* (Anura, Discoglossidae) from the lower Miocene of France. *Amphibia-Reptilia* 14: 237–245.
- Howes GJ (1991). Systematics and biogeography: An overview. In: Winfield IJ, Nelson JS, editors. *Cyprinid Fishes, Systematics, Biology and Exploitation*. London: Chapman & Hall, pp. 1–33.
- Huvaz O (2009). Comparative petroleum systems analysis of the interior basins of Turkey: implications for petroleum potential. *Mar Petrol Geol* 26: 1656–1676.
- Irrlitz W (1972). Lithostratigraphie und tektonische Entwicklung des Neogens in Nordostanatolien. *Beih Geol Jahrb* 120: 1–111.
- Ivanov M, Böhme M (2011). Snakes from Griesbeckerzell (Langhian, Early Badenian), North Alpine Foreland Basin (Germany), with comments on the evolution of snake faunas in Central Europe during the Miocene Climatic Optimum. *Geodiversitas* 33: 411–449.
- Kottelat M, Freyhof J (2007). Handbook of European Freshwater Fishes. Vol. 13. Berlin: Publications Kottelat.
- Linnaeus C (1758). Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata Aufl. Stockholm: L. Salvii.
- Lister AM, Sher AV, van Essen H, Wei G (2005). The pattern and process of mammoth evolution in Eurasia. *Quatern Int* 126–128: 49–64.
- Masini F, Abbazzi L, Lippi P, Sala B, Torre D (1998). Review and new finds of *Microtus (Allophaiomys)* (Rodentia, Arvicolidae) from the Early Pleistocene of the Italian peninsula. *Paludicola* 2: 78–90.
- Mayhew DF (2013). West European arvicolid evidence of intercontinental connections during the Early Pleistocene. *Quatern Int* 284: 62–73.
- Meller H (2010). Elefantenreich: Eine Fossilwelt in Europa. Saale: Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt.
- Mendelssohn H, Steinitz H (1943). A new frog from Palestine. *Copeia* 4: 231–233.
- Müller OF (1774). Vermium terrestrium et fluviatilium, seu, Animalium infusoriorum, helminthicorum, et testaceorum, non marinorum succincta historia. Leipzig: Apud Heineck et Faber.

- Neubauer TA, Schneider S, Böhme M, Prieto J (2012). First records of freshwater rissooidean gastropods from the Palaeogene of Southeast Asia. *J Mollus Stud* 78: 275–282.
- Obrhelová N (1971). Vergleichende Osteologie der Gattung *Leuciscus* (Pisces) aus tertiären Schichten der nördlichen und westlichen ČSSR. *Palaeont Abh A* 4: 550–660.
- Rabeder G (1981). Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem alteren Pleistozän von Niederösterreich. *Beitr Palaeont Geol Oester* 8: 1–343.
- Rage JC, Hossini S (2000). Les Amphibiens du Miocène moyen de Sansan. *Mem Mus Natl Hist* 183: 177–217.
- Rekovets L, Nadachowski A (1995). Pleistocene voles (Arvicolidae) of the Ukraine. *Paleont Evol* 28–29: 145–245.
- Repenning CA (1992). *Allophaiomys* and the age of the Olyor Suite, Krestovka Sections, Yakutia. *B Us Geol Surv* 2037: 1–98.
- Roček Z (1994). Taxonomy and distribution of Tertiary discoglossids (Anura) of the genus *Latonia* v. Meyer, 1843. *Geobios-Lyon* 27: 717–751.
- Rutte E (1962). Schlundzähne von Süßwasserfischen. *Palaeont Abt A* 120: 165–212.
- Sala B, Masini F (2007). Late Pliocene and Pleistocene small mammal chronology in the Italian peninsula. *Quatern Int* 160: 4–16.
- Sanchíz B (1998). Vertebrates from the Early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria). *Ann Nathist Mus Wien* 99A: 13–29.
- Schütt H (1964). Die Molluskenfauna eines relikitären Quellsees der südlichen Türkei. *Arch Molluskenkd* 93: 173–180.
- Schütt H (1991). Fossile Mollusken dreier anatischer Ovas. *Arch Molluskenkd* 120: 119–129.
- Schütt H (1997). Altpleistozäne Mollusken im Becken von Pasinler bei Erzurum, Türkei. *Geol Palaeont* 31: 275–284.
- Szyndlar Z (1991). A review of Neogene and Quaternary snakes of central and eastern Europe. Part 2: Natricinae, Elapidae, Viperidae. *Estud Geol-Madrid* 47: 237–266.
- Terzea E (1973). A propos d'une faune villafranchienne finale de Betfia (Bihor, Roumanie). *Trav I Speol* 12: 229–242.
- Turan D, Kottelat M, Ekmekçi GF (2008). *Capoeta erhani*, a new species of cyprinid fish from Ceyhan River, Turkey (Teleostei: Cyprinidae). *Ichthyol Explor Fres* 19: 263–270.
- Ünay E (1998). *Allophaiomys* from Turkey. *Paludicola* 2: 106–109.
- Ünay E, De Bruijn H (1998). Plio-Pleistocene rodents and lagomorphs from Anatolia. In: van Kolfschoten T, Gibbard PL, editors. *The Dawn of the Quaternary*; *Med Ned I Toeg Geowet* 60: 431–465.
- Van der Meulen AJ (1973). Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtis* (Arvicolidae, Rodentia). *Quaternaria* 17: 1–144.
- Van der Meulen AJ (1974). On *Microtus* (*Allophaiomys*) *deucalion* (Kretzoi, 1969), (Arvicolidae, Rodentia), from the Upper Villanyian (Lower Pleistocene) of Villany-5, S. Hungary. *P N Ned Akad B Phys* 77: 259–266.
- Venczel M (2001). Anurans and squamates from the Lower Pliocene (MN 14) Osztramos 1 locality (Northern Hungary). *Palaeont Hung* 19: 79–90.
- Venczel M (2004). Middle Miocene anurans from the Carpathian Basin. *Palaeont Abt A* 271: 151–174.