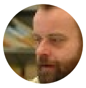
Ericek, a new Pliocene vertebrate locality in the Çameli Basin (southwestern Anatolia, Turkey)

ARTICLE *in* PALAEOBIODIVERSITY AND PALAEOENVIRONMENTS · JULY 2015

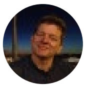
DOI: 10.1007/s12549-015-0202-3



Lars van den Hoek Ostende
Naturalis Biodiversity Center
100 PUBLICATIONS **654** CITATIONS
SEE PROFILE

M. Cihat Alçiçek
Pamukkale University
66 PUBLICATIONS **409** CITATIONS
SEE PROFILE

Alison M Murray
University of Alberta
73 PUBLICATIONS **514** CITATIONS
SEE PROFILE



Frank Wesselingh
Naturalis Biodiversity Center
80 PUBLICATIONS **1,304** CITATIONS
SEE PROFILE

Palaeobio Palaeoenv
DOI 10.1007/s12549-015-0202-3

SENCKENBERG

ORIGINAL PAPER

Ericek, a new Pliocene vertebrate locality in the Çameli Basin (southwestern Anatolia, Turkey)

Lars W. van den Hoek Ostende[1] **· James D. Gardner**[2] **· Lysanne van Bennekom**[1] **·**
M. Cihat Alçiçek[3] **· Alison Murray**[4] **· Frank P. Wesselingh**[1] **· Hülya Alçiçek**[3] **·**
Alexey Tesakov[5]

Received: 26 January 2015 / Accepted: 21 May 2015

Abstract The Çameli Basin in southwestern Anatolia preserves a sequence of fossiliferous sediments that record the Pliocene and early Pleistocene faunal development in the area. Here, we present the fauna of Ericek, a locality near the bottom of the sequence. The locality is rich in fish remains, particularly pharyngeal teeth of the cyprinids *Barbus*, *Carassius* and *Capoeta*, but also includes rare tooth-bearing bones of a possible cobitid and gobiid. The abundant fish remains agree with the geological interpretation that the Ericek sediments were deposited in a palaeolake. That interpretation is further supported by the abundance of mollusc fossils. The gastropod fauna is dominated by *Pseudamnicola*, *Valvata* and other freshwater prosobranch taxa. The dominance of prosobranch taxa over freshwater pulmonate species indicates a well-oxygenated lake environment. A range of aquatic, swamp and terrestrial tetrapod taxa are also represented. The amphibian fauna, documented mainly by anuran skull and postcranial bones and by a single salamander jaw, is consistent with a lacustrine setting for Ericek. Notable among the amphibian fossils are two jaws that may document the second record of palaeobatrachid frogs from Anatolia. Reptiles are represented by a few, incomplete vertebrae of colubroid and indeterminate snakes. Micromammal molars suggest the presence of a forested environment surrounding the palaeolake. Muridae are represented by three species, of which *Apodemus* cf. *dominans* is the most abundant. The shrew *Asoriculus* is the second most abundant species, which argues for a humid palaeoenvironment. The co-occurrences of the vole

---

This article is a contribution to the special issue "Old worlds, new ideas. A tribute to Albert van der Meulen"

✉ Lars W. van den Hoek Ostende
Lars.vandenHoekOstende@naturalis.nl

James D. Gardner
james.gardner@gov.ab.ca

Lysanne van Bennekom
lysanne_bennekom@msn.com

M. Cihat Alçiçek
alcicek@pau.edu.tr

Alison Murray
ammurray@ualberta.ca

Frank P. Wesselingh
Frank.Wesselingh@Naturalis.nl

Hülya Alçiçek
halcicek@pau.edu.tr

Alexey Tesakov
tesak@ginras.ru

[1] Naturalis Biodiversity Center, Darwinweg 2, 2333
CR Leiden, The Netherlands

[2] Royal Tyrrell Museum of Palaeontology, Box 7500, Midland
Provincial Park, Drumheller, AB, Canada T0J 0Y0

[3] Department of Geological Engineering, Pamukkale University,
20070 Denizli, Turkey

[4] Department of Biological Sciences, University of Alberta,
Edmonton, AB, Canada T6G 2EG

[5] Russian Academy of Sciences, Geological Institute, Staromonetny
per., 119017 Moscow, Russia

Mimomys occitanus and of the murids *Orientalomys* cf. *similis* and *Rhagapodemus* cf. *primaevus* indicate a late MN 15 age for the fauna, at an estimated age of 3.4 Ma.

Keywords Turkey · *Mimomys* · Palaeobiogeography · Palaeobatrachidae · Palaeolake · Palaeoenvironment

Introduction

Anatolia, the Asian part of Turkey, is biogeographically interesting due to its location at the junction between Africa, Asia and Europe. It has been an important overland route for the movement of non-marine animals and, thus, is potentially informative for deciphering the evolution of faunas and ecosystems in western Eurasia and elsewhere in the region. Unfortunately, the fossil vertebrate record of Anatolia is still poorly known. For example, our understanding of micromammal faunas that are important for dating Cenozoic fossil localities in western Eurasia is still incomplete and fragmentary. The vertebrate fossil record in Anatolia is especially limited for the Plio-Pleistocene, which is unfortunate because that is a critical interval leading up to the establishment of modern faunal distributions in the region. Although a large number of localities are known for this time frame (e.g. Ünay and De Bruijn 1998), the number of specimens per locality is too limited for drawing definitive palaeoenvironmental conclusions or biostratigraphic schemes.

The Çameli Basin, located in southwestern Anatolia (Fig. 1), is notable for containing several non-marine fossil localities of Plio-Pleistocene age (Alçiçek 2001; Saraç 2003; Alçiçek et al. 2005: table 1, fig. 4). The geological setting and tectonic-sedimentary development of the Çameli Basin is well understood (Alçiçek et al. 2005): it is a northeast-trending, graben-type basin formed during the Neogene by three pulses of crustal rifting, which were part of the larger scale and more complex regional history of tectonism that occurred during that period throughout the eastern portion of the Mediterranean (Alçiçek et al. 2005). The present-day basin is filled with terrestrial sediments that represent deposition in fluvial, alluvial-fan and lacustrine settings from about the late Miocene (Tortonian) through to the early Pleistocene (Gelasian). A lacustrine succession within the basin is bracketed above and below by palustrine deposits (Fig. 1c); collectively, these deposits document the expansion and contraction of a freshwater lake and wetlands. There are localities within the lower (Ericek) and upper (Bıçakçı) palustrine deposits that contain fossils of vertebrates (fish teeth and bones; amphibian and reptile bones; micromammal teeth), molluscs (shells), pollen and macroplant plant remains. Bıçakçı and Ericek were sampled at the same time during field work conducted between 2010 and 2013. It soon became clear that there were intriguing differences among the preserved vertebrate remains at the two localities: Bıçakçı yielded mainly large numbers of rodent teeth, whereas Ericek was rich in fish teeth and bones, yielded some amphibian and reptile bones and—compared to Bıçakçı—contained relatively few micromammal molars. The fauna and palaeoenviromental setting of Bıçakçı and its age determination have recently been reported (Van den Hoek Ostende et al. 2015), with the palaeoenvironment at the very end of the Villanyian, at around 2 Ma, shown to consist of open landscapes. Here, we present a first attempt at reconstructing the environment at Ericek. Our accounts for certain of the groups known from Ericek (e.g. mammals) are preliminary; more detailed studies are planned for the future.

Material and methods

Vertebrate fossils reported in this paper were recovered from a bulk sample of 200 kg of fossiliferous sediment collected from various parts of the section that was subsequently screen washed through 0.7-mm mesh. Matrix samples for molluscs were taken from three levels and were processed separately (Fig. 2).

Figured fish, amphibian and reptile fossils were all lightly coated with ammonium chloride before being photographed using either a Nikon DCM1500 digital camera (Niko Corp., Tokyo, Japan) mounted on a Zeiss V8 Discovery stereo microscope (fish) (Carl Zeiss GmbH, Jena, Germany) or a Leica IC80 HD digital camera (Leica Camera AG, Wetzlar, Germany) mounted on a Leica MZ75 stereo microscope (amphibians and reptiles) (Leica Microsystems GmbH). Arvicolid molars were drawn using a camera lucida, whereas the other mammal teeth were photographed using a JEOL electron microscope (JEOL Ltd., Tokyo, Japan). The vertebrate material will be stored at Natural History Museum of EGE University, Izmir, Turkey, and bear catalogue numbers prefixed with the abbreviation "EUNHM". The molluscs are stored at the Naturalis Biodiversity Center (prefix RGM).

The Ericek fauna

Molluscs

Molluscs were collected from three different levels in the Ericek section (Fig. 2). Samples ErA and ErB are dominated by *Pseudamnicola* spec., whereas sample ErC is dominated by *Valvata* aff. *macrostoma* (Fig. 3d). Indeterminate opercula of *Bythinia* are common in samples ErA and ErC. The lymnaied *Galba* indet. is present in low numbers in all three samples, as are a variety of unidentifiable "Gyrauliform"gastropods. Finally, shells and remains of some rare landsnails (*Vertigo* s.l. spec.) and a slug were found in sample ErC. No taxa could be identified to the species level due to (1) limited experience with continental

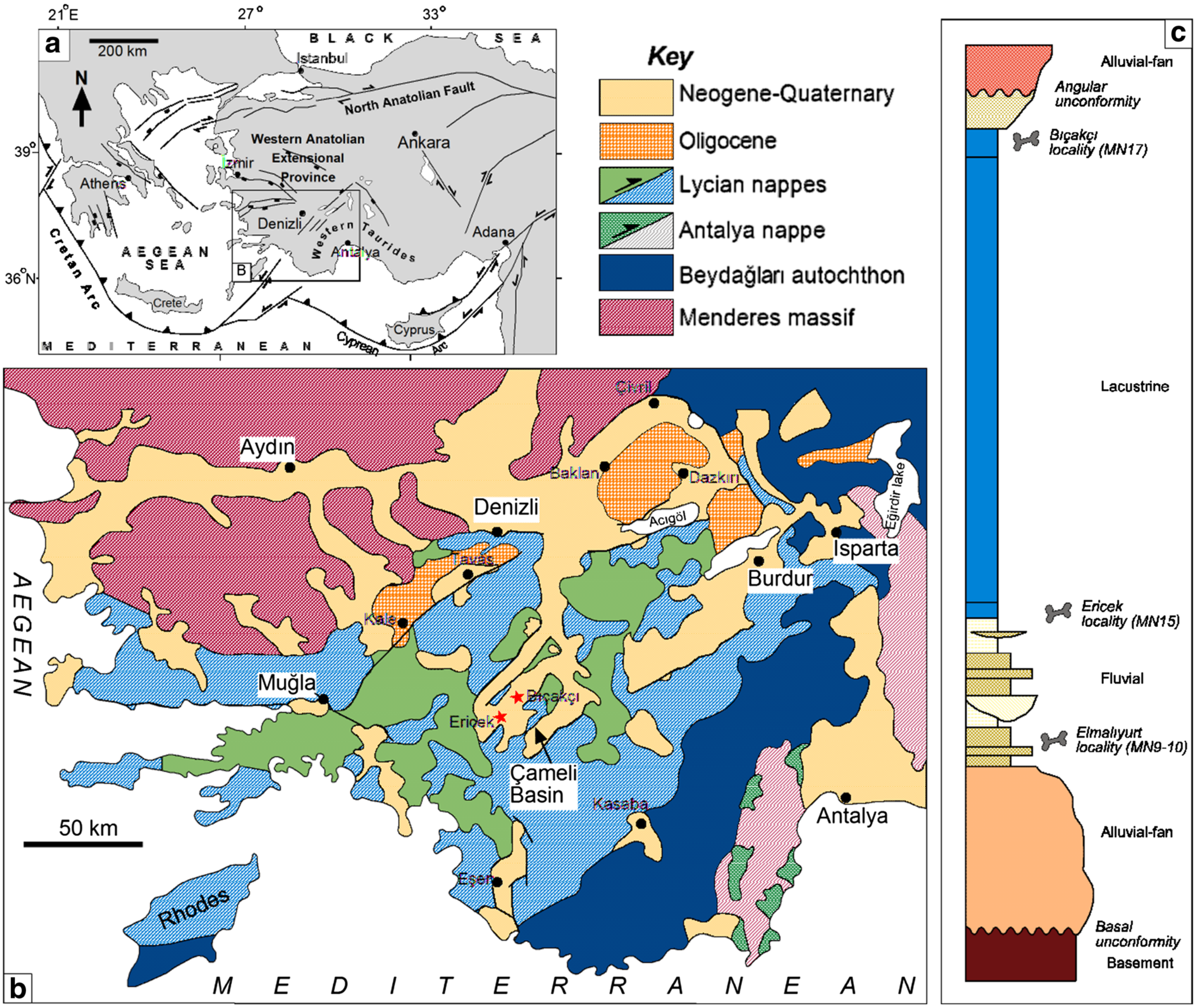


Fig. 1 Geological setting of the Ericek locality. **a** Regional map showing the location of Anatolia. **b** Simplified geological map of southwestern Anatolia (based on Senel 1997), showing the geographic positions of the Ericek locality within the Cameli Basin. **c** Composite stratigraphy of the Çameli Basin-fill succession, showing the stratigraphic positions of Ericek in basal and Bıçakçı in upper palustrine portions of the lacustrine sequence (not to scale; based on Alçiçek et al. 2005)

fresh water faunas in the region and (2) a lack of modern Eurasian species. The latter are common in the Pliocene of the nearby Baklan Basin (FW, personal observation). Even with the very incomplete identification it is possible to assess the crude ecology of the fauna (see below).

Samples differ in terms of preservation. Sample ErA consists of very well-preserved shells with details of microsculpture. Two colouration types are present, with one being bluish slightly translucent and the other having a beige opaque colour. The absence of any wear indicates lack of transport of the material. Sample ErB consists of uniformly well-preserved partially translucent shells. Fine details of microscupture are present and traces of wear are lacking, implying that the material has been preserved in situ. By contrast, Er-C contains an admixture of preservation styles. Very well-preserved shells, some translucent, with fine microscopic details do occur, but indurated, strongly worn (glossy) and discoloured shells were also found in the sample. Almost all species occur in various preservation states, indicating only local reworking and possibly minimal time averaging. Part of the worn material may derive from a "beach" setting, suggesting that ErC represents an environment closer to the fringes of the lake than the other two samples.

Fishes

The majority of the fish material from the site is represented by pharyngeal teeth from a variety of cyprinids. Pharyngeal teeth and the associated fifth pharyngobranchial bones of cyprinids are considered to be of systematic value, particularly in

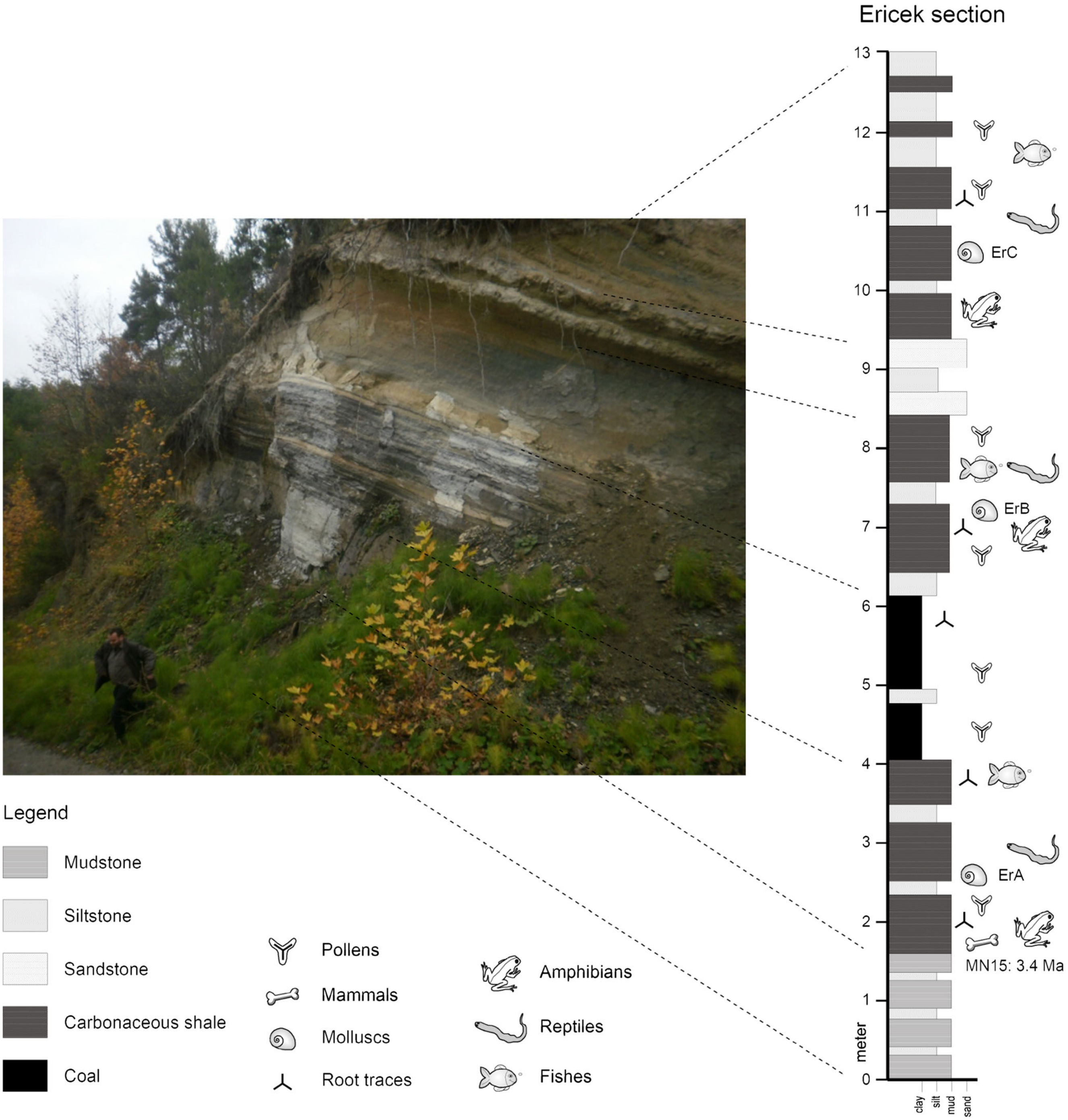


Fig. 2 The Ericek section showing the levels in which the different types of fossils were collected

terms of the arrangement and number of teeth (e.g., Simons and Mayden 1997); however, isolated pharyngeal teeth are difficult to identify to lower taxonomic levels. The teeth on a single pharyngobranchial of an individual may vary in morphology depending on its position on the bone, ontogeny, wear and frequency of replacement (e.g. Tadajewska 1998; Wautier et al. 2001). Teeth vary among species based on the fishes' diet; however, similar diets among individuals of different species may also lead to similar tooth morphologies. For these reasons, our identifications of the Ericek teeth to the generic level are considered somewhat tentative.

The Ericek pharyngeal teeth represent a diversity of taxa (Fig. 4), mostly from members of the Cyprininae, identified as *Barbus*, *Carassius*, *Capoeta* and *Capoeta* cf. *C. damascina* or cf. *C. sieboldi*. A single tooth is reminiscent of *Squalius*, of the subfamily Leuciscinae (EUNHM PV-11028; Fig. 4j). However, because we found only a single tooth that appears to be from *Squalius* among hundreds attributable to other

Fig. 3 Some common and ecological important gastropod species. **a** RGM.794476. *Bythinia* indet., operculum, L 4.6 mm; **b** RGM.794477. *Hydrobia* s.l. sp.1, H 2.2 mm; **c** RGM.794478. *Pseudamnicola* sp. 1, H 3.2 mm; **d** RGM.794479. *Valvata* aff. *macrostoma*, H 1.6 mm; **e** RGM.794480. ?*Gyraulus* sp. 1, H 1.4 mm; **f** RGM.794481. *Galba* sp. 1, H 2.9 mm; **g** RGM.794482. *Vertigo* sp. 1, H 1.8 mm; **h** RGM.794483. unidentified pulmonate gastropod, H 1.7 mm; **i** RGM.794476. unidentified slug remains, L 4.2 mm. *L* Length, *H* height

actinopterygian families, we are hesitant to positively identify it as such and suggest it may instead be an aberrant tooth belonging to one of the other genera found in the sample. *Tinca*, the only genus of the cyprinid subfamily Tincinae, may also be represented in the sample, but this identification is also tentative. Although we have identified these teeth as belonging to living genera, there are also extinct genera known from articulated specimens from Anatolia, but, unfortunately, their pharyngeal tooth morphology is unknown (Rückert-Ülkümen 1987; Gaudant 1993). Additional cyprinid material includes centra and unbranched serrate fin rays. There are also non-cyprinid fishes in the locality, with a single tooth and attached partial pharyngeal bone (EUNHM PV-11036; Fig. 4q) identified as probably belonging to a loach (Cobitidae). A small jaw (EUNHM PV-11037; Fig. 4r) that appears to belong to a fish was also collected from the deposits, but its identity is not certain. It has a low coronoid process and a single row of tooth sockets. We tentatively suggest it may be from a gobiid fish, mainly because it has a gobiid-like structure and because members of this family are today found in Turkey, but a lack of comparative material prevents certainty. Other teeth that remain unidentified in our sample may also represent jaw and pharyngeal teeth from gobiids.

About 450 km north of Ericek, at Yalova, on the Sea of Marmora and about 40 km southwest of Istanbul, Rückert-Ülkümen and Yiğıtbaş (2007) found a similar diversity of cyprinids in upper Miocene to lower

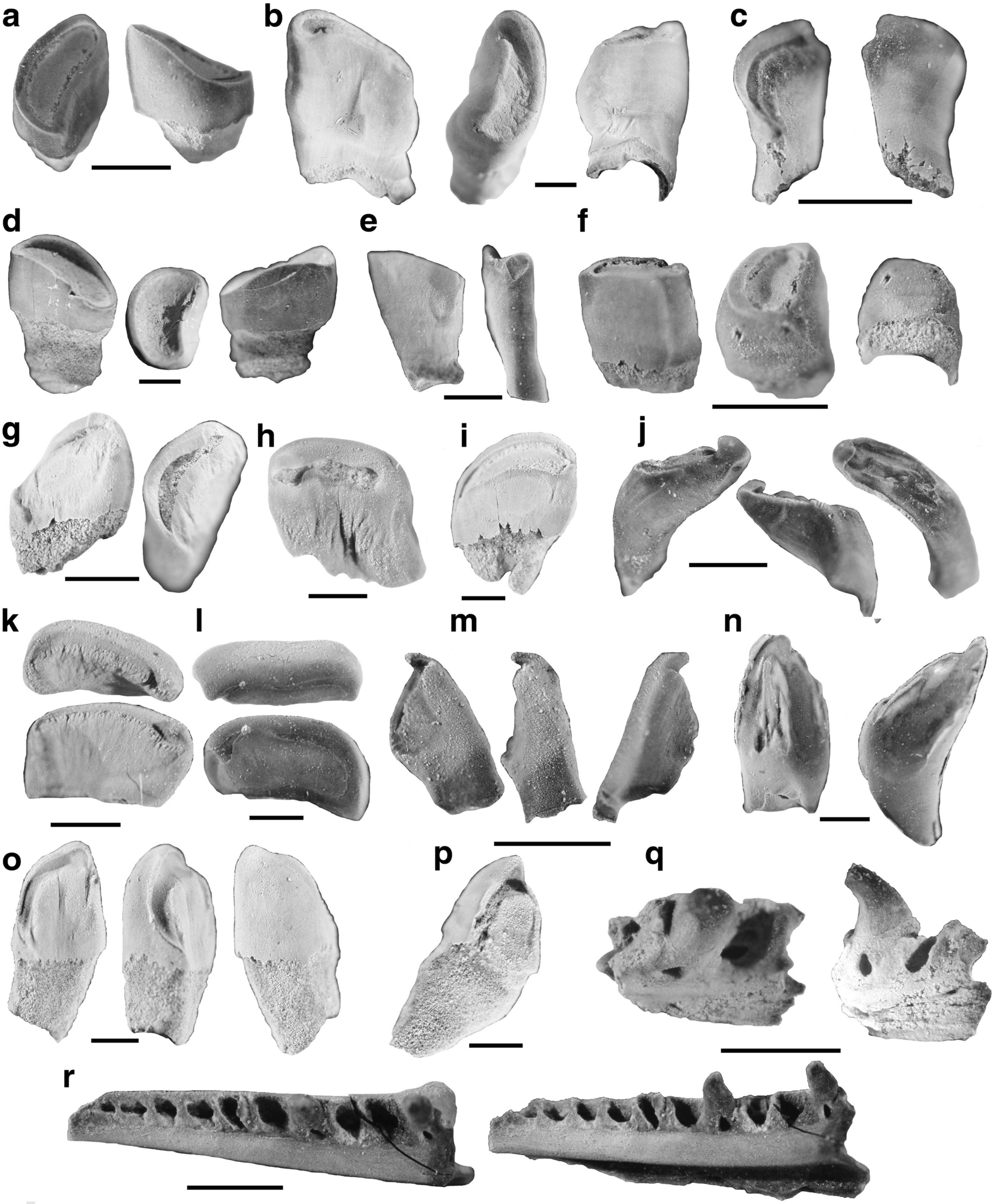


Fig. 4 Representative fish fossils from the Ericek locality, Turkey. **a–p** Cyprinidae pharyngeal teeth, **q–r** jaw bones. **a-d** Cyprininae, *Capoeta* sp., EUNHM PV-11019 (**a**), EUNHM PV-11020 (**b**), EUNHM PV-11022 (**c**), EUNHM PV-11021 (**d**); **e**, **f** *Capoeta* cf. *C. damascina*or cf. *C. sieboldi*, EUNHM PV-11024 (**e**), EUNHM PV-11023 (**f**); **g–i** Cyprininae, *Carassius* sp., EUNHM PV-11025 (**g**), EUNHM PV-11026 (**h**), EUNHM PV-11027 (**i**); **j** Leuciscinae, ? *Squalius* sp., EUNHM PV-11028; **k-m** Tincinae, *Tinca* sp., EUNHM PV-11030 (**k**), EUNHM PV-11031 (**l**), EUNHM PV-11032 (**m**); **n–p** Cyprininae, *Barbus* sp., EUNHM PV-11034 (**n**), EUNHM PV-11035 (**o**), EUNHM PV-11033 (**p**); **q** EUNHM PV-11036 partial pharyngeal bone with tooth, cf. Cobitidae; **r** EUNHM PV-11037 right dentary with two teeth, ?Gobiidae, in occlusal (*left*) and medial (*right*) views. *Scale bars*: 1 mm

Pliocene deposits. Despite being of roughly a similar age and location, the cyprinids reported and figured by them differ from the Ericek fauna. Only the pharyngeal teeth of *Barbus* sp. (Rückert-Ülkümen and Yiğıtbaş 2007: fig. 3-10) are very similar to those identified as *Barbus* sp. from Ericek (Fig. 4n, p). The Yalova pharyngeal teeth of *Tinca* sp. are somewhat similar to those from Ericek, and those of *Carassius* are somewhat comparable between the two faunas, but the similarities end there. Rückert-Ülkümen and Yiğıtbaş (2007) reported two additional cyprinids, *Scardinius* and *Leuciscus*, from Yalova along with a catfish (*Silurus*) and the pike (*Esox*); none of these were found in Ericek. However, at Ericek we have probably at least two species of the cyprinid genus *Capoeta*, the tooth reminiscent of *Squalius*, as well as a potential gobiid, none of which were reported from Yalova. Both sites have produced a loach; however, the teeth identified as *Cobitus* sp. from Yalova (Rückert-Ülkümen and Yiğıtbaş 2007: figs. 3-11, 3-12) are quite different from the partial jaw with teeth in Ericek (Fig. 4q).

Amphibians and reptiles

Amphibians are represented by a moderate number (*n*=14) of fragmentary bones, all but one of which belong to anurans. The ten anuran upper jaw bones include eight maxillae (Fig. 5a–l) and two premaxillae (Fig. 5m, n). Each bears teeth, and the external surface of the bone is essentially smooth, except for scattered external nutritive foramina in some maxillary specimens. The eight maxillary specimens (e.g. Fig. 5a–l) each preserve a portion of the bone below or posterior to the orbital region. Collectively, those specimens show that the maxilla is low, becomes shallower posteriorly and is probably elongate, that its orbital margin is essentially straight and that its lingual (medial) surface bears a lamina horizontalis in the form of a shallow and narrow shelf. The two premaxillae are even more fragmentary. One example each of a maxilla and a premaxilla [EUNHM PV-11000 (Fig. 5a–c) and EUNHM PV-11009 (Fig. 5m, n), respectively] are notable for having broken and slightly inflated vertical bony struts (see arrows in Fig. 5c) between their tooth bases. Although broken, those bony struts are reminiscent of the so-called “osseous knobs” that are characteristic of at least some palaeobatrachid species (e.g. Sanchiz 1998, p. 41; Roček 2004, text-fig. 8c; Venczel 2004, text-fig. 3g, I, j; Wuttke et al. 2012, table 1), and their presence suggests that those jaws may pertain to that family. Two other maxillae [EUNHM PV-11001 (Fig. 5d–f) and EUNHM PV-11007 (Fig. 5g–i)] each preserve an intact tooth that is weakly pedicellate and bears a labio-lingually bicuspid crown; these differ from the non-pedicellate and monocuspid teeth of palaeobatrachids. The largest maxillary specimen [EUNHM PV-11003 (Fig. 5j, l)] lacks any intact teeth, but the apical ends of its tooth pedicels are preserved as smoothly rounded rims that suggest these teeth were also pedicellate. The taxonomic identities of the non-palaeobatrachid jaws are uncertain. Of the other seven anuran families known from the Pliocene to Recent of Turkey (e.g. Rage and Sen 1976; Böhme and Ilg 2003; Venczel and Sen 1994; Frost 2014), the jaws can be excluded only from Bufonidae on the basis of having teeth and from Pelobatidae and the discoglossid *Latonia gigantea* in lacking external ornament on the maxilla. Both iliac specimens are from the right side and preserve incomplete acetabular regions. Differences in the preserved features suggest that the ilia pertain to different taxa, but neither specimen can be reliably assigned to a particular taxon. EUNHM PV-11011 (Fig. 5o) is broken through the base of the iliac shaft, so nothing can be said about that portion of the bone. However, the ventrally projecting lower rim of the acetabulum and what appears to be the broken base of an inter-iliac tubercle on the medial surface of EUNHM PV-11011 are reminiscent of palaeobatrachids and the bombinatorid *Bombina*. EUNHM PV-11012 (Fig. 5p) preserves the basal portion of the shaft and that region bears a dorsal tubercle along the posteriormost portion of a low dorsal crest. Among anurans known from the Pliocene to Recent of Turkey, an iliac crest is absent in palaeobatrachids, *Bombina*, pelobatids, pelodytids and bufonids, but it is present in *Latonia* and many neobatrachians, including ranids and hylids. The final anuran specimen [EUNHM PV-11010 (Fig. 5q, r)] is a taxonomically indeterminate vertebral centrum.

A fragmentary left dentary [EUNHM PV-11013 (Fig. 5s, t)] that is broken anteriorly and posteriorly and preserves only empty tooth slots can be identified as belonging to a urodele, rather than a squamate, on the basis of the following suite of features: (1) tooth slots are tall, narrow and loosely spaced (which indicates the teeth had highly pleurodont attachments and were small and closely spaced); (2) subdental shelf is shallow and lingually narrow and dorsally lacks a subdental sulcus; (3) Meckelian is groove deep and poorly demarcated; (4) ventral edge of bone is not strongly curved inwards, lacks a ventral notch or facet and is inclined anteriorly; (5) labial surface of bone is smooth and lacks external nutritive foramina. Salamandrids are the only urodele family known from the Pliocene to Recent of Turkey (e.g. Böhme and Ilg 2003; Frost 2014), but EUNHM PV-11013 is too fragmentary to be reliably assigned to that or any other family.

Reptiles are documented by four incomplete snake vertebrae (Fig. 5u–gg). The most nearly complete specimen [EUNHM PV-11014 (Fig. 5u–z)] is a caudal vertebra preserving the centrum and most of the neural arch, except for the pre- and postzygapophyseal processes on the left side. The lightly built structure, well-developed prezygapophyseal process and overall appearance of the specimen support assigning it to Colubroidea (e.g. Rage 1984; Holman 2000), but because caudal vertebrae are not taxonomically informative (e.g.

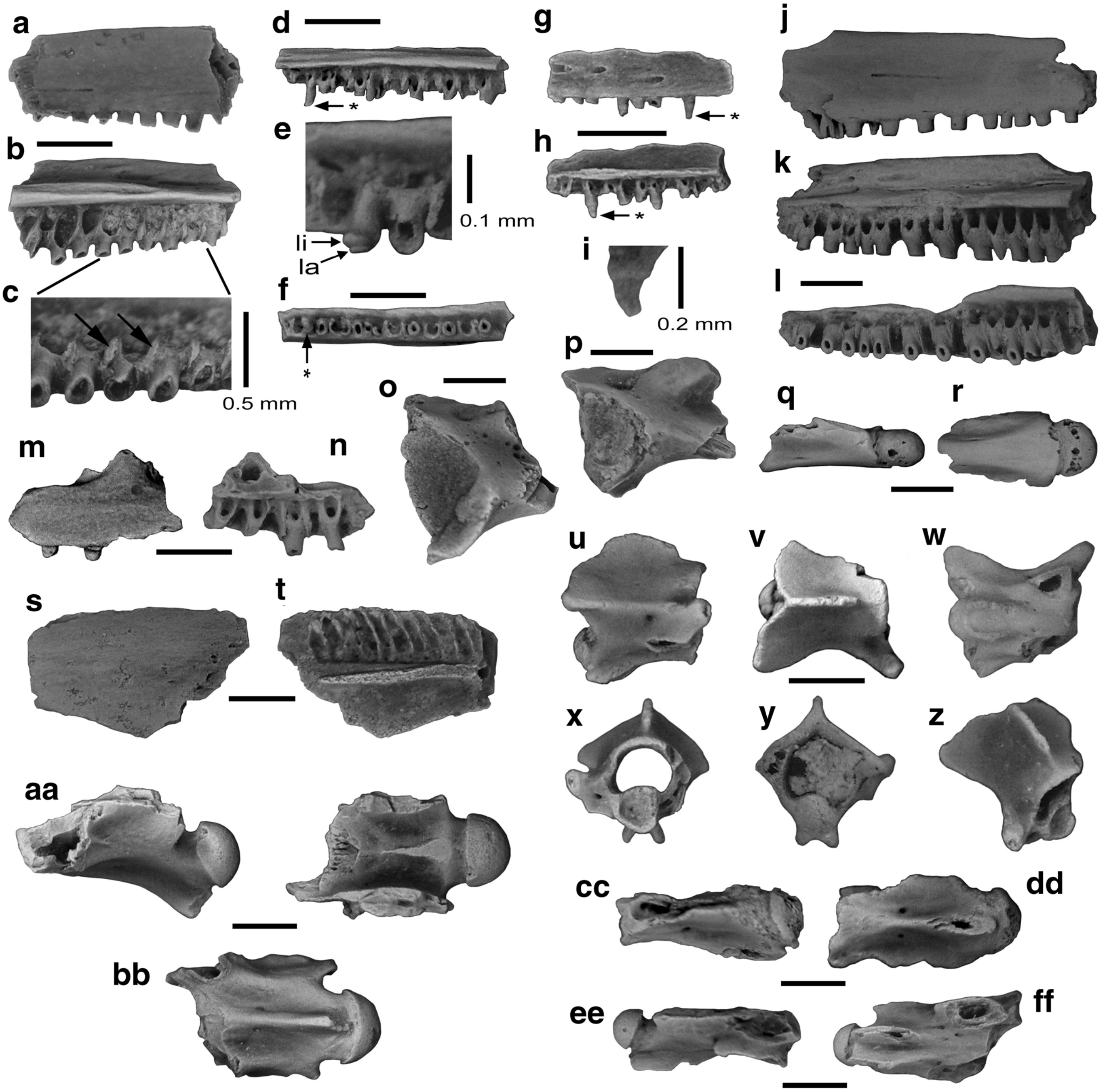


Fig. 5 Representative frog (**a**–**r**), salamander (**s**, **t**) and snake (**u**–**z**) fossils from the Ericek locality, Turkey. **a**–**c** ?Palaeobatrachidae indet. (Anura), EUNHM PV-11000, fragmentary right maxilla, entire specimen in labial (**a**) and lingual (**b**) views and close-up of part of tooth row in oblique lingual-occlusal view (**c**), with *arrows* pointing at remnants of what appear to be osseous knobs between bases of teeth. **d**–**r** Anura indet.: **d**–**f** EUNHM PV-11001, fragmentary left maxilla, entire specimen in lingual (**d**) and occlusal (**f**) views, both with *arrow* and *asterisk* pointing at intact tooth, and close-up of intact tooth in oblique lingual-occlusal view (**e**) with labelled *arrows* pointing at lingual (*li*) and labial (*la*) cuspules of bicuspid tooth crown; **g**–**i** EUNHM PV-11007, fragmentary right maxilla, entire specimen in labial (**g**) and lingual (**h**) views, both with *arrow* and *asterisk* pointing at intact tooth, and close-up of intact tooth in distal (= posterior) view (**i**); **j**, **l** EUNHM PV-11003, fragmentary left maxilla, in labial (**j**), lingual (**k**) and occlusal (**l**) views; **m**, **n** EUNHM PV-11009, fragmentary right premaxilla, in labial (**m**) and lingual (**n**) views; **o** EUNHM PV-11011, incomplete acetabular region of right ilium, in lateral view; **p** EUNHM PV-11012, incomplete acetabular region of right ilium, in lateral view; **q**, **r** EUNHM PV-11010, anteriorly incomplete trunk vertebral centrum, in left lateral (**q**) and ventral (**r**) views. **s**, **t** Urodela indet., EUNHM PV-11013, fragmentary left dentary in labial (**s**) and lingual (**t**) views. **u**–**z** Colubridae indet. (Serpentes), EUNHM PV-11014, anterior or mid-caudal vertebra in right lateral (**u**), dorsal (**v**), ventral (**w**), anterior (**x**), posterior (**y**) and oblique anterior-dorsal-right lateral (**z**) views. **aa**–**cc** “natricine” Colubridae indet. or Elapidae indet., EUNHM PV-11017, posterior trunk vertebra (centrum + bases of neural arch walls), in left lateral (**aa**), dorsal (**bb**) and ventral (**cc**) views. **dd**–**gg** Serpentes indet.: **dd**–**ee** EUNHM PV-11015, posterior trunk vertebra (centrum only), in left lateral (**dd**) and ventral (**ee**) views; **ff**–**gg** EUNHM PV-11016, anterior or mid-caudal vertebra (centrum only), in right lateral (**ff**) and ventral (**gg**) views. All images are photographs. Images are at different scales: *horizontal scale bars* are for entire specimens and are all 1 mm, *vertical scale bars* are for close-up views and are at indicated magnifications

LaDuke 1991), EUNHM PV-11014 cannot be identified more precisely. The next most nearly complete specimen [EUNHM PV-11017 (Fig. 5aa–cc)] is a posterior trunk vertebra preserving an intact centrum and basal parts of the neural arch walls. The elongate proportions and not especially robust build of the centrum indicate it too is referable to the Colubroidea (e.g. Rage 1984; Holman 2000). Among colubroids, the presence on the ventral midline of a shallow, blade-like, and ventroposteriorly-projecting hypapophysis is suggestive of “natracines” and elapids (Rage 1984, personal communication 2014); viperids also have a prominent hypapophysis, but in that family the hypapophysis typically is much deeper and also the cotyle and condyle are relatively larger. The other two specimens are centra from a posterior trunk vertebra [EUNHM PV-11015 (Fig. 5dd, ee)] and from a caudal vertebra [EUNHM PV-11016 (Fig. 5ff, gg)]. Although their elongate proportions are reminiscent of colubroids, considering their fragmentary and otherwise unremarkable appearances both centra are best regarded as being from indeterminate snakes.

The Pliocene record of amphibians and reptiles in Turkey is limited to the earlier part of the epoch. The youngest occurrences are at Ericek (this study) and Çalta (Rage and Sen 1976), both of which are latest early to earliest middle Pliocene (Ruscinian or MN 15) in age (e.g. Sen et al. 1998; Alçiçek et al. 2005; this study). Older Ruscinian occurrences are at Develiköy H 67, H 69 and H 128 (Rückert-Ülkümen et al. 2002) and at Tekman (33-4)–K 161c and Tekman (33-5)–K161d (Sickenberg et al. 1975). The Safran coal section (undifferentiated late Miocene to early Pliocene in age) near Yalova has produced turtle shell fragments (Rückert-Ülkümen and Yiğıtbaş 2007). The Turkish localities listed above have yielded only modest numbers of amphibian and reptile fossils and contain low-diversity herpetofaunas when compared, for example, to assemblages of comparable age in eastern and central Europe (e.g. Ivanov 2007) or to the modern Turkish herpetofauna (37 amphibian species: Frost 2014; 138 reptile species: The Reptile Database 2013). The non-Ericek Pliocene localities are dominated by anurans and lizards, with salamanders and turtles being less commonly represented. The Ericek herpetofauna is notable for documenting the first records of Pliocene snakes and, potentially, only the second occurrence of palaeobatrachid frogs in Turkey.

Mammals

Thirty-four isolated molars were recovered from Ericek. These pertain to at least seven species distributed among four rodent families (Arvicolidae, Muridae, Cricetidae, Gliridae) and one insectivoran family (Soricidae). Our accounts below for these specimens and taxa are brief; systematic descriptions will be presented elsewhere.

The small collection of arvicolid (vole) fossils from Ericek includes 13 molars and molar fragments representing a single species of medium-sized brachyodont vole. The molar reentrants lack cement, and the hypsodonty level is very basal with indentations of linea sinuosa not exceeding 1.0 mm at the highest positions. The enamel is undifferentiated in thickness in younger (higher crowned) specimens and shows a negative (*Mimomys*) pattern in worn molars. The Schmelzmuster was not studied, but the visually observable whitish rims along the outer sides of trailing edges indicate tangental enamel, whereas two discernible zones in leading edges may point to the development of lamellar enamel. Therefore, we tentatively interpret the presence of at least primitive pachyknem Schmelzmuster typical for mimomyoid voles since the late early Pliocene. Lower molars have two roots, and upper ones (M2, M3) have three roots, although in M3, the anterior roots are fused at the base (Fig. 6e, f). The most characteristic first lower molar is represented in the material by three fragments. The most complete specimen shows the anteroconid cap and three basic triangles (Fig. 6a). This molar represents a very young individual with a slightly worn occlusal surface and high crown [crown height (H)=2.85 mm]. The posterior lobe is not preserved. The island reentrant is deep and insulates at the crown’s basal part at approximately 1.5 mm above the crown base. The well-developed *Mimomys*-ridge is present. The anteroconid cap bears six to seven juvenile folds less than 1 mm deep. The reconstructed length of this molar is close to 3 mm. Another m1 fragment (Fig. 6b) shows a structure of a heavily worn (H = 0.85) anteroconid complex with just a pinched-off enamel islet.

The morphology of the posterior root of the second lower molar is visible (Fig. 6c), indicating its position above the incisor (acrorhiz condition). Two nearly complete third upper molars and one fragmentary specimen are present in the material. The youngest specimen (H=1.45) shows a transversely elongated posterior enamel islet and a deep antero-labial reentrant (BRA1), which insulates at the crown height of 1.0 mm (Fig. 6g). An older specimen (H=0.75) shows anterior and posterior enamel islets (Fig. 6g).

The overall dental appearance and stage of hypsodonty indicate a late early Pliocene mimomyoid vole of medium to large size. In European taxonomic tradition, this morphology is assigned to the species *Mimomys occitanus*, originally described from the late Ruscinian (late early Pliocene) locality of Sète (France) and well characterised in subsequent publications (Michaux 1971; Chaline 1974; among others) and later recognized in a number of coeval assemblages in France, Spain and central and southeastern Europe. The species has been frequently erroneously referred to the Villanyian species *M. stehlini*. The late closure of the insular fold of m1 and the seemingly increasing complexity of occlusal structure (transition from original 3 to 5 dental triangles) prompted Maul (1996) to transfer the species to the genus *Dolomys*, a

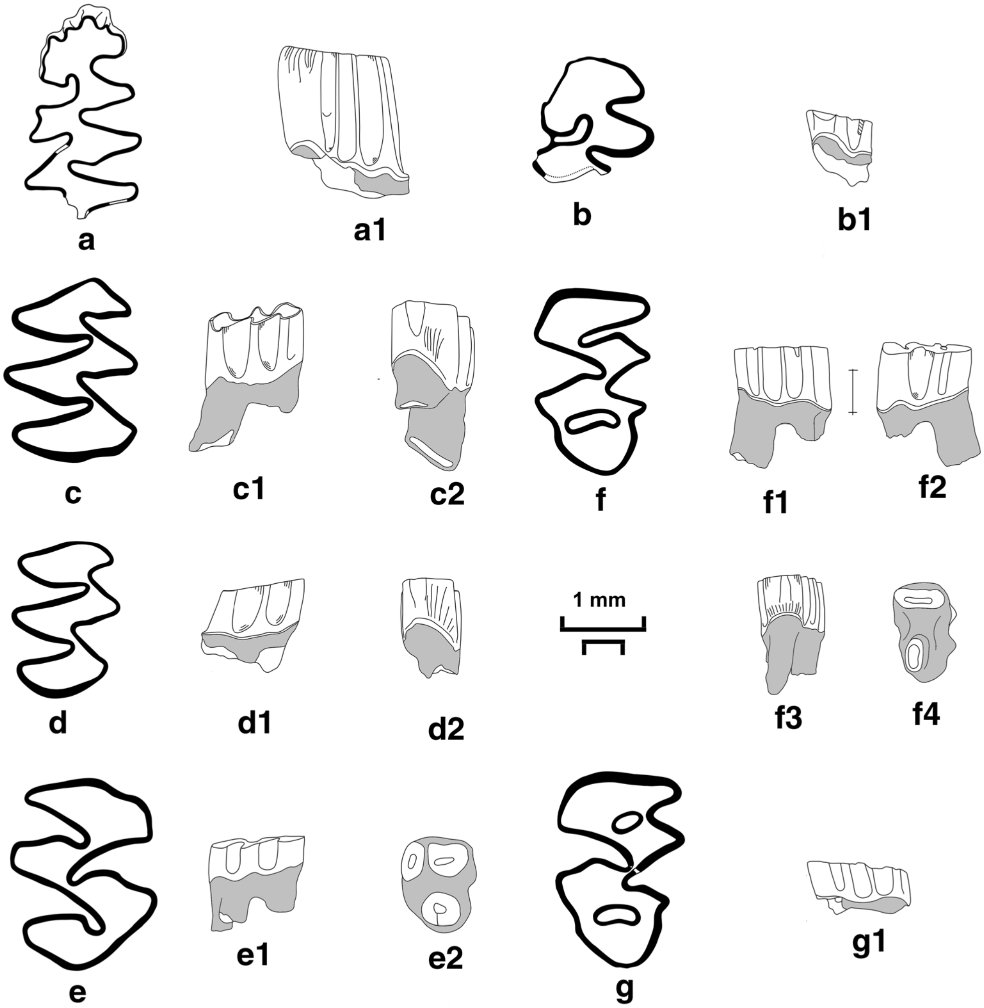


Fig. 6 Representative *Mimomys occitanus* molars, from the Ericek locality, Turkey. **a**–**g** Occlusal view of lower (**a**–**d**) and upper (**e**–**g**) molars. **a** EUNHM PV-11072, m1 sin., fragment, **a1** labial view; **b** EUNHM PV-11073, m1 sin. fragment, **b1** labial view; **c** EUNHM PV-11074, m2 dex., **c1** labial view, **c2** anterior view; **d** EUNHM PV-11075, m3 dex., **d1** labial view, **d2** anterior view; **e** EUNHM PV-11076, M2 dex., **e1** labial view, **e2** root view; **f** EUNHM PV-11077, M3 sin., **f1** labial view, **f2** lingual view, **f3** posterior view, **f4** root view; **g** EUNHM PV-11078, M3 sin., **g1** labial view. *Scale bars* are for occlusal (*above*) and lateral views (*below*)

suggestion followed by authors of many subsequent publications (e.g. Fejfar et al. 1997; Minwer-Barakat et al. 2004; Popov 2004). However, the genus *Dolomys*, based on *D. milleri* 1898, is quite different in terms of the structure of M3 (persistently deep LRA3 and loss or strong reduction of insulation of BRA2). This morphology is traced back in time to late Ruscinian (*D. gromovorum*) and latest Ruscinian/earliest Villanyian (*D. nehringi*) species of central and eastern Europe (Topachevsky and Nesin 1989; Radulescu et al. 1997), indicating that *M. occitanus*, with persistently present posterior insulation in M3, may represent an independent lineage of generic rank. Advanced mimomyoid voles and species of *Dolomys* share the "*Mimomys*" (= pachyknem) Schmelzmuster (Rabeder 1981). von Koenigswald (1980) found only radial enamel in leading edges of the topotypic *M. occitanus*, which indicates a still very primitive evolutionary stage.

The taxonomy of European mimomyoid voles of the early Pliocene is not yet resolved. There are concerns with the straightforward use of the name *Mimomys* for brachyodont cementless arvicolids of Ruscinian age (Gromov and Polyakov 1977; Tesakov 1998, 2004). Many of these forms belong to phyletic lineages giving rise to a number of vole genera (*Dolomys*, *Pliomys*, *Pitymimomys*, etc.) that are distinct from the clade containing the type species of the genus *Mimomys*, namely *M. pliocaenicus* of the late Villanyian. The phyletic status of "*Mimomys*" *occitanus* is not clear. This group should not be mixed with the mid-early Pliocene array of the medium-sized mimomyoid groups that show lower hypsodonty stages and lack delayed insulation of the insular fold, including "*Mimomys*" *moldavicus*, "*Mimomys*" *davakosi* and *Promimomys antiquus*. Alternatively, the group of *Mimomys occitanus* may be a basal member of a Plio-Pleistocene large *Mimomys* group related to *M. pliocaenicus* (Chaline 1974; Fejfar and Heinrich 1982), an independent blind lineage of the Ruscinian mimomyoid radiation (for reasoning, see Maul 1996), or a polymorphic group containing members of different lineages (Kowalski 1960; Bachelet 1990; Fejfar et al. 1990). More data on morphotypes of M3 in the type and other representative faunas are needed to help resolve this issue. Pending taxonomic clarification, we classify the *occitanus* group under the genus *Mimomys* F. Major.

Muridae (rats and mice) are represented by at least three genera and species. The most common is a species of *Apodemus* documented by ten molars, for which examples from all positions are available, except M1 (Fig. 7a–e). These teeth fit well within the known size range for *Apodemus dominans* (Van de Weerd 1976; Storch and Dahlmann 1995), a rather common species in the Pliocene of Europe (Van de Weerd 1979). Our material is on average larger than the Ruscinian-Villanyian *A. atavus* and smaller than *A. gudrunae*. On morphological grounds, assignment to *A. dominans* is supported by the presence of a t7 in M2, a large antero-central cuspid and well-developed accessory cusps on the labial cingulum in m1. However, *Apodemus* species are similar in terms of molar morphology, especially in their M2 and M3, and exhibit variable size and morphology across species (Pasquier 1974). Therefore, for now we conservatively classify the Ericek species as *A.* cf. *dominans*. The other two murid species are represented by fewer molars. A single M1 closely resembles those described for *Orientalomys similis* from Tourkabounia (De Bruijn and Van der Meulen 1975) in both size and morphology (Fig. 6h). However, because only a single tooth is available, we conservatively identify it as *O.* cf. *similis*. Two molars (one each of M2 and m3; Fig. 7f, g) are referable to *Rhagapodemus*. The M2 has a well-developed t1 (with t1 bis present) and t3, t7 is separated from t4 and t12 is well developed. These characters fit well with *Rhagapodemus hautimagnensis* from Ptolemais as reported by Van de Weerd (1979), although the two Ericek molars seem to be larger than examples from Greece (Van de Weerd 1979). Recently, Hordijk and De Bruijn (2009) included all the material described by Van de Weerd (1979) from Ptolemais in the morphologically close *R. primaevus*, noting that this action meant an overlap in stratigraphic ranges with *R. hautimagnensis* from western Europe. This suggests that the distinction between the two species needs to be revised. We follow Hordijk and De Bruijn (2009) in using the name *R. primaevus*, but note that both of our specimens are much larger and more morphologically advanced than the M2 and m3 of *R. primaevus* as described from the latest Miocene locality of Maramena by Storch and Dahlmann (1995). The Ericek material is smaller than the material reported in the type descriptions for *R. vanderweerdi* De Bruijn and Van der Meulen (1975) and *R. ballesioi* Mein and Michaux (1970).

Cricetidae (hamsters) are represented in the Ericek assemblage by an M3 and m3 of *Cricetulus* sp. (Fig. 7i, j) [note that we follow Mayhew (1978) in considering *Allocricetus* to be a junior synonym of *Cricetulus*]. Gliridae (dormice) are documented by a fragment of an m1, which, unfortunately, was damaged beyond repair before we could photograph it. Although incomplete, that lower molar preserved a pair of characteristic transverse ridges which indicate it belongs to *Muscardinus* sp.

Insectivores are well represented in the Ericek sample by ten isolated molars that collectively document each position, except for M3 (Fig. 7k–o). Based on comparisons with material described by Reumer (1984) and Doukas et al. (1995), the Ericek molars are referable to an indeterminate species of the shrew *Asoriculus*, a genus which is also known from older deposits in the region (De Bruijn et al. 1970).

Discussion

Age of the Ericek fauna

Alçiçek et al. (2005) estimated the age of the Ericek locality at between 3.8 and 3.2 Ma. That preliminary estimate was based on the presence of *Mimomys occitanus*, a species that is only known from MN 15 of Eurasia. The other mammalian species identified from Ericek also have temporal ranges outside of the Çameli Basin that are known to include at least a portion of MN 15 (Fig. 8). Three different species of Muridae were identified in the Ericek material: *Apodemus* cf. *dominans*, *Rhagapodemus* cf. *primaevus* and *Orientalomys* cf. *similis*. Because *Apodemus dominans* is a wide-ranging species known from MN 13 through to MN 17 (Van de Weerd 1976, 1979; Storch and Dahlmann 1995), it cannot be used to further refine the age estimate for Ericek. The other two murid species have far shorter ranges: *R. primaevus* ranges from latest MN 13 up to late MN 15 (Hordijk and De Bruijn 2009), whereas *O. similis* ranges from late MN 15 through MN 16 (De Bruijn and Van der Meulen 1975). The presence of *R.* cf. *primaevus* and *O.* cf. *similis* at Ericek is the first reported instance of these species co-occurring at a locality and further constrains the locality's age to the late, but not latest, MN 15, within the late Ruscinian. We note that because our taxonomic identifications are based on limited material and stratigraphic ranges established for occurrences outside of Anatolia, caution is advised in accepting our age estimate. The ranges for the remaining mammalian genera (*Cricetulus*: MN 12 to present (Ünay 2006); *Muscardinus*: MN 5 to present (Daams 1999); *Asoriculus*: MN 14 to 17; Reumer 1984; Furió and Angelone 2010) do not contradict our late MN 15 age estimate. None of the fish, amphibian or squamate taxa reported here from Ericek are informative for assessing the locality's age.

Biogeographical considerations

From a biogeographical point of view, the fish fauna of Ericek reflects the position of Anatolia at the cross roads of continents. The cyprinid fishes represent a mix of lineages from diverse places. *Barbus* is the most diverse cyprinid genus found in Ericek (over 300 accepted species; Froese and Pauly 2013), with living species found throughout Europe, Asia and Africa. Species of *Squalius*, a genus tentatively identified in Ericek, are also more widespread, but predominantly found in Europe around the north shore of the Mediterranean, from Spain and France in the west to Greece, Bulgaria and

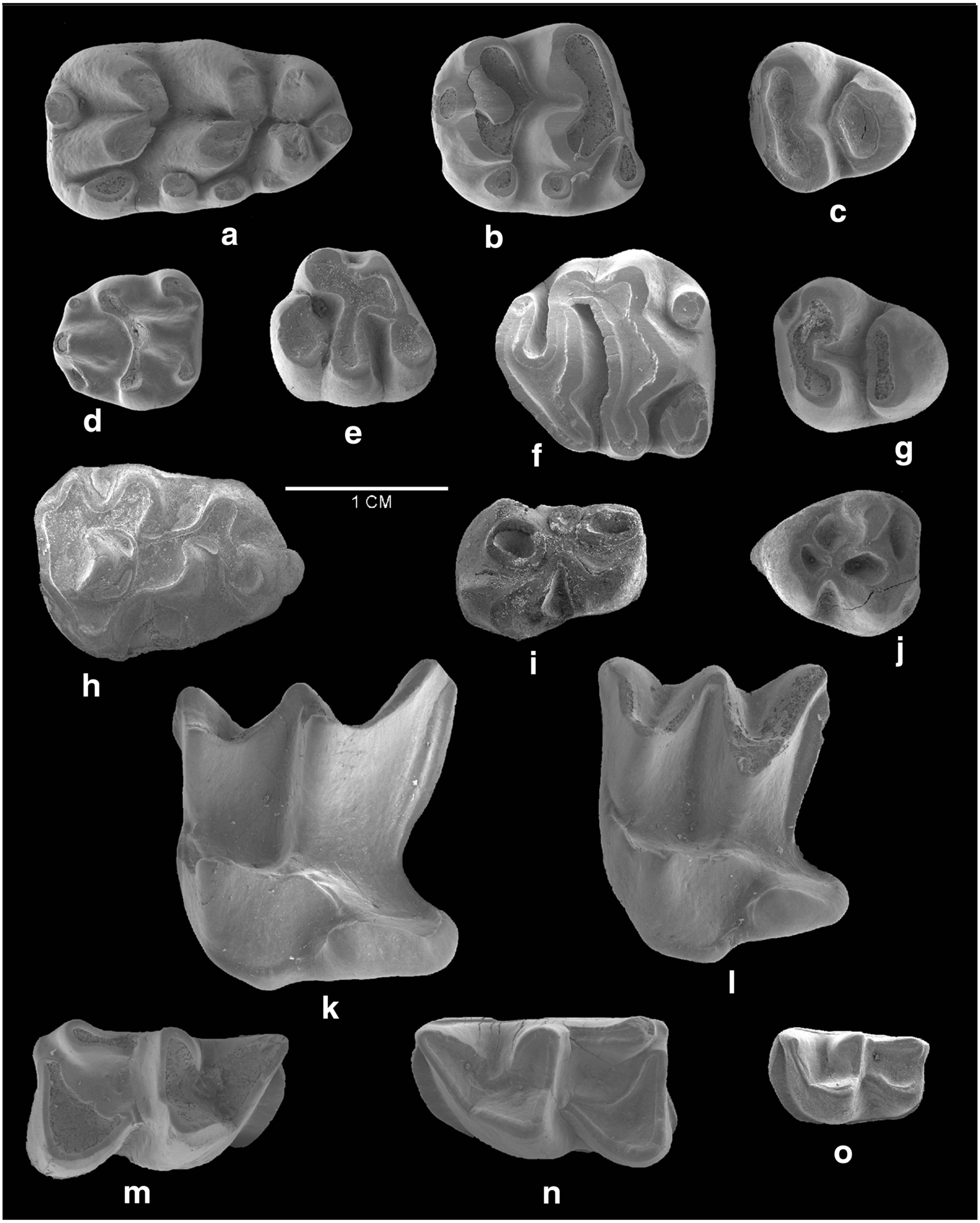
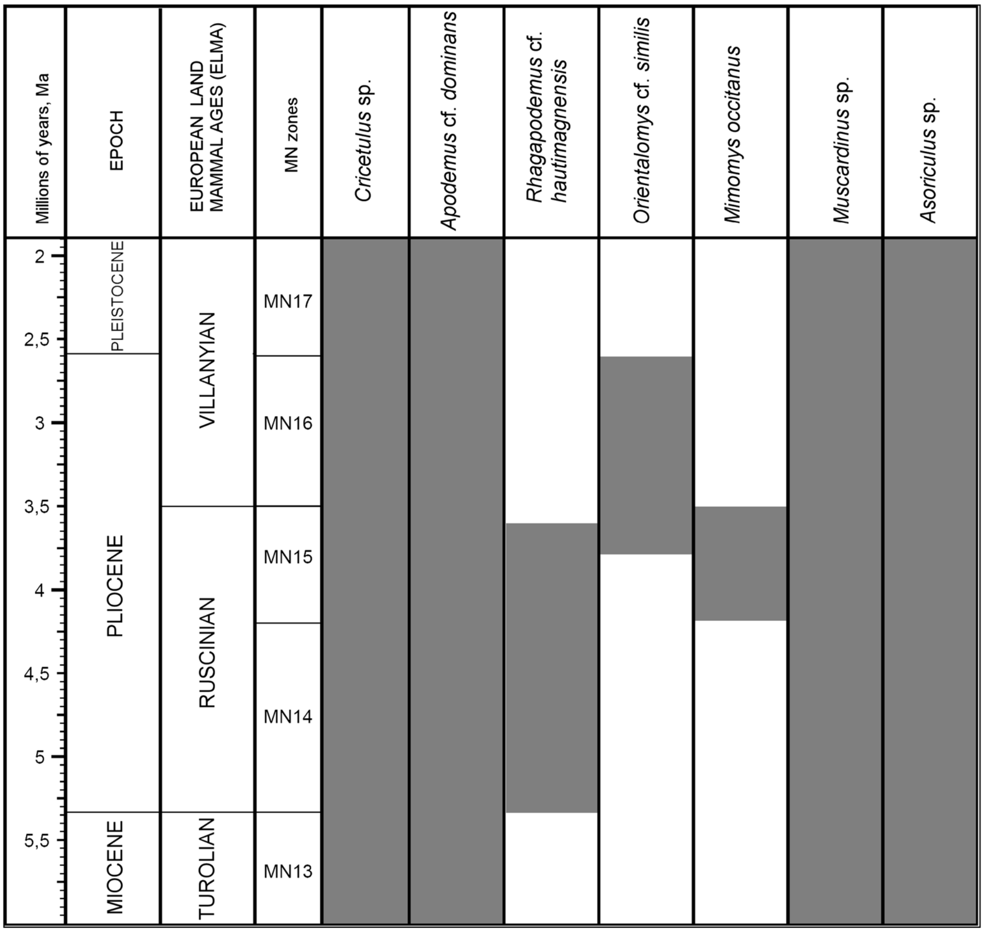


Fig. 7 Representative Muridae (**a–h**), Cricetidae (**i**, **j**) and Soricidae (**k–o**) molars from the Ericek locality, Turkey. **a–h** *Apodemus* cf. *dominans*: **a** EUNHM PV-11051, m1 dex., **b** EUNHM PV-11070, m2 dex., **c** EUNHM PV-11064, m3 sin., **d** EUNHM PV-11063, M2 dex., **e** EUNHM PV-11062, M3 dex. *Rhagapodemus* cf. *primaevus*, **f** EUNHM PV-11059, M2 dex., **g** EUNHM PV-11071, m3 sin. *Orientalomys* cf. *similis*, **h**. EUNHM PV-11069, M1 dex. *Cricetulus* sp. **i**, **j** Cricetidae: **i** EUNHM PV-11048, M3 sin., **j** EUNHM PV-11049, m3 dex. *Asoriculus* sp. **k–o** Soricidae: **k** EUNHM PV-11045, M1 sin., **l** EUNHM PV-11046, M2 sin., **m** EUNHM PV-11044, m1 dex., **n** EUNHM PV-11039, m2 dex., **o** EUNHM PV-11042, m3 sin

Fig. 8 Stratigraphic ranges of mammal taxa found in Ericek. Based on these, the assemblage is best placed in the later part of unit MN 15 (see text for details)



Turkey in the east. They also range into Iran and Azerbaijan. Modern species of the genus *Capoeta* are found in Turkey and areas to the east and south, including Iran, Mesopotamia, western Pakistan and the Jordan River drainage into the Levant (Froese and Pauly 2013), and may represent the more endemic element of the ichtyofauna. The five living species of *Carassius* are essentially Asian (China, Japan, Taiwan and Siberia), with only two species found in central or eastern Europe.

Because the non-palaeobatrachid anuran specimens, the urodele dentary and the snake vertebrae (Colubroidea indet. and Serpentes indet.) from Ericek cannot be identified more precisely, they are not biogeographically informative. The possible presence of palaeobatrachids at Ericek is notable because the only report of that family in Turkey to date is based on as-yet undescribed material from an unspecified locality of early Miocene age (Claessens 1997; Wuttke et al. 2012), on which a paper is currently being prepared (Leon Claessens, personal communication). The presence of palaeobatrachids in Turkey during the early Miocene and early Pliocene is consistent with the notion that these frogs were pushed eastwards out of western and central Europe after the Eocene due to changing climatic conditions, before finally becoming extinct in the middle Pleistocene (Wuttke et al. 2012).

Palaeoenvironmental interpretation

The Ericek mollusc fauna is dominated by freshwater snails. Based on our preliminary investigations, we identity about 15 species of aquatic snails and only four terrestrial species. The fauna is dominated by *Pseudamnicola* and contains several strict freshwater taxa (e.g. *Galba*, *Planorbis*, *'Gyraulus'*). Prosobranch snails dominate over pulmonate snails. The occurrence of prosobranchs suggest a permanent (non-ephemeral) lake, while that of *Bythinia* suggests a relatively warm temperature, as the hatching of eggs is strongly delayed in cool water (approx. 13 °C) (Richter and Wächtler 1999). The lack of unionoid bivalves might indicate isolation of the lake from adjacent river systems. *Galba* and *Vertigo* likely indicate that the lake margin was nearby.

The palaeoenvironment of the Ericek locality has been reconstructed as marginal lake deposits; this is best supported by the abundant fish remains that indicate the presence of permanent freshwater bodies. Taking into account that most of the vertebrate remains belong to fishes, we suspect the locality predominantly samples more open parts of the palaeolake. The differences between the three mollusc samples show that both intervals of more open lakes and 'beach' conditions are preserved in the section, and as the vertebrates come from a bulk sample, these environments would be mixed. Indeed, the occurrence of certain fish taxa (e.g. some species of *Carassius*) also indicates the presence of vegetation and slow-moving or still waters, whereas that of others (e.g. some species of *Barbus*) indicates faster moving waters that suggest the presence of nearby streams or rivers. Because palaeobatrachids are obligate aquatic frogs (e.g. Špinar 1972; Wuttke et al. 2012), their presence in the Ericek assemblage is consistent with geological interpretations (Alçiçek et al. 2005) and the fish assemblage that the deposit formed in a marginal lacustrine setting. Other components of the herpetofauna (non-palaeobatrachid anurans, salamander and snakes) are consistent with that palaeoenvironmental setting because these animals typically are plentiful close to permanent water bodies.

The surrounding landscape can be reconstructed on the basis of the micromammal fauna. In total, 34 small mammal molars were identified. Slightly more than a quarter of the molars belong to insectivores (in this case the shrew *Asoriculus* sp.), whereas the rest belong to the Rodentia. This is a rather striking pattern because, whereas soricids usually are present at clearly lower percentages in most Eurasian Neogene localities, at Ericek, they are the second largest family group. Litter decomposers (e.g. insects and worms) are an important food source for insectivores; consequently, we expect them to be relatively more abundant in wooded areas than in grasslands (Van den Hoek Ostende 2001; Furió et al. 2011). Thus, a high percentage of insectivores in a fossil fauna is suggestive of a more humid and wooded biotope. Despite the relative abundance of insectivore teeth, it is notable that just one species—namely *Asoriculus* sp.—appears to be represented in the sample. Although most insectivores today are found in moist environments, some shrews are known to live in semi-arid areas.

The largest mammalian family group at Ericek is the Muridae, representing nearly 40 % of Ericek fauna. A total of 14 murid molars were found, with the largest share belonging to the wood mouse *Apodemus* cf. *dominans*. Most extant *Apodemus* species have frugivorous to omnivorous diets, which implies a rather humid and wooded environment for the food source, rather than grasslands (Suata-Alpaslan 2010). *Rhagapodemus* is considered to be closely related (Martín Suarez and Mein 1998) and presumably had a similar ecological preference. *Orientalomys* is represented by a single molar. Its species were adapted to relatively open and dry environments based on their molars having a relatively large width:length ratio and bearing a well-developed longitudinal valley, indicating a strong power stroke. Their diet probably included a more substantial fibrous component, which may suggest a relatively drier and relatively more open environment (Van Dam 1997).

The third largest mammalian family group, which makes up exactly a quarter of the molars found in Ericek, is the Arvicolidae. All of the arvicolid specimens belong to the same species, namely *Mimomys occitanus*. Unfortunately, not much is known about the ecological preferences of this species.

The two smallest mammalian family groups in the Ericek fauna are the Cricetidae and Gliridae. Recent *Cricetulus* species are found in open dry country, such as steppes and the borders of deserts; fossil species are presumed to also have favoured similar environments (García-Alix et al. 2008). Some species of *Cricetulus* are still present in Anatolia nowadays. The glirid *Muscardinus*, by contrast, is considered indicative of forested environments. Its only recent species, *M. avellanarius*, is a typical inhabitant of woodlands, where it forages for food in shrubs (Bright and Morris 2009).

Overall, the micromammals from Ericek suggest that the palaeolake lay in forested surroundings. This early Pliocene palaeoenvironment of the Çameli Basin stands in sharp contrast to the far more open, early Pleistocene landscape reconstruction suggested by the fauna from Bıçakçı (Van den Hoek Ostende 2001).

Conclusions

The locality of Ericek in the Çameli Basin has yielded a variety of fossils, including many remains of fishes, amphibians, snakes and small mammals. The fauna, in combination with that from the nearby early Pleistocene locality of Bıçakçı, testifies to the tremendous changes which occurred in palaeoenvironmental conditions in the basin between the Pliocene and Pleistocene. On the basis of the small mammals, deposition of the Ericek section is placed in the late Ruscinian, at an estimated age of 3.4 Ma. The fish and amphibian fauna suggest a permanent water body that was connected to streams or rivulets. In sharp contract to Bıçakçı, the landscape appears to have been forested, and the high number of insectivores (shrews) in combination with a predominance of wood mice suggests relative humid surroundings. Sample sizes for the amphibians, reptiles and mammals are still relatively small and consist entirely of isolated elements. Not surprisingly, our taxonomic identifications for these groups are preliminary. Nevertheless, the fact that Ericek and Bıçakçı are clearly fossiliferous and show a pronounced localized change in palaeoenvironmental settings within a relatively short time span of just a few million years demonstrates that the Çameli Basin provides an excellent area to study changes in the Anatolian ecosystems leading to the onset of the Quaternary.

Acknowledgements We dedicate this paper to Albert J. van den Meulen, in recognition of his contribution to our knowledge of the Plio-Pleistocene faunas of the eastern Mediterranean. Albert's thesis stands as the starting point for the modern studies on arvicolid palaeontology, and as such he was a major inspiration and help in the career of Alexey Tesakov. Lysanne van Bennekom is grateful for the help provided by

Wilma Wessels in studying the fossil murid collections at Utrecht University and for the discussions and help in identification by Hans de Bruijn. James Gardner thanks Jean-Claude Rage (Paris) for assistance with identifying the snake specimens and August Ilg (Düsseldorf) for running a search in the fosFARbase database for records of Pliocene amphibian and reptiles in Turkey. M. Cihat Alçiçek benefited from both a Temminck fellowship and a SYNTHESYS grant for consecutive visits to Naturalis. Alexey Tesakov and Hülya Alçiçek received Temminck and Martin fellowships, respectively, for their visits to the same institute. M. Cihat Alçiçek, Alexey Tesakov and Hülya Alçiçek benefited from the bilateral project of TUBITAK-RFBR (111Y192) and MCA granted by TUBA-GEBIP (Outstanding Young Scientist Award by the Turkish Academy of Sciences). We are grateful for the comments of Leon Claessens and an anonymous reviewer, which helped to improve our paper. Delia van Oijen (Naturalis) assisted with the electron microscope photographs and in making the figures. This is a contribution to NECL IME.

References

Alçiçek, M. C. (2001). *Sedimentological investigation of the Çameli Basin (late Miocene – late Pliocene, Denizli, SW Anatolia)*. Ph.D. Dissertation, 101 p., Ankara University, Turkey.

Alçiçek, M. C., Kazancı, N., & Özkul, M. (2005). Multiple rifting pulses and sedimentation pattern in the Çameli Basin, southwestern Anatolia, Turkey. *Sedimentary Geology, 173*, 409–431.

Bachelet, B. (1990). Revision of the population of Arvicolids from the Pliocene fauna of Sete (Herault, France). Evidence of the *Mimomys capettai* lineage. In O. Fejfar & W.-D. Heinrich (Eds.), *International symposium evolution, phylogeny and biostratigraphy of arvicolids* (pp. 33–40). Prague: Geological Survey of Czechoslovakia.

Böhme, M., & Ilg, A. (2003). fosFARbase. Electronic database. Accessible at: http://www.wahre-staerke.com/. Accessed 28 Feb 2014.

Bright, P. W., & Morris, P. A. (2009). Foraging behaviour of dormice *Muscardinus avellanarius* in two contrasting habitats. *Journal of Zoology, 230*, 69–85.

Bruijn, H. de, & Meulen, A. J. van der (1975). Early Pleistocene Rodents from Tourkoubounia-1 (Athens, Greece). I. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B, 78*, 314–338.

Bruijn, H. de, Dawson, M. R., & Mein, P. (1970). Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece), I, II, III. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B, 73*(5), 535–595.

Chaline, J. (1974). Un nouveau critère d'étude des *Mimomys*, et les rapports de *Mimomys occitanus-Mimomys stehlini* et *Mimomys polonicus* (Arvicolidae, Rodentia). *Acta Zoologica Cracoviensia, 19*(16), 337–356.

Claessens, L. P. A. M. (1997). On the herpetofauna of some Neogene eastern Mediterranean localities and the occurence of *Palaeobatrachus* and *Bufo* (Amphibia, Anura) in the lower Miocene of Turkey. *Journal of Vertebrate Paleontology, 17*[Supplement to 3] 39A.

Daams, R. (1999). Family Gliridae. In: Rössner, G. E., & Heissig, K. (eds.). *The Miocene Land Mammals of Europe* (pp. 301–318). Munich: Verlag Dr. Friedrich Pfeil.

Dam, J. A. van (1997). The small mammals from the Upper Miocene of the Teruel-Alfambra region (Spain): palaeobiology and paleoclimatic reconstructions. *Geologica Ultraiectina, 156*, 1–204.

Doukas, C. S., Hoek Ostende, L. W. van den, Theocharopoulos, C., Reumer, J. W. F. (1995). Insectivora (Erinaceidae, Talpidae, Soricidae, Mammalia). In: Schmidt–Kittler, N. (ed), The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary. Münchner *Geowissenschaftliche Abhandlungen*, *A28*: 4364.

Fejfar, O., & Heinrich, W.-D. (1982). Zur Evolution von *Mimomys* (Rodentia, Mammalia) im Csarnótanum und Villafranchium Europas. *Eclogae Geologicae Helvetiae, 75*(3), 779–793.

Fejfar, O., Heinrich, W.-D., Pevzner, M. A., & Vangengeim, E. A. (1997). Late Cenozoic sequences of mammalian sites in Eurasia: an updated correlation. *Palaeogeography Palaeoclimatology Palaeoecology, 133*, 259–288.

Fejfar, O., Mein, P., & Moissenet, E. (1990). Early Arvicolids from the Ruscinian (Early Pliocene) of the Teruel Basin. In O. Fejfar & W.-D. Heinrich (Eds.), *International symposium: Evolution, phylogeny and biostratigraphy of arvicolids (Rodentia, Mammalia)* (pp. 133–164). Prague: Geological Survey, Czechoslovakia.

Froese, R., & Pauly, D. (eds.) (2013). FishBase. World Wide Web electronic publication. Version (10/2013). Available at: www.fishbase.org.

Frost, D. R. (2014). Amphibian species of the world: An online reference. Version 6.0. Electronic database. Accessible at http://research.amnh.org/herpetology/amphibia/index.html. Accessed 26 Feb 2014.

Furió, M., & Angelone, C. (2010). Insectivores (Erinaceidae, Soricidae, Talpidae; Mammalia) from the Pliocene of Capo Mannu D1 (Mandriola, central-western Sardinia, Italy). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 258*, 229–242.

Furió, M., Casanovas-Vilar, I., & van den Hoek Ostende, L. W. (2011). Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Palaeogeography Palaeoclimatology Palaeoecology, 304*, 219–229.

García-Alix, A., Minwer-Barakat, R., Martín Suárez, E., Freudenthal, M., & Martín, J. M. (2008). Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeography Palaeoclimatology Palaeoecology, 265*(3-4), 214–225.

Gaudant, J. (1993). L'ichthyofaune lacustre du Miocène d'Etili (Anatolie occidentale, Turquie): un réexamen. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 6*, 335–344.

Gromov, V. J., & Polyakov, I. Y. (Eds.). (1977). *Fauna of the SSSR.Mammals, III, 8: voles (Microtinae)*. Leningrad: Nauka.

Hoek Ostende, L. W. van den (2001). Insectivore faunas from the lower Miocene of Anatolia. Part 8: stratigraphy, palaeoecology, palaeobiogeography. *Scripta Geologica, 122*, 101–122.

Hoek Ostende, L. W. van den, Diepenveen, F., Tesakov, A. S., Saraç, G., Mayhew, D., & Alçiçek, M. C. (2015). On the brink: micromammals from the latest Villanyian from Bıçakçı (Anatolia). *Geological Journal*. doi:10.1002/gj.2622.

Holman, J. A. (2000). *Fossil snakes of North America: origin, evolution, distribution, paleoecology* (p. 357). Bloomington: Indiana University Press.

Hordijk, K., & Bruijn, H. de (2009). The succession of rodent faunas from the Moi/Pliocne lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). *Hellenic Journal of Geosciences, 44*, 21–103.

Ivanov, M. (2007). Herpetological assemblages from the Pliocene to middle Pleistocene in Central Europe: palaeoecological significance. *Geobios, 29*, 297–320.

Koenigswald, W. von (1980). Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 539*, 1–129.

Kowalski, K. (1960). Cricetidae and Microtidae (Rodentia) from the Pliocene of Weze (Poland). *Acta Zoologica Cracoviensia, 5*(11), 447–506.

LaDuke, T. C. (1991). The fossil snakes of Pit 91, Rancho La Brea, California. *Natural History Museum of Los Angeles County Contributions in Science, 424*, 1–28.

Martín Suarez, E., & Mein, P. (1998). Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios, 31*, 87–97.

Maul, L. (1996). A discussion on the referal of *Mimomys occitanus* Thaler, 1955 (Rodentia, Arvicolidae) to the genus *Mimomys. Acta Zoologica Cracoviensia, 39*(1), 343–348.

Mayhew, D. F. (1978). Late Pleistocene small mammals from Arnissa (Macedonia, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B, 81*, 302–323.

Mein, P., & Michaux, J. (1970). Un nouveau stade dans l'évolution des rongeurs pliocenes de l'Europe sud-occidentale. *Comptes Rendus de l'Academie des Sciences Paris, 270*(D), 2780–2783.

Michaux, J. (1971). Arvicolinae (Rodentia) du Pliocène terminal et du Quaternaire ancien de France et d'Espagne. *Palaeovertebrata, 4*, 137–214.

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., & Freudenthal, M. (2004). Arvicolidae (Rodentia) from the Pliocene of Tollo de Chiclana (Granada, SE Spain). *Geobios, 37*(5), 619–629.

Pasquier, L. (1974). Dynamique evolutive d'un sous-genre de Muridae, *Apodemus* (*Sylvaemus*). Etude biometrique des caracteres dentaires de populations fossils et actuelles d'Europe occidentale. *Universite des sciences et techniques du Languedoc*, 1-183.

Popov, V. (2004). Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria). *Geodiversitas, 26*(3), 403–491.

Rabeder, G. (1981). Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie von Österreich, 8*, 1–373.

Radulescu, C., Samson, P., Sen, S., Stiuca, E., Horoi, V. (1997). Les Mammiféres Pliocénes de Dranic (Bassin Dacique, Roumanie). Acte du Congrès BiochroM'97. In: Aguilar, J.-P., Legendre, S., Michaux, J. (eds.). *Memoires et Travaux de l'École Pratique des Hautes Études, Institut Montpellier*, 21, 635–647.

Rage, J.–C. (1984). *Serpentes*. In P. Wellnhofer (Ed.), *Encyclopedia of Paleoherpetology, Part 11* (pp. 1–80). Stuttgart: Gustav Fischer Verlag.

Rage, J.–C., & Sen, S. (1976). Les amphibians et les reptiles du Pliocène supérieur de Çalta (Turquie). *Géologie Mediterranéenne, 3*, 127–134.

Reumer, J. W. F. (1984). Ruscinian and early Pleistocene Soricidae (Insectivorea, Mammalia from Tegelen (The Netherlands) and Hungary. *Scripta Geologica, 73*, 1–173.

Richter, T., & Wächtler, K. (1999). Zur Reproduktionsbiologie von *Bithynia tentaculata* (L. 1758) in Norddeutschland. *Heldia, 4*, 47–52.

Roček, Z. (2004). Late Miocene Amphibia from Rudabánya. *Palaeontographica Italica, 90*, 11–29.

Rückert-Ülkümen, N. (1987). Muş ve Aladağ'ın fauna ve florası hakkında (On fauna and flora of Muş and Aladağ). *Bulletin Geological Society of Turkey, 30*, 15–18.

Rückert-Ülkümen, N., & Yiğıtbaş, E. (2007). Pharyngeal teeth, lateral ethmoids, and jaw teeth of fishes and additional fossils from the late Miocene (Late Khersonian / Early Maeotian) of Eastern Paratethys (Yalova, near Istanbul, Turkey). *Turkish Journal of Earth Sciences, 16*, 211–224.

Rückert-Ülkümen, N., Böhme, M., Reichenbacher, B., Heissig, K., Witt, W., & Bassler, B. (2002). Die Fossilführung des kontinentalen Neogens (Ober-Miozän/Unter-Pliozän) von Develiköy (Manisa, Türkei). *Mitteilungen Bayerische Staatssammlung für Paläontologie Historische Geologie, 42*, 51–74. + 3 plates.

Sanchiz, B. (1998). Salientia. In P. Wellnhofer (Ed.), *Encyclopedia of Paleoherpetology, Part 4* (pp. 1–275). München: Verlag Dr. Friedrich Pfeil.

Saraç, G. (2003). *Vertebrate fossil localities of Turkey.* Scientific Report No. 10609. Ankara: The General Directorate of the Mineral Research and Exploration of Turkey (MTA).

Sen, S., Bouvraine, G., & Geraads, D. (1998). Pliocene vertebrate locality of Çalta, Ankara, Turkey. 12. Paleoecology, biogeography and biochronology. *Geodiversitas, 20*, 497–510.

Şenel, M. (1997). *Geological maps of Turkey in 1:250000 scale: Fethiye sheet*. Ankara: Mineral Research and Explanation Directorate of Turkey.

Sickenberg, O., Becker-Platen, J. D., Benda, L., Berg, D., Engesser, B., Gaziry, W., Heissig, K., Hünermann, K. A., Sondaar, P. Y., Schmidt-Kittler, N., Staesche, K., Staesche, U., Steffrens, P., & Tobien, H. (1975). Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie. *Geologisches Jahrbuch Reihe B, Hefte, 15*, 1–167.

Simons, A. M., & Mayden, R. L. (1997). Phylogenetic relationships of the creek chubs and the spine-fins: an enigmatic group of North American cyprinid fishes (Actinopterygii: Cyprinidae). *Cladistics, 13*, 187–20.

Špinar, Z. V. (1972). *Tertiary frogs from Central Europe* (p. 286). The Hague: Dr. W. Junk N.V.

Storch, G., & Dahlmann, T. (1995). Murinae (Rodentia, Mammalia). In Schmidt-Kittler, N. (ed.) The vertebrate locality Maramena. *Münchner Geowissenschaftliche Abhandlungen A*, *28*, 121–132.

Suata-Alpaslan, F. (2010). The paleoecology of the continental early Pliocene of the eastern Mediterranean, a construction based on rodents. *Cumhuriyet Üniversitesi Fen-Edebiyat Fakültesi Fen Bilimleri Dergisi, 31*(2), 29–48.

Tadajewska, M. (1998). Pharyngeal teeth and shape of the ossa pharyngea inferiora during development of *Abramis brama* (L.) and *Blicca bjoerkna* (L.) (Cyrprinidae). *Cybium, 22*, 123–147.

Tesakov, A. S. (1998). Voles of the Tegelen fauna. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 60*, 71–134.

Tesakov, A. S. (2004). *Biostratigraphy of middle Pliocene* (Eopleistocene of Eastern Europe (based on small mammals), p. 247). Moscow: Nauka.

The Reptile Database (2013). Electronic database, Accessible at: http://reptile-database.org/ Accessed 26 Feb 2014.

Topachevsky, V. A., & Nesin, V. A. (1989). *Rodents of the Moldavian and the Khaprovian faunistic complexes of the Kotlovina section* (p. 134). Kiev: Naukova Dumka.

Ünay, E. (2006). Rodents from the upper Miocene hominoid locality Çorakyerler (Anatolia). *Beiträge zur Paläontologie, 30*, 453–467.

Ünay, E., & Bruijn, H. de (1998). Plio-Pleistocene rodents and lagomorphs from Anatolia. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 60*, 431–466.

Weerd, A. van de (1979). Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B, 82*(2), 127–170.

Venczel, M. (2004). Middle Miocene anurans from the Carpathian Basin. *Palaeontographica Abteilung A, 271*, 151–174.

Venczel, M., & Sen, S. (1994). Pleistocene amphibians and reptiles from Emirkaya-2, Turkey. *Herpetological Journal, 4*, 159–165.

Wautier, K., Heyden, C. van der, & Huysseune, A. (2001). A quantitative analysis of pharyngeal tooth shape in the zebrafish (*Danio rerio*, Teleostei, Cyprinidae). *Archives of Oral Biology, 46*, 67–75.

Weerd, A. van de (1976). Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropalaeontological Bulletin Special Publication, 2*, 1–217.

Weerd, A. van de (1979). Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B, 82*(2), 127–170.

Wuttke, M., Přikryl, T., Ratnikov, V. Y., Dvořák, Z., & Roček, Z. (2012). Generic diversity and distributional dynamics of the Palaeobatrachidae (Amphibia: Anura). *Palaeobiodiversity and Palaeoenvironments, 92*(3), 367–395.