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Research Paper

Early Pliocene Spalacinae from the locality of Afşar, western Turkey ☆

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ABSTRACT

Spalacinae are an unusual component of the fossil record around the world with a limited geographical distribution. The revisited section of Afşar includes one of the richest collections of Spalacinae in Turkey. From Afşar 1, near the base of the section we recovered *Pliospalax* cf. *macoveii* while in Afşar 2, at the top of the section we distinguish the species *P. tourkobouniensis*. The current research includes the first record of the last-mentioned species outside of Europe. Both spalacines indicate a dry and open space environment and, in accordance with the Arvicolinae, suggest that Afşar 1 can be attributed to MN 15 while Afşar 2 is correlated to MN 16.

1. Introduction

Turkey, positioned as a bridge between Europe, Asia and Africa, has always been an area of particular interest to palaeontologists. Focusing on the Late Miocene-Early Pliocene of this vast region, a transition in the paleo-environment period can be observed. The warm and seasonally arid environment of the Miocene, was succeeded by the cooler conditions and the humid–arid climate cyclicity of the Pliocene (Eronen et al., 2009; Jiménez-Moreno et al., 2015). This transition enriched the Eurasian vertebrate faunas (Koufos, 2013; Koufos and Vasileiadou, 2015; Koufos, 2016; Van den Hoek Ostende et al., 2020). However, despite the importance of both periods, our understanding of the Pliocene of Turkey is limited (Erdal, 2017). Despite a large number of localities (Ünay and De Bruijn, 1998), the fossil record remains largely unpublished (Van den Hoek Ostende et al., 2015).

Field campaigns of the project "Surveys for the identification of fossil localities of Neogene and Pleistocene periods in the province of Afyon and Burdur" led by one of us (FAD) from Burdur Mehmet Akif Ersoy University, revealed a vast number of promising new localities. Part of this project was revisiting the Afşar section, which was recognized as important for fossil mammals in the early 1990s by Gerçek Saraç (geologist at the MTA; Mineral Research and Exploration General Directorate) (Saraç, 2003; Demirel et al., 2019). The Afşar section is represented in the Dombayova graben of the Western Anatolia, a territory of late Neogene postorogenic crustal extension which is prominent with a broad array of NE-trending orogen-top basins represented by a synchronic, rather uniform superimposition of alluvial, fluvial, and lacustrine sediments (Alçiçek et al., 2019). In Afşar section, two different fossiliferous layers were recognized at the bottom and the top of the lacustrine sediments, and they were designated as the Afşar 1 and Afşar 2 localities, respectively (Skandalos et al., 2023; Fig. 1). The two assemblages comprise a rich variety of micromammal taxa. The occurrence of *Mimomys* cf. *gracilis* (Kretzoi, 1959), *Pliomys* sp. Méhely, 1914, and *Cricetulus* cf. *ehiki* (Schaub, 1930) in Afşar 1 places it in MN 15 or early MN 16, while *Mimomys hassiacus* Heller, 1936, *M. gracilis*, *Pliomys graecus* De Bruijn and Van der Meulen, 1975, *Cricetulus* sp. Milne-Edwards, 1867, and *Mesocricetus primitivus* De Bruijn et al., 1970 in Afşar 2 correlate it to MN 16 (Skandalos et al., 2023). However, the rest of the fauna will better test the proposed ages of both Afşar assemblages as well as render a better assumption of their paleoenvironments.

In this paper, we describe the Spalacinae from the Afşar assemblages. The taxonomy of the group is complicated, even at the suprageneric level. In zoological literature, blind moles are commonly referred to as the family Spalacidae, comprising the rhizomyines, myospalacines, tachyorictines, and spalacines (Steppan and Schenk, 2017; He et al., 2019). Paleontologists tend to empha-

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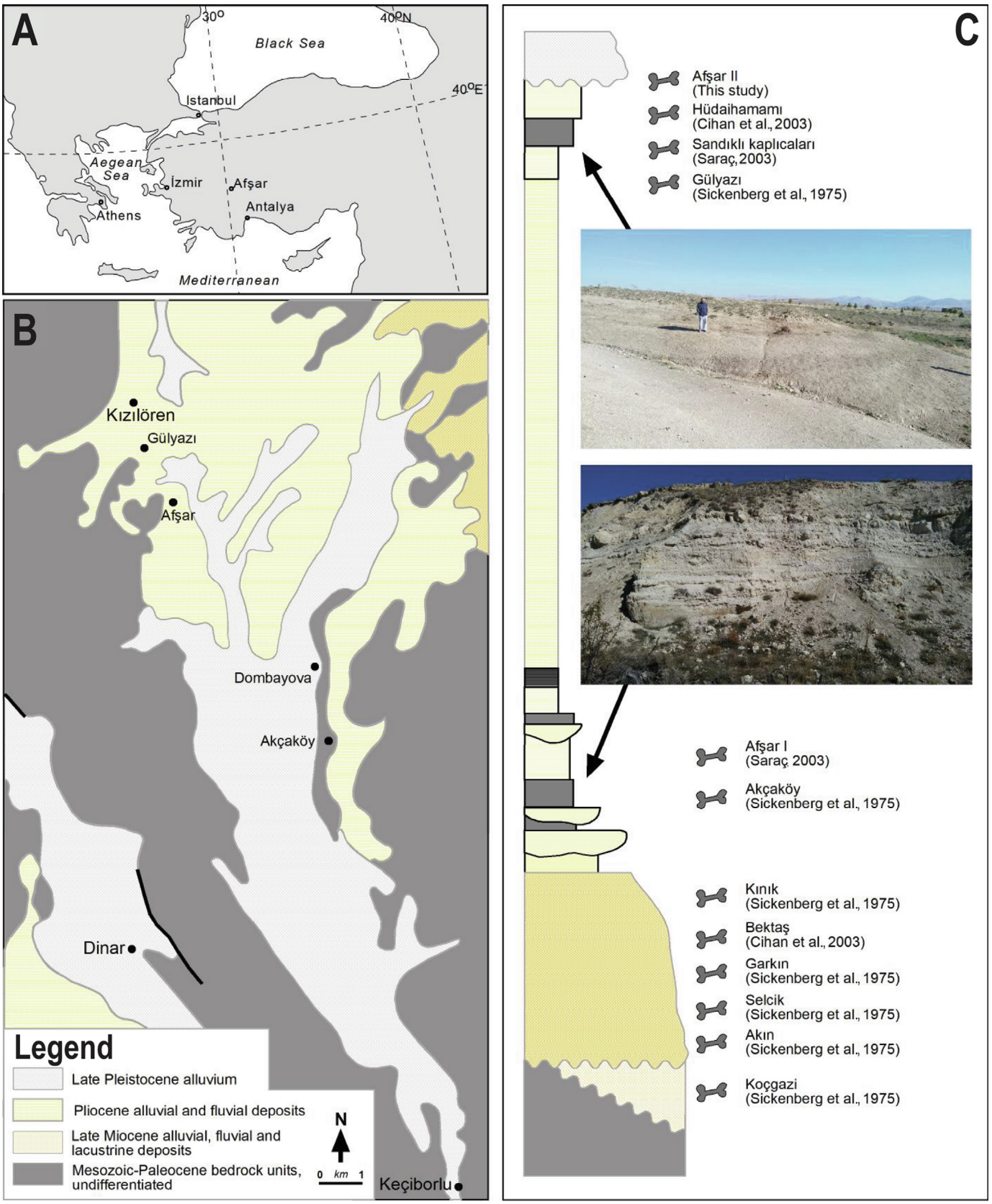

Fig. 1. A. Geographic position of the Afşar locality. **B.** Geological map of the Dombayova Graben with the Afşar locality (after Turan, 2002). **C.** Stratigraphy of Dombayova Graben based on fossil data from Sickenberg et al. (1975), Saraç (2003), Cihan et al. (2003), Balcı (2011) and this study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sise the separate development of the subfamilies. Flynn (2009) retained Spalacinae and Rhizomyinae (including the tachyorictines) as subfamilies within the Spalacidae and considered the myospalacines presumably "derivatives of early rhizomyine evolution". The same author underlines the need for additional research on the relationship between the various taxa. De Bruijn et al. (2015) state that spalacines and rhizomyines do not share the same murid ancestor and recognize them as separate subfamilies within the Muridae. This seems in sharp contrast to the tree given by Steppan and Schenk (2017: fig. 1), that separates the spalacid stock from murids. However, as these authors point out, the molecular data only provide information on the recent diversification. Based on these data, we cannot assess the diversification of the Oligocene stem group murids, which may provide the link between the modern murid lineages and the, presumably separate, development of the spalacine lineages. Therefore, we follow De Bruijn et al. (2015) in their classification.

The Spalacinae have a restricted range in eastern Europe, Asia Minor, parts of the Middle East up to western Siberia. They are adapted to a subterranean life as inhabitants of steppic environments and grasslands (Sarıca and Şen, 2003). Notably, the fossil range of the subfamily reflects very much its current geographic distribution (Ünay, 1999; De Bruijn et al., 2015; He et al., 2019). The fossil record is long and fairly continuous, dating back to the Late Oligocene of southeastern Europe (De Bruijn et al., 2013, 2015). It comprises seven genera: *Spalax* Güldenstädt, 1770, *Pliospalax* Kormos, 1932, *Heramys* Klein Hofmeijer and De Bruijn, 1985, *Debruijnia* Ünay, 1996, *Sinapospalax* Sarıca and Şen, 2003, *Vetusspalax* De Bruijn et al., 2013, and *Pannoniamys* van de Weerd et al., 2022. Although the subfamily appears in many fossil assemblages, it is usually represented by a few elements per locality only. Presumably, the rarity in assemblages is linked to the fossorial lifestyle, which makes spalacines a difficult target for birds of prey, one of the main agents for the accumulation of fossil remains (Andrews, 1990). Similar to other rare and remarkably rich localities such as Çalta (Şen, 1977), the Afşar assemblages stand out in having a high number of specimens compared to other occurrences of spalacines. As such, the spalacines of the Afşar sections provide not only an important reference point for resolving taxonomical problems of the genus, but also a chance to follow evolutionary trends within a section.

2. Material and methods

The studied material has been collected from two stratigraphic levels outside of the Afşar village in Afyonkarahisar Province of Turkey. The specimens were collected by wet screening on a set of sieves with the finest mesh used being 500 μm. The Afşar assemblages include 52 Spalacinae molars of which 10 (1 M1, 3 M2, 3 M3, 1 m1, 2 m3) occur in Afşar 1 and 42 (6 M1, 9 M2, 3 M3, 8 m1, 12 m2, 4 m3) are from Afşar 2. The complete collection of the locality is stored in the Natural Museum of Ege University of Izmir in Turkey. The specimens were illustrated as if they were all right molars. The generic classification and the terminology for the dental descriptions follow Sarıca and Şen (2003: fig. 1). The maximum length (L) and width (W) of the occlusal surface of cheek molars have been measured with a Leica 16A microscope with Leica application suite software and are given in mm. In order to describe the wear stages of the molars, we follow Skandalos and Van den Hoek Ostende (2023: fig. 12).

3. Systematic palaeontology

Class Mammalia Linnae, 1758
Order Rodentia Bowdich, 1821.
Family Muridae Illiger, 1811.
Subfamily Spalacinae Gray, 1821.
Genus ***Pliospalax*** Kormos, 1932.

Species included: *P. macoveii* (= *P. sotirisi*) (Simionescu, 1930), *P. compositodontus* (Topachevski, 1969), *P. tourkobouniensis* De Bruijn and Van der Meulen, 1975, *P. complicatus* Şen and Sarıca, 2011.

Pliospalax cf. *macoveii*
Fig. 2
Type locality: Măluşteni, Romania.
Locality: Afşar 1.
Measurements: see Table 1.

Description: The M1 (Fig. 2(A)) is elongated and has three roots. The only available specimen is worn. The anterocone is fused as almost perpendicular to the length of the anteroloph; the latter connects to the protocone. The wide paracone is anteriorly oriented, the mesoloph is absent and the metacone is fused into the posteroloph. The anterosinus, the mesosinus and the sinus create a "W" shape pattern. The presence of a posterosinus cannot be observed due to the advanced wear stage of the molar.

The M2s (Fig. 2(B)) have a square shape and three roots. The anterocone is fused into the anteroloph ending freely on the anterior side of the paracone. The mesoloph is absent. The anterosinus, the mesosinus and the sinus are deep and well-developed. The metalophule and the posteroloph enclose a shallow posterosinus that disappears in later wear stages.

The M3s (Fig. 2(C)) have a sub-triangular outline with one wide root. The anteroloph connects to the protocone and the paracone. A small emargination in the labial part of the anterior outline indicates the presence of a shallow anterosinus that disappears in early wear stages. The sinus is closed. The metalophule is connected to the small hypocone. The posteroloph connects to the metacone and together they enclose the shallow posterosinus.

The m1 (Fig. 2(D)) has two roots. The only available specimen is in late wear stage C. The anterior border of the molar is rounded with the anteroconid fused into the anterolophulid. The labial anterolophulid connects to the protoconid lingually to the metaconid. The long posterior metalophulid connects to the hypolophulid and the short mesolophid. This connection forms a shallow enamel island. The sinusid and the mesosinusid are well-developed. The posterolophid connects to the metaconid and the posterosinusid is closed, shaped as an enamel island.

The m3s (Fig. 2(E)) have a sub-triangular shape and two roots. The labial anterolophid connects to the protoconid. The well-developed lingual anterolophid connects to the metalophulid with its lingual end at the lingual border of the molar. A small anterosinusid is present. The short hypolophulid connects to the weak ectolophid. The hypoconid is fused into the posterolophid, which is connected to the entoconid. The mesosinusid and the sinusid are well-developed and deep. One of the two m3s has an enclosed posterosinusid (PV-AFS-473).

Remarks: The small to medium molar size, the round anterior border of the m1 without the anterosinusid, the lack of the mesoloph in the M1 and M2, the incorporated protocone of the M1 into the anteroloph and the posteriorly oblique metalophule indicate that the spalacine from the lower layer of Afşar belongs to *Pliospalax* (Table 2). Its molars are similar in size to *P. complicatus* Şen and Sarıca, 2011 from Amasya in Turkey (Figs. 3–5). However, the sample differs morphologically due to the absence of a long mesolophid in the m1. The material from Afşar 1 differs from *P. compositodontus* Topachevski, 1969 from Andreevka in Ukraine in not having a well-developed mesoloph in M1 and M2. The size of the M1, m1 and m3 from Afşar 1 is close to those of *P. tourkobouniensis* De Bruijn and Van der Meulen, 1975. The M3s,

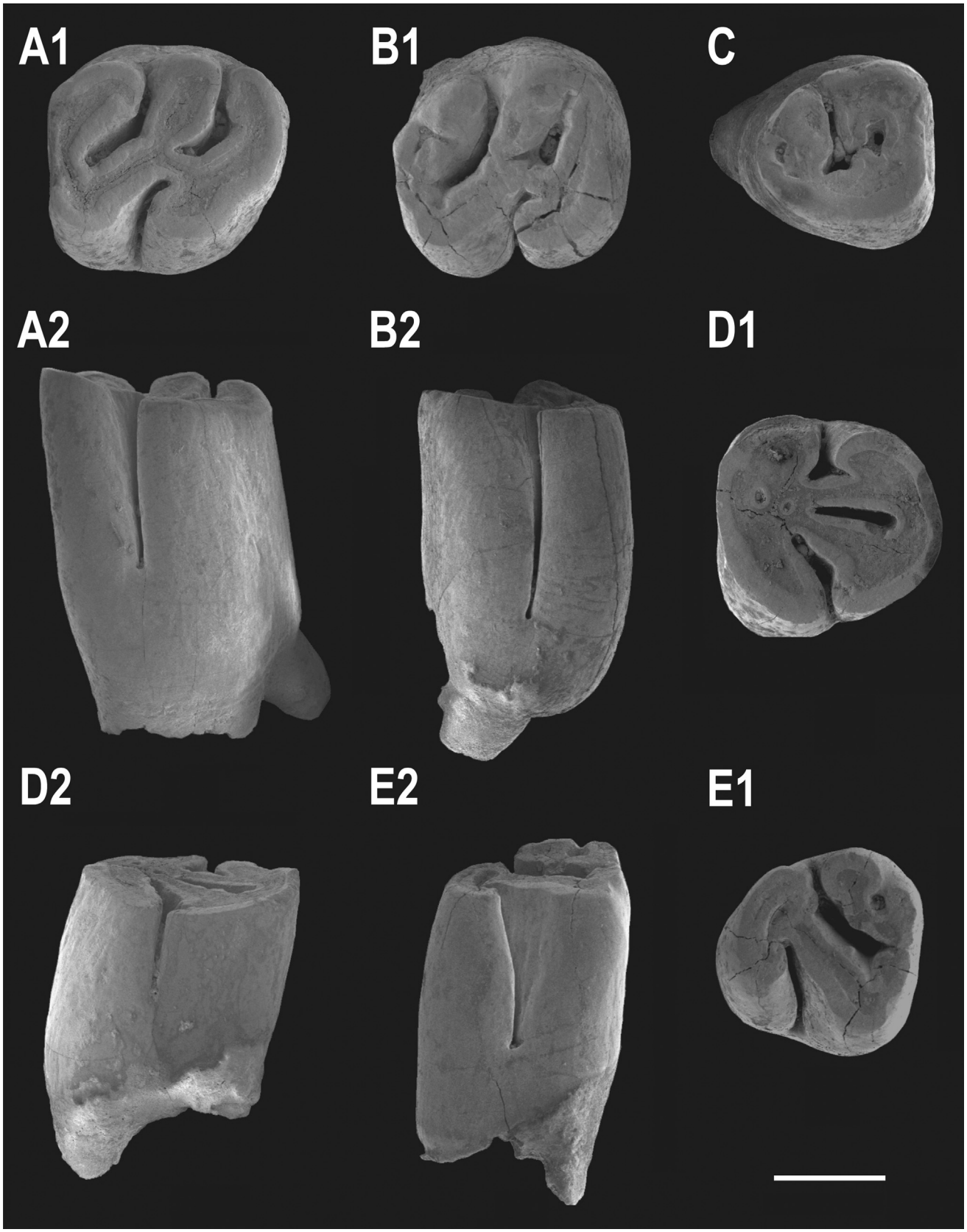

Fig. 2. Upper and lower molars of *Pliospalax* cf. *macoveii* from Afşar 1. **A.** M1, PV-AFS-465, in occlusal (A1) and labial (A2) views. **B.** M2, PV-AFS-466, in occlusal (B1) and labial (B2) views (mirrored images). **C.** M3, PV-AFS-469, in occlusal view. **D.** m1, PV-AFS-472, in occlusal (D1) and labial (D2) views (mirrored images). **E.** m3, PV-AFS-473, in occlusal (E1) and labial (E2) views. Scale bar: 1 mm.

Table 1
Measurements (in mm) of *Pliospalax* cf. *macoveii* from Afşar 1.

	Length				Width			
Tooth	**N**	**Min**	**Max**	**Mean**	**N**	**Min**	**Max**	**Mean**
M1	1	2.48	2.48	2.48	1	2.25	2.25	2.25
M2	3	2.03	2.25	2.13	3	1.90	2.13	2.04
M3	3	1.70	1.88	1.76	3	1.67	1.87	1.75
m1	1	2.22	2.22	2.22	1	2.12	2.12	2.12
m2	–	–	–	–	–	–	–	–
m3	2	1.74	1.99	1.86	2	1.78	1.83	1.80

Table 2
Stratigraphic and geographic distribution of the *Pliospalax* species (Simionescu, 1930; Topachevski, 1969; De Bruijn et al., 1970; De Bruijn and Van der Meulen, 1975; Şen, 1977; Popov, 2004; Şen and Sarıca, 2011).

Species	**Locality**	**Country**	**MN**
P. tourkobouniensis De Bruijn and Van der Meulen, 1975	Tourkobounia-1	Greece	16
P. macoveii (Simionescu, 1930)	Măluşteni	Romania	15
	Bereşti		15
	Çalta	Turkey	15
	Muselievo	Bulgaria	15
	Maritsa	Greece	14
P. compositodontus (Topachevski, 1969)	Andreevka	Ukraine	13
P. complicatus Şen and Sarıca, 2011	Amasya	Turkey	13

however, are larger than those from the Greek locality. The size difference and the lack of the lingual re-entrant fold in the M3, differentiate the species from *P. tourkobouniensis*. The m1 from Afşar 1 is similar to *P. macoveii* (Simionescu, 1930) from the type locality of Măluşteni (Topachevski, 1969; Crespo et al., 2023). The m3s, however, are larger than those from the type locality. Furthermore, the M1s and M2s are larger in size than those from Bereşti in Romania (Crespo et al., 2023). The material from Afşar 1 is within the size range of *P. macoveii* from Çalta. Despite the smaller M1 and the larger M3, the material from Afşar 1 resembles *P. macoveii* (De Bruijn et al., 1970) from Maritsa, on Rhodes Island. The M1 and M2 are similar to *P.* cf. *macoveii* from Muselievo in Bulgaria (Popov, 2004). The M3 and m1 are larger in size than those in the Bulgarian locality. Morphologically, the spalacine from Afşar 1 is similar to *P. macoveii* in the lack of the mesoloph in the M1 and M2, the sole re-entrant fold in the M3, the lack of the anterosinusid, the short mesolophid in the m1 and the size of the molars. Notably, the *P. macoveii* assemblage from Muselievo does have a mesoloph in the M1. De Bruijn and Van der Meulen (1975) stated that *P. macoveii* and *P. sotirisi* are closely related and possibly synonymous species. Skandalos and Van den Hoek Ostende (2023), using virtual reconstruction techniques to analyse the molars from diverse *Pliospalax* species, distinguished different wear stages and categorising *P. sotirisi* as an early phase C of *P. macoveii*, synonymized the two species. In this study we follow these findings. However, since the material from Afşar 1 is limited and the wear stage of the sole m1 and M1 does not allow to observe important characters like the anterosinusid and the protosinusid of the m1, it is classified as *Pliospalax* cf. *macoveii*.

Pliospalax tourkobouniensis De Bruijn and Van der Meulen, 1975.
Figs. 6, 7

Type locality: Tourkobounia-1, Greece.

Locality: Afşar 2.

Measurements: see Table 3.

Description: The M1 (Fig. 6(A, B)) have a rectangular outline and three roots. The anterocone and the protocone are fused into the anteroloph. The paracone is wide and anteriorly oriented. The mesoloph is absent. The metalophule is directed backwards and connects to the strong posteroloph. The latter is developed perpendicular to the length of the molar, ending on the labial border of the molar, behind the metacone. The molars have four well-developed re-entrant folds. Three are on the labial side of the molar. These are the anterosinus, the mesosinus and the posterosinus. In later wear stages, the specimens lack the latter (wear stage C). The lingual side of the molar has one re-entrant fold, the sinus.

The M2s (Fig. 6(C)) have a square shape with three roots. The anterocone is fused into the anteroloph. The paracone is elongated with a posteriorly directed arm and the mesoloph is absent. The metalophule is directed posteriorly. The posteroloph is developed perpendicular to the length, ending freely at the labial border of the molar. The anterosinus, the mesosinus, the sinus and the posterosinus are present. In later wear stages, the anterosinus is closed and the posterosinus disappears (wear stages B and C).

The M3s (Fig. 6(D) have a sub-triangular outline and a single wide root. The anteroloph is connected both to the protocone and to the protolophule. The protocone is fused to the latter. The ectoloph is present and the molars lack the mesoloph. The metalophule is connected to the small hypocone. The mesosinus communicates with the sinus. The posteroloph encloses a shallow posterosinus that disappears in worn specimens (wear stage C).

The m1s (Fig. 7(A, B)) are elongated and have two roots. The anteroconid is incorporated into the anterolophid. The labial anterolophid meets the anterior part of the protoconid and its labial end ends at the border of the molar. The posterior part of the lingual anterolophid connects to the metalophulid. In early stages of wear (wear stage B), the metaconid is incorporated into the anterolophid. Both the anterosinusid and the protosinusid are present. They are shallow and disappear in worn specimens (wear stages C and D). The mesosinusid, the sinusid and the posterosinusid are present. The posterior metalophulid connects to the hypolophulid or it ends freely in the mesosinusid. The hypolophulid connects with the posterolophid. The latter is rather perpendicular to the length of the molars. The posterosinusid is present and in worn specimens it forms an enamel island (Fig. 7 (B1)). One of the eight specimens (PV-AFS-441) has the hypolophulid with an additional, posteriorly directed ridge forming two enamel islands (Fig. 7(A1)).

The m2s (Fig. 7(C, D)) have a square-shaped outline and two roots. The labial anterolophid connects to the protoconid. The lingual anterolophid connects to the metalophulid and to the metaconid, enclosing a shallow anterosinusid; the latter disappears in a later wear stage (wear stage B). The sinusid, the mesosinusid and the posterosinusid are well-developed. The mesolophid is short and ends freely in the mesosinusid. The posterolophid ends in the lingual border of the molar. In worn specimens, it connects to the entoconid, enclosing the posterosinusid (wear stage C).

The m3s (Fig. 7(E, F)) have a sub-triangular shape and two roots. One of the four specimens (PV-AFS-459) has the metalophulid isolated. The other molars have the lingual anterolophid connected to the metalophulid. The labial anterolophid encloses the shallow protosinusid, which disappears in worn specimens (wear stage

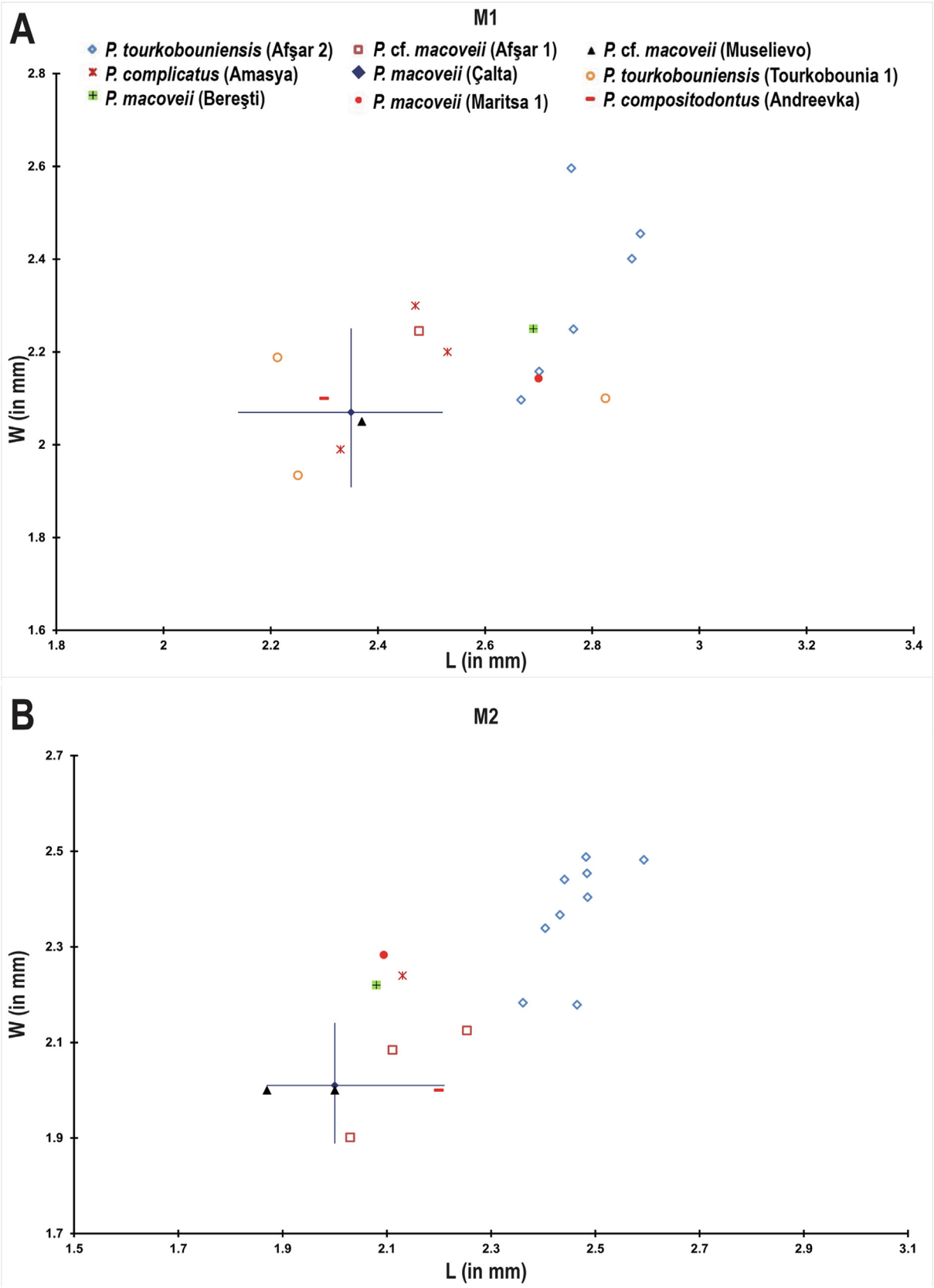

Fig. 3. L/W scatter plot of M1 (**A**) and M2 (**B**) molars of *Pliospalax macoveii* (and *P.* cf. *macoveii*) from Afşar 1, Bereşti, Maritsa 1, Çalta and Muselievo (De Bruijn et al., 1970; Şen, 1977; Crespo et al., 2023); *P. tourkobouniensis* from Afşar 2 and Tourkobounia-1 (De Bruijn and Van der Meulen, 1975); *P. complicatus* from Amasya (Şen and Sarıca, 2011); *P. compositodontus* from Andreevka (Topachevski, 1969). Measurements in mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

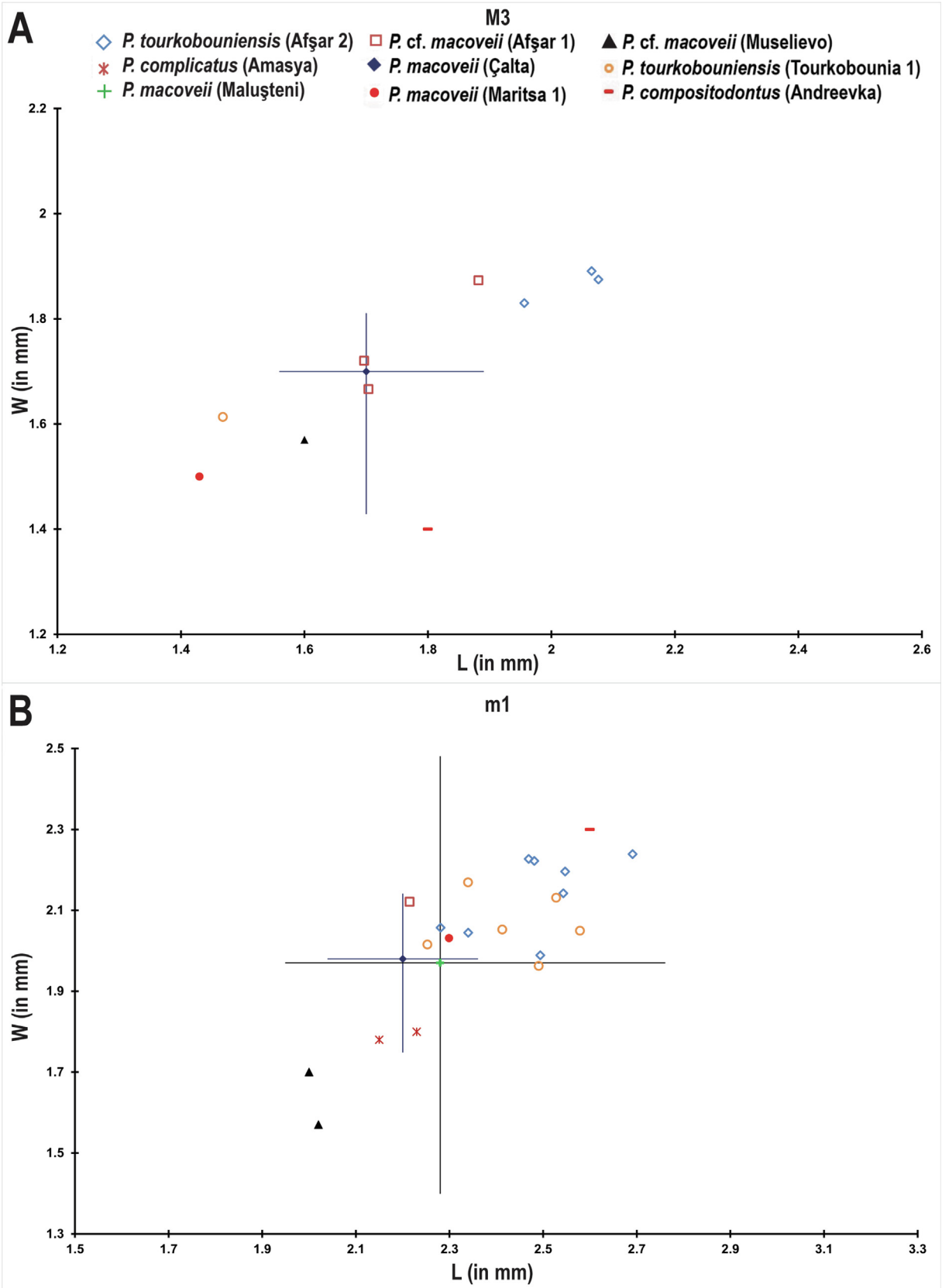

Fig. 4. L/W scatter plot of the M3 (**A**) and m1 (**B**) molars of *Pliospalax macoveii* (and *P.* cf. *macoveii*) from Afşar 1, Măluşteni, Maritsa 1, Çalta and Muselievo (Simionescu, 1930; De Bruijn et al., 1970; Şen, 1977; Crespo et al., 2023); *P. tourkobouniensis* from Afşar 2 and Tourkobounia-1 (De Bruijn and Van der Meulen, 1975); *P. complicatus* from Amasya (Şen and Sarıca, 2011); *P. compositodontus* from Andreevka (Topachevski, 1969). Measurements in mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

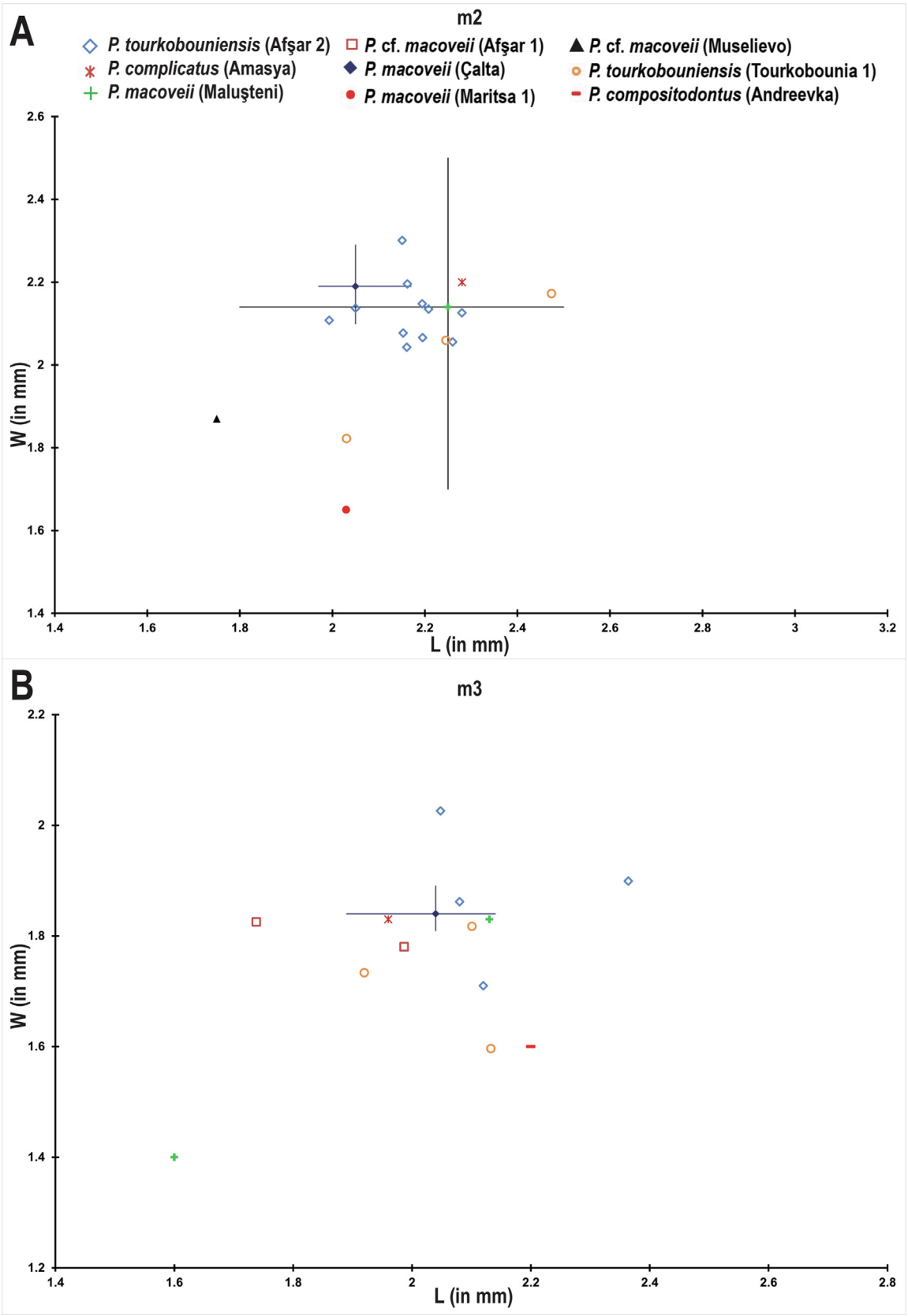

Fig. 5. L/W scatter plot of the m2 (**A**) and m3 (**B**) molars of *Pliospalax macoveii* (and *P.* cf. *macoveii*) from Afşar 1, Măluşteni, Maritsa 1, Çalta and Muselievo (Simionescu, 1930; De Bruijn et al., 1970; Şen, 1977; Crespo et al., 2023); *P. tourkobouniensis* from Afşar 2 and Tourkobounia-1 (De Bruijn and Van der Meulen, 1975); *P. complicatus* from Amasya (Şen and Sarıca, 2011); *P. compositodontus* from Andreevka (Topachevski, 1969). Measurements in mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

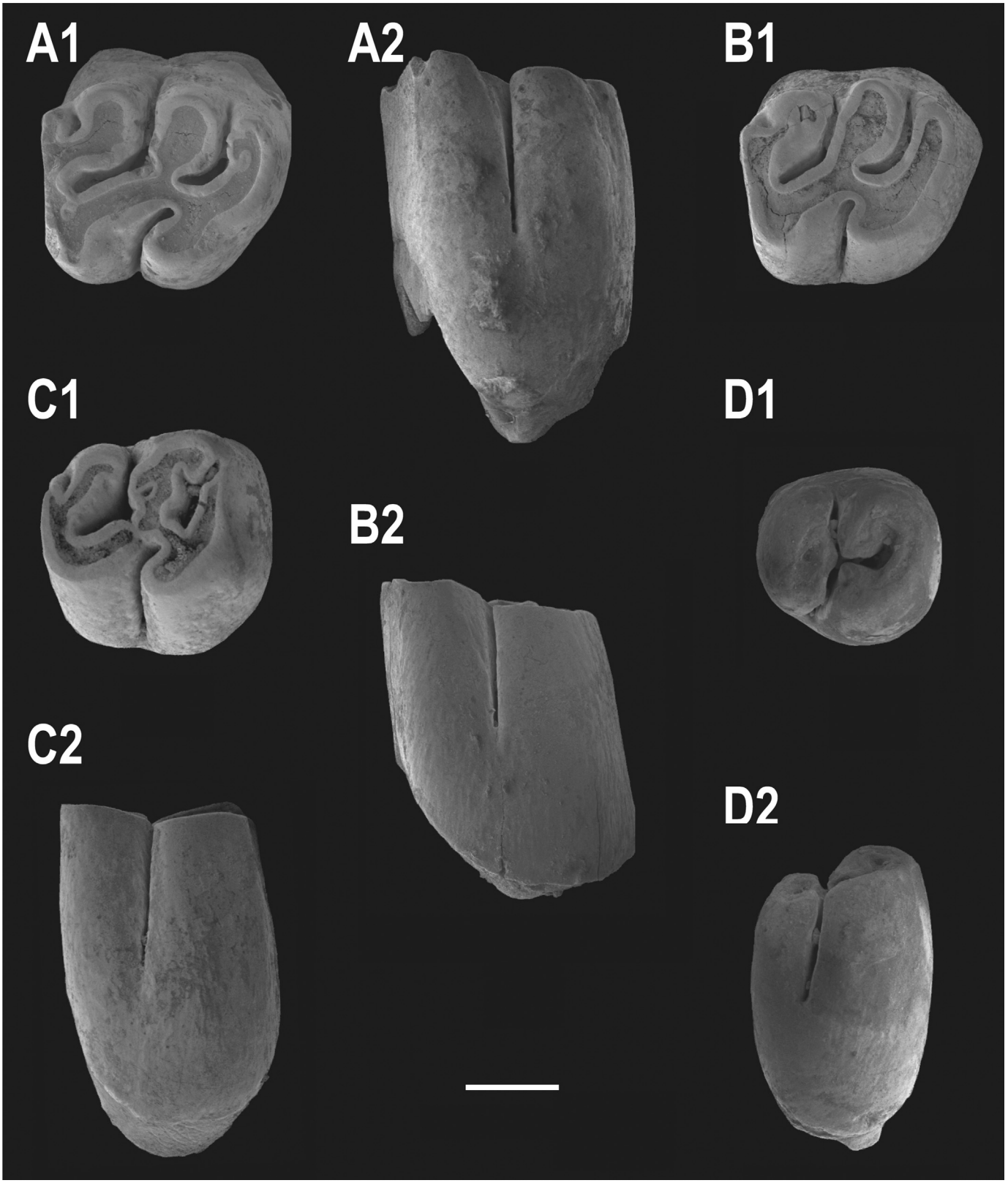

Fig. 6. Upper molars of *Pliospalax tourkobouniensis* from Afşar 2. **A.** M1, PV-AFS-420, in occlusal (A1) and labial (A2) views (mirrored images). **B.** M1, PV-AFS-421, in occlusal (B1) and labial (B2) views (mirrored images). **C.** M2, PV-AFS-433, in occlusal (C1) and labial (C2) views (mirrored images). **D.** M3, PV-AFS-435, in occlusal (D1) and labial (D2) views. Scale bar: 1 mm.

C). The anterosinusid, the mesosinusid and the sinusid are well-developed. A short mesolophid is developed. The hypolophulid connects to the short ectolophid. The hypoconid is fused into the posterolophid, which is connected to the entoconid. The posterolophid encloses the small posterosinusid, which disappears in a later wear stage (wear stage C).

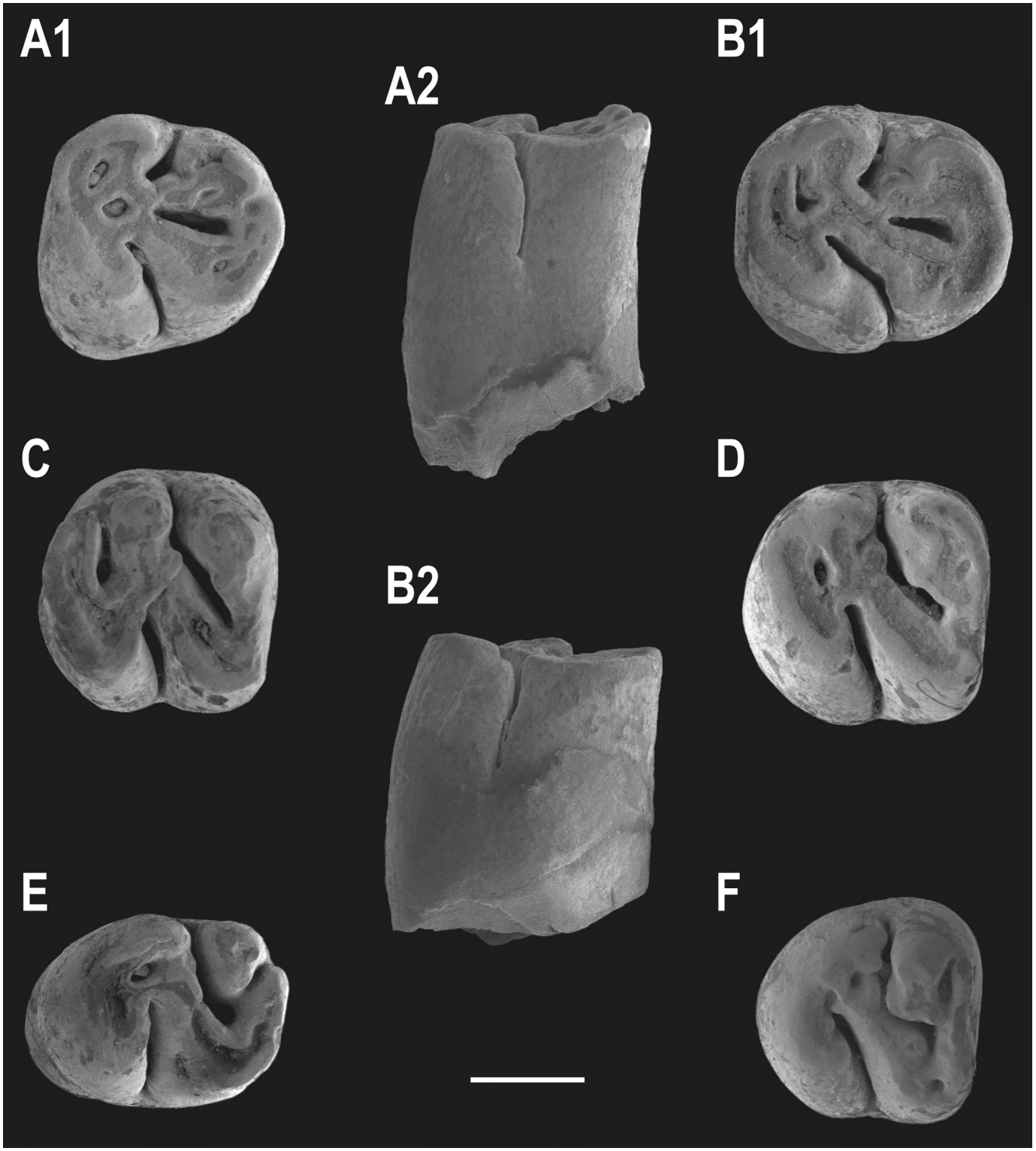

Fig. 7. Lower molars of *Pliospalax tourkobouniensis* from Afşar 2. **A.** m1, PV-AFS-441, in occlusal (A1) and labial (A2) views. **B.** m1, PV-AFS-439, in occlusal (B1) and labial (B2) views. **C.** m2, PV-AFS-449, in occlusal view. **D.** m2, PV-AFS-451, in occlusal view. **E.** m3, PV-AFS-459, in occlusal view. **F.** m3, PV-AFS-460, in occlusal view (mirrored image). Scale bar: 1 mm.

Remarks: The four re-entrant folds in the m1, two in the labial and two in the lingual side, the rounded anterior side, the short mesolophid in the m2 and the protocone entirely incorporated into the anteroloph in the M1 and M2 indicate that the species belongs to *Pliospalax* (Sarıca and Şen, 2003; Şen and Sarıca, 2011). Except for its m1s, the spalacine from Afşar 2 has larger-sized molars than *P. compositodontus* and it lacks the well-developed mesoloph in the M1 and the mesolophid in the m1 (Topachevski, 1969). Despite the larger-sized m3s, the material from Afşar 2 has similarly-sized molars as *P. macoveii* from the type locality of Măluşteni (Topachevski, 1969). Crespo et al. (2023) provided new measurements for the Măluşteni assemblage, but these show a huge

Table 3
Measurements (in mm) of *Pliospalax tourkobouniensis* from Afşar 2.

	Length				Width			
Tooth	N	Min	Max	Mean	N	Min	Max	Mean
M1	6	2.67	2.89	2.78	6	2.10	2.60	2.33
M2	9	2.36	2.59	2.46	9	2.18	2.49	2.37
M3	3	1.96	2.08	2.03	3	1.83	1.89	1.87
m1	8	2.28	2.69	2.48	8	1.99	2.24	2.14
m2	11	1.99	2.28	2.16	11	2.04	2.30	2.13
m3	4	2.05	2.36	2.15	4	1.71	2.03	1.87

variation for the m1 and m2 (Figs. 4, 5), casting some doubt on the homogeneity of that sample. The molar size of the Afşar 2 assemblage is larger than those of the same species from Çalta. The highest values of Çalta's m1 reach those of Afşar 2. The molars are also larger in size than *P.* cf. *macoveii* from Muselievo (Popov, 2004) and from Bereşti (Crespo et al., 2023). Finally, other than the similar sized m1s, the other molars from Afşar 2 are larger than those of *P.* cf. *macoveii* from Afşar 1. Regardless of the size differences, the *Pliospalax* species from Afşar 2 differs from *P. macoveii* (including *P. sotirisi*) from the former localities, by the presence of the anterosinusid in the m1 and the well-developed posteroloph in the M1. In addition, the material of this study differs from *P.* cf. *macoveii* from Muselievo by the lack of the mesoloph in the M1. The M1, M2, m1 and m3 are larger in size than those from *P. complicatus* from Amasya in Turkey (Şen and Sarıca, 2011). The presence of the anterosinusid in the m1 is a character similar in both species. However, m1 lacks the well-developed mesolophid of the species from Amasya. In addition, the m2s have a much shorter mesolophid compared to the strong one of *P. complicatus*. The size of the molars from Afşar 2, especially that of the m1s, fits well within the size range of *P. tourkobouniensis* from Tourkobounia-1 (De Bruijn and Van der Meulen, 1975). However, the size of the M1 and M3 is larger than that from the Greek locality. It differs from material from the type locality in the presence of a weak mesolophid in the m3. The first description of the Greek species by De Bruijn and Van der Meulen (1975) does not mention the presence of the anterosinusid in the m1. However, additional material from Tourkobounia-1 published by Skandalos and Van den Hoek Ostende (2023) indicated that the character is present. In addition, the presence and size of the M1 mesoloph varies. It can be strong, weak or even absent (De Bruijn and Van der Meulen, 1975: pl. 6). Based on the similar size, the presence of the anterosinusid and both variations with one or two enamel islands between the hypolophulid and the posterolophid in the m1, the well-developed posteroloph in the M1 and the presence of two re-entrant folds in the M3, the spalacine from Afşar 2 is classified as *P. tourkobouniensis*. It is worth mentioning that one of its m1s (PV-AFS-441) has a posteriorly oriented ridge on the posterior side of the hypolophid. This character is similar to the hypolophid folds present in older species like *Debruijnia tintinnabulus* from Zvonce in Serbia (De Bruijn et al., 2022: fig. 1). It is also present in one of the m1s of *P. macoveii* from Çalta (Şen, 1977: ACA-857, pl. 14, fig. 3a).

4. Discussion

Spalacinae are an unusual component in the fossil faunas. Even though they have been found in numerous localities, they are generally represented by only a few specimens. In Afşar they represent ca. 8% of the fauna which has been studied by Skandalos et al. (2023) as part of the Ph.D. thesis of the first author (PS). The Arvicolinae and the Cricetinae material from the two localities of Afşar indicate that the top part of the section, Afşar 2, is richer than the lower, Afşar 1. Spalacines follow the same pattern with 41 and 10 molars, respectively. From Afşar 1, near the base of the section, Skandalos et al. (2023) recovered *Mimomys* cf. *gracilis*, *Pliomys* sp., Arvicolinae gen. et sp. indet., and *Cricetulus* cf. *ehiki*. From Afşar 2, they recognized the species *Mimomys hassiacus*, *M. gracilis*, *Pliomys graecus*, *Cricetulus* sp., and *Mesocricetus primitivus* (Skandalos et al., 2023). In the classification followed here, the oldest representatives of *Pliospalax* occurred at the end of the Late Miocene of eastern Europe and Anatolia (Şen and Sarıca, 2011). Sarıca and Şen (2003) separated the Middle and early Late Miocene species of *Pliospalax* into a genus of their own, *Sinapospalax*. De Bruijn et al. (2022), however, tentatively grouped the genus in *Pliospalax*. Here, we follow the classification of Sarıca and Şen (2003) and Şen and Sarıca (2011). *Pliospalax* is present in nine assemblages with a reliable amount of material. In Greece, it is present in the MN 12 locality of Samos, the MN 13/14 locality of Silata, and the MN 14 locality of Maritsa with *P. macoveii* (De Bruijn et al., 1970; Vasileiadou et al., 2003; Vasileiadou and Sylvestrou, 2009), as well as the MN 16 locality of Tourkobounia-1 with *P. tourkobouniensis* (De Bruijn and Van der Meulen, 1975). The genus is also present in Turkey with *P. complicatus* in Amasya (MN 13; Şen and Sarıca, 2010) and *P. macoveii* in Çalta (MN 15; Şen, 1977). It is present in Ukraine with *P. compositodontus* in the MN 13 locality of Andreevka (Topachevski, 1969), in Romania with *P. macoveii* in the MN 15 locality of Măluşteni and Bereşti (Simionescu, 1930; Crespo et al., 2023), and also in the MN 15 locality of Muselievo in Bulgaria (Popov, 2004). Afşar 2 is the first record of *P. tourkobouniensis* in Turkey. The presence of *P. tourkobouniensis* is in line with the suggestion of Skandalos et al. (2023) to place the locality in MN 16. The number and the condition of the spalacine material from Afşar 1, like its few cricetines and its arvicolines, do not provide us enough information to confidently correlate the locality at this point (Skandalos et al., 2023). However, the presence of *Mimomys* cf. *gracilis* (Skandalos and Van den Hoek Ostende, 2023) and *P.* cf. *macoveii* (present work) in combination with its stratigraphic position would suggest MN 15.

The *Pliospalax* species and their comparison with *P.* cf. *macoveii* and *P. tourkobouniensis* from Afşar 1 and Afşar 2 highlighted a significant obstacle on Spalacinae research. The occlusal morphology of their molars changes rapidly with wear during the individual life span of these species, some taxonomical problems arise (von Koenigswald, 1993; Lopatin, 2003; Van Weers, 2005; Skandalos and Van den Hoek Ostende, 2023). Skandalos and Van den Hoek Ostende (2023) distinguish the wear stages of the *Pliospalax* m1s. They identified morphological characters that are influenced by wear and vary between the different spalacine species, including *P. macoveii* and *P. tourkobouniensis*. One of these characters is a distinct and short ridge that starts from the hypolophulid and meets the posterior metalophulid observed on the m1s of *Pliospalax macoveii* from Çalta (Şen, 1977: ACA-857, pl. 14, fig. 3a), Maritsa (Skandalos and Van den Hoek Ostende, 2023: fig. 7) and in the older spalacine species *Debruijnia tintinnabulus* (De Bruijn et al., 2022: fig. 1). De Bruijn et al. (2022: fig. 1) name this character hypolophid fold. The current paper adds to the work of Skandalos and Van den Hoek Ostende (2023), providing an additional species carrying this variable character, namely *Pliospalax tourkobouniensis*.

Following García-Alix et al. (2008), we presume that the fossil species had the same preferences as their recent counterparts. Thus, the cricetines inhabit mainly steppic environments (Musser and Carleton, 1993), while Arvicolinae inhabit the temperate and arctic zones of the Northern Hemisphere (Chaline et al., 1999). The fauna of Afşar 1 and 2 indicate dry and open spaced habitats (Skandalos et al., 2023). The Spalacinae are known as inhabitants of steppic environments and grasslands (Sarıca and Şen, 2003). The current research confirms the assumptions of Skandalos et al. (2023) about the paleoenvironmental conditions of Afşar as well as Jiménez-Moreno et al. (2015), who proposed an open steppic environment in general for SW Turkey.

5. Conclusion

In the small mammal assemblages of the Afşar section from the Pliocene of Turkey, the spalacines are well represented and two species are distinguished. In the lower section (Afşar 1) we recognize the species *Pliospalax* cf. *macoveii*. From the top section (Afşar 2) we distinguish the species *P. tourkobouniensis*. This is the first record of the species in Anatolia, which increases its geographical range to the East. Furthermore, the current research complements the work of Skandalos et al. (2023), providing additional information on the environmental conditions and the age of the Afşar section. The species found are in line with assigning an MN 16 age to Afşar 2 and an MN 15 correlation for Afşar 1. The abundant material of Spalacinae, particularly in Afşar 2, confirms that the Pliocene environments of Afşar were steppe-like at that time.

CRediT authorship contribution statement

Panagiotis Skandalos: Visualization, Project administration, Investigation, Formal analysis. **Fatma Arzu Demirel:** Resources, Project administration. **Mehmet Cihat Alçiçek:** Resources, Investigation. **Serdar Mayda:** Resources, Investigation. **Lars W. van den Hoek Ostende:** Supervision, Conceptualization.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Alçiçek, M.C., Mayda, S., Ten Veen, J.H., Boulton, S.J., Alçiçek, H., Tesakov, A., Saraç, G., Hakyemez, Y., Göktaş, F., Murray, A., Wesselingh, F.P., Jimenez-Moreno, G., Büyükmeriç, Y., Bouchal, J.M., Demirel, F.A., Kaya, T.T., Halaçlar, K., Bilgin, M., van den Hoek Ostende, L.W., 2019. Reconciling the stratigraphy and sedimentation history of the Lycian orogen-top basins, SW Anatolia. Palaeobiodiversity and Palaeoenvironments 99, 551–570.

Andrews, P., 1990. In: Owls, Caves and Fossils. University of Chicago Press, Chicago, p. 231.

Balcı, V., 2011. 1/100 000 ölçekli Türkiye Jeoloji Haritaları, Afyon-L25 paftası: Maden Tetkik ve Arama Genel Müdürlüğü. Jeoloji Etüdleri Dairesi Yayını No: 161, Ankara, Türkiye (in Turkish).

Bowdich, T.E., 1821. In: An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers. Smith J. Paris, France, p. 115.

Chaline, J., Brunet-Lecomte, P., Montuire, S., Viriot, L., Courant, F., 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaecoecological history and evolutionary data. Annales Zoologici Fennici 36, 239–267.

Cihan, M., Saraç, G., Gökçe, A.O., 2003. Insights into biaxial extensional tectonics: an example from the Sandıklı Graben, West Anatolia, Turkey. Geological Journal 38, 47–66.

Crespo, V.D., Vasile, Ş., Petculescu, A., Răţoi, B.G., Haiduc, B.S., 2023. The Early Pliocene small mammals (Eulipotyphla, Rodentia, Lagomorpha) from Bereşti and Măluşteni (eastern Romania): a fresh look at old collections. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 114, 49–63.

de Bruijn, H., Bosma, A.A., Wessels, W., 2015. Are the Rhizomyinae and the Spalacinae closely related? Contradistinctive conclusions between genetics and palaeontology. Palaeobiodiversity and Palaeoenvironments 95, 257–269.

de Bruijn, H., Dawson, M.R., Mein, P., 1970. Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the isle of Rhodes (Greece) 3. The Rodentia, Lagomorpha and Insectivora. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Ser. B 73, 568–584.

de Bruijn, H., Marković, Z., Wessels, W., 2013. Late Oligocene rodents from Banovići (Bosnia and Herzegovina). Palaeodiversity 6, 63–105.

de Bruijn, H., Marković, Z., Wessels, W., van de Weerd, A.A., 2022. On the antiquity and status of the Spalacidae, new data from the late Eocene of south-East Serbia. Palaeobiodiversity and Palaeoenvironments 103, 433–445.

de Bruijn, H., van der Meulen, A.J., 1975. The early Pleistocene rodents from Tourkobounia-1 (Athens, Greece). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B 78, 314–338.

Demirel, F.A., Mayda, S., Alçiçek, M.C., Eryılmaz, D., 2019. Burdur ve Afyonkarahisar İlleri ve İlçelerinde Neojen ve Pleistosen Dönem Fosil Lokalitelerinin Tespiti Yüzey Araştırması-2017. Araştırma Sonuçları Toplantısı 36, 193–202 (in Turkish).

Erdal, O., 2017. Küçük Memeli Paleontolojisinin Türkiye'deki Kuvaterner Çalışmalarına Katkısı: Tanımlar ve Uygulamalar [Contribution of Micromammal Palaeontology to Quaternary Studies in Turkey: Definitions and Applications]. Geological Bulletin of Turkey 60, 637–664 (in Turkish).

Eronen, J.T., Ataabadi, M.M., Micheels, A., Karme, A., Bernor, R.L., Fortelius, M., 2009. Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. Proceedings of the National Academy of Sciences of the United States of America 106, 11867–11871.

Flynn, L.J., 2009. The antiquity of *Rhizomys* and independent acquisition of Fossorial traits in subterranean Muroids. Bulletin of the American Museum of Natural History 331, 128–156.

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, 214–225.

Gray, J.E., 1821. On the natural arrangement of vertebrose animals. London Medical Repository 15, 296–310.

Güldenstädt, A.J., 1770. *Spalax*, novum glirium genus. Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae 14, 409–440.

He, Y., Hu, S., Ge, D., Yang, Q., Connor, T., Zhou, C., 2019. Evolutionary history of Spalacidae inferred from fossil occurrences and molecular phylogeny. Mammal Review 50, 11–24.

Heller, F., 1936. Eine oberpliocäne Wirbeltierfauna aus Rheinhessen. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Abt. B 76, 99–160.

Hofmeijer, K.G., de Bruijn, H., 1985. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece) 4. The Spalacidae and Anomalomyidae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B 88, 185–198.

Illiger, C., 1811. Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione germanica. Salfeld C. Berlin, Germany, 301 p.

Jiménez-Moreno, G., Alcicek, H., Alcicek, M.C., van den Hoek Ostende, L.W., Wesselingh, F.P., 2015. Vegetation and climate changes during the late Pliocene and early Pleistocene in SW Anatolia, Turkey. Quaternary Research 84, 448–456.

Kormos, T., 1932. Neue Pliozäne Nagetiere aus der Moldau. Palaeontologische Zeitschrift 14, 193–200.

Koufos, G.D., 2013. Neogene mammal biostratigraphy and chronology of Greece. In: Wang, X., Flynn, L.J., Fortelius, M. (Eds.), Fossils Mammals of Asia: Neogene Biostratigraphy and Chronology. New York (NY), CUP, pp. 595–626.
Koufos, G.D., 2016. Neogene and Quaternary continental biostratigraphy of Greece based on mammals. Bulletin of the Geological Society of Greece Vol. L. Thessaloniki, Greece.
Koufos, G.D., Vasileiadou, K., 2015. Miocene/Pliocene mammal faunas of southern Balkans: implications for biostratigraphy and palaeoecology. Palaeobiodiversity and Palaeoenvironments 95, 285–303.
Kretzoi, M., 1959. Insectivoren, Nagetiere und Lagomorphen der jüngstpliozänen Fauna von Csarnóta im Villáyer Gebirge (Südungarn). Vertebrata Hungarica 1, 237–246.
Lopatin, A.V., 2003. The revision of the Early Miocene beavers (Castoridae, Rodentia, Mammalia) from the North Aral Region. Russian Journal of Theriology 2, 15–25.
Milne-Edwards, A., 1867. Description de quelques espèces nouvelles d'écureuils de l'ancien continent. Revue et Magasin de Zoologie pure et appliquée 2, 225–234.
Musser, G.G., Carleton, M.D., 1993. Family Muridae. In: Wilson, D.E., Reeder, D.M. (Eds.), Mammal Species of the World. A Taxonomic and Geographic Reference. second ed. Smithsonian Institution Press and The American Society of Mammalogists, Washington, USA, pp. 501–755.
Popov, V., 2004. Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha. Rodentia) from Muselievo (North Bulgaria). Geodiversitas 26, 403–491.
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).
Sarıca, N., Şen, S., 2003. Spalacidae. In: Fortelius, M., Kappelman, J., Bernor, R.L. (Eds.), Geology and Paleontology of the Miocene Sinap Formation, Turkey. CUP, New York, pp. 141–163.
Schaub, S., 1930. Quartäre und jungtertiäre Hamster. Abhandlungen der Schweizerischen paläontologischen Gesellschaft 49 (6), 1–49.
Şen, S., 1977. La faune de rongeurs pliocène de Çalta (Ankara, Turquie). Bulletin du Muséum National d'Histoire Naturelle, Section c, Sciences de la Terre, Paléontologie, Géologie, Minéralogie 61, 89–171.
Şen, S., Sarıca, N., 2011. Middle-Late Miocene Spalacidae (Mammalia) From Western Anatolia, and the Phylogeny of the Family. Bulletin of the Earth Sciences Application and Research Centre of Hacettepe University. Yerbilimleri 32, 21–50.
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., Steffens, 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 15, 1–167.
Simionescu, I., 1930. Vertebratele Pliocene de la Malusteni (Covurlui) [Les Vertébrés Pliocène de Malusteni (Roumanie)]. Academia Romana. Publicatiunile Fondului Vasile Adamachi. București: Cultura Nationala, 9, pp. 83–151.
Skandalos, P., Hoek Ostende, L.W., 2023. Wear-dependent molar morphology in hypsodont rodents: the case of the spalacine Pliospalax. Palaeontologia Electronica 26 (3), a47.
Skandalos, P., Lansing, K., Demirel, F.A., Alçiçek, M.C., Mayda, S., Dieleman, F.E., Hoek Ostende, L.W., 2023. Early Pliocene Arvicolinae and Cricetinae from the locality of Afşar, western Turkey. Turkish Journal of Earth Sciences 32, 27–62.
Steppan, S.J., Schenk, J.J., 2017. Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. PLS ONE 12 (8), e0183070.
Topachevski, V.O., 1969. Fauna of the USSR: Mammals, molerats, Spalacidae. Fauna of the USSR: Mammals, molerats, Spalacidae. Akademia Nauk USSR, n.s. 99, pp. 1–247.
Turan, N., 2002. Geological map of Turkey in 1:500000 scale: Ankara sheet. Publication of Mineral Research and Exploration Directorate of Turkey (MTA), Ankara.
Ünay, E., 1996. On fossil Spalacidae (Rodentia). In: Bernor, R.L., Falbusch, V., Mittmann, H.W. (Eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. CUP, New York, pp. 246–252.
Ünay, E., 1999. Family Spalacidae. In: Rössner, G.E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Verlag Dr. F. Pfeil, München, pp. 421–425.
Ünay, E., de Bruijn, H., 1998. Plio-Pleistocene rodents and lagomorphs from Anatolia. NITG-TNO 60, 431–466.
van den Hoek Ostende, L.W., Casanovas-Vilar, I., Furió, M., 2020. Stuck in the middle. A geographical appraisal of the oldest insectivores and a marsupial from the Vallès-Penedès Basin (early Miocene, Catalonia, Spain). Comptes Rendus Palevol 19, 1–25.
van den Hoek Ostende, L.W., Diepenveen, F., Tesakov, A., Saraç, G., Mayhew, D., Alçiçek, M.C., 2015. On the brink: micromammals from the latest Villanyian from Bıçakçı (Anatolia). Geological Journal 50, 230–245.
van de Weerd, A.A., de Bruijn, H., Wessels, W., Marković, Z., 2022. New late Oligocene rodent faunas from the Pannonian basin. Palaeobiodiversity and Palaeoenvironments 102, 465–492.
van Weers, D.J., 2005. A taxonomic revision of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia with notes on the evolution of the family. Contributions to Zoology 74, 301–312.
Vasileiadou, K., Koufos, G.D., Syrides, G.E., 2003. Silata, a new locality with micromammals from the Miocene/Pliocene boundary of the Chalkidiki peninsula, Macedonia, Greece. Deinsea 10, 549–562.
Vasileiadou, K., Sylvestrou, I.A., 2009. The Late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 4. Micromammals. Beiträge zur Paläontologie 31, 189–205.
von Koenigswald, W., 1993. Heterochronies in Morphology and Schmelzmuster of hypsodont molars in the Muroidea (Rodentia). Quaternary International 19, 57–61.
von Méhely, L., 1914. Fibrinae Hungariae. Annales Historico-Naturales Musei Nationalis Hungarici 12, 157–243 (in Hungarian and German).