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Prospalax priscus jaw from the site of Węże 2 (southern Poland, Pliocene)

Čeljust vrste *Prospalax priscus* iz najdišča Węże 2 (južna Poljska, pliocen)

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Abstract

The ecology and adaptations of the Anomalomyidae (Muroidea) have been long debated in the scientific literature. A jaw belonging to *Prospalax priscus* (Anomalomyidae) was found at the Late Pliocene site of Węże 2 in southern Poland. The presence of this species at the site agrees with the interpretation of *P. priscus* and the Anomalomyidae in general as adapted to forest environments.

Izvleček

V znanstveni literaturi se že dolgo razpravlja o ekologiji in prilagoditvah družine Anomalomyidae (Muroidea). Čeljust, ki pripada vrsti *Prospalax priscus* (Anomalomyidae), je bila najdena na najdišču Węże 2 iz zgornjega pliocena na južnem Poljskem. Prisotnost te vrste na tem najdišču se ujema z interpretacijo, da sta bili vrsta *P. priscus* in družina Anomalomyidae na splošno kot prilagojeni gozdnemu okolju.

Introduction

The Muroidea (mouse-like rodents) is a highly diverse superfamily of rodents (Rodentia) encompassing around 1750 species, which amounts to circa 75 % of all rodent species. Six main extant clades may be distinguished among the Muroidea, namely the Muridae, the Cricetidae, the Spalacidae, the Platacanthomyidae, the Calomyscidae and the Nesomyidae (Michaux et al., 2001; D'Elía et al., 2003; Jansa & Weksler, 2004; Steppan et al., 2004; Musser & Carleton, 2005; Jansa et al., 2009; Schenk et al., 2013). Moreover, the extinct family Anomalomyidae has been recognized, which cladistically should be supposedly included in the Cricetidae (Bolliger, 1999; López-Guerrero et al., 2017; Nesin & Kovalchuk, 2020). The Muroidea, having probably originated in Eurasia during the Eocene, now inhabit every continent except Antarctica, thriving in a wide range of habitats and occupying many different ecological niches (Lindsay, 1977; Flynn et al, 1985; D'Elía et al., 2003; Musser & Carleton, 2005; Jansa et al., 2009; Schenk et al., 2013; Li et al., 2016). The Anomalomyidae is an example of a muroid clade of which ecology has been long debated and apparently not well understood (Kalthoff, 2000; Hordijk & de Bruijn, 2009; Nesin & Kovalchuk, 2020). Thus, each newly described discovery may bring about important information clarifying the mode of life of this enigmatic family. The purpose of this paper is to present part of the anomalomyid fossil material (a fragmentary left lower jawbone of *Prospalax priscus*) collected at the Late Pliocene site of Węże 2, and subsequently to argue that the presence of this species in the Węże 2 assemblage further supports the interpretation of the Anomalomyidae as adapted to forest environments.

Geological and stratigraphical settings

The Węże 2 site is situated on the NW slope of the Zelce Hill (51°05′52″N 18°47′30″E; 228 m a.s.l.), near the village of Węże, in the vicinity of the town of Działoszyn (Pajęczno County), in the Wieluń Upland, southern Poland. The site comprises a vertical crevice etched in the Upper Jurassic (Oxfordian) limestone by karst processes, originally infilled with late Pliocene fossiliferous sediment of the terra rossa type. The crevice itself is a part of a larger karst cave system of the hill and is located about 150–200 m north from the better known Węże 1 site, which has been dated at MN 15 (Sulimski, 1962; Stefaniak et al., 2020; Szynkiewicz, 2015 A and B).

The locality of Węże 2 was discovered and preliminary explored between 1958 and 1961 by Sulimski. The terra rossa deposits (~3.5 t in total) were collected during field work organized by the Department of Paleozoology of the Polish Academy of Sciences in Warsaw (currently the Institute of Paleobiology PAS) and the Department of Paleozoology of the Wrocław University. Three to four clayey fossiliferous strata of slightly differing lithology were distinguished. These were initially named D1, D2 and D3 by Sulimski (1962) and then renamed D (= upper D1), E (= lower D1), F, and G. Additionaly, there was a stratum of quartz sand at the bottom in which some specimens were also found (this stratum was initially named D4 and then renamed as H). However, only part of the fossil material collected has been attributed to a particular stratum and the faunal lists are generally given for the site as a whole, which is also the case for the nearby and better known site of Węże 1. The faunal composition of the Węże 2 fossil assemblage is currently dated at the late Pliocene (Early Villafranchian) and is considered to belong to the MN 16b zone in the European Land Mammal Age chronology, i.e. 2.9–2.6 mya (Sulimski, 1962; Nadachowski et al., 2015; Szynkiewicz, 2015 A and B; Stefaniak et al., 2020; Marciszak et al., 2023).

The rodents thus far described from Węże 2 include the previously unknown species of a flying squirrel, *Pliopetaurista dehneli* (originally named *Pliosciuropterus dehneli*) (Sulimski, 1964; Hordijk & de Bruijn, 2009), the dormice *Glis minor* and *G. sackdillingensis* (Czernielewski, 2021), the beavers *Trogontherium minus* and *Dipoides* ex gr. *problematicus-sigmodus* (Czernielewski, 2022) and the porcupine *Hystrix refossa* (Czernielewski, 2023), see Table 1. Several non-rodent mammalian taxa have also been recognized. These include the lagomorph *Hypolagus beremendensis* (Fostowicz-Frelik, 2007), the cervids *Croizetoceros ramosus* and *Metacervocerus pardinensis*, (Stefaniak, 1995; Stefaniak et al., 2020), the talpid *Rzebikia skoczeni*, defined based on material from Węże 2 (Rzebik-Kowalska, 1990, 2014; Skoczeń, 1976, 1993; Zijlstra, 2010; Sansalone et al., 2016), a proboscidean ?*Anancus* sp. (Stefaniak et al., 2020), as well as the chiropterans *Rhinolopus* sp. and *Myotis* sp. (Kowalski, 1990). Moreover, the presence of several carnivorans was attested, including the canids *Nyctereutes donnezani* and *Canis etruscus* (Marciszak et al., 2023).

In addition to mammals, some other vertebrate remains have been found in Węże 2. Reptiles were represented by the turtle *Emys orbicularis antiqua*, the serpents *Elaphe paralongissima* and *Natrix* cf. *longivertebrata*, as well as the lizards *Ophisaurus pannonicus*, *Anguis* cf. *fragilis*, *Lacerta* cf. *viridis* and *Lacerta* sp. (Młynarski et al., 1984). The amphibian fauna included a new species of salamander named *Mioproteus wezei* and the anurans *Palaeobatrachus* sp., *Pliobatrachus* cf. *langhae*, *Pelobates fuscus*, *Pelobates* sp., *Bufo bufo*, *Rana dalmatina*, *Rana* sp. and *Pelophylax* kl. *esculentus* (Młynarski et al., 1984; Młynarski & Szyndlar, 1989). Moreover, remains of unidentified birds were uncovered (Bocheński et al., 2012) as well as isolated vertebrae of salmonid fishes (Nadachowski et al., 2015). In general, the fauna of Węże 2 is considered to be suggestive of a forest environment, which is supported by the presence of genera strongly associated with woodland habitats, such as *Glis*, *Sciurus*, *Pliopetaurusta*, *Blackia*, *Trogontherium* and *Dipoides* (Sulimski, 1964; Szynkiewicz, 2015 A; Stefaniak et al., 2020; Czernielewski, 2021, 2022).

Material and methods

The *Prospalax* specimen here described (Fig. 1) was discovered and handpicked at the site of Węże 2 in the late 1950's / early 1960's during excavations conducted by Andrzej Sulimski, the Department of Paleozoology of the Polish Academy of Sciences in Warsaw, and the Department of Paleozoology of the Wrocław University. The exact provenance of the mandible (the stratum in which it was found) is not known. In addition, each of the strata contained several dozens of isolated teeth morphologically and morphometrically identical to the *P. priscus* specimens from Węże 1 (Sulimski 1964). This material is part of the collection of the Institute of Paleobiology, Polish Academy of Sciences (abbreviated as ZPAL). The described specimen was examined, measured and photographed with Keyence VHX 900-F Digital Microscope System.

Systematic palaeontology

Superfamily Muroidea Illiger, 1811
Family Anomalomyidae Schaub, 1925
Genus *Prospalax* Méhely, 1908
Prospalax priscus (Nehring, 1897)

Material

A fragmentary left mandible of *Prospalax priscus* with m1-m2 preserved *in situ* (ZPAL M. VIII/b/P1/1), Fig. 1.

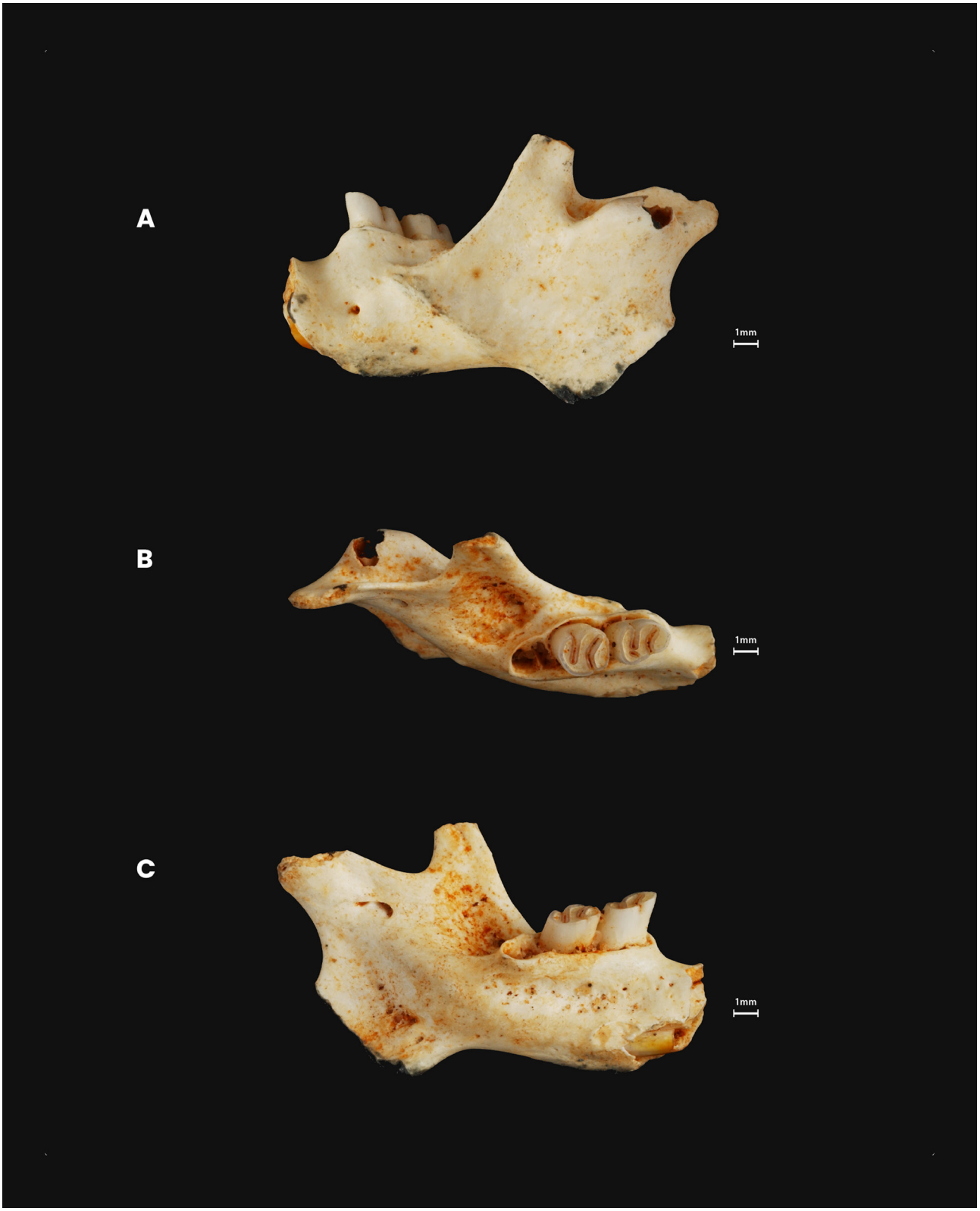

Fig. 1. Left mandible of *Prospalax priscus* (ZPAL M. VIII/b/P1/1) in labial (A), occlusal (B) and lingual (C) views.

Table 1. Rodent material from Węże 2 present in the collection of the Institute of Paleobiology PAS according to taxa and stratigraphic units.

Stratigraphic unit	Rodent taxa present
D	*Glis* ex gr. *sackdillingensis-minor* (Gliridae) *Muscardinus pliocaenicus* (Gliridae) *Pliopetaurista dehneli* (Sciuridae) *Blackia miocaenica* (Sciuridae) *Tamias orlovi* (Sciuridae) *Prospalax priscus* (Anomalomyidae) *Baranomys* sp. (Cricetidae) *Mimomys* sp. (Cricetidae) Cricetidae indet.
E	*Glis* ex gr. *sackdillingensis-minor* (Gliridae) *Muscardinus pliocaenicus* (Gliridae) *Pliopetaurista dehneli* (Sciuridae) *Tamias orlovi* (Sciuridae) *Prospalax priscus* (Anomalomyidae) *Trogontherium minus* (Castoridae) *Hystrix refossa* (Hystricidae) *Baranomys* sp. (Cricetidae) *Mimomys* sp. (Cricetidae) Cricetidae indet.
F	*Glis* ex gr. *sackdillingensis-minor* (Gliridae) cf. *Pliopetaurista dehneli* (Sciuridae) *Tamias orlovi* (Sciuridae) *Prospalax priscus* (Anomalomyidae) *Trogontherium minus* (Castoridae) *Hystrix* sp. (Hystricidae) *Baranomys* sp. (Cricetidae) *Mimomys* sp. (Cricetidae) Cricetidae indet.
G	*Glis* ex gr. *sackdillingensis-minor* (Gliridae) *Blackia miocaenica* (Sciuridae) *Tamias orlovi* (Sciuridae) *Prospalax priscus* (Anomalomyidae) *Trogontherium minus* (Castoridae) *Dipoides* ex gr. *problematicus-sigmodus* (Castoridae) *Hystrix* sp. (Hystricidae) *Baranomys* sp. (Cricetidae) *Mimomys* sp. (Cricetidae) Cricetidae indet.

Description

The specimen exhibits the sigmoid pattern of the occlusal dental surfaces typical for the genus *Prospalax*. It is an adult specimen (cf. Sulimski 1964) and corresponds with other mandibles attributed to *P. priscus* and illustrated by Méhely (1908), Sulimski (1964) and Topachevskii (1976) by its relatively robust appearance compared to the *P. petteri* specimens (including the holotype) illustrated by Bachmayer and Wilson (1970). In the Węże 2 specimen the height of the horizontal branch at the level of the posterior edge of the alveolus of m1 is ca. 5.00 mm measured at the labial side. The shape of the angular process is typical

for *P. priscus*, while in the holotype of *P. rumanus* it exceeds the length of m1–m2 which is a diagnostic trait for this species (Simionescu 1930; Topachevskii 1976). The dimensions of the preserved teeth in the Węże 2 specimen are 2.07/1.54 mm (m1) and 2.02/1.88 mm (m2). The alveolar m1–m3 length is 6.43 mm which corresponds to the lower end of the range typical for *P. priscus*, i.e. 6.0–9.0 mm (Jánossy 1972; Topachevskii 1976). Topachevskii (1976) points out to the smaller size of *P. rumanus* as defined by the length of the mandibular tooth row which in the described specimens of *P. rumanus* equals 6.0 and 6.2 mm, but as the dimensions of the measured specimens of *P. rumanus* overlap with the measurements of the smaller mandibles of *P. priscus*, it would apparently not be possible to distinguish between the species based on morphometric traits alone. However, the dimensions of m2 (2.02/1.88 mm) and the alveolar length of the Węże 2 specimen are also much smaller than in the holotype specimen of *P. kretzoii* (2.8/2.4 mm, and 10.2 mm), a species that has been diagnosed as being significantly larger than *P. priscus* (Jánossy 1972).

Discussion

Prospalax priscus is now recognized as a representative of the Anomalomyidae. Apparently restricted to the Old World, this family is known to have lasted since the Early Miocene till the beginning of MN 18 (Marković & Milivojević, 2010; López-Guerrero et al. 2017; Nesin and Kovalchuk 2020). The family includes three genera (*Anomalomys*, *Anomalospalax*, *Prospalax*), all of which were previously assigned to the Cricetidae (i.e. the family that comprises hamsters, voles, lemmings, muskrats and the so called New World rats and mice) or the Spalacidae (i.e. the family that includes mole-rats, bamboo rats and zokors) (Bachmayer & Wilson 1978; Kordos 1985; Hugueney & Mein 1993; Bolliger 1999; Jansa & Weksler, 2004; Musser & Carleton, 2005; Nesin & Kovalchuk 2020). It is hypothesized that the Anomalomyidae originated within the Cricetidae, with *Argyromys aralensis* from the Oligocene of Kazakhstan being the immediate ancestor, even though the oldest anomalomyids have been attested in southern Europe (López-Guerrero et al. 2017; Nesin and Kovalchuk 2020). Another hypothesis holds that the origins of the Anomalomyidae are associated with the primitive cricetid *Eumyarion intercentralis* from western Asia (de Bruijn 2009). Among anomalomyids the eponymous genus *Anomalomys* is the most species-rich and is also considered to be the most primitive, while *Prospalax* and *Anomalospalax* are described as being more derived (Kordos 1985, 2005; Nesin & Kovalchuk 2020). The evolutionary lineage *Anomalomys – Prospalax* has been inferred from the fossil record (Bachmayer & Wilson 1970; Nesin & Kovalchuk 2020).

P. priscus is known from several sites in Central Europe and Greece, dated from the Upper Miocene (Daxner-Höck 1970; Temper 2005) till the beginning of MN 18 (Marković & Milivojević, 2010). In Poland it was attested at the MN 15 sites of Draby 1, Mokra 1, Raciszyn 1 (Nadachowski 1989; Nadachowski et al. 1989) and Węże 1 (Sulimski, 1964), as well as the MN 16 site of Rębielice Królewskie 1A (Kowalski, 1960). In Hungary *P. priscus* was reported from the Late Pliocene / Early Pleistocene sites of Csarnóta (Kretzoi 1956; Jánossy 1986; Szentesi et al. 2015) and Beremend (Méhely 1908; Kretzoi 1956; Jánossy 1986; Hordijk & de Bruijn 2009; Pazonyi et al. 2019), the Early/Middle Pleistocene site of Nagyharsány (Nehring 1897; Kretzoi 1956; Jánossy 1986; Pazonyi et al. 2021), the MN 16? sites of Osztramos 7 and Villány 3 (Kretzoi 1956; Jánossy 1986; Kessler 2019), the Late Villanyian site of Dunaalmás IV, as well as from Kisláng, supposedly also of the Late Villanyian age (Jánossy, 1986). Romanian localities of *P. priscus* include the Pliocene sites of Măluşteni and Barault Capeni (= Barót-Köpec) (Simionesciu, 1930; Kormos, 1932). Moreover, the species was attested at the MN 15? site of Notio 1 in Greece (Hordijk & de Bruijn, 2009), MN 16 of Hajnáčka I in Slovakia (Sabol, 2003), and MN 18 of Riđake in Serbia (Marković & Milivojević, 2010). It was also reported from the Upper Miocene of Eichkogel in Austria (Daxner-Höck, 1970; Temper, 2005). The localities are summed up in Table 2.

Supposedly by analogy to the extant Eurasian blind mole rats (the genus *Spalax*), to which it was once considered closely related (Méhely, 1908; Topachevskii, 1976), *Prospalax* has been described as a burrowing animal of the steppe and open grasslands, similar in their behavior and adaptations to the modern spalacids (Kowalski, 1964; Sulimski, 1964; Bachmayer and Wilson, 1970; Sabol, 2003) which was also considered true for the Anomalomyidae in general (Bachmayer & Wilson, 1970; Kowalski, 1994; Bolliger, 1999). However, the interpretation of anomalomyid ecology has been shifting towards understanding them as animals dwelling in forest environments, behaviorally similar to the extant burrowing shrews, and not well adapted to strictly underground lifestyle (Kalthoff, 2000; Hordijk & de Bruijn, 2009; Nesin & Kovalchuk, 2020). Such a shift has been caused by findings of anomalomyid remains within faunal

Table 2. Anomalomyid occurrences unequivocally referred to as *Prospalax priscus*.

No.	Locality	Age	References
1.	Eichkogel (Austria)	Upper Miocene	Daxner-Höck 1970; Temper 2005
2.	Măluşteni (Romania)	Pliocene	Simionesciu 1930; Kormos 1932
3.	Barault Capeni (Romania)	Pliocene	Simionesciu 1930; Kormos 1932
4.	Beremend (Hungary)	Late Pliocene / Early Pleistocene	Méhely 1908; Kretzoi 1956; Jánossy 1986; Pazonyi et al. 2019
5.	Csarnóta (Hungary)	Late Pliocene / Early Pleistocene	Kretzoi 1956; Jánossy 1986; Szentesi et al. 2015
6.	Draby 1 (Poland)	MN 15, Late Ruscinian	Nadachowski 1989; Nadachowski et al. 1989
7.	Mokra 1 (Poland)	MN 15, Late Ruscinian	Nadachowski 1989; Nadachowski et al. 1989
8.	Raciszyn 1 (Poland)	MN 15, Late Ruscinian	Nadachowski 1989; Nadachowski et al. 1989
9.	Węże 1 (Poland)	MN 15, Late Ruscinian	Nadachowski 1989; Nadachowski et al. 1989; Sulimski 1964
10.	Notio 1 (Greece)	MN 15?	Hordijk and de Bruijn 2009
11.	Hajnáčka I (Slovakia)	MN 16	Sabol 2003
12.	Osztramos 7 (Hungary)	MN 16?	Kretzoi 1956; Jánossy 1986; Kessler 2019
13.	Rębielice Królewskie 1A (Poland)	MN 16	Kowalski 1960
14.	Villány 3 (Hungary)	MN 16?	Kretzoi 1956; Jánossy 1986; Kessler 2019
15.	Węże 2 (Poland)	MN 16	Sulimski 1962; Stefaniak 1995; Stefaniak et al. 2020
16.	Dunaalmás IV (Hungary)	Late Villanyian	Jánossy 1986
17.	Kisláng (Hungary)	Late Villanyian?	Jánossy 1986
18.	Nagyharsány (Hungary)	Early/Middle Pleistocene	Nehring 1897; Kretzoi 1956; Jánossy 1986; Pazonyi et al. 2021
19.	Riđake (Serbia)	MN 18	Marković and Milivojević 2010

assemblages otherwise typical for forest habitats (Hordijk & de Bruijn, 2009; Nesin & Kovalchuk, 2020) as well as by the reinterpretation of the anomalomyid incisors as not being proficient digging tools (Kalthoff, 2000; Nesin & Kovalchuk, 2020). Also the relationships between Anomalomyidae and Spalacidae seem to be more distant than previously thought and the presence of burrowing adaptations in these two clades is now described as a result of an evolutionary convergence (Nowakowski et al., 2018; Nesin & Kovalchuk, 2020). It is noteworthy that *P. priscus* itself has not infrequently been found in association with species suggestive for arboreal environments, i.e. flying squirrels (Sciuridae: Petauristini) and dormice (Sulimski, 1964; Daxner-Höck, 1970;

Jánossy, 1986; Nadachowski, 1989; Sabol, 2003; Hordijk & de Bruijn, 2009; Marković & Milivojević, 2010).

Attributing the Węże 2 specimen to *P. priscus* seems well supported due to the robust appearance of the jaw, the shape of the angular process, and the smaller dimensions than the holotype of *P. kretzoii*. Moreover, it can be inferred that the isolated *Prospalax* teeth found at Węże 2 also belong to *P. priscus*, although this cannot be proved by the occlusal morphology as it does not seem to differ significantly between the species and possible interspecific differences were never cited as diagnostic while defining new species within *Prospalax* (Nehring, 1897; Simionescu, 1930; Bachmayer and Wilson, 1970; Jánossy 1972). The presence of *P. priscus* at the site of Węże 2 agrees with the interpretation of this species as adapted to forest rather than steppe environments.

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