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New data on the Sciuridae (Rodentia) from the Villafranchian site of Wężę 2 in southern Poland

Michał CZERNIELEWSKI[1, *]

[1] Polish Academy of Sciences, Institute of Paleobiology, Twarda 51/55, 00-818 Warszawa, Poland; ORCID: 0000-0001-8880-3964

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In addition to specimens attributable to *Pliopetaurista dehneli* (Pteromyini), already described by Sulimski (1964), the fossil tooth material collected at the Upper Pliocene (MN 16b) site of Wężę 2 in southern Poland comprises specimens assignable to other representatives of the Sciuridae. These include *Tamias orlovi* (Marmotini), *Blackia miocaenica* (Pteromyini) and *Sciurus warthae* (Sciurini). All these species are otherwise relatively rare in the fossil record. Along with another MN 16b site, Frechen, as well as the MN 16 sites of Rębielice Królewskie 1A and Rębielice Królewskie 2, Wężę 2 thus represents one of the youngest occurrences of *B. miocaenica* in the fossil record. *P. dehneli*, *B. miocaenica* and *S. warthae* are considered to have inhabited dense forests while *T. orlovi* probably also lived in more open wooded environments.

Key words: Early Villafranchian, Pliocene, rodent, squirrels, Wężę.

INTRODUCTION

The Sciuridae (squirrels) are a family of small to medium-sized, mostly herbivorous rodents represented by ~60 extant genera that comprise almost 300 living species. They inhabit a wide range of environments, from temperate and tropical forests to open grassy, rocky or desert areas. Likewise, they display a variety of modes of life, from climbing trees (with some species being adapted to glide) to fossoriality associated with living in ground-dwelling colonies. The supposedly monophyletic tribes recognized within the Sciuridaeare, among others, the Sciurini (the "tree squirrels", including the widespread genus *Sciurus*), the Pteromyini (also known as the Petauristini or "flying squirrels"), and the Marmotini (marmots, prairie dogs, chipmunks and susliks). However, the phylogenetical relationships between them, as well as their monophyly, are not entirely clear (Mercer and Roth, 2003; Steppan et al., 2004; Thorington Jr. et al., 2012). Fossil taxa are commonly defined based on differences in morphology of occlusal dental surfaces (e.g., Sulimski, 1964; Mein, 1970; Emry and Korth, 2007; Li et al., 2023; see Fig. 1).

It has not yet been resolved if the Sciuridae originated in North America or in Eurasia. The earliest known fossil sciurid is possibly *Hesperopetes thoringtoni*, described on the basis of dental material recovered from the Upper Eocene White River Formation of Wyoming (Emry and Korth, 2007). Another early North American form that may belong to the Sciuridae, *Douglassciurus jeffersoni*, is known from the Upper Eocene / Lower Oligocene of northern USA and it has been interpreted as a tree-dwelling animal (Emry and Korth, 1996, 2001; Mercer and Roth, 2003; Steppan et al., 2004). However, according to an alternative view, *Hesperopetes* and *Douglassciurus* should be reinterpreted as more closely related to the Aplodontidae, which may be a sister clade to the Sciuridae (Rocha et al., 2016). *Protosciurus*, spanning from the Early Oligocene to the Middle Miocene, and known from fossils including a nearly complete skeleton, is apparently the earliest undisputed member of the Sciuridae reported from North America (Black, 1963; Emry and Thorington Jr., 1982; McKenna and Bell, 1997; Li et al., 2023).

Recently, *Junggarisciurus jeminaiensis* and *Eopetes irtyshensis* have been described based on tooth material from the Upper Eocene of northwestern China. They represent respectively "tree-squirrel" and "flying squirrel" morphotypes and make a strong case for the Asiatic origin of the family (Li et al., 2023). The oldest fossil representatives of the Sciuridae in Europe, dated from the Early Oligocene, include the genera *Palaeosciurus* (Mercer and Roth, 2003), *Oligopetes* (de Bruijn and Unay, 1989; Lu et al., 2013) and *Heteroxerus* (Alvarez Sierra et al., 1990), although *Oligopetes* may have been an aplodontid (McKenna and Bell, 1997). Regardless of their area

* E-mail: m.czernielewski@twarda.pan.pl

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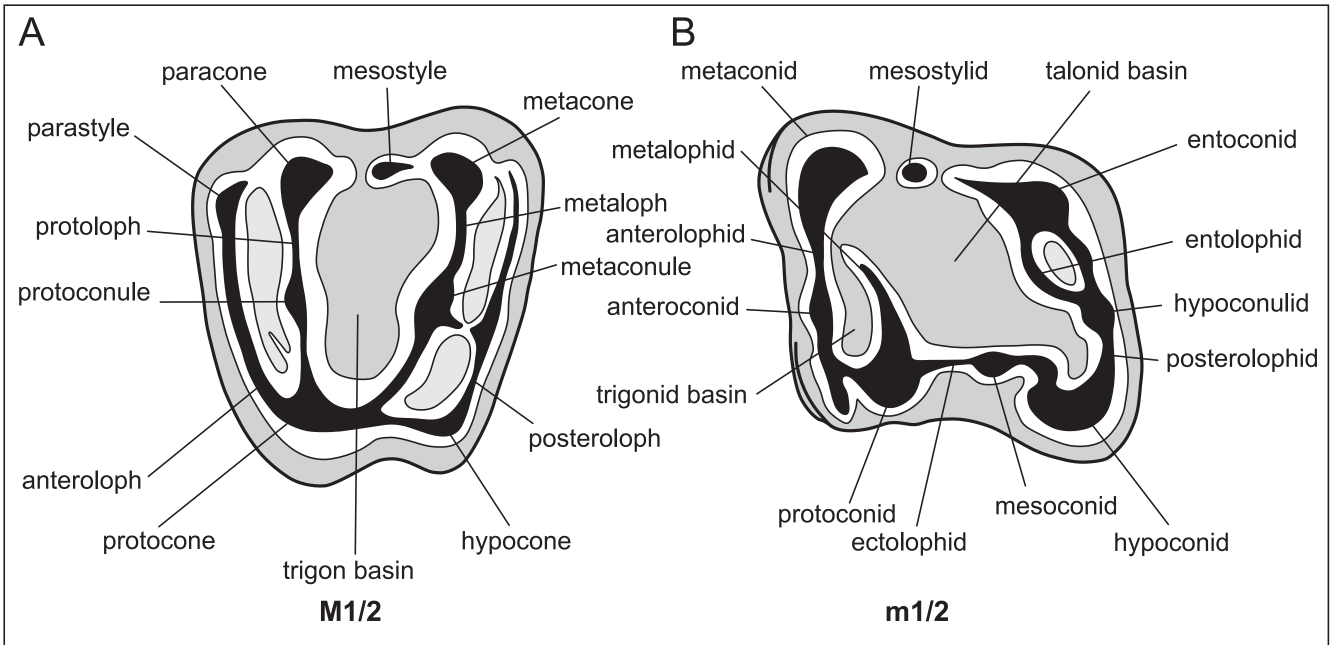

Fig. 1. Idealized occlusal morphology of sciurid cheek teeth (after Qiu, 1996, 2019; Li et al., 2023)

of origin, squirrels are considered to have undergone a rapid adaptive radiation shortly after their appearance in the fossil record. They spread to Africa during the Miocene and colonized South America relatively lately, after the formation of the Panamanian land bridge during the Late Pliocene at ~3.1 Ma (Mercer and Roth, 2003; Steppan et al., 2004; Li et al., 2023).

Early occurrences of squirrels in Poland include the presence of the Sciuridae indet. in assemblages from the Lower/Middle Miocene (MN 4/5) of Bełchatów C, the Lower/Middle Miocene (MN 5/6) of Bełchatów B, and the Middle/Upper Miocene (MN 8/9) of Bełchatów A (Garapich, 2002). Moreover, *Miopetaurista gibberosa* (Pteromyini) was recorded from the Middle Miocene (MN 6?) site of Opole 1, and *M. gibberosa*, *M. gaillardi, Palaeosciurus* cf. *fissurae* as well as *Spermophilinus bredai* (Marmotini) from the Middle Miocene (MN 7?) site of Opole 2 (Kowalski, 1967; Black and Kowalski, 1974; Nadachowski, 1989; Nadachowski et al., 1989).

The species *Blackia polonica* (Pteromyini) was named by Black and Kowalski (1974) based on material from the Lower Pliocene (MN 14) of Podlesice, although de Bruijn (1998) questioned the validity of this species and Hellmund and Ziegler (2012) considered it a junior synonym of *B. miocaenica* as is followed in this study. Other sciurids present at that site included *Pliopetaurista* sp., *Pliopetaurista* cf. *dehneli*, *Hylopetes hungaricus* (Pteromyini), ?*Sciurotamias* sp. (Marmotini), *Sciurus* cf. *warthae* and *Tamias orlovi* (Marmotini) (Black and Kowalski, 1974; van de Weerd, 1979; Nadachowski, 1989; Nadachowski et al., 1989).

The genus *Pliosciuropterus* (Pteromyini), encompassing two species, *P. schaubi* and *P. dehneli*, was described based on material from Węże 1 (MN 15) and Węże 2 (MN 16b), respectively, with *P. dehneli* being the type species (Sulimski, 1964; Stefaniak et al., 2020). Both *P. schaubi* and *P. dehneli* were later included in *Pliopetaurista* (Hordijk and de Bruijn, 2009). Furthermore, the species *Sciurus warthae* and *Eutamias orlovi* (Marmotini) were established based on material from Węże 1 (Sulimski, 1964), but the latter species was later included in the genus *Tamias* by Black and Kowalski (1974).

Additionally, *Blackia polonica* and *Pliopetes* cf. *hungaricus* were also recorded at that site (Sulimski, 1964), though *B. polonica* is here treated as a junior synonym of *B. miocaenica* and the species *Pliopetes hungaricus* was transferred to *Hylopetes* by van de Weerd (1979).

Moreover, the species *Pliopetaurista meini* was established by Black and Kowalski (1974) based on material from the Lower Pleistocene site of Zalesiaki, and the species *Citellus polonicus* (Marmotini) was named by Gromov (Gromov et al., 1965) based on material from the Lower Pleistocene of Kamyk, although the latter species was subsequently transferred to *Spermophilus* (Nadachowski, 1989). The Miocene, Pliocene and Early Pleistocene occurrences of fossil sciurids in Poland are given in Table 1.

The purpose of this paper is to present previously undescribed fossil tooth material of the Sciuridae from the site of Węże 2, which in addition to *Pliopetaurista dehneli*, already described and illustrated by Sulimski (1964), includes *Tamias orlovi*, *Blackia miocaenica* and *Sciurus warthae* (Tables 2 and 3). In terms of sciurid diversity, Węże 2 is thus virtually identical to the roughly contemporaneous and nearby site of Rębielice Królewskie 2 (Table 1). All the sciurid species present at Węże 2 indicate a woodland habitat.

GEOLOGICAL SETTING AND AGE OF THE FAUNA

The locality of Węże 2 is situated in the Wieluń Upland (southern Poland), on a slope of Zelce Hill, near the town of Działoszyn (Pajęczno County, Łódź Voivodeship). Originally it comprised the infilling of a small (~10 m long, ~4 m wide) vertical karst crevice formed in Oxfordian limestone. The fossiliferous deposits (~3.5 t in total) of Late Pliocene age were collected during fieldwork organized in the early 1960s by the Department of Paleozoology of the Polish Academy of Sciences in Warsaw (currently the Institute of Paleobiology PAS) and the

Table 1

Miocene, Pliocene and Early Pleistocene occurrences of fossil Sciuridae in Poland; after taxonomic revisions by Black and Kowalski (1974), van de Weerd (1979), de Bruijn (1998), Hordijk and de Bruijn (2009) and Hellmund and Ziegler (2012)

Site	Species present	Dating	Reference
Bełchatów C	Sciuridae indet.	MN 4/5	Garapich (2002)
Bełchatów B	Sciuridae indet.	MN 5/6	Garapich (2002)
Bełchatów A	Sciuridae indet.	MN 8/9	Garapich (2002)
Zamkowa Dolna Cave B	*Pliopetaurista* cf. *pliocaenica*, *Sciurus* cf. *warthae*	Early Pliocene	Black and Kowalski (1974); Nadachowski (1989); Nadachowski et al. (1989)
Mała Cave	*Pliopetes* sp.	Early Pliocene, MN 14	Nadachowski (1989); Nadachowski et al. (1989)
Pańska Góra	*Tamias* sp.	Early Pliocene, MN 14	Nadachowski (1989); Nadachowski et al. (1989)
Podlesice	*Blackia miocaenica*, *Pliopetaurista* sp., *Pliopetaurista* cf. *dehneli*, *Hylopetes hungaricus*, cf. *Sciurotamias* sp., *Sciurus* cf. *warthae*, *Tamias orlovi*	Early Pliocene, MN 14	Black and Kowalski (1974); Nadachowski (1989); Nadachowski et al. (1989)
Ewa's Cave	*Sciurus* sp.	Early Pliocene, MN 15	Nadachowski (1989); Nadachowski et al. (1989)
Mokra 1	*Pliopetes* sp.	Early Pliocene, MN 15	Nadachowski (1989); Nadachowski et al. (1989)
Raciszyn 1	*Pliopetes* cf. *hungaricus*, *Spermophilinus* sp., ?*Tamias* sp.	Early Pliocene, MN 15	Nadachowski (1989); Nadachowski et al. (1989)
Węże 1	*Blackia miocaenica*, *Pliopetaurista schaubi*, *Pliopetes* cf. *hungaricus*, *Sciurus warthae*, *Tamias orlovi*	Early Pliocene, MN 15	Sulimski (1964); Black and Kowalski (1974); Nadachowski (1989); Stefaniak et al. (2020)
Rębielice Królewskie 1A	*Blackia miocaenica*, *Miopetaurista* cf. *thaleri*, *Pliopetaurista dehneli*, *Sciurus* cf. *warthae*, *Tamias orlovi*	Late Pliocene, MN 16	Black and Kowalski (1974); Nadachowski (1989); Nadachowski et al. (1989)
Rębielice Królewskie 2	*Blackia miocaenica*, *Pliopetaurista dehneli*, *Sciurus* cf. *warthae*, *Tamias orlovi*	Late Pliocene, MN 16	Black and Kowalski (1974); Nadachowski (1989); Nadachowski et al. (1989)
Węże 2	*Blackia miocaenica*, *Pliopetaurista dehneli*, *Sciurus warthae*, *Tamias orlovi*	Late Pliocene, MN 16b	Sulimski (1964); Stefaniak et al. (2020); this paper
Kadzielnia 1	*Spermophilus polonicus*	Pliocene/Pleistocene	Black and Kowalski (1974); Nadachowski (1989)
Kamyk	*Spermophilus polonicus* ?*Tamias* sp.	Early Pleistocene	Black and Kowalski (1974); Nadachowski (1989)
Kielniki 3A	*Sciurus* sp.	Early Pleistocene	Nadachowski (1989)
Zalesiaki 1A	*Pliopetaurista meini*, *Spermophilus polonicus*	Early Pleistocene	Black and Kowalski (1974); Nadachowski (1989)
Zamkowa Dolna Cave C	*Spermophilus polonicus*	Early Pleistocene	Black and Kowalski (1974); Nadachowski (1989)
Żabia Cave	*Sciurus* sp.	Early Pleistocene	Nadachowski (1989)
Kozi Grzbiet	*Pliopetaurista meini*	Early/Middle Pleistocene	Black and Kowalski (1974); Nadachowski (1989)

Department of Paleozoology of Wrocław University. Four, and later five clay-rich beds containing fossils were distinguished that differed slightly in lithology; nevertheless, only part of the fossil material collected was attributed to a particular bed and the faunal lists were generally given for the site as a whole (Sulimski, 1962; Szynkiewicz, 2015).

The faunal composition of the Węże 2 fossil assemblage is currently dated as Late Pliocene (Lower Villafranchian) and is

Table 2

Measurements (mm) of isolated sciurid teeth from Węże 2

Species/tooth locus	N	Length: min.	Length: mean	Length: max.	Width: min.	Width: mean	Width: max
Tamias orlovi							
P4	4	1.2	1.3	1.4	1.2	1.2	1.3
M1/2	8	1.5	1.7	1.9	1.5	1.6	1.8
p4	4	1.2	1.3	1.5	1.1	1.2	1.3
m1/2	11	1.5	1.8	1.9	1.4	1.6	1.8
m3	3	1.9	2.0	2.0	1.5	1.5	1.6
Blackia miocaenica							
M3	3	1.6	1.6	1.7	1.4	1.5	1.5
Sciurus warthae							
M3	1	–	–	2.5	–	–	2.5

Table 3

Sciurids present at Węże 2 according to stratigraphic units

Stratigraphic unit	Species present
D	*Pliopetaurista dehneli, Tamias orlovi, Blackia miocaenica*
E	*Pliopetaurista dehneli, Tamias orlovi*
F	cf. *Pliopetaurista dehneli, Tamias orlovi*
G	*Tamias orlovi, Blackia miocaenica*
Indet.	*Pliopetaurista dehneli, Tamias orlovi, Blackia miocaenica, Sciurus warthae*

considered to belong to the MN 16b zone in the European Land Mammal Age chronology, i.e. 2.9–2.6 Ma (Nadachowski et al., 2015; Stefaniak et al., 2020; Marciszak et al., 2023). Remains of several amphibian (Młynarski et al., 1984; Młynarski and Szyndlar, 1989), reptilian (Młynarski et al., 1984), rodent (Sulimski, 1964; Czernielewski, 2021, 2022, 2023), eulipotyphlan (Skoczeń, 1976, 1993; Rzebik-Kowalska, 1990, 2014; Zijlstra, 2010; Sansalone et al., 2016), artiodactyl (Stefaniak, 1995; Stefaniak et al., 2020), carnivoran (Marciszak et al., 2023) and other mammalian (Kowalski, 1990; Fostowicz-Frelik, 2007; Stefaniak et al., 2020) taxa were recovered from the site, as well as some bird (Bocheński et al., 2012) and fish (Nadachowski et al., 2015) remains. In general, the fossil fauna of Węże 2 reflects an arboreal environment, located near to a constant freshwater source, and characterized by a warm, Mediterranean-like climate (Nadachowski et al., 2015; Stefaniak et al., 2020).

MATERIAL AND METHODS

The material comprises isolated teeth belonging to *Tamias orlovi*, *Blackia miocaenica* and *Sciurus warthae*, as well as a lower jaw belonging to *T. orlovi* with m1 and m2 preserved *in situ*. The remains were handpicked during fieldwork conducted in the early 1960s and are now housed in the collection of the Institute of Paleobiology of the Polish Academy of Sciences (abbreviated ZPAL). For the purpose of this study, the material was examined and photographed using a *Keyence VHX 900-F Digital Microscope System*.

SYSTEMATIC PALAEONTOLOGY

Family Sciuridae Fischer, 1817
Tribe Marmotini Pocock, 1923
Genus *Tamias* Illiger, 1811
Type species: *Tamias striatus* (Linnaeus, 1758)
Tamias orlovi (Sulimski, 1964)

Material. – 30 isolated teeth (ZPAL M. VIII/b/S1/2–31). See Table 2 and Fig. 2A–D

Right lower jaw with m1 and m2 *in situ* (ZPAL M. VIII/b/S1/1). Figure 3.

DESCRIPTION OF THE MATERIAL

Remark. – The occlusal morphology of these teeth is virtually identical to the *Tamias orlovi* teeth described and illustrated by Sulimski (1964: fig. 4, pl. III: figs. 6c, 7 and 8).

P4 – these teeth are approximately triangular in shape and three-rooted. The protoloph and the metaloph are high and well-developed, creating a U-shape in the central part of the occlusal surface. Close to the labial edge of the crown they merge into the paracone and the metacone respectively. Close to the lingual edge, the protoloph blends into the protocone and the metaloph into the hypocone. The protocone and the hypocone are also fused, forming a ridge. The parastyle is prominent, while the anteroloph and the posteroloph are less noticeable.

M1/2 – both are roughly trapezoid in shape, three-rooted and virtually identical with regard to occlusal morphology. The protoloph, the metaloph, the paracone and the metacone are all

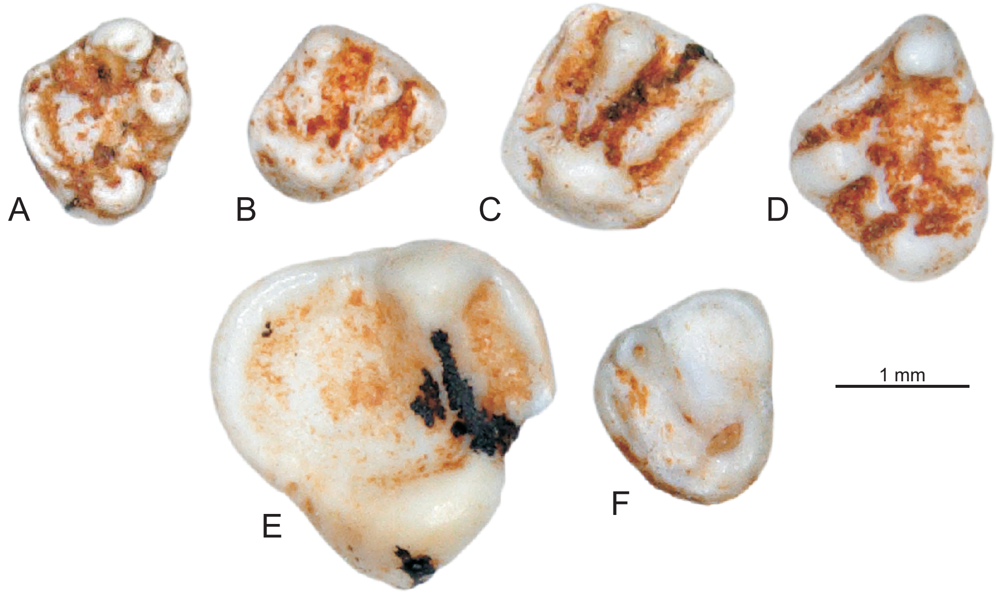

Fig. 2. Isolated sciurid teeth from Węże 2

A – *Tamias orlovi*, right p4 (ZPAL M. VIII/b/S1/29); **B** – *Tamias orlovi*, right P4 (ZPAL M. VIII/b/S1/25); **C** – *Tamias orlovi*, left M1/2 (ZPAL M. VIII/b/S1/8); **D** – *Tamias orlovi*, left m3 (ZPAL M. VIII/b/S1/23); **E** – *Sciurus warthae*, right M3 (ZPAL M. VIII/b/S3/1); **F** – *Blackia miocaenica*, left M3 (ZPAL M. VIII/b/S2/3)

Fig. 3. *Tamias orlovi* right lower jaw from Węże 2 (ZPAL M. VIII/b/S1/1) with m1-m2 *in situ*

well-developed. Especially the protoloph and the metaloph are easily noticeable and form a conspicuous V-shape in the central part of the crown. Another conspicuous feature of the occlusal surface is the prominent ridge formed by the protocone and the hypocone. The parastyle is present but not well developed. The anteroloph and the posteroloph are barely discernible.

p4 – the specimens from Węże are of a roughly trapezoid shape (although the posterior edge is visible curved) and are two-rooted. The metaconid and the protoconid are very close to each other, although clearly separated. The entoconid and the hypoconid are connected with a prominent ridge formed by the entolophid and the posterolophid.

m1/2 – these teeth are virtually indistinguishable on the grounds of occlusal morphology, rhomboid in shape, and four-rooted. The metaconid, the protoconid and the hypoconid are protruding and hook-shaped. The entoconid is more flattened and less elevated. The mesoconid is not as well-developed as in m3. The entolophid and the posterolophid form a prominent ridge. The talonid basin is low and featureless.

m3 – the general shape of the occlusal surface and its morphology are similar to m1/2 but the posterolabial edge is less curved, making the tooth look more elongated. The entoconid is underdeveloped while the mesoconid is more conspicuous than in m1/2. The protoconid is very prominent. The tooth is three-rooted.

The right lower jaw with m1 and m2 *in situ* is very similar to the *Tamias orlovi* material from Węże 1 described by Sulimski (1964: fig. 4, pl. III: figs. 5 and 6). The length/width measurements are 1.6/1.4 for m1 and 1.8/1.5 for m2.

Tribe Pteromyini Brandt, 1855
Genus *Blackia* Mein, 1970
Type species: *Blackia miocaenica* Mein, 1970
Blackia miocaenica Mein, 1970

Material. – 3 isolated M3 specimens (ZPAL M. VIII/b/S2/1–3). Figure 2F.

DESCRIPTION OF THE MATERIAL

M3 – it is of a roughly triangular shape. The central field of the occlusal surface is divided by the protoloph into a large, deep trigon basin and a narrow, elongated anterior valley. The protoloph is the most distinctive loph and it also connects the paracone and the protocone. The anteroloph, the posteroloph and the metacone are discernible but less conspicuous. The anteroloph runs parallel to the protoloph. The tooth is 3-rooted. These specimens closely resemble the *B. miocaenica* and *Blackia* sp. specimens illustrated and described by Mein (1970: figs. 75 and 79) as well as the *B. miocaenica* specimen from Hambach 11C illustrated and described by Van Laere and Mörs (2023: fig. 8A).

Tribe Sciurini Fischer, 1817
Genus *Sciurus* Linnaeus, 1758
Type species: *Sciurus vulgaris* Linnaeus, 1758
Sciurus warthae Sulimski, 1964

Material. – 1 isolated M3 specimen (ZPAL M. VIII/b/S3/1). Figure 2E.

DESCRIPTION OF THE MATERIAL

M3 – the shape of the tooth resembles a triangle with rounded corners. The main feature of the occlusal surface is the very high and conspicuous protocone which is connected with the paracone by a distinctive, high protoloph. The protoloph also divides the occlusal surface into a craterlike trigon basin and a narrow, elongated anterior valley. The anteroloph, the posteroloph and the metacone are less distinctive. The anteroloph runs parallel to the protoloph. There is no discernible metaloph. The tooth is 3-rooted. It is the only specimen from Węże 2 and is slightly damaged, with part of the anterior valley broken off. This is also the largest tooth of all the specimens studied. The morphology of the occlusal surface is very similar to that of the *S. warthae* specimen illustrated by Sulimski (1964: pl. III: fig. 1).

DISCUSSION

Tamias orlovi was first described as *Eutamias orlovi* by Sulimski (1964) on the basis of material from Węże 1, and included in *Tamias* by Black and Kowalski (1974). The genera *Tamias* and *Eutamias* are very closely related and *Eutamias* is sometimes considered a junior synonym of the former. These genera represent the tribe Marmotini that comprises forms adapted to a terrestrial lifestyle, supposedly descended from a *Palaeosciurus*-like ancestor (Piaggio and Spicer, 2001; Kryštufek and Vohralík, 2012; Patterson and Norris, 2016; Bosma et al., 2019). The oldest recognized species belonging to these genera are *Tamias eviensis* from MN 4 of Aliveri on the Greek island of Evia (de Bruijn et al., 1980) and *Eutamias sihongensis* from MN 4? of Xiacaowan in the Chinese province of Jiangsu located on the Pacific coast (Qiu and Liu, 1986), which shows that the lineage was widespread in Eurasia already from the Early Miocene. However, according to the recently accepted taxonomy, the only surviving representatives of these genera are the North American *Tamias striatus* and the Eurasian *Eutamias sibiricus* (Piaggio and Spicer, 2001; Kryštufek and Vohralík, 2012; Patterson and Norris, 2016).

In Poland *Tamias* was present at several Pliocene sites, the majority of the occurrences having been referred to as *T. orlovi*. Moreover, ?*Tamias* sp. was recorded at the Early Pleistocene site of Kamyk (Table 1). Other occurrences of *T. orlovi* include the Pliocene sites of Muselievo in Bulgaria (Popov, 2004) and Simbugino in Bashkortostan, western Russia (Danukalova et al., 2009). The *Tamias* teeth from Węże 2 are very similar to the material uncovered at the *T. orlovi* type locality of Węże 1 and are considered herein to belong to the same species.

B. miocaenica belongs to the Petauristini tribe of the Sciuridae family. The genus *Blackia* and the species *B. miocaenica* were established by Mein (1970) based on material from La Grive-Saint-Alban in the province of Isère, southwestern France (MN 7/8). Another species, *B. woelfersheimensis*, was recognized in the same study, the type locality of which is Wölfersheim (MN 15). Baudelot (1972) then created the taxon *B. parvula* for some Middle Miocene *Blackia* material from Greece. Moreover, Black and Kowalski (1974) established *B. polonica* (MN 14 of Podlesice, southern Poland), and Werner (1994) described an early (MN 2) *Blackia* from southern Germany as another species, *B. ulmensis*. However, later studies (de Bruijn et al., 1980; de Bruijn, 1998; Daxner-Höck, 2004; Hellmund and Ziegler, 2012; Van Laere and Mörs, 2023) tend to find these other species to be junior synonyms of *B. miocaenica*. Especially, Hellmund and Ziegler (2012) make a case that *B. miocaenica* and *B. polonica* are synonymous, which is followed here. The earliest fossil material attributed to *Blackia* is of Oligocene age and apparently has not yet been assigned to a particular species (Lu et al., 2013). An isolated P4 from the Upper Oligocene (MP 30) of Rott in Germany was described as *B.* aff. *miocaenica* by Mörs (1996).

Although *Blackia* is considered to rarely occur at Pliocene, and especially Upper Pliocene sites (Hellmund and Ziegler, 2012; Van Laere and Mörs, 2023), some material belonging to this genus has been reported from the Upper Pliocene of Rębielice Królewskie 1A and Rębielice Królewskie 2, whereas the other reported Polish occurrences are from the Lower Pliocene sites of Podlesice and Węże 1 (Table 1) The Węże 2 material consists of several detached teeth morphologically very similar to the *B. miocaenica* and *Blackia* sp. specimens described and illustrated by Mein (1970) as well as to the single *B. miocaenica* tooth illustrated and described by Van Laere and Mörs (2023). Thus, along with the MN 16b site of Frechen (Kolfschoten et al., 1998), and the MN 16 sites of Rębielice Królewskie 1A and Rębielice Królewskie 2, Węże 2 becomes one of the youngest occurrences of *B. miocaenica* and the genus *Blackia* in general, attesting to the longevity of the genus and the respective species (Lu et al., 2013; Van Laere and Mörs, 2023).

S. warthae is another species that was first recognized and described on the basis of material from Węże 1 (Sulimski, 1964). The genus itself is probably of North American origin, *Sciurus olsoni* from the Upper Miocene (Clarendonian) of Nevada being the oldest known representative (Emry et al., 2005).

Sciurus is considered to be morphologically extremely primitive, to the point of being described as a living fossil (Emry and Thorington Jr., 1982, 1984), and species thought to be very early squirrels were once routinely assigned to the Sciurini, the tribe of which *Sciurus* is the type species. These include *Protosciurus* (Black, 1963), *Douglassciurus* (Emry and Korth, 1996) and *Palaeosciurus* (Mercer and Roth, 2003).

In addition to the Lower Pliocene locality of Węże 1, which is the type site of *S. warthae*, fossil specimens from the Lower Pliocene site of Podlesice and the Upper Pliocene sites of Rębielice Królewskie 1A and Rębielice Królewskie 2 have been assigned to *Sciurus* cf. *warthae* (Table 1). Later, *S. warthae* was reported from the Lower Pliocene locality of Wölfersheim in central Germany (Dahlmann, 2001), as well as from the Pleistocene site of Monte la Mesa (Marchetti et al., 2000), while the Late Miocene (Turolian, MN 13) occurrence of *S. warthae* from Moncucco Torinese is also the oldest known occurrence of *Sciurus* in Europe (Colombero and Carnevale, 2016). The Węże 2 record of *S. warthae* consists of a single large M3 displaying similar morphology to a specimen from the species' type site of Węże 1, illustrated and described by Sulimski (1964).

The fossil sciurid fauna of Węże 2 consists of both tree-dwelling and ground-dwelling species. The former ecological type is represented by *P. dehneli*, *B. miocaenica* and *S. warthae*, and the latter by *T. orlovi*. All the genera present at Węże 2 are associated with arboreal environments, although the tree-dwelling forms are considered to indicate dense, continuous forests (Lu et al., 2013; Colombero and Carnevale, 2016) while *Tamias* is known to inhabit also more open, sometimes rocky areas (Svendsen and Yahner, 1979; Mahan and Yahner, 1999). Each of the species may also be considered relatively infrequent in the fossil record, which may be partly due to forest-dwelling faunas in general not being prone to fossil preservation (Colombero and Carnevale, 2016).

CONCLUSIONS

The fossil sciurid fauna of the MN 16b site of Węże 2 consists of specimens attributable to *P. dehneli*, *T. orlovi*, *B. miocaenica* and *S. warthae*. All these species are considered to be typical of arboreal environments, although the "flying squirrels" (Petauristini) *P. dehneli* and *B. miocaenica*, as well as the "tree squirrel" (Sciurini) *S. warthae* are thought to be more indicative of dense forests than the ground-dwelling *Tamias* (Marmotini). The site of Węże 2 is apparently one of the youngest occurrences of *B. miocaenica* (along with the MN 16b site of Frechen and the MN 16 sites of Rębielice Królewskie 1A and Rębielice Królewskie 2). Dated to the Late Pliocene, it is also one of the younger occurrences of *T. orlovi*. The composition of the sciurid fauna is apparently identical to that of the site of Rębielice Królewskie 2. The sciurid species of Węże 2 represent both the main ecological types evolved among squirrels, i.e. the arboreal and terrestrial modes of life.

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