Instytut Paleobiologii Polskiej Akademii Nauk

Rodents (Rodentia, Mammalia) from the Late Pliocene site of Węże 2: systematics, biogeography and ecomorphology

Gryzonie (Rodentia, Mammalia) z późnoplioceńskiego stanowiska Węże 2: systematyka, biogeografia i ekomorfologia

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Spis treści

Acknowledgements 4

Streszczenie 5

Summary 8

Introduction 11

Chapter 1. Gliridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland 18

Chapter 2. Castoridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland 38

Chapter 3. A new species of *Hystrix* (Rodentia: Hystricidae) from the Pliocene site of Węże 1 in southern Poland..51

Chapter 4: New data on the Sciuridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland 69

Chapter 5. *Prospalax priscus* jaw from the site of Węże 2 (Southern Poland, Pliocene) 86

Chapter 6. Fossil caries in a Pliocene rodent with a plausible case of in situ preservation of bacterial remains 98

Chapter 7. Orzesznice (*Muscardinus* spp.) i popieliczka *Glirulus pusillus* z późnoplioceńskiego stanowiska Węże 2 (Wyżyna Wieluńska) / Dormice *Muscardinus* spp. and *Glirulus pusillus* from the late Pliocene site of Węże 2 (Wieluń Upland) 117

Chapter 8. *Baranomys longidens* Kowalski, 1960 (Cricetidae: Baranomyinae) z późnoplioceńskiego stanowiska Węże 2 (Wyżyna Wieluńska) / *Baranomys longidens* Kowalski, 1960 (Cricetidae: Baranomyinae) from the Late Pliocene locality of Węże 2 (Wieluń Upland) 127

Conclusions 140

Future perspectives 141

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Streszczenie

Węże 2 to późnoplioceńskie (MN 16b, ok. 2.9–2.6 Ma) stanowisko paleontologiczne zlokalizowane na Wyżynie Wieluńskiej w południowej Polsce. Gatunki należące do co najmniej siedmiu rodzin gryzoni (Mammalia, Rodentia) zostały zidentyfikowane w materiale kopalnym pochodzącym z tego stanowiska. Do rodzin tych należą Gliridae (popielicowate), Sciuridae (wiewiórkowate), Hystricidae (jeżozwierzowate), Castoridae (bobrowate), Anomalomyidae, Cricetidae (chomikowate) i Muridae (myszowate). Wszystkie taksony zostały rozpoznane na podstawie zachowanych zębów lub szczęk, co stanowi powszechną praktykę przy badaniu kopalnych gryzoni. Anomalomyidae to jedyna wymarła rodzina reprezentowana w Wężach 2, podczas gdy wszystkie pozostałe mają żyjących przedstawicieli, włączając w to gatunki pospolicie występujące. Kopalna fauna gryzoni zachowana na stanowisku jest dość typowa dla późnego pliocenu i podobna do fauny pobliskiego stanowiska Rębielice Królewskie 2, które jest również podobnie datowane.

Popielicowate (Gliridae) są w Wężach 2 reprezentowane przez pięć gatunków: *Glis sackdillingensis*, *G. minor*, *Muscardinus pliocaenicus*, *M. dacicus* i *Glirulus pusillus*. *G. minor* i *G. sackdillingensis* różnią się między sobą jedynie rozmiarami zębów policzkowych, a materiał kopalny należący do zespołu *G. sackdillingensis-minor* często był dość arbitralnie przypisywany jednemu lub drugiemu gatunkowi. Striczky i Pazonyi (2014) opracowali metodę rozróżniania przynależności gatunkowej niektórych zębów policzkowych na podstawie lepiej ugruntowanych badań morfometrycznych. Dzięki temu można było w przekonujący sposób wykazać występowanie w Wężach 2 obu gatunków. Ponadto przeprowadzono rewizję taksonomiczną wystąpień *G. minor* i *G. sackdillingensis* na innych stanowiskach, w wyniku której skorygowano przynależność gatunkową części materiału. Struktura szkliwa *Glis* z Wężów 2 również została poddana analizie, co pozwoliło wykazać, że jest ono uformowane głównie ze szkliwa radialnego. Cienka warstwa lamelarnego szkliwa może występować jedynie w pobliżu miejsc, w których szkliwo przechodzi w zębinę. Taka struktura szkliwa jest typowa dla Myomorpha, czyli kladu gryzoni obejmującego Muroidea (myszowe) i Gliridae.

M. pliocaenicus jest uważany za bezpośredniego przodka współczesnej orzesznicy leszczynowej (*M. avellanarius*). Okazy przypisywane *M. dacicus* mogą reprezentować ten sam gatunek, co *M. avellanarius*, lub też siostrzaną dla *M. pliocaenicus – M. avellanarius* linię ewolucyjną. Zarówno *M. dacicus*, jak i *Glirulus pusillus* są bardzo rzadkie w zapisie kopalnym i nie były do tej pory notowane na listach faunistycznych sporządzonych dla Wężów 2.

Szczególnym odkryciem poczynionym podczas analizy szkliwa popielicowatych z Wężów 2 było znalezienie prabdopodobnej skamieniałej mikroflory bakteryjnej w asocjacji z ubytkiem

spowodowanym przez próchnicę w zębie *Glis sackdillingensis*. Opisany okaz jest najprawdopodobniej pierwszym znanym pochodzącym sprzed holocenu przykładem zachowania się w zapisie kopalnym śladów stanu chorobowego (na zębach, kościach czy innych tkankach), gdzie mikroby odpowiedzialne za jego rozwój zachowały się *in situ* jako skamieniałości. Niemniej brak doniesień o tego rodzaju znaleziskach może być spowodowany kwestiami metodologicznymi, co również jest poddane dyskusji.

Sciuridae (wiewiórkowate) w Wężach 2 reprezentowane są przez *Pliopetaurista dehneli* (materiał należący do tego gatunku, a znaleziony w Wężach 2 został opisany przez Sulimskiego, 1964), *Tamias orlovi*, *Blackia miocaenica* and *Sciurus warthae*. Wszystkie te gatunki są relatywnie rzadkie w zapisie kopalnym. Obok innego datowanego na MN 16b stanowiska Frechen oraz datowanych na MN 16 stanowisk Rębielice Królewskie 1A i Rębielice Królewskie 2 Węże 2 są jednym z najmłodszych wystąpień *B. miocaenica* w zapisie kopalnym. Obecność tylu gatunków prowadzących najprawdopodobniej nadrzewny tryb życia (*P. dehneli*, *B. miocaenica*, *S. warthae* i pięć gatunków popielicowatych) wskazuje na to, iż kopalny zespół faunistyczny Wężów 2 odpowiada środowisku leśnemu.

Castoridae (bobrowate) z Wężów 2 reprezentowane są przez *Trogontherium* (*Euroxenomys*) *minus* i *Dipoides* ex gr. *problematicus-sigmodus*. Rodzaj *Dipoides* oraz *Trogontherium* (*Euroxenomys*) *minus* nie były wcześniej notowane z Polski. Jako że kopalny zespół faunistyczny z Wężów 2 wskazuje na zalesione środowisko oraz bliskość stałego źródła słodkiej wody, obecność tych gatunków na stanowisku sugeruje, że ci mniej znani i wymarli przedstawiciele Castoridae byli przystosowani do podobnych warunków jak współczesne gatunki (*Castor fiber* i *C. canadensis*).

O obecności jeżozwierza *Hystrix refossa* w Wężach 2 świadczy fragmentaryczna żuchwa, która może być z pewnością przypisana do tego gatunku, a także pewna liczba izolowanych zębów należących do *Hystrix* sp. Odkrycie to pokazuje, że zasięg występowania *H. refossa* był w późnym pliocenie szerszy, niż wcześniej przypuszczano, i że gatunek ten zaczął rozprzestrzeniać się po Europie Środkowo-Wschodniej przez nastaniem wczesnego plejstocenu. Znalezisko rodzaju *Hystrix* w Wężach 2 czyni to stanowisko (razem z pobliskim stanowiskiem Węże 1) jednym z najbardziej wysuniętych na północ stanowisk kopalnych jeżozwierzowatych w Europie. Ponadto porównanie materiału jeżozwierzowatych z kilku stanowisk doprowadziło do wyróżnienia nowego gatunku *H. velunensis* na podstawie plioceńskiego (MN 15) materiału ze stanowiska Węże 1. Materiał ten był poprzednio zaliczany do *H. primigenia* lub *H. depereti*, lecz różni się od tych gatunków oraz od *H. refossa* morfologią powierzchni zgryzowych.

Innym rzadkim gatunkiem obecnym w Wężach 2 jest *Prospalax priscus* (Anomalomyidae). Ekologia i adaptacje Anomalomyidae (Muroidea) są od dawna kwestią debaty w literaturze przedmiotu. Obecność tego gatunku na stanowisku wspiera interpretację *P. priscus* oraz Anomalomyidae w ogólności jako zaadaptowanych do środowisk leśnych.

Gatunkiem występującym pospolicie w Wężach 2 jest *Baranomys longidens* reprezentujący chomikowate gryzoń blisko spokrewniony z karczownikami (Arvicolinae). Gatunek ten był notowany na listach faunistycznych opracowanych dla tego stanowiska, niemniej jednak materiał z Wężów 2 nie został wcześniej poddany badaniom morfometrycznym ani zilustrowany. Analiza morfologii powierzchni zgryzowych oraz badanie morfometryczne wykonane na potrzeby niniejszej pracy potwierdziły, że okazy z Wężów 2 należą do tego samego gatunku, co materiał z Wężów 1, które są *locus typicus* gatunku *B. longidens*. Niemniej z uwagi na niewielką liczbę dostępnych informacji na temat innych gatunków należących do rodzaju *Baranomys* (*B. loczyi* i *B. kowalskii*), różnice morfometryczne i morfologiczne pomiędzy tymi gatunkami nie są dobrze udokumentowane. Pojawienie się nowego materiału *Baranomys* z innych stanowisk w Europie może pomóc w lepszym zrozumieniu tych różnic bądź też podważeniu ich.

Ponadto w kolekcji Instytutu Paleobiologii PAN znajdują się szczątki innych chomikowatych pochodzące z Wężów 2 i reprezentujące rodzaje *Mimomys*, *Germanomys* i *Trilophomys*, a także bardzo nieliczne szczątki myszowatych (Muridae). Dalsze analizy są konieczne w celu kompletnego rozpoznania składu gatunkowego fauny chomikowatych i myszowatych z Wężów 2.

Summary

Węże 2 is a Late Pliocene (MN 16b, i.e. 2.9–2.6 Ma) paleontological site located in the Wieluń Upland, southern Poland. Species belonging to at least seven rodent (Mammalia, Rodentia) families have been detected in the fossil assemblage of the site. These families include Gliridae (dormice), Sciuridae (squirrels), Hystricidae (porcupines), Castoridae (beavers), Anomalomyidae, Cricetidae (hamster-like rodents) and Muridae (mice and rats). All the taxa were identified based on dental specimens and/or jaws as is commonly practiced while dealing with fossil rodents. Anomalomyidae is the only extinct family represented at Węże 2 while all the other families have also extant representatives, including very common species. The fossil rodent fauna of the site is quite typical for the Late Pliocene and similar to the nearby site of Rębielice Królewskie 2 which is also similarly dated.

The dormouse (Gliridae) fauna of Węże 2 is represented by five species – *Glis sackdillingensis*, *G. minor*, *Muscardinus pliocaenicus*, *M. dacicus* and *Glirulus pusillus*. *G. sackdillingensis* and *G. minor* differ only by the dimensions of their cheek teeth and fossil material belonging to *G.* ex gr. *sackdillingensis-minor* was often fairly arbitrarily assigned to one of the species. Striczky and Pazonyi (2014) elaborated a method of distinguishing some of the cheek teeth as belonging to either *G. minor* or *G. sackdillingensis* based on stronger morphometric grounds. Thus, the presence of both species at the Węże 2 site could be more convincingly shown. Moreover, a taxonomic revision of *G. minor* and *G. sackdillingensis* occurrences from other sites led to reassigning of some material to the other species. The enamel structure in the glirids from Węże 2 was also examined and proved to be formed predominantly by radial enamel. A thin layer of lamellar enamel, occurring close to the enamel-dentine junction, may be also present. Such enamel structure is typical for the Myomorpha, the clade of rodents encompassing the Muroidea (the mouse-like rodents) and the Gliridae.

M. pliocaenicus is considered to be a direct ancestor of the extant hazel dormouse (*M. avellanarius*). Specimens assigned to *M. dacicus* may represent either the same species as *M. avellanarius* or a sister evolutionary lineage to *M. pliocaenicus* – *M. avellanarius*. Both *M. dacicus* and *G. pusillus* are rare in the fossil record and were not listed on the faunal lists for Węże 2 before.

A striking finding made during the analyses of the enamel of the Gliridae from Węże 2 was the discovery of probable fossil bacterial microflora associated with a cavity caused by caries in a *Glis sackdillingensis* tooth. The described specimen is apparently the only known pre-Holocene example of a pathological condition (dental, osteological or of another type) where the microbes

responsible for its development were preserved *in situ* as fossils. However, potential methodological factors that may have caused such cases to be overlooked are also discussed.

The Sciuridae (squirrels) present at Węże 2 include the species *Pliopetaurista dehneli* (material belonging to this species and found at Węże 2 was already described by Sulimski, 1964), *Tamias orlovi*, *Blackia miocaenica* and *Sciurus warthae*. All the species are otherwise relatively rare in the fossil record. Along with another MN 16b site of Frechen, as well as the MN 16 sites of Rębielice Królewskie 1A and Rębielice Królewskie 2, Węże 2 is also one of the youngest occurrences of *B. miocaenica* in the fossil record. The presence of so many species of most probably associated with arboreal environments (*P. dehneli*, *B. miocaenica*, *S. warthae* and five species of glirids) indicates that the fossil assemblage of Węże 2 corresponds to a woodland environment.

The Castoridae (beavers) of Węże 2 include *Trogontherium* (*Euroxenomys*) *minus* and *Dipoides* ex gr. *problematicus-sigmodus*. The genus *Dipoides* and the species *Trogontherium* (*Euroxenomys*) *minus* have not previously been reported from Poland. As the Węże 2 fossil assemblage is otherwise suggestive of a fauna inhabiting a woodland environment with a constant freshwater source nearby, the presence of these species at the site suggests that these lesser-known and extinct representatives of the Castoridae were adapted to similar conditions as the modern species (*Castor fiber* and *C. canadensis*).

The presence of the porcupine *Hystrix refossa* in Węże 2 is supported by one fragmentary mandible that can be certainly assigned to this species as well as some dental specimens belonging to *Hystrix* sp. The discovery shows that the late Pliocene range of *H. refossa* was wider than previously indicated and that it started to spread across East-Central Europe before the onset of the early Pleistocene. The finding of a *Hystrix* specimen at Węże 2 makes this site (along with the nearby site of Węże 1) one of the northernmost occurrences of fossil porcupines in Europe. Moreover, comparison of hystricid material from several sites, led to establishing a new species, *H. velunensis*, present at the Pliocene (MN 15) site of Węże 1. This specimen was previously assigned either to *H. primigenia* or *H. depereti* but it differs from these species as well as from *H. refossa* by distinct occlusal morphology.

Another rare species present at the site of Węże 2 is *Prospalax priscus* (Anomalomyidae). While the ecology and adaptations of the Anomalomyidae (Muroidea) have been long debated in the scientific literature, 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.

A species that appears frequently at Węże 2 is *Baranomys longidens*, a rodent belonging to the Cricetidae and closely related to voles (Arvicolinae). This species was listed on the faunal lists prepared for this site but the Węże 2 fossil material has not previously been subjected to morphometric studies or illustrated. Examination of the morphology of occlusal surfaces and a morphometric analysis made for the purpose of this work confirmed that the specimens from Węże 2 belong to the same species as the fossil material from Węże 1 which is the type site of *B. longidens*. However, because of the scarcity of published data on the other species within the genus *Baranomys* (*B. loczyi* and *B. kowalskii*), morphometric and morphological differences between them are not well documented. Appearance of new fossil material of *Baranomys* from other sites may help to either understand these differences better or call them into question.

Moreover, in the collection of the Institute of Paleobiology are remains of other cricetid rodents from Węże 2, belonging to the genera *Mimomys*, *Germanomys* and *Trilophomys*, as well as some very rare teeth of fossil mice (Muridae). Further examinations are needed to better understand the specific composition of the Węże 2 cricetid and murid material.

Introduction

Rodents

The order Rodentia, commonly known as rodents, encompasses approximately 1500 extant species out of the approximately 4000 extant species of mammals (Carleton and Musser 2005). The evolutionary history of rodents, as documented in the fossil record, extends back to the Paleocene (Wodd 1962, Rose 2006). However, some molecular data suggest that rodents might have been present even in the Late Cretaceous (Suárez et al. 2011). The order can be classified into five extant suborders: Anomaluromorpha, Castorimorpha, Hystricomorpha, Myomorpha and Sciuromorpha. Anomaluromorpha comprises small sub-Saharan African rodents, including the eponymous Anomaluridae. Castorimorpha consists of Castoridae (beavers), Geomyidae (gophers), Heteromyidae (e.g. kangaroo rats and kangaroo mice), along with several extinct families. Representatives of this suborder inhabit Eurasia, as well as North and South America. Hystricomorpha contains numerous extant and extinct families, including Hystricidae (porcupines) and Caviidae (cavies, capybaras and guinea pigs). Hystricomorphs colonized all the continents except for Australia and Antarctica. Sciuromorpha includes the well-known families Sciuridae (squirrels) and Gliridae (dormice), along with the so-called „mountain beavers" (Aplodontidae), which contain only one extant species with particularly primitive morphology, as well as some extinct families. This suborder is indigenous to the Americas, Eurasia and Africa. Myomorpha is the most species-rich suborder of the Rodentia, comprising over 1500 extant species. The vast majority belong to the family Muridae which includes mice and rats. Other notable families within Myomorpha in the context of the Polish Pliocene are the Cricetidae (containing hamsters, voles, lemmings etc.), as well as the extinct Anomalomyidae. The Myomorpha inhabit all continents except Antarctica (Carleton and Musser 2005, Freudenthal and Martín-Suárez 2015).

Basic methodology of paleontological research on rodents

Fossil rodent taxa are commonly defined based on differences in the morphology of occlusal dental surfaces (the surfaces used for ripping, tearing or grinding food). This is because compared to other hard body parts of mammals, teeth are the most likely to fossilize and are also the most diagnostically significant due to clear inter-specific differences in occlusal morphology. Among the four kinds of teeth present in mammals, the incisors (I, i), the canines (C, c), the premolars (P, p) and the molars (M, m), rodents notably lack any sorts of canines (a characteristic obviously linked to their evolutionary rooted herbivory) while the incisors are rarely diagnostic for inter-specific differences. The standard rodent dental formula is I1/1, C0/0, P1/1, M3/3, signifying that the animal possesses one incisor, no canines, one premolar and three molars in each half of both the upper and the lower jaw. However, the actual formula varies between families (for example many rodents lack premolars, leaving the molars as the sole diagnostic teeth).

The designation of specific teeth for purposes such as indicating the number of found specimens of a specific kind, providing measurements, or illustrating important specimens involves a standardized system. Upper dentition teeth are typically marked with upper case letters (I, P, M), while lower dentition teeth are marked with lower case letters (i, p, m). Additionally, their position in the upper or the lower jaw relative to the other teeth of the same kind is marked with Roman numerals. The higher the number, the farther within the mouth (more posteriorly) the tooth is situated. For instance, "M2" signifies an upper molar which is situated farther inside the mouth than M1, but closer to the mouth's tip (more anteriorly) than M3. It is worth noting, that rodents exhibit differences in occlusal morphology not only between different kinds of teeth (I, P, M), but also between the upper and lower teeth of the same kind and locus within the jaw. Consequently, an upper second molar (M2) will display distinct occlusal morphology from its counterpart in the lower jaw (m2). Differences exist also among teeth of the same kind, depending on their position in the jaw (e.g. m1 differing in occlusal morphology from m2). Furthermore, it is also possible to distinguish the teeth belonging to the same jaw, kind and locus, based on whether they come from the left or right half of the jaw, as their occlusal morphologies are mirror images. In summary, rodents display well-developed heterodonty, wherein there is intra-individual variability of tooth morphology. While this feature can be valuable in distinguishing between species present in fossil material, it may also introduce confusion as it is not always clear if differences in morphology between isolated teeth are inter-specific or caused by intra-individual variability. There is also considerable diversity in dental morphology between different clades of rodents caused by adaptations to consuming different kinds of food (Tapaltsyan et al. 2016, Berkovitz and Shellis 2018).

Chronology of European Pliocene

The Pliocene epoch spans from 5.333 to 2.58 million years ago (mya). It is divided into the Zanclean, also referred to as the early Pliocene (5.333–3.6 mya) and the Piacenzian, known as the late Pliocene (3.6 –2.58 mya) (Cohen et al. 2023). In the context of European Cenozoic localities housing mammal fossils, the so-called Mammal Neogene Zonation (MN) and European Land Mammal Ages serve as standard tools for dating and biostratigraphically correlating sites with each other. The relevant MN biozones and geologic time periods for the study of the Polish Pliocene are MN 13 (ca. 7.0–4.9 mya), MN 14 (4.9–4.2 mya), MN 15 (4.2–

3.2 mya), MN 16 (3.2–2.5 mya), the Turolian (9.0–5.3 mya), the Ruscinian (5.3–3.4 mya), and the Villafranchian (3.5–1.0 mya) (Lindsay et al. 1989, Rook and Martínez-Navarro 2010, Gibbard and Head 2020*).* Węże 2 is among several Pliocene sites in Poland where rodent fossil material has been discovered. Notable sites in this category include Podlesice (MN 14), Węże 1 (MN 15), Rębielice Królewskie 1A (MN 16) and Rębielice Królewskie 2 (MN 16) (Nadachowski, 1989; Nadachowski et al., 1989). Węże 2, based on its vertebrate fauna, is dated at 2.9–2.6 mya (late Pliocene, Villafranchian, MN 16b) (Nadachowski et al. 2015; Stefaniak et al. 2020; Marciszak et al. 2023).

Rodent clades present at Węże 2

The rodent species present at Węże 2 and studied here in considerable detail are *Glis minor*, *G. sackdillingensis*, *Muscardinus pliocaenicus*, *M. dacicus*, *Glirulus pusillus* (Sciuromorpha, Gliridae), *Trogontherium minus* (Castorimorpha, Castoridae), *Dipoides* ex gr. *problematicus-sigmodus* (Castorimorpha, Castoridae), *Sciurus warthae* (Sciuromorpha, Sciuridae), *Blackia miocaenica* (Sciuromorpha, Sciuridae), *Tamias orlovi* (Sciuromorpha, Sciuridae), *Hystrix refossa* (Hystricomorpha, Hystricidae), *Prospalax priscus* (Myomorpha, Anomalomyidae) and *Baranomys longidens* (Myomorpha, Cricetidae) (Fig. 1). Moreover the presence of several other cricetid species, including *Mimomys* spp. (Myomorpha, Cricetidae) has been confirmed, as well as the presence of some murid teeth. Among these species, *Glis sackdillingensis, G. minor, Sciurus warthae*, *Blackia miocaenica*, *Tamias orlovi*, *Prospalax priscus*, *Muscardinus pliocaenicus*, *M. dacicus*, *Glirulus pusillus*, *Baranomys longidens* and several *Mimomys* species have been previously identified in other Polish Pliocene localities. However, *Hystrix refossa*, *Trogontherium minus* and the genus *Dipoides* appear exlusive to the Węże 2 site. Additionaly, a novel species, *Hystrix velunensis* (Hystricomorpha, Hystricidae), has been identified based on material from Węże 1.

The species present at Węże 2 exhibit diverse ecological and behavioral characteristics and belong to different evolutionary lineages, a distinction mirrored in their dental morphologies. Despite their differences, all species are quite typical representatives of their respective families, showcasing adaptations and modes of life unique to each. Most of the studied species exhibit a dental formula of I1/1, C0/0, P1/1, M3/3, with Anomalomyidae and Cricetidae being exceptions, possessing a dental formula of I1/1, C0/0, P0/0, M3/3.

Previous research on the site of Węże 2

Sulimski (1962) reported the discovery of the site and published preliminary information on the fossil fauna. Subsequently, Sulimski (1964) described a new species of flying squirrel, *Pliosciuropterus dehneli*, based on fossil material from Węże 2. However, this species was later included in *Pliopetaurista* by Hordijk and de Bruijn (2009). Młynarski et al. (1984) described amphibian and reptilian remains from the site. Skoczeń (1993) then examined eulipotyphlan fossil material from Węże 2 and described a new species of mole, *Neurotrichus minor*, which was renamed *N. skoczeni* by Zijlstra (2010) and then *Rzebikia skoczeni* by Sansalone et al. (2016). Stefaniak (1995) and Stefaniak et al. (2020) described the cervid fauna of Węże 2, confirming the presence of *Croizetoceros ramosus, Matacervocerus pardinensis, Procapreolus moldavicus* and *Arvenoceros* cf. *ardei*. Fostowicz-Frelik (2007) examined the remains of the leporid *Hypolagus beremendensis*. The site and its fossil fauna were also briefly described by Szynkiewicz (2015) and Nadachowski et al. (2015). Moreover, Marciszak et al. (2023) confirmed the presence of the canids *Canis etruscus*, *Vulpes* cf. *alopecoides*, and *Nyctereutes* sp.

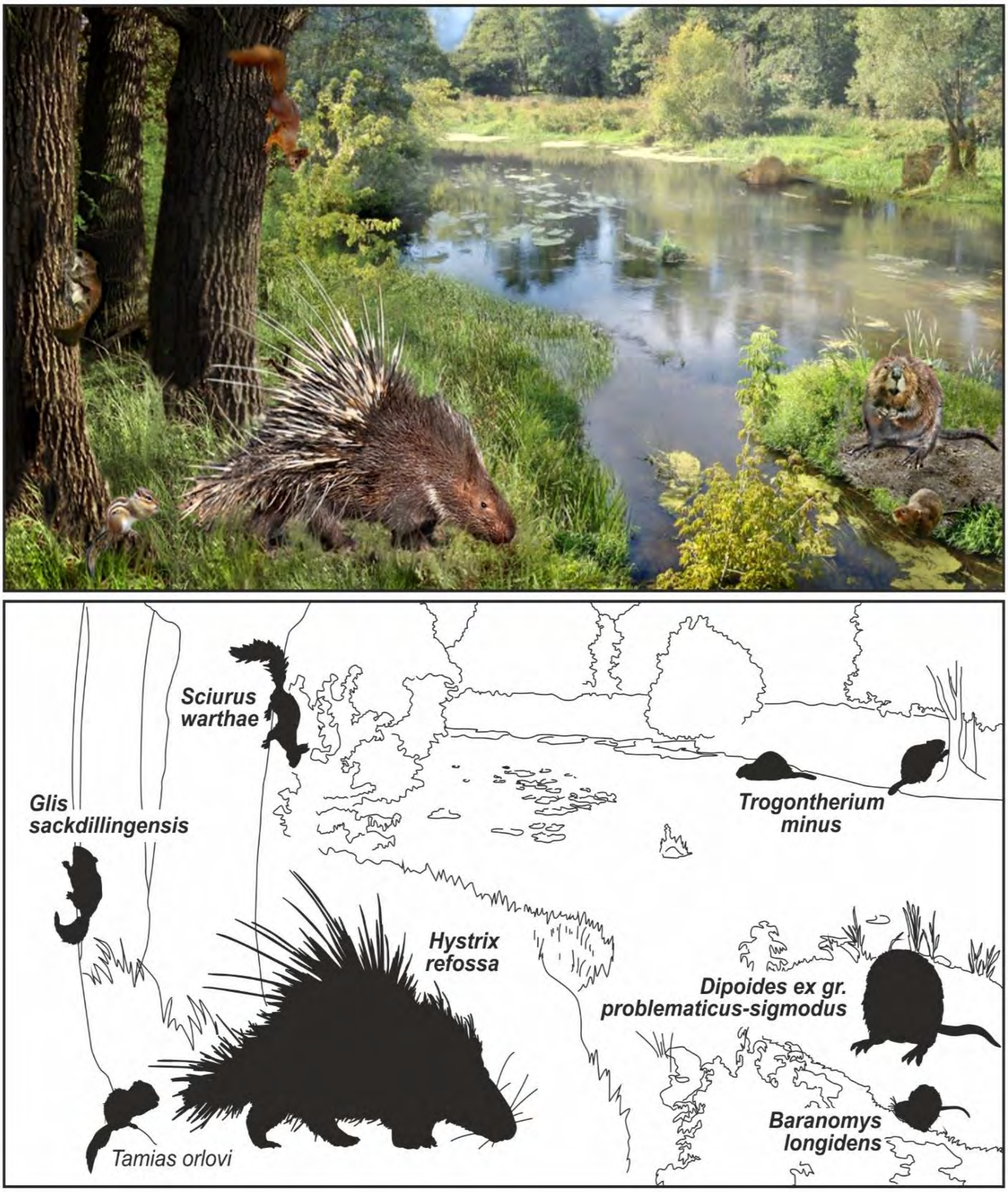

Fig. 1. Reconstruction of the ecosystem of Węże 2 with some rodent species present in the fossil assemblage. Illustrated species are *Sciurus warthae* (Sciuridae), *Tamias orlovi* (Sciuridae), *Glis sackdillingensis* (Gliridae), *Hystrix refossa* (Hystricidae), *Trogontherium minus* (Castoridae), *Dipoides* ex gr. *problematicus-sigmodus* (Castoridae) and *Baranomys longidens* (Cricetidae).

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Chapter 1.

Gliridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland[1]

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Abstract

A fossil assemblage of dormice (Rodentia: Gliridae) was uncovered at the (Lower?) Villafranchian site of Węże 2 in southern Poland. Based on morphometric criteria, the diagnostic M1 and m1 specimens are assignable to *Glis minor* and *Glis sackdillingensis*, two species which differ only by the dimensions of their cheek teeth. The presence of dormice at Węże 2 implies that the fossil assemblage of this site represents an at least partly wooded environment. The enamel structure in the glirids from Węże 2 is formed predominantly by radial enamel. A thin layer of lamellar enamel, occurring close to the enamel-dentine junction may be present. Such a type of enamel structure is typical of the Myomorpha, the clade of rodents encompassing the Muroidea (the mouse-like rodents) and Gliridae.

Key words: Villafranchian; rodents; dormice; Węże; karst

Introduction

This paper describes the fossil assemblage of dormice (Rodentia: Gliridae) uncovered at the Villafranchian (MN 16b?) site of Węże 2 in southern Poland. Although the site has been known since the early 1960s (Sulimski 1962), much of the fossil material collected still awaits a systematic description. This study is part of a larger project intended to provide a comprehensive report on the rodent fauna of Węże 2. The data provided will contribute to current knowledge on the palaeobiogeography, palaeoecology and evolution of particular taxa.

The Gliridae (dormice) are an ancient family of omnivorous Old World rodents. They first appeared in the Eocene and underwent a major radiation during the Miocene. Nonetheless, at the end of the Miocene several phyletic lineages became extinct, which resulted in the modern genera being rather distantly related (Nadachowski 1989, Daoud 1993, Rose 2006, Kurtén 2007).

The oldest glirid fossils from Poland are probably the *Glirudinus* sp. remains from the MN 5–6 (Lower Miocene) of Bełchatów (Kowalski 1990).

Modern dormice are mostly associated with various kinds of arboreal and shrubby habitats, and generally are capable climbers, nesting in tree hollows or among branches. Caves are also sometimes inhabited and used as hibernacula, and areas with caves may be preferred by some species (Nadachowski 1989, Kurtén 2007, Kryštufek 2010). It has been suggested that fossil dormice displayed greater ecological diversity than the surviving taxa (Nadachowski 1989). Out of the recent genera, *Eliomys* differs from the typical Gliridae as it is known to thrive in open rocky environments and semi-desert areas of Northern Africa (Daoud 1993, Amori et al. 2008).

There are nine extant genera of glirids comprising 29 species and grouped into three subfamilies (Holden 2005). The *Glis* genus is today represented by the fat dormouse, *G. glis.* This species, as well as *Glirulus japonicus* (the Japanese dormouse) belong to the Glirinae subfamily, which is thought to have originated in the Oligocene (Holden 2005, Kurtén 2007, Holden and Levine 2009). The evolutionary lineage *G. minor* – *G. sackdillingensis* – *G. glis* is commonly inferred from the fossil record (Nadachowski 1989, Daoud 1993, Siori et al. 2014, Striczky and Pazonyi 2014). Here I report the presence of *G. minor* and *G. sackdillingensis* at the Villafranchian (MN16?) site of Węże 2 in southern Poland. Both species are considered to be associated with arboreal environments (de Bruijn 1998, Popov 2004, Hellmund and Ziegler 2012, Siori et al. 2014, Striczky and Pazonyi 2014, Colombero et al. 2017).

Geological setting

Węże 2 is a Villafranchian site situated on the NW slope of the Zelce Hill (51°06′00″N 18°47′30″E; 228 m a.s.l.) in the Wieluń Upland, near the village of Węże, in the vicinity of the town of Działoszyn, in Pajęczno County, southern Poland (Fig. 1). The site comprises a vertical karst crevice etched in the Upper Jurassic (Oxfordian) limestone and infilled with fossiliferous sediment of the terra rossa type. The crevice itself is a part of a larger karst cave system of the hill (Sulimski 1962, Stefaniak 1995, Stefaniak et al. 2020) and is located about 150–200 m north from the better known Węże 1 site, which has been dated at MN 15 (e.g. Sulimski 1964, Fostowicz-Frelik 2007).

The Węże 2 site (abbreviated as W2) was discovered and preliminary explored between 1958 and 1961 by Sulimski who detected an abundant fossil vertebrate fauna dominated by small mammal remains, whereas the big mammal fossils were rare and highly fragmented (Sulimski 1962, Stefaniak et al. 2020). The terra rossa deposits (~3.5 t in total) were collected during field work organized by the Department of Paleozoology (now: Institute of Paleobiology) PAS in Warsaw and the Department of Paleozoology of the Wrocław University (Sulimski, 1962).

So far, the fossil remains have been described only in part, more detailed studies concerning cervids (Stefaniak 1995, Stefaniak et al. 2020), rhinoceroses and elephantids (Stefaniak et al. 2020), and lagomorphs (Fostowicz-Frelik 2007). The presence of diverse rodent and lipotyphlan faunas was mentioned (Sulimski 1962, Nadachowski 1989, Rzebik-Kowalska 1989), but these were not studied in detail. The accompanying, generally scarce reptilian remains included *Lacerta* sp., *Anguis* cf. *fragilis*, *Ophisaurus pannonicus*, *Testudo* sp. and *Emys wermuthi*, while amphibians were represented by rare and fragmented long bones of *Rana* sp. (Sulimski 1962). The age of the Węże 2 fossil assemblage was preliminary established as the Late Pliocene (Lower Villafranchian) MN 16b zone (2.9–2.6 Ma) based on its faunal composition compared to the nearby site of Rębielice Królewskie 1 (Sulimski 1962, 1964, Stefaniak 1995, Stefaniak et al. 2020).

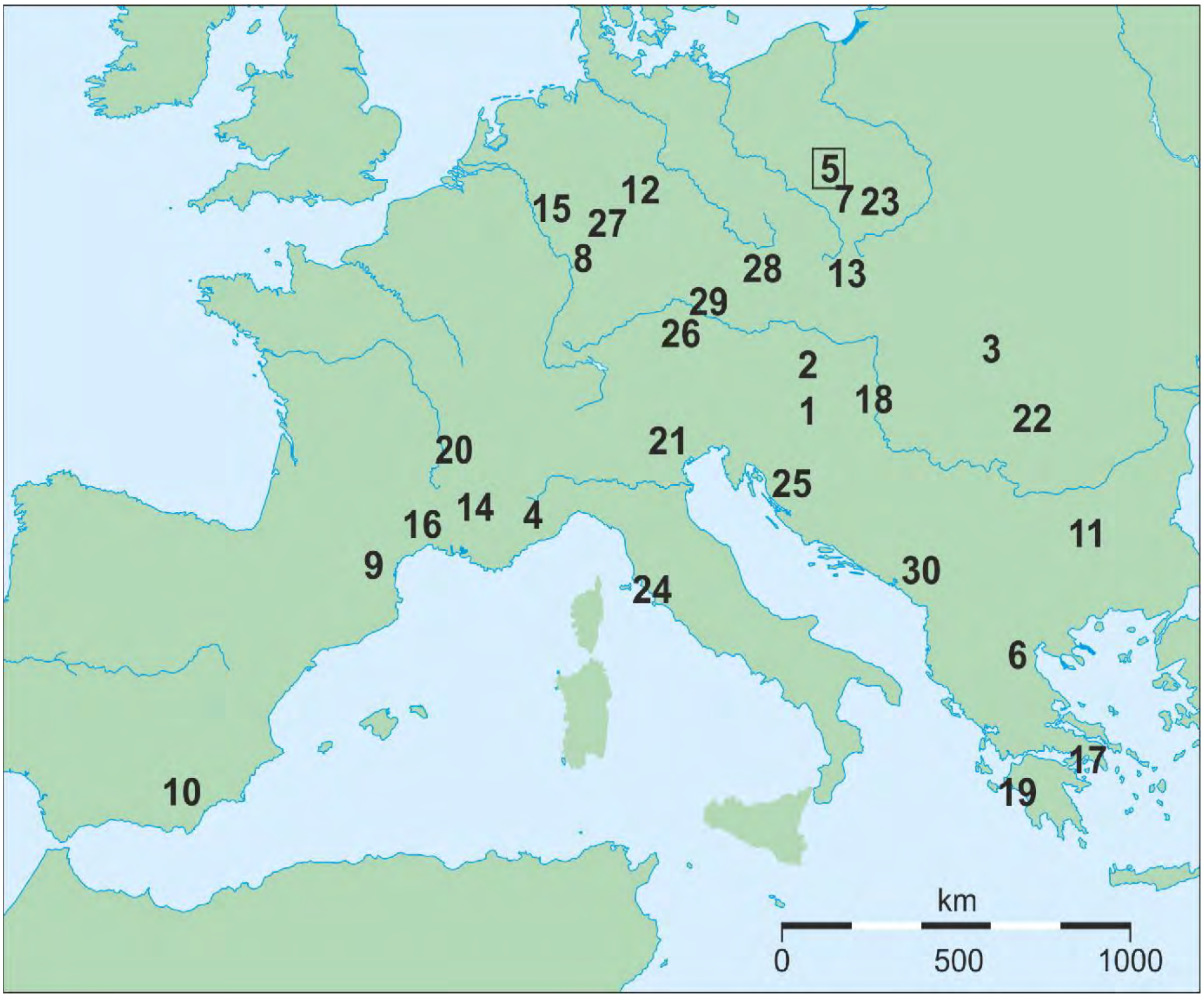


Fig. 1. Locations of sites mentioned in Table 2. 1 – Oberdorf, Kohfidisch; 2 – Richardhof; 3 – Rudabánya, Osztramos, Kövesvárad, Tarkő, Uppony Rock Shelter 1; 4 – Moncucco Torinese; 5 – Mała Cave, Raciszyn 1, Węże 1, Węże 2; 6 – Komanos 1, Notio 1; 7 – Pańska Góra, Podlesice,

Rębielice Królewskie, Kamyk, Kielniki, Żabia Cave; 8 – Wölfersheim; 9 – Mont Hélène; 10 – Moreda; 11 – Muselievo; 12 – Sondershausen; 13 – Vitošov; 14 – Grand Serre; 15 – Hambach; 16 – Mas Rambault; 17 – Tourkovounia 1; 18 – Csarnóta, Somssich Hill 2, Beremend 14, Villány-Kalkberg-Nord; 19 – Kaiafas; 20 – Les Valerots; 21 – Monte la Mesa; 22 – Betfia; 23 – Kadzielnia, Kozi Grzbiet; 24 – Monte Argentario; 25 – Razvodje, Podumci; 26 – Schernfeld; 27 – Untermassfeld; 28 – Chlum; 29 – Sackdillinger Cave; 30 – Trlica.

Material and methods

The *Glis* material consists of isolated teeth and one mandible fragment with m1–m2 in situ (Fig. 2). All dental loci are represented in the sample, although the most numerous are m1/M1 and m2/M2, whereas m3/M3 and p4/P4 are underrepresented in the sample (see Table 1). The bias results most probably from the size factor, the premolars and the ultimate molars being the smallest teeth in the dental row, and thus easier to overlook during collecting and preparation. The morphology of the teeth is typical of *Glis* teeth described from coeval localities in Poland (Kowalski 1960b, 1963, Daoud 1993).

The remains were recovered from the bone breccia site of Węże 2 by hand picking. Some larger portions of more calcified sediment were dissolved using acetic acid and then the residue was sifted. The specimens were examined, measured and photographed with the Keyence VHX 900-F Digital Microscope System.

The glirid dental terminology follows Striczky and Pazonyi (2014) and is illustrated in Figure 3. The enamel microstructure of the cheek teeth was made visible using the method described in Fostowicz-Frelik et al. (2012). It was then studied under SEM (Philips XL20) at the Institute of Paleobiology (PAS). The material is housed in the collection of the Institute of Paleobiology PAS (abbreviated ZPAL).

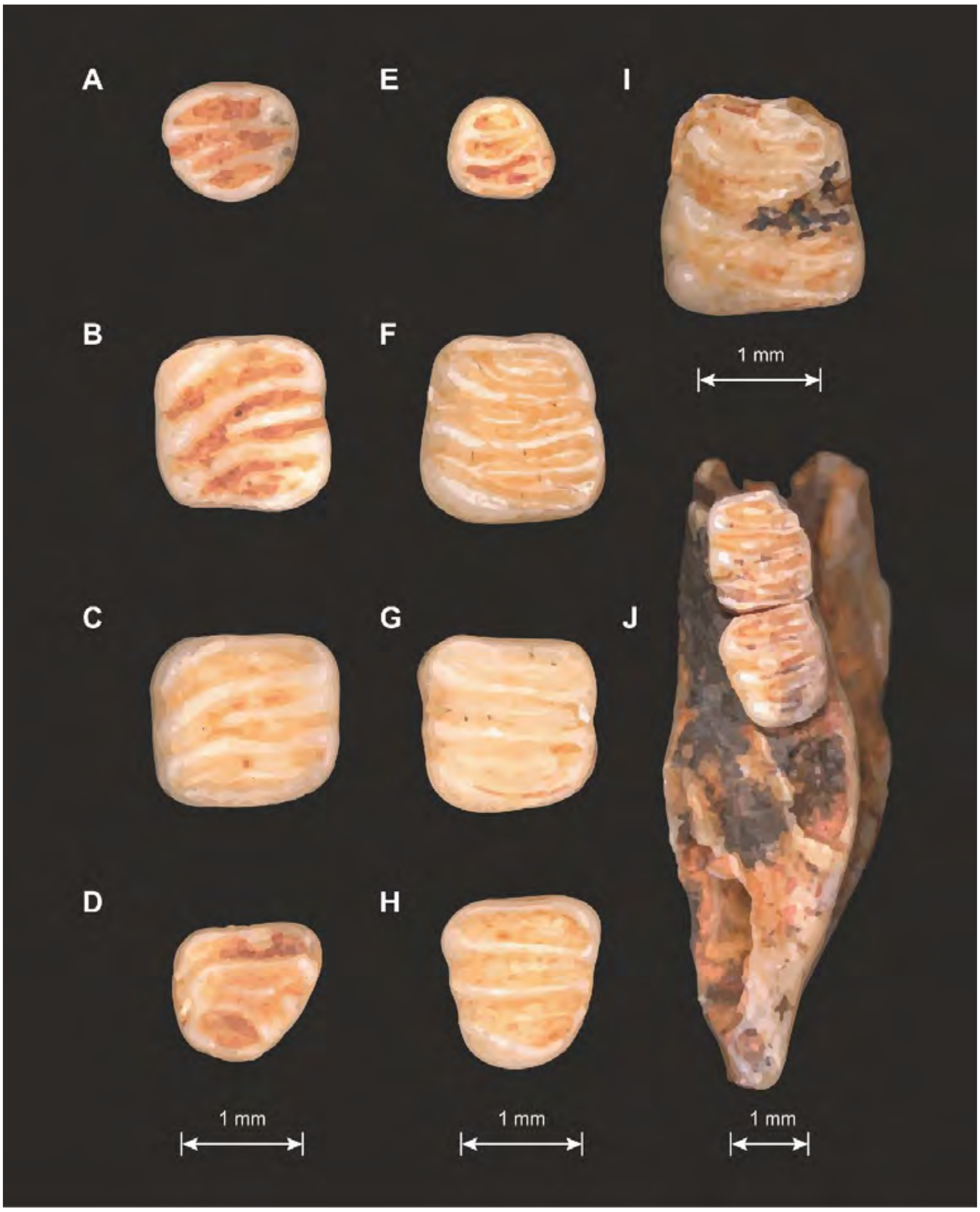


Fig. 2. *Glis* ex gr. *minor-sackdillingensis* from Węże 2. A, C, D, E, G, H – *G.* ex gr. *minor-sackdillingensis*; B, F, J – *G. minor*; I – *G. sackdillingensis*; A – P4, B – M1, C – M2, D – M3, E – p4, F – m1, G – m2, H – m3, I – m1, J – left mandible with m1 and m2; all in occlusal view

Species/tooth locus	N	Length: min.	Length: mean	Length: max.	Width: min.	Width: mean	Width: max
Glis ex gr. *minor-sackdillingensis*							
p4	6	0.87	0.99 ± 0.0793	1.06	0.89	0.97 ± 0.0563	1.02
m2	48	1.4	1.51 ± 0.0606	1.63	1.4	1.52 ± 0.0610	1.64
m3	11	1.3	1.42 ± 0.0741	1.56	1.3	1.33 ± 0.0773	1.45
P4	8	0.97	1.01 ± 0.0294	1.04	1.05	1.11 ± 0.0353	1.14
M2	29	1.35	1.45 ± 0.0494	1.56	1.48	1.59 ± 0.0538	1.7
M3	4	1.17	1.2 ± 0.025	1.23	1.31	1.34 ± 0.0424	1.4
Glis minor							
m1	61	1.34	1.52 ± 0.068	1.63	1.32	1.48 ± 0.0731	1.65
M1	62	1.38	1.5 ± 0.0557	1.66	1.32	1.49 ± 0.0611	1.62
Glis sackdillingensis							
m1	6	1.65	1.7 ± 0.0715	1.84	1.53	1.58 ± 0.045	1.66

Table 1. Isolated teeth of Gliridae from Węże 2 – material and measurements

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Gliridae Muirhead, 1819

Subfamily Glirinae Thomas, 1897

Genus *Glis* Brisson, 1762

Glis sackdillingensis (Heller, 1930)

Glis minor Kowalski, 1956

Material

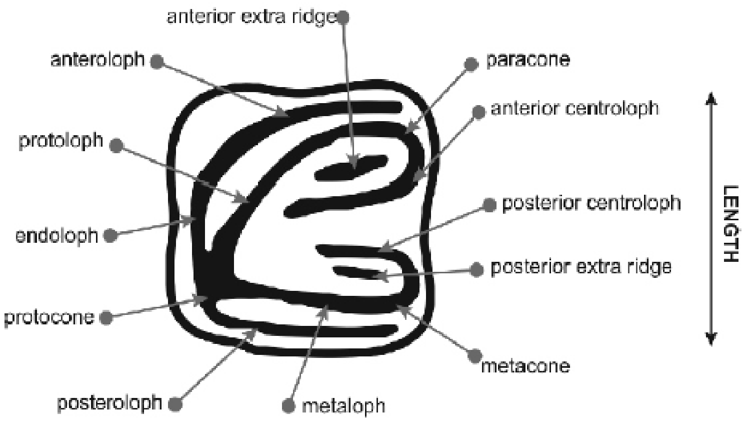
Glis sackdillingensis, isolated teeth: 6 m1 (ZPAL M.VIII/b/G2/1–6).

Glis minor, isolated teeth: 61 m1 (ZPAL M.VIII/b/G1/16–76), 62 M1 (ZPAL M.VIII/b/G1/77–138).

Glis minor, a fragment of the left mandible body with m1–m2 *in situ* (ZPAL M.VIII/b/G1/1).

Glis ex gr. *sackdillingensis-minor*, isolated teeth: 6 p4 (ZPAL M.VIII/b/G1/2–7), 8 P4 (ZPAL M.VIII/b/G1/8–15), 48 m2 (ZPAL M.VIII/b/G1/139–186), 29 M2 (ZPAL M.VIII/b/G1/187–215), 11 m3 (ZPAL M.VIII/b/G1/216–226) and 4 M3 (ZPAL M.VIII/b/G1/227–230).

Occlusal surface of M1



Occlusal surface of m1

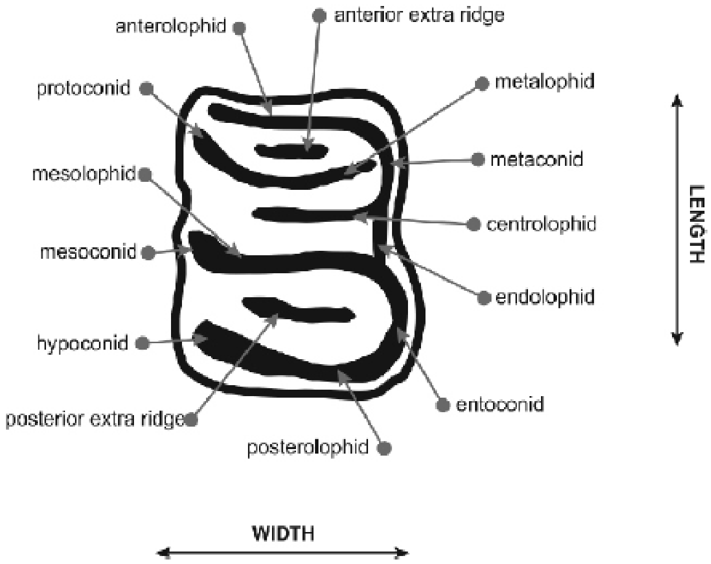


Fig. 3. Schematic drawing of the M1 and m1 occlusal surface of *Glis* ex gr. *minor-sackdillingensis*

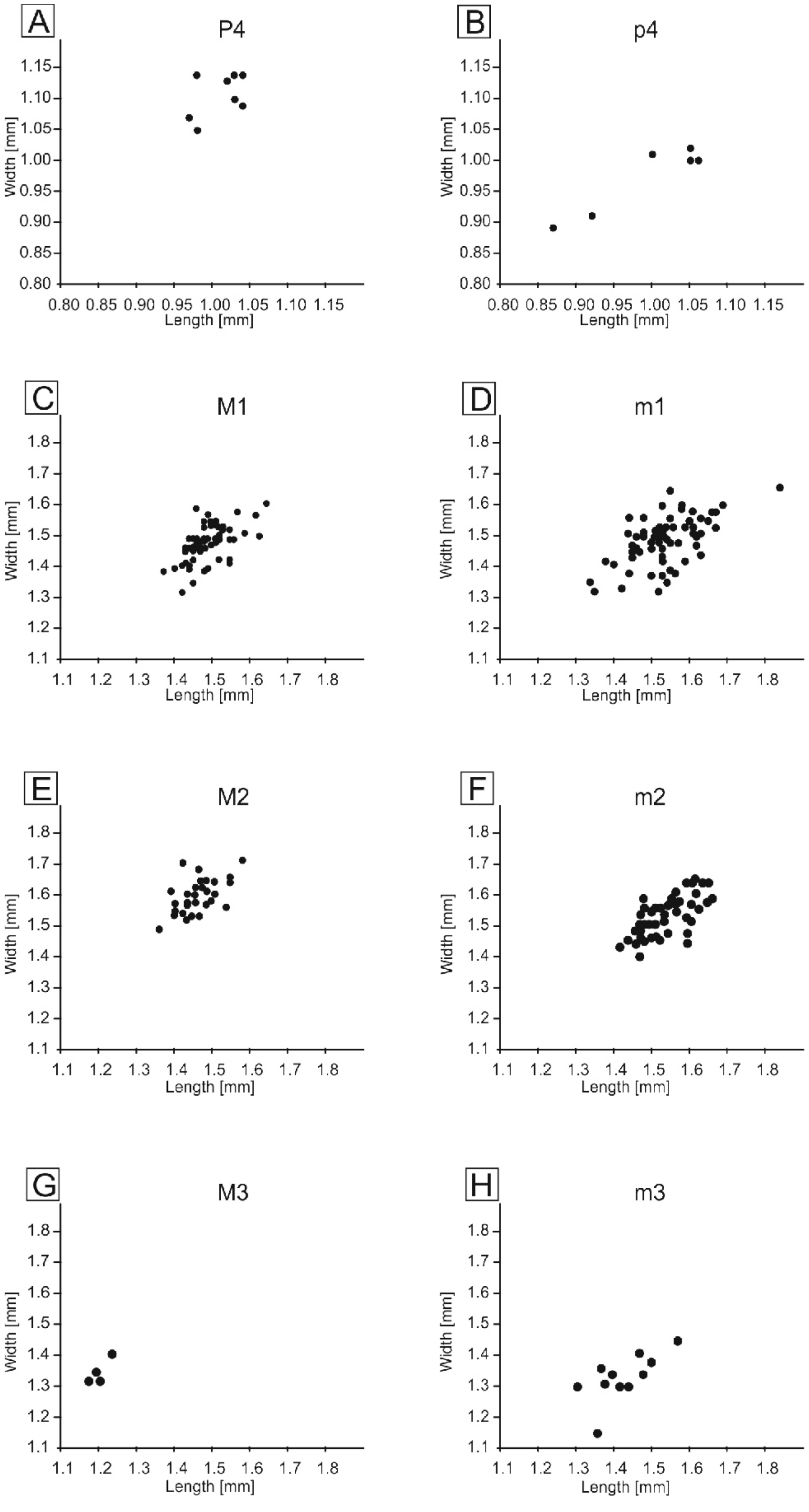


Fig. 4. Bivariate plots showing the measurements of *Glis* teeth from Węże 2

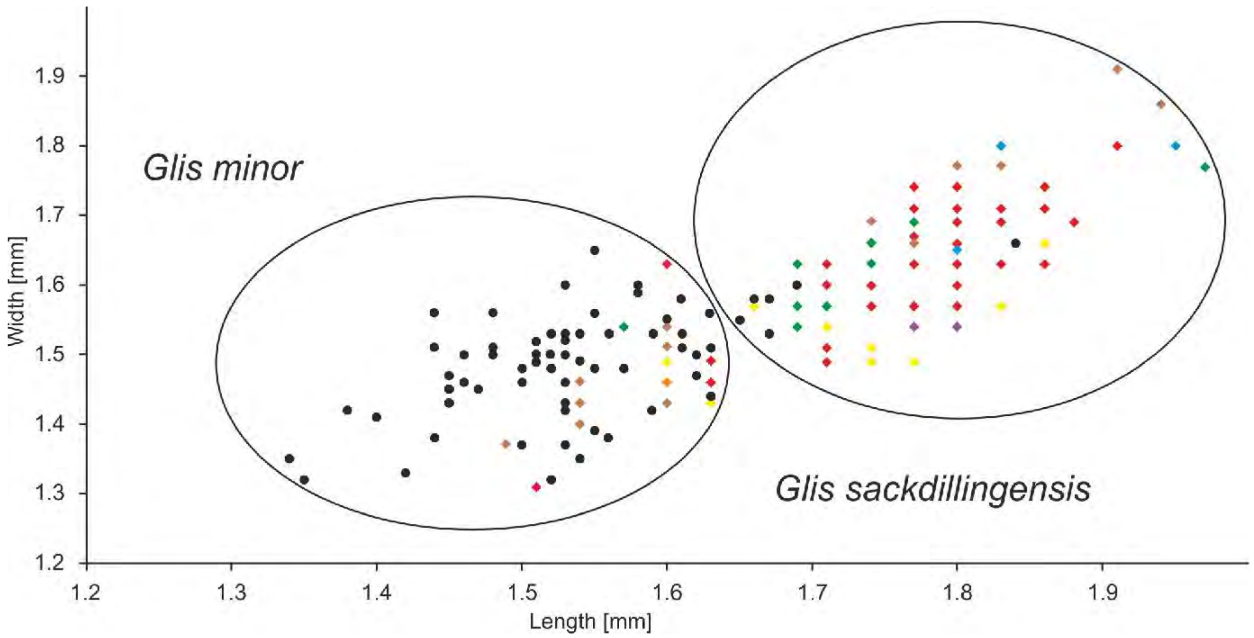


Fig. 5. Bivariate plots showing the measurements of G. minor and G. sackdillingensis specimens from Węże 2 (black circles) and several other central European sites studied by Striczky and Pazonyi 2014 (diamond shapes). Brown – Sommsich Hill 2; yellow – Osztramos 1; orange – Osztramos 1/E; red – Tarkő; green – Kövesvárad; violet – Uppony Rock Shelter 1; blue – Sackdillinger Cave.

No.	Locality	Age	Species detected	References
1.	Oberdorf (Austria)	MN 4	*G. minor*	de Bruijn (1998)
2.	Richardhof-Golfplatz (Austria)	MN 9	*G. minor*, **G. sackdillingensis*	Daxner-Höck and Höck (2009)
3.	Rudabánya (Hungary)	MN 9	*G. minor*, **G. sackdillingensis*	Daxner-Höck (2005)
4.	Richardhof-Wald (Austria)	MN 10	*G. minor* (* = *G. sackdillingensis*)	Daxner-Höck and Höck (2009)
5.	Kohfidisch (Austria)	MN 11	*G. minor*	Daxner-Höck and Höck (2009)
6.	Moncucco Torinese (Italy)	MN 13 (5.41–5.33 Ma)	*G. minor*, **G. sackdillingensis*	Colombero et al. (2014, 2017)
7.	Mała Cave (Poland)	MN 14	*G. minor*, **G. sackdillingensis*	Sulimski et al. (1979); Nadachowski et al. (1989)
8.	Komanos 1 (Greece)	Late Turolian	(?) *G. minor*	Hordijk and de Bruijn (2009)
9.	Notio 1 (Greece)	Late Turolian	*G. minor*	Hordijk and de Bruijn (2009)
10.	Pańska Góra (Poland)	Early Pliocene	*G. minor*, **G. sackdillingensis*	Bednarczyk (1993); Daoud (1993)
11.	Wölfersheim (Germany)	Early Pliocene	*G. minor*	Dahlmann (2001)
12.	Podlesice (Poland)	MN 14	*G. minor*, **G. sackdillingensis*	Kowalski (1956, 1963); Sulimski et al. (1979); Daoud (1993)

13.	Mont Hélène (France)	Ruscinian	*G. sackdillingensis* (* = *G. minor*)	Aguilar et al. (1986)
14.	Moreda (Spain)	Ruscinian	*G. sackdillingensis*	Martin-Suarez (1998)
15.	Muselievo (Bulgaria)	MN 15	*G. minor*	Popov (2004)
16.	Raciszyn 1 (Poland)	MN 15	(?) *G. minor*	Nadachowski (1989); Nadachowski et al. (1989)
17.	Sondershausen (Germany)	MN 15	*G. minor*, **G. sackdillingensis*	Hellmund and Ziegler (2012)
18.	Węże 1 (Poland)	MN 15	*G. minor*, **G. sackdillingensis*	Sulimski (1964); Daoud (1993); Stefaniak et al. (2020);
19.	Vitošov (Czechia)	MN 15/16	*G. minor* (* = *G. sackdillingensis*)	Čermák et. al. (2016)
20.	Grand Serre (France)	Late Pliocene	*G. sackdillingensis*	Aguilar et al. (1993)
21.	Hambach (Germany)	Late Pliocene	*G. minor* (* = *G. sackdillingensis*)	Mörs et al. (1998)
22.	Mas Rambault (France)	Late Pliocene	*G. sackdillingensis*	Aguilar et al. (2002)
23.	Rębielice Królewskie (Poland)	MN 16	*G. minor*, **G. sackdillingensis*	Kowalski (1963); Daoud (1993); Stefaniak et al. (2020)
24.	Tourkovounia 1 (Greece)	MN 16	(?) *G. sackdillingensis*	Koufos (2001)
25.	Węże 2 (Poland)	MN 16?	*G. minor*, *G. sackdillingensis*	Sulimski (1962); Stefaniak et al. (2020);
26.	Csarnóta (Hungary)	Late Pliocene / Early Pleistocene	(?) *G. minor*	Kretzoi (1959); Jánossy (1986)
27.	Kamyk (Poland)	Late Pliocene / Early Pleistocene	**G. minor*, *G. sackdillingensis*	Kowalski (1960a, 1963); Daoud (1993)
28.	Osztramos 1 (Hungary)	Late Pliocene / Early Pleistocene	*G. minor*, *G. sackdillingensis*	Jánossy (1986); Striczky and Pazonyi (2014)
29.	Osztramos 1/E (Hungary)	Late Pliocene / Early Pleistocene	*G. minor*, *G. sackdillingensis*	Striczky and Pazonyi (2014)
30.	Osztramos 7 (Hungary)	Late Pliocene / Early Pleistocene	(?) *G. minor*	Jánossy (1986)
31.	Osztramos 9 (Hungary)	Late Pliocene / Early Pleistocene	*G. minor*	Striczky and Pazonyi (2014)
32.	Kaiafas (Greece)	MNQ 19	(?) *G. sackdillingensis*	Koufos (2001)
33.	Les Valerots (France)	Early Biharian	*G. minor*	Chaline (1972)
34.	Monte la Mesa (Italy)	Early Biharian	*G. sackdillingensis*	Marchetti et al. (2000)

35.	Betfia (Romania)	Biharian	(?) *G.* cf. *minor*, (?) *G. sackdillingensis*	Terzea (1996)
36.	Beremend 14 (Hungary)	Early Pleistocene	*G. minor*, **G. sackdillingensis*	Pazonyi et al. (2016)
37.	Kadzielnia (Poland)	Early Pleistocene	**G. minor*, *G. sackdillingensis*	Daoud (1993); Urban et al. (2019)
38.	Kielniki 3A (Poland)	Early Pleistocene (Early Biharian)	(?) *G. sackdillingensis*	Nadachowski (1989); Nadachowski et al. (1989)
39.	Kielniki 1 (Poland)	Early Pleistocene (Late Biharian)	*G. sackdillingensis* (*= *G. minor*)	Nadachowski (1989); Nadachowski et al. (1989); Daoud (1993)
40.	Monte Argentario (Italy)	Early Pleistocene	(?) *G. sackdillingensis*	Siori et al. (2014)
41.	Osztramos 3 (Hungary)	Early Pleistocene	(?) *G. sackdillingensis*	Jánossy (1986)
42.	Osztramos 14 (Hungary)	Early Pleistocene	(?) *G. sackdillingensis*	Jánossy (1986)
43.	Razvodje (Croatia)	Early Pleistocene	(?) *G. sackdillingensis*	Paunovic and Rabeder (1996)
44.	Schernfeld (Germany)	Early Pleistocene	**G. minor*, *G. sackdillingensis*	Dehm (1962)
45.	Untermassfeld (Germany)	Early Pleistocene	*G. sackdillingensis*	Maul (2001)
46.	Villány-Kalkberg-Nord (Hungary)	Early Pleistocene	(?) *G. sackdillingensis*	Jánossy (1986)
47.	Żabia Cave (Poland)	Early Pleistocene	(?) *G. sackdillingensis*	Stefaniak et al. (2009); Nadachowski et al. (2011)
48.	Somssich Hill 2 (Hungary)	Late Early Pleistocene	*G. minor*, *G. sackdillingensis*	Striczky and Pazonyi (2014)
49.	Chlum 4 (Czechia)	Early/Middle Pleistocene	(?) *G. sackdillingensis*	Horáček et al. (2016)
50.	Kozi Grzbiet (Poland)	Early/Middle Pleistocene	*G. minor**, *G. sackdillingensis*	Nadachowski (1989); Nadachowski et al. (1989); Daoud (1993)
51.	Podumci (Croatia)	Early Middle Pleistocene	*G. sackdillingensis*	Malez and Rabeder (1984)
52.	Sackdillinger Cave (Germany)	Early Middle Pleistocene	*G. sackdillingensis*	Heller (1930); Striczky and Pazonyi (2014)
53.	Trlica (Montenegro)	Early Middle Pleistocene	(?) *G. sackdillingensis*	Agadzhanian et al. (2017)
54.	Kövesvárad (Hungary)	Middle Pleistocene	*G. minor*, *G. sackdillingensis*	Striczky and Pazonyi (2014)
55.	Tarkő (Hungary)	Middle Pleistocene	*G. minor*, *G. sackdillingensis*	Jánossy (1986); Striczky and Pazonyi (2014)
56.	Uppony Rock Shelter 1 (Hungary)	Middle Pleistocene	*G. minor*, *G. sackdillingensis*	Jánossy (1986) Striczky and Pazonyi (2014)

Table 2. Occurrences of *Glis* ex gr. *minor-sackdillingensis*
* – revised according to the criteria given by Striczky and Pazonyi (2014)
(?) – measurements of diagnostic teeth not provided

Description

Glis sackdillingensis

m1 (Fig 2: F). A vaguely rectangular, anteriorly narrowed tooth. The anterolophid, the metalophid, the centrolophid, the mesolophid and the posterolophid are present. The metalophid, the mesolophid and the posterolophid are clearly curved. Extra ridges may be present (Fig. 1). In W2 the length of the tooth ranges from 1.65 to 1.84 mm and the width from 1.53 to 1.66 mm (Table 1, Fig. 3D).

Glis minor

M1 (Fig 2: B). A squarish tooth with rounded corners. The anteroloph, the protoloph, the anterior centroloph, the metaloph and the posteroloph are present. The anteroloph is clearly rounded. Extra ridges may be present (Fig. 1). In W2 the length of the tooth ranges from 1.38 to 1.66 mm, and the width from 1.32 to 1.62 mm (Table 1, Fig 3C).

m1 (Fig 2: F). Morphologically indistinguishable from *G. sackdillingensis* (Fig. 1). The anterolophid, the metalophid, the centrolophid, the mesolophid and the posterolophid are present. The length of the teeth from W2 ranges from 1.34 to 1.63 mm and the width from 1.32 to 1.65 mm (Table 1, Fig. 3D).

Glis ex gr. *minor-sackdillingensis*

P4 (Fig. 2: A). The outline of the occlusal surface is roughly oval. The anteroloph, the protoloph, the metaloph, and the posteroloph are present. The length of the Węże 2 specimens ranges from 0.97 to 1.04 mm, and the width from 1.05 to 1.14 mm (Table 1, Fig. 3A). These specimens, as all the other non-diagnostic teeth, are attributed to *G.* ex gr. *minor-sackdillingensis* as an exact specific assignment is not possible with a satisfying certainty and both species are present at the site (see Striczky and Pazonyi, 2014).

M2 (Fig 2: C). A broad, squarish tooth with its corners slightly rounded. The anteroloph, the protoloph, the anterior centroloph, the metaloph and the posteroloph are present. The length of the Węże 2 specimens ranges from 1.35 to 1.56 mm, and the width from 1.48 to 1.7 mm (Table 1, Fig. 3E).

M3 (Fig 2: D). It is approximately triangular in shape, posteriorly narrowed. The anteroloph, the protoloph, the anterior centroloph, the metaloph and the posteroloph are present, as well as a residual posterior centroloph, located posteriorly to the anterior centroloph. The length of the

M3 specimens collected from Węże 2 ranges from 1.17 to 1.23 mm and the width from 1.31 to 1.4 mm (Table 1, Fig. 3G).

p4 (Fig 2: E). The shape of the occlusal surface resembles a circular triangle. It is also the smallest of the teeth (Fig. 3B). The anterolophid, the metalophid, the mesolophid and the posterolophid are present. The length of the Węże 2 specimens ranges from 0.87 to 1.06 mm and the width from 0.89 to 1.02 mm (Table 1, Fig 3B).

m2 (Fig 2: G). A vaguely rectangular tooth, posteriorly narrowed. The anterolophid, the metalophid, the centrolophid, the mesolophid and the posterolophid are present. The length of the teeth collected at Węże 2 ranges from 1.4 to 1.63 mm and the width from 1.4 to 1.64 mm (Table 1, Fig. 3F).

m3 (Fig 2: H). It is similar to m2 but still more narrowed posteriorly. The anterolophid, the metalophid, the centrolophid, the mesolophid and the posterolophid are present. The length of the Węże 2 specimens ranges from 1.3 to 1.56 mm and the width from 1.3 to 1.45 mm (Table 1, Fig. 3H).

Preliminary observations of the Węże 2 material show the ridges at the occlusal surfaces of the cheek teeth in *Glis* ex gr. *minor-sackdillingensis* as being low and delicate. The enamel layer covering the circumference of the teeth and the ridges is relatively thin, ranging from 38 to 93 µm. It is usually the thickest along the ridges and at the lingual and buccal margins of the teeth. Also, its thickness changes from the root to the crown (in vertical sections, as demonstrated by Koenigswald, 2004). The most even enamel layer is observed in p4 (Fig. 6).

Remarks

In the inferred *G. minor* – *G. sackdillingensis* – *G. glis* lineage a general increase of molar dimensions is supposed to be observed in the fossil record (Kowalski 1956, Daoud 1993, Striczky and Pazonyi 2014). It is however noteworthy that the cheek teeth of *G. minor* are morphologically indistinguishable from those of *G. sackdillingensis* (Striczky and Pazonyi 2014). Instead, the two species either have been quite arbitrary distinguished by the size of their molars, or by their supposedly complementary stratigraphic ranges, with geologicaly older material being routinely assigned to *G. minor* (see: Table 2). Using statistical tools, Striczky and Pazonyi (2014) have established that in *G. minor* the length of m1 is < 1.65 mm (Fig. 4) while the width of M1 is < 1.7 mm.

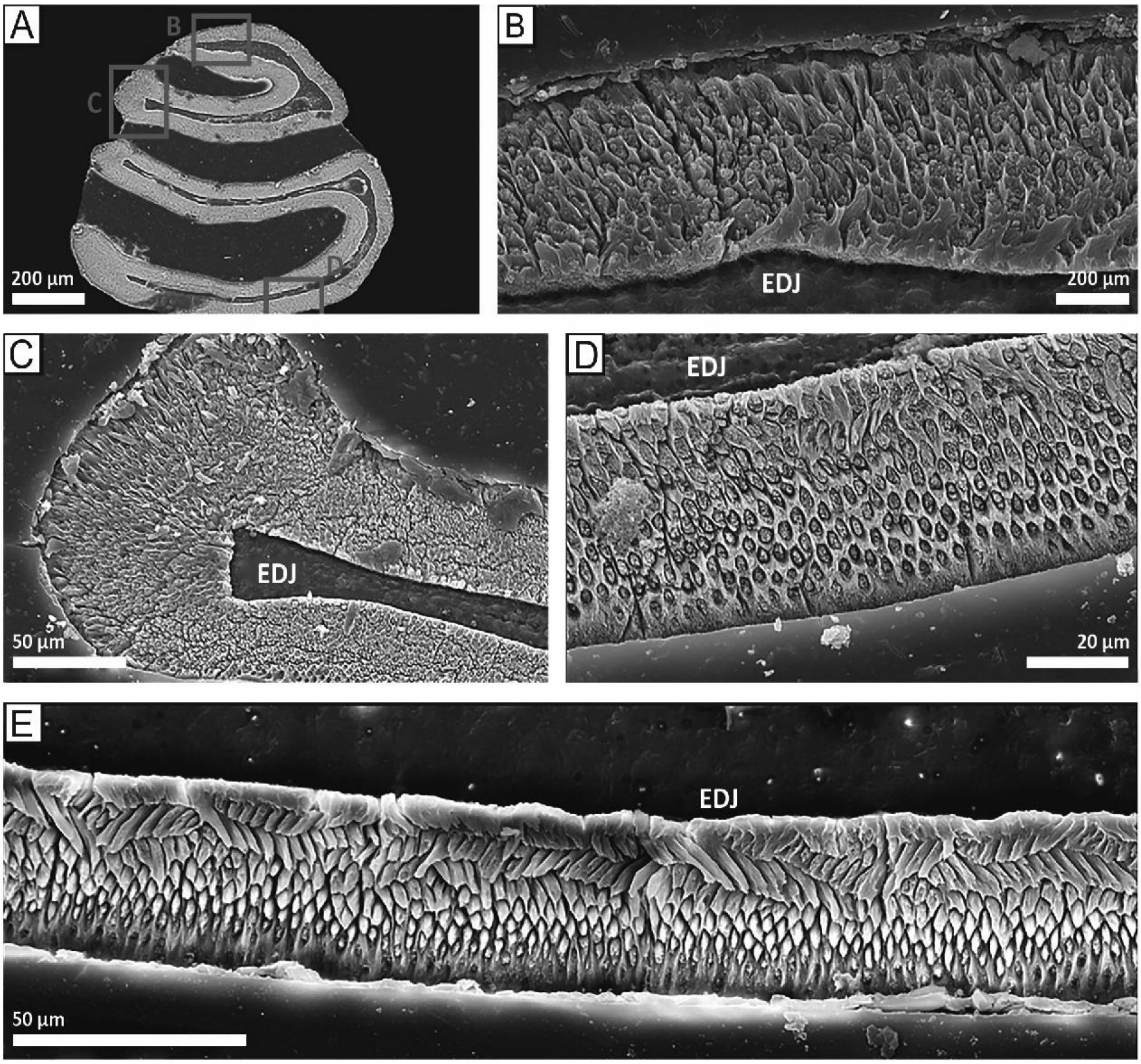


Fig. 6. Enamel structure of some *Glis* teeth from Węże 2 in cross section. A–D – p4: A – general view, B – anterolophid, C – protocinid, D – posterolophid; E – enamel structure of the posterolophid of m1 showing a BRLE (basal ring of lamellar enamel) near the base of the crown; EDJ – enamel-dentine junction

Discussion

The genus *Glis*, which represents the Glirinae lineage of the Gliridae family, is considered to have originated in the Middle Oligocene of Anatolia and to be descended from *Gliravus* (Daams and de Bruijn 1995). Several extinct and one extant species (*G. glis*) are known (Daams and de Bruijn 1995, Holden 2005, Holden and Levine 2009, Kryštufek 2010). The stratigraphic range of the *G. minor-sackdillingensis* complex spans from the Late Early Miocene to the Late Early Pleistocene and both forms are known predominantly from Central Europe, with clusters of sites located in Austria, Hungary and Poland (Table 2, Fig. 5). *G. minor* was first described by Kowalski (1956) as *G. sackdillingensis minor*, based on the material from Podlesice, as the dimensions of the Podlesice form "are distinctly smaller than all the corresponding dimensions of specimens from Germany, which strongly suggests its establishment as a separate subspecies". This smaller form was then raised to the rank of a species (*G. minor*) by Kretzoi (1959), a decision which was supported by Kowalski (1963).

Two specimens of p4 seem significantly smaller than the rest (Fig. 3: B) but specimens narrower than 0,95 mm were already known from Węże 1 (Kowalski 1963) and Sondershausen, and the measurements of the *Glis* teeth from Węże 1, Węże 2 and Rębielice Królewskie often fall quite close to the lower end of the typical *G.* ex gr. *sackdillingensis-minor* ranges (Hellmund and Ziegler 2012). It is, however, worth noting that Kowalski, in his description of some fossil rodent fauna from Rębielice Królewskie, reported a finding of a small (0.9 mm long, 0.9 mm wide) detached p4 that he classified as cf. *Glis* sp. and considered to possibly represent "a thus far unknown, very minute form of the genus *Glis* Brisson" (Kowalski 1960b).

G. minor is considered to be the immediate ancestor of *G. sackdillingensis* which in turn is thought to have evolved into the modern *G. glis* (Nadachowski 1989, Daoud 1993, Siori et al. 2014, Striczky and Pazonyi 2014). The direct ancestor of *G. minor* has not been recognized. Although a synonymy between *G. sackdillingensis* and *G. minor* has been proposed (de Bruijn and van der Meulen 1975), this suggestion was not generally followed (see Table 2) and "complementary stratigraphic ranges" have been cited as an argument in favor of keeping the specific status of the alleged smaller form (Popov 2004). However, when the criteria elaborated by Striczky and Pazonyi (2014) are applied to the previously described *G. minor* / *G. sackdillingensis* material, the perceived complementarity hardly seems to be the case. At the same time, the statistical analyses performed by Striczky and Pazonyi (2014) seem to support the existence of two separate species, distinguishable only by morphometric criteria.

So far, the incisor enamel of the Glires (rodents and lagomorphs) has been studied more extensively than that of the molars. In the case of the Gliridae, Koenigswald (1993) provided a detailed study of their incisor enamel structure only. A more comprehensive study by Koenigswald (2004) provides a survey of the molar enamel structure in both fossil and extant rodents, concerning three types of schmelzmuster (spatial organization of enamel types) and their distribution across the phylogenetic tree. The Gliridae are virtually not mentioned there, apart from *Muscardinus* and *Leithia*, a large, insular form from the Pleistocene of the Mediterranean.

The observations performed for the purpose of this study show that the enamel structure is simple and similar along the whole tooth perimeter. It is formed predominantly by the radial enamel. A thin layer of lamellar enamel, occurring close to the enamel-dentine junction (EDJ) may be present (Fig. 6). The lamellar enamel forms a structure known as *the basal ring of lamellar enamel* (BRLE). Such a type of schmelzmuster, where radial and lamellar enamel co-occur, was recognized as the C-type (Koenigswald 2004). Generally, it is typical of the Myomorpha, the species-rich clade of rodents encompassing the Muroidea (the mouse-like rodents) and the Gliridae (Koenigswald 2004, see also Nowakowski et al. 2018).

Conclusions

At the Villafranchian site of Węże 2 the genus *Glis* is represented by over 200 isolated teeth and a partially preserved mandible. The material belongs to *G. minor* and *G. sackdillingensis*, two species that differ only by the dimensions of their cheek teeth. Based on the morphometric criteria elaborated by Striczky and Pazonyi (2014), the mandible, all 62 isolated M1 specimens, as well 61 m1 specimens are assigned to *Glis minor*, while 6 m1 specimens are assigned to *Glis sackdillingensis*. The remaining material is assigned to *G.* ex gr. *sackdillingensis*-*minor*, due to the lack of clear morphometric or morphological criteria permitting to attribute them to one of the species with sufficient certainty. The presence of the dormouse genus *Glis* suggests that the fossil assemblage of Węże 2 represents at least a partly arboreal environment.

The traditional two species paradigm for *G.* ex gr. *minor-sackdillingensis* is maintained in this study as the statistical analysis performed by Striczky and Pazonyi (2014) on the *Glis* material collected at several central European sites seems to support it. However, applying the criteria elaborated through that analysis to the previously described *G. minor* / *G. sackdillingensis* material also shows these two species as having almost parallel stratigraphic ranges and not infrequently coexisting at the same site which was not thought to be the case. A more comprehensive statistical analysis may be needed to confirm or disprove the existence of two separate species, as opposed to one species, *G. sackdillingensis*, which displays some intraspecific variability of morphometric traits and a general evolutionary tendency to grow in size.

It is also possible that further studies of enamel structures are going to provide some additional means of distinguishing these species as differences in diet and lifestyle could have led to differences in enamel structure. Preliminary observations of the enamel of the dormice from Węże 2 show that the structure typical of the Myomorpha is discernible, formed predominantly by radial enamel, with a thin layer of lamellar enamel occurring close to the enamel-dentine junction.

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Chapter 2. Castoridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland[1]

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Abstract

Several isolated teeth and jaw fragments of beavers (Rodentia: Castoridae), discovered at the Villafranchian (MN 16b?) site of Węże 2 in southern Poland, are attributable to two species: *Dipoides* ex gr. *problematicus-sigmodus* and *Trogontherium* (*Euroxenomys*) *minus*. The genus *Dipoides* and the species *Trogontherium* (*Euroxenomys*) minus have not previously been reported from Poland. Their presence at the Węże 2 site suggests that these lesser-known and extinct representatives of the Castoridae were adapted to similar conditions as the modern species (*Castor fiber* and *C. canadensis*).

Key words: Villafranchian; rodents; beavers; Węże, karst

Introduction

This study describes the fossil dental beaver (Castoridae) remains from the Villafranchian (MN 16b) site of Węże 2 in southern Poland. Although few, they are significant as they belong to taxa that apparently have not yet been reported from Polish sites, namely the genus *Dipoides* and the species *Trogontherium minus*. The Castoridae (true beavers) are a family of herbivorous rodents that, throughout their evolutionary history, developed large body sizes and, by adapting to a semi-aquatic lifestyle, became strongly associated with fresh-water environments. Today the family is represented only by the genus Castor, consisting of two extant species – the North American *C. canadensis* and the Eurasian *C. fiber*. However, the fossil recoed of the Castoridae comprises around 30 valid genera (Hugueney and Escuilié 1996, Rose 2006, Rybczynski 2007, Rybczynski et al. 2010, Stefen 2011, Li et al. 2017). Present-day beavers are known from their iconic dam-building behavior, which allows them to create ponds that they subsequently inhabit, such an adaptation supposedly being driven by habitual acquiring and consumption of wood (Rosell et al. 2005, Rybczynski 2007, Pint et al. 2020). Both *Dipoides* and *Trogontherium* (as well as the subgenus *Euroxenomys*) are thought to also represent the branch of the beaver evolutionary tree that encompasses woodcutting and a semi-aquatic lifestyle (Rybczynski 2007, Rybczynski et al. 2010, Xu et al. 2017, Plint et al. 2020).

The earliest recognized member of Castoridae, *Agnotocastor*, has been described from the latest Eocene of Wyoming. In the Early Oligocene the family was already present in Eurasia, *Propalaeocastor* (perhaps synonymous with *Agnotocastor*) being the earliest beaver found outside of North America (Rose 2006, Li et al. 2017). Early occurrences of fossil Castoridae in Poland include the presence of *Steneofiber jaegeri* in the Early/Middle Miocene sites of Przeworno 1, Opole 1 and Opole 2, dated respectively at MN 5–6?, MN 6? and MN 7?. Moreover, *Steneofiber eseri* and *Trogontherium* (*Euroxenomys*) *minutum* have been recorded from Opole 2 (Kowalski 1967, Kubiak and Wolsan 1986, Nadachowski 1989).

Out of the *several* genera of beavers inhabiting Europe through the Miocene, *Steneofiber* is the dominant one and it is sometimes considered to be ancestral to *Trogontherium*. Although the purported transition from *Steneofiber* to *Trogontherium* is not well understood, the evolutionary lineage *S. eseri – T. minutum – T. minus – T. cuvieri* has been inferred from the fossil record (Mayhew 1978, Stefen 2011). The phylogenetical analysis performed by Rybczynski (2007) puts *S. eseri* and *Trogontherium* in separate clades, with *Steneofiber* closely related to *Castor* (within the clade Castorinae) and *Trogontherium* as a probable descendant of *Dipoides* (within Castoroidinae). Rybczynski et al. (2010) considered *Castor* to be a close relative of *Sinocastor* with Steneofiber as an outgroup. Another study (Li et al. 2017) again argues for a very close relationship between *Steneofiber* and *Castor*, as well as between *Trogontherium cuvieri* and *Dipoides*. *Trogontherium* (*Euroxenomys*) *minutum*, however, has been placed at the stem of the clade encompassing *Steneofiber eseri*, *Castor canadensis*, *Trogontherium cuvieri* and *Dipoides majori*.

Geological setting

The Węże 2 site is situated on the NW slope of the Zelce Hill, near the village of Węże, in the Wieluń Upland, southern Poland (Pajęczno County). Upon its discovery, it comprised a vertical karst crevice (ca. 10 m long and ca. 4 m wide) carved in Upper Jurassic (Oxfordian) limestone and infilled with clayey sediments containing fossil material. The bone breccia is considered to have originated at least partly by means of water transportation of the bones into the crevice, although it is possible that some small animals were buried in situ at the place of their death. The fossiliferous deposits (~3.5 t in total) were collected during field work organized in the early sixties 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 (Samsonowicz 1936, Sulimski 1962, Szynkiewicz 2015). Four to five clayey fossiliferous strata of slightly differing lithology were distinguished. These were initially named D1, D2, D3 and D4 by Sulimski (1962) and then renamed D (= upper D1), E (= lower D1), F, G and H (unpublished notes referred to in Szynkiewicz 2015A). However, not all fossil material collected has been attributed to a particular stratum and the faunal lists are generally given for the site as a whole (Szynkiewicz 2015A), which is also the case for the nearby and better known site of Węże 1 (Szynkiewicz 2015B).

The mammalian taxa described so far from Węże 2 include the the flying squirrel *Pliopetaurista dehneli* (Sulimski 1964, Hordijk and de Bruijn 2009), the lagomorph *Hypolagus beremendensis* (Fostowicz-Frelik 2007), the cervids *Croizetoceros ramosus* and *Metacervocerus pardinensis*, an unindentified rhinocerotid, an elephantid probably assignable to the genus *Anancus* (Stefaniak et al. 2020), and the dormice *Glis minor* and *G. sackdillingensis* (Czernielewski, 2021). The presence of many other taxa was preliminary reported (Sulimski 1962, Nadachowski 1989, Rzebik-Kowalska 1989, Nadachowski et al. 2015). These include the carnivorans *Canis etruscus*, *Vulpes praeglacialis*, *Ursus minimus*, *Mustela pliocaenica*, *Homotherium latidens* and *Felis lunensis* (Sulimski 1962, Nadachowski et al. 2015), the eulipotyphlans *Talpa minor*, *Condylura kowalskii*, *Desmana* cf. *kormosi*, *Petenya hungarica* and *Sorex* cf. *minutus* (Sulimski 1962, Rzebik-Kowalska 1989, Nadachowski et al. 2015), and the rodents *Hystrix* cf. *primigenia*, *Baranomys longidens*, *Mimomys gracilis*, *Prospalax priscus*, *Pliospalax* sp. and *Sciurus warthae* (Sulimski 1962, Nadachowski 1989, Nadachowski et al. 2015). In general, the fossil assemblage of Węże 2 is suggestive of warm, Mediterranean-like climate and an arboreal environment formed around a constant freshwater source. Based on its faunal composition, the Węże 2 fossil assemblage is currently dated at the Late Pliocene (Lower Villafranchian) and is 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).

Material and methods

The material here examined consists of five specimens clearly attributable to the Castoridae and belonging to two species of beavers: *Dipoides* ex gr. *problematicus-sigmodus* and *Trogontherium* (*Euroxenomys*) *minus*. *Trogontherium minus* is represented by four specimens – a fragment of the left maxilla with P4 *in situ*, an isolated left M1, an isolated right M3, and a fragment of the left mandible with m1 *in situ*. An isolated right M1/2 is assignable to *Dipoides* ex gr. *problematicus-sigmodus*.

The material was collected by handpicking during the fieldwork conducted in the early 1960s and is now housed in the collection of the Institute of Paleobiology of the Polish Academy of Sciences (abbreviated ZPAL). For the purpose of this study it was examined with Keyence VHX

900-F Digital Microscope System and photographed with the Nikon D1X camera with MC 50 mm f/2.8.

Systematic palaeontology

Family Castoridae Hemprich, 1820

Subfamily Castoroidinae Allen, 1877

Genus *Dipoides* Jäger, 1835

Dipoides ex gr. *problematicus-sigmodus*

Genus *Trogontherium* Fischer de Waldheim, 1809

Trogontherium minus Newton, 1890

Material

Dipoides ex gr. *problematicus-sigmodus*: isolated right M1/2 (ZPAL VM/I–127/1; Fig. 1A and Table 1)

Trogontherium (*Euroxenomys*) *minus*: fragment of left maxilla with P4 *in situ* (ZPAL VM/I–124/1; Fig. 1D); isolated left M1 (ZPAL VM/I–125/1; Fig. 1C); isolated right M3 (ZPAL VM/I–123/1; Fig. 1B); fragment of left mandible with m1 in situ (ZPAL VM/I–122/1; Fig. 1E).

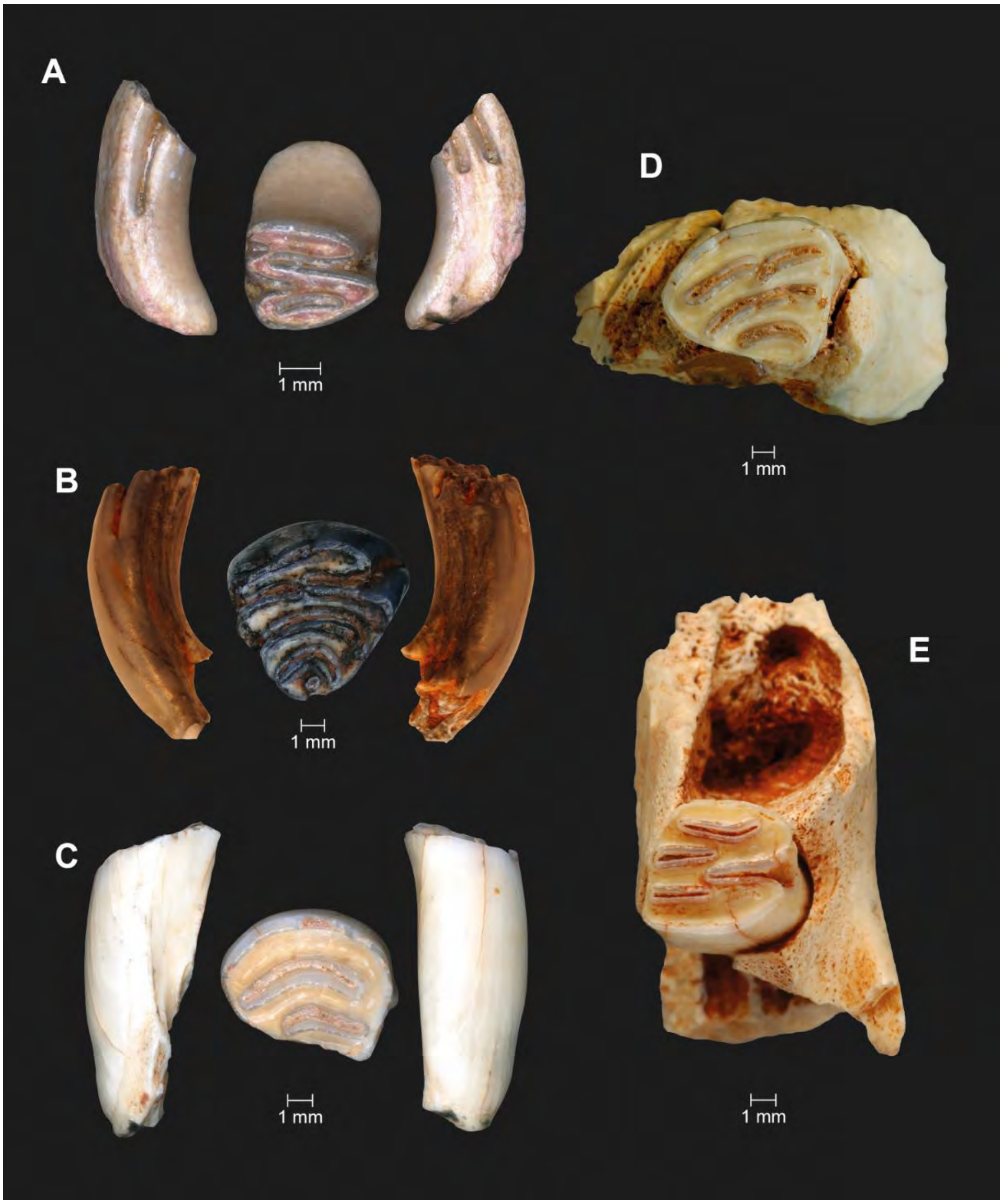

Fig. 1. Dental beaver (Castoridae) remains from Węże 2. A – *Dipoides* ex gr. *problematicus-sigmodus* (M1/2); B – *Trogontherium minus* (M3); C – *Trogontherium minus* (M1); D – *Trogontherium minus* (fragment of maxilla with P4); E – *Trogontherium minus* (fragment of mandible with m1).

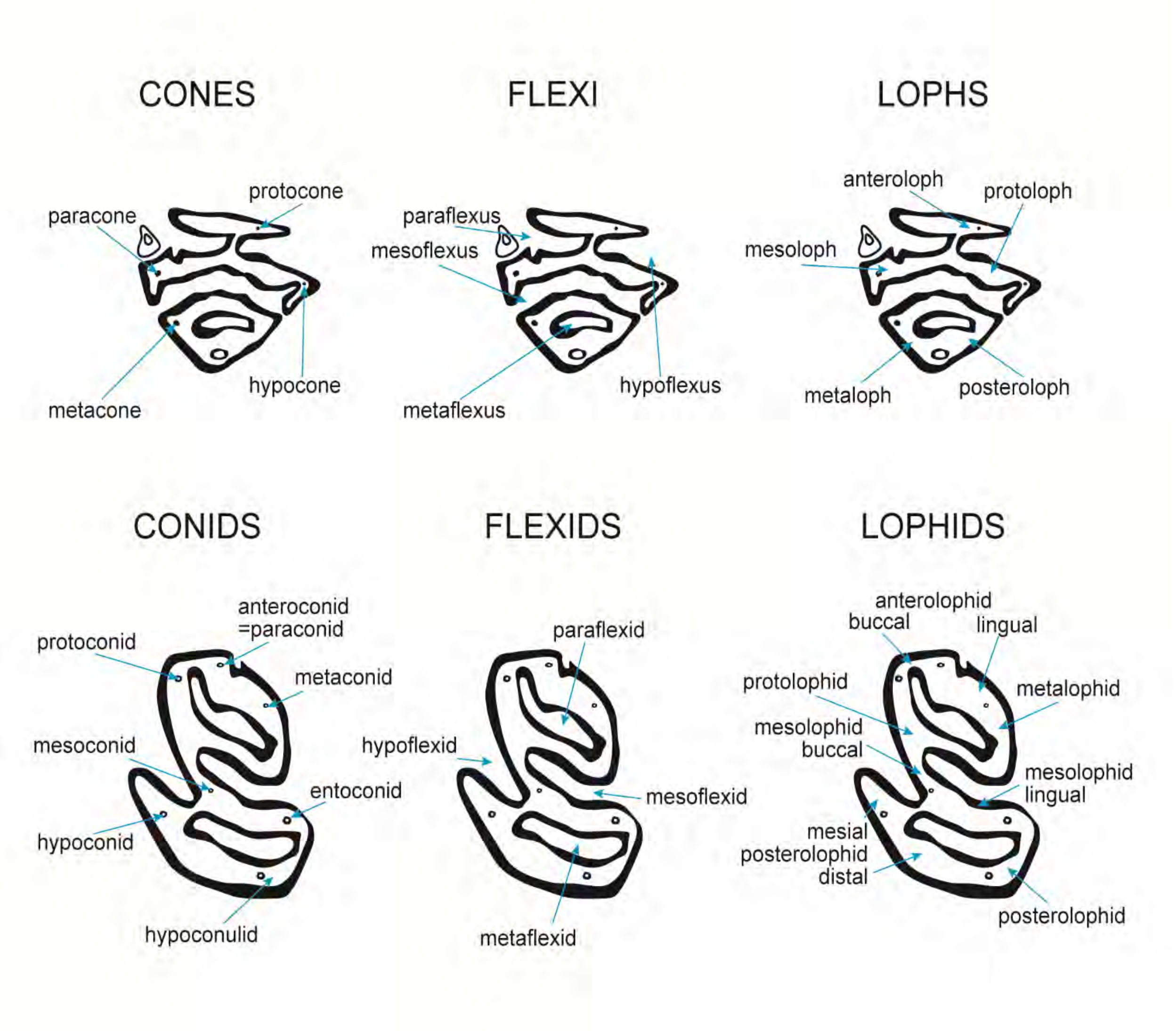

Fig. 2. Morphology of castorid cheek teeth exemplified by *Trogontherium* sp. P4 (upper row) and p4 (lower row). The vertical axis is the height and the horizontal axis is the width of the specimens (after Kordos 2020).

Species/tooth locus	**Length [mm]**	**Width [mm]**	**Provenience**
Dipoides ex gr. *problematicus-sigmodus*			
M1/2	2.7	2.9	W2/G
Trogontherium minus			
P4	7.4	8.6	W2/?
M1	6.0	6.0	W2/?
M3	6.5	7.0	W2/G
m1	5.5	5.7	W2/E

Table 1. Measurements of the Castoridae cheek teeth from Węże 2

Description

Dipoides ex gr. *problematicus-sigmodus*

M1/M2 (Fig. 1A). The occlusal surface displays the typical sigmoid pattern of the genus *Dipoides* formed by the paraflexus, the hypoflexus, the mesoflexus and the metaflexus (van de Weerd 1976, García-Alix et al. 2007, Li et al. 2017, Xu et al. 2017; see: Fig 2), although the paraflexus and the mesoflexus are barely discernible. Morphologically it strongly resembles the *Dipoides problematicus* material from the Pliocene localities of the Teruel-Alfambra region of Spain (van de Weerd 1976, García-Alix et al. 2007). However, the dimensions of the occlusal surface (the length is 2.7 and the width equals 2.8 mm) are significantly smaller than the typical ranges of both *D. problematicus* and *D. sigmodus* (van de Weerd 1976, Dema 2000, García-Alix et al. 2007, Xu et al. 2017).

Trogontherium minus

P4 (Fig. 1D). The occlusal surface resembles a circular triangle. The hypoflexus, the paraflexus, the mesoflexus and the metaflexus are discernible, showing the pattern typical of the genus *Trogontherium* (Stefen and Rummel 2003, Fostowicz-Frelik 2008, Kordos 2020) The length of the occlusal surface is 7.4 while the width equals 8.6 mm. That puts the specimen within the typical range for *T. minus* with regard to the length and very close to that range in terms of the width, the Węże 2 specimen being slightly wider than the expected range for *T. minus* but nonetheless much narrower than the expected rante for *T. cuvieri* (Fostowicz-Frelik 2008).

M1 (Fig. 1C). The occlusal surface is roughly kidney-shaped. Only the hypoflexus and the metaflexus are discernible, which is probably indicative of tooth wear. Both the length and the width of the occlusal surface equal 6 mm, such dimensions being substantially larger than the typical range of *Trogontherium minutum* (Stefen and Rummel 2003, Stefen 2011, Apoltsev and Rekovets 2015, Kordos 2020) but smaller than expected for *T. cuvieri* (Stefen 2011, Langeveld 2013).

M3 (Fig. 1B). The shape of the occlusal surface resembles a circular triangle. The hypoflexus, the paraflexus, the mesoflexus and the metaflexus are present, showing the pattern typical for *Trogontherium* (Stefen and Rummel 2003, Kordos 2020). The length of the tooth is 6.5 mm and the width equals 7 mm which is larger than the expected range for *Trogontherium minutum* (Stefen and Rummel 2003, Apoltsev and Rekovets 2015, Kordos 2020) but smaller than would be expecred for *T. cuvieri* (Stefen 2011, Langeveld 2013).

m1 (Fig. 1E). The occlusal surface is roughly rectangular. The paraflexid, the hypoflexid, the metaflexid and the mesoflexid are visible (see Fig. 2), displaying the pattern typical of *Trogontherium*. The length is 5.5 and the width 5.7 mm, such dimensions being larger than expected for *Trogontherium minutum* (Stefen and Rummel 2003, Apoltsev and Rekovets 2015, Kordos 2020) but smaller than the typical range of *T. cuvieri* (Stefen 2011, Langeveld 2013, Yang et al. 2019).

Discussion

The Mio-Plio-Pleistocene genus *Dipoides* includes several species, most of which are described from North America (Shotwell, 1955). In Eurasia it is represented by *D. problematicus*, *D. sigmodus*, *D. anatolicus*, *D. majori* and *D. mengensis*, the former two comprising the Western/Central European branch, and the last three forming the Eastern Mediterranean / Asiatic branch. The Eurasian representatives of the genus are poorly known as compared to the American ones; their record is relatively sparse, and morphological differences between them are elusive (van de Weerd 1976, García-Alix et al. 2007, Rekovets et al. 2009, Xu et al. 2017). It was suggested that the genus *Dipoides* is actually polyphyletic, with the Eurasian species having evolved independently in Europe from a *Eucastor*-like ancestor and not constituting a clade with the New World *Dipoides* (Hugueney,1999). The Węże 2 tooth, which apparently is the first *Dipoides* specimen described from Poland, displays the usual sigmoid occlusal pattern of the *D. problematicus-sigmodus* species complex, which is also present in *Eucastor* (van de Weerd 1976, Hugueney 1999, García-Alix et al. 2007, Xu et al. 2017). Morphologically, the tooth seems most similar to *Dipoides problematicus* from the Teruel-Alfambra region of Spain (van de Weerd 1976). Nonetheless, the stratigraphic position of the Węże 2 specimen suggests assigning it to *D. sigmodus*, which is considered a direct descendant of the former species (Montoya 1993, García-Alix et al. 2007, Rekovets et al. 2009, Xu et al. 2017). The find would apparently be the second easternmost occurrence of a representative of the *D. problematicus-sigmodus* species complex besides the *D*. ex gr. *sigmodus* finding from the Ukrainian MN 17 site of *Kotlovina* 2 (Dema, 2000, Rekovets et al. 2009). However, the measurements of the Węże 2 specimen are significantly smaller than the typical ranges of both *D. problematicus* and *D. sigmodus* (van de Weerd 1976, García-Alix et al. 2007, Xu et al. 2017). The specimen probably belongs to a hitherto unknown minute *subspecies* or species of *Dipoides*.

Within the genus *Trogontherium*, *T. cuvieri*, lasting from the Late Pliocene to the Late Pleistocene, is by far the best known, owing to its widespread distribution across Eurasia and the relative abundance of the fossil material (Fostowicz-Frelik 2008, Stefen 2011). *T.* (*Euroxenomys*) *minutum* (MN 3? – MN 15?) and *T.* (*Euroxenomys*) *minus* (MN 13? – MN 17?)

are distinguished from *T. cuvieri* mainly by the size of their cheek teeth, *T. minutum* being the smaller and *T. minus* the larger of the two forms, and they are known mainly from Western and Central Europe (Newton 1890, Mayhew 1978, Stefen and Rummel 2003, Stefen 2011, Apoltsev and Rekovets 2015, Kordos 2020). However, the earliest representative of the subgenus *Euroxenomys* may be either *T.* (E.) *nanus* from the Early Miocene of Japan (Mörs and Tomida 2018) or *T.* (*E.*) wilsoni from the Early Miocene of North America (Korth 2001). Another Early Miocene form, *T.* (*E.*) *inconnexus*, is younger and may be considered a possible descendant of *T.* (*E.*) *wilsoni* (Sutton and Korth 1995, Korth 2001). *Trogontherium* (*Euroxenomys*) *minus* itself was first described from eastern England (Newton 1890) but is also known from mainland Europe. Seemingly it has not yet been reported from Poland, although it appears in fossil faunal assemblages of Germany (Mörs et al. 1998, Mörs 2002), Slovakia (Sabol 2001) and Ukraine (Apoltsev and Rekovets 2015). Two Węże 2 specimens are attributed to *T.* (*E.*) *minus* on the basis of the occlusal morphology characteristic of *Trogontherium* and the occlusal measurements larger than the typical ranges of *T. minutum* but smaller than expected for *T. cuvieri* (Stefen and Rummel 2003, Stefen 2011, Langeveld 2013, Apoltsev and Rekovets 2015, Kordos 2020).

The genus *Castor* is the only extant genus belonging to the once species-rich family Castoridae, a clade that underwent a substantial decline in diversity during the Pleistocene (Hugueney and Escuillié 1996, Rose 2006, Rybczynski 2007, Rybczynski et al. 2010, Stefen 2011, Li et al. 2017). Thus, *C. fiber*, present in Europe since at least the Late Miocene (Belyaeva 1962, Zelenkov and Panteleyev 2015), and *C. canadensis*, may be both considered relict species in modern faunas and are the only castorids the ecology of which can be directly observed. As they are both strongly specialized for utilizing freshwater and woodland habitats, their presence in a fossil fauna is also a reliable indication for such environmental conditions. The constant presence of forest within the Węże 2 area during the formation of the fossil assemblage is also indicated by the appearance of the dormouse *Glis* ex gr. *sackdillingensis-minor* in each of the stratigraphic units (Czernielewski 2021), while other modern mammalian genera linked to a semiaquatic lifestyle and recorded at Węże 2 include the talpids *Condylura* and *Desmana* (Sulimski 1962, Rzebik-Kowalska 1989, Nadachowski et al. 2015). The presence of *Trogontherium minus* and *Dipoides* ex gr. *problematicus-sigmodus* at Węże 2 agrees with the hypotheses that they were also woodcutting and semi-aquatic animals (Rybczynski 2007, Rybczynski et al. 2010, Xu et al. 2017, Pint et al. 2020).

Conclusions

The Villafranchian (MN16b?) site of Węże 2 in southern Poland yielded a relatively diverse fossil assemblage of rodents including some beaver remains. These are attributable to two species: *Dipoides* ex gr. *problematicus-sigmodus* and *Trogontherium* (*Euroxenomys*) *minus*. The species *T.* (*E.*) *minus* and the genus *Dipoides*, although previously recorded in Central Europe, had apparently not previously been found in Poland. As the fossil assemblage of Węże 2 is considered to represent a forested environment close to a constant freshwater source, the presence of *T.* (*E.*) *minus* and *Dipoides* ex gr. *problematicus-sigmodus* at the site suggests that these lesser known and extinct representatives of the Castoridae, although, ultimately unsuccessful, were adapted to similar environments as are the modern species. The Eurasian *Dipoides*, despide having a wide range, apparently was never common, and its fossil record has a patchy geographical distribution, suggesting dependence on very specific environmental conditions.

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Chapter 3. A new species of *Hystrix* (Rodentia: Hystricidae) from the Pliocene site of Węże 1 in southern Poland[1]

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Abstract

The specific name *velunensis* is established to encompass porcupine remains (*Hystrix* Linnæus, 1758) recovered from the Pliocene site of Węże 1 in southern Poland. The studied specimen was previously assigned either to *H. primigenia* (Wagner, 1848) or *H. depereti* Sen, 2001, however it can be distinguished from these species and other fossil Hystricidae by its distinct occlusal morphology, most importantly the presence of an anterolingual flexus dissecting the anteroloph of P4. *Hystrix velunensis* sp. nov. was probably closely related to *H. primigenia* and *H. depereti*. A previously undescribed specimen from the nearby site of Węże 2 most probably belongs to *H. refossa* Gervais, 1852b, which would be the first known occurrence of this species in Poland.

Key words: Pliocene; rodents; porcupines; Węże; karst.

Introduction

The Hystricidae Fischer, 1817 (Old World porcupines) are a family of large herbivorous rodents recognizable by their characteristic spiny covering formed by modified body hair. The family comprises three extant genera – *Hystrix* Linnæus, 1758, *Atherurus* Cuvier, 1829 and *Trichys* Günther, 1877. Out of these three, *Hystrix* is by far the most species-rich genus (Carleton and Musser 2005, Woods and Kilpatrick 2005, Sheng et al. 2020). The Hystricidae are classified in the suborder Hystricomorpha Brandt, 1855, which also encompasses, among others, the so-called New World porcupines (the family Erethizontidae Bonaparte, 1845), the Caviidae Fischer, 1817 (including the capybara and the guinea pigs), and the African mole-rats, i.e., the Bathyergidae Waterhouse, 1841 (Carleton and Musser 2005, Woods and Kilpatrick 2005). Early representatives of the Hystricomorpha are known from the middle Eocene of South America (Antoine et al. 2012) while the Hystricidae themselves may have originated either in Southeast Asia (van Weers 2005) or in Africa (Lazaridis et al. 2019). The oldest fossil specimen clearly attributable to this family is probably an isolated unerupted tooth recovered from the late

Miocene of Egypt and assigned to *Atherurus* indet. (Mein and Pickford 2010, Lazaridis et al. 2019). Extant Old World porcupines are typically limited to tropical and subtropical climate zones, being widespread in Africa and Asia while in Europe they are confined to the southernmost part of the continent. They thrive in a wide range of warm habitats, from tropical forests to deserts, and their foraging mode is considered to be of a generalist type (Alkon 1999, Mori et al. 2013, Lovari et al. 2017, Sheng et al. 2020).

The purpose of this paper is to provide a formal description of a newly recognized porcupine (Rodentia: Hystricidae) species, present at the Pliocene site of Węże 1 in southern Poland (Wieluń Upland, Pajęczno County; Fig. 1). Although a distinct specific or even generic status of the Węże 1 form was previously hypothesized (Sulimski 1960, Shevyreva 1986, Lopatin et al. 2003), a new taxon has never been formally established. Further material of *Hystrix* from the younger site of Węże 2 is also described as assignable to *H. refossa* Gervais, 1852b which would be the first occurrence of this species known from a Polish site.

Geological setting

The Węże 1 site (also known as the Samsonowicz's Cave) is situated on the western slope of Zelce Hill, near the village of Węże (Pajęczno County), in the Wieluń Upland, southern Poland (Fig. 1). It comprises a karst cave system developed in Oxfordian (Upper Jurassic) limestone. It was initially examined by Jan Samsonowicz in the 1930s and after the Second World War was extensively studied by researchers from the Museum of the Earth of the Polish Academy of Sciences in Warsaw, the Department of Systematics and Experimental Zoology of the Polish Academy of Sciences in Cracow, and the Department of Palaeozoology of Wrocław University. The site is composed of a pit, c. 8 m deep, leading to a system of small corridors. Water transportation was probably the key factor in the formation of the bone breccias that constitute the infilling of the cave. It was also hypothesized that the cave might have acted as a trap for animals (Samsonowicz 1936, Sulimski 1959, Szynkiewicz 2015a). Three main sedimentary cycles were distinguished at Węże 1 based on mammal biostratigraphy, dated respectively at MN 13 (Messinian, upper Miocene), MN 15 (lower to upper Pliocene, Zanclean/Piacenzian, 4.2–3.4 Ma) and MNQ 20 (lower to middle Pleistocene) (Głazek et al. 1975; Agustí et al. 2001; Szynkiewicz, 2015a; Stefaniak et al. 2020). Węże 1 yielded an abundant fossil vertebrate fauna (Stach 1951, 1953, 1957, 1959, 1961, Młynarski 1956a, b, 1961, Czyżewska 1958, 1960, 1968, 1969, 1978, 1981a, b, 1982, 1985, Sulimski 1959, 1962b, c, 1964, Kowalski 1960, 1962, Sych 1965, 1980, Skoczeń 1976, 1993, Bocheński 1989, Dybka 1990, Rzebik-Kowalska 1990, Zijlstra 2010, Sansalone et al. 2016; Stefaniak et al. 2020). The mammalian fauna of the site represented in the Pliocene assemblage includes the badger *Arctomeles pliocaenicus* Stach, 1951, the bears

Ursus wenzensis Stach, 1953 and *Agriotherium intermedium* Stach, 1957, the rhinoceros *Dicerorhinus* sp. (Czyżewska 1958), the eulipotyphlans *Erinaceus samsonowiczi* Sulimski, 1959, *Rzebikia polonica* (Skoczeń, 1980), *R. skoczeni* (Zijlstra, 2010), *Desmana nehringi* Kormos, 1913, *Sorex runtonensis* Hinton, 1911, *Blarinoides mariae* Sulimski, 1959, *Zelceina soriculoides* Sulimski, 1959, *Beremendia fissidens* Petényi, 1864, *Petenyia hungarica* Kormos, 1934, *Crocidura* sp. and *Paenelimnoecus pannonicus* (Kormos, 1934) (Sulimski 1959, 1962b, Skoczeń 1976, 1993, Rzebik-Kowalska 1990, Zijlstra 2010, Sansalone et al. 2016), the lagomorph *Hypolagus beremendensis* (Kormos, 1930) (Sulimski 1964, Sych 1965, 1980, Czyżewska 1985, Fostowicz-Frelik 2007), the cervids *Muntiacus polonicus* Czyżewska, 1968, *Praeelaphus warthae* (Czyżewska, 1968), *Arvernoceros* cf. *ardei* Croizet and Jobert, 1828, and *Procapreolus moldavicus* (Janovskaya, 1954) (Czyżewska 1968, 1982, Stefaniak et al. 2020), as well as the saber-toothed cat *Machairodus* sp. (Dybka 1990). Numerous rodent taxa were also recognized, including the sciurids *Sciurus warthae* Sulimski, 1964, *Pliosciuropterus schaubi* Sulimski, 1964 and *Eutamias orlovi* Sulimski, 1964, the castorid *Steneofiber wenzensis* Sulimski, 1964, the muroids *Trilophomys pyrenaicus* Depéret, 1890, *Baranomys longidens* (Kowalski, 1960), *Germanomys weileri* Heller, 1936, *Mimomys gracilis* (Kretzoi, 1959), *Plioselevinia gromovi* Sulimski, 1962, *Sminthozapus janossyi* Sulimski, 1962 and *Prospalax priscus* (Nehring, 1897) (Kowalski 1960, Sulimski 1962b, c, 1964), as well as the glirids *Glis minor* Kowalski, 1963 and *G. sackdillingensis* Heller, 1930 (Kowalski 1963, Sulimski 1964, Czernielewski 2021). The Pliocene fauna of Węże 1 presumably reflects a Mediterranean-like climate and a mixture of arboreal and open habitats (Czyżewska 1968, Stefaniak et al. 2020).

Fig. 1. Location of the village of Węże in Poland (A) and the Wieluń Upland (B).

The nearby Węże 2 site upon its discovery comprised a vertical karst crevice (c. 10 m long and c. 4 m wide) infilled with clayey fossiliferous strata. These deposits (~3.5 t in total) were collected during field work organized in the early 1960s by the Department of Palaeozoology of the Polish Academy of Sciences in Warsaw (currently the Institute of Paleobiology PAS) and the Department of Palaeozoology of Wrocław University (Sulimski 1962a, Szynkiewicz 2015b). Based on its faunal composition the site is presently dated at 2.9–2.6 Ma, i.e., the late Pliocene (Piacenzian), early Villafranchian Mammal Age and MN 16b zone in the Mammal Neogene zonation (Agustí et al. 2001, Nadachowski et al. 2015, Stefaniak et al. 2020). However, this might be modified since the material collected is still under study. The mammalian taxa thus far described from Węże 2 include the flying squirrel *Pliopetaurista dehneli* (Sulimski, 1964) (Sulimski 1964, Hordijk and de Bruijn 2009), the lagomorph *Hypolagus beremendensis* Kormos, 1930 (Fostowicz-Frelik 2007), the cervids *Croizetoceros ramosus* (Croizet and Jobert, 1828) and *Metacervocerus pardinensis* (Croizet and Jobert, 1828), an unindentified rhinocerotid, an elephantid probably assignable to the genus *Anancus* Aymard, 1855 (Stefaniak et al. 2020), the talpids *Rzebikia polonica* and *R. skoczeni* (Rzebik-Kowalska 1990, 2014, Skoczeń 1993, Zijlstra 2010, Sansalone et al. 2016), the dormice *Glis minor* and *G. sackdillingensis* (Czernielewski

2021), as well as the beavers *Trogontherium minus* Newton, 1890 and *Dipoides* sp. (Czernielewski 2022). The presence of several carnivoran, eulipotyphlan, rodent and chiropteran taxa was briefly reported (Sulimski 1962a, Nadachowski 1989, Rzebik-Kowalska 1989, Nadachowski et al. 2015). In general, the fossil assemblage of Węże 2 is suggestive of an arboreal environment and a warm, Mediterranean-like climate (Nadachowski et al. 2015, Stefaniak et al. 2020).

Matherial and methods

The specimen MZ VIII-Vm/731-1 (a fragmentary palate, Fig. 2) was etched out from the calcareous breccia of Węże 1 in 1933, probably by Jan Samsonowicz (Sulimski 1960). It is part of the collection of the Museum of the Earth of the Polish Academy of Sciences in Warsaw. More specimens from Węże 1, including an isolated lower premolar, two lower and one upper incisors, and a fragmentary right mandible with p4–m2 can be attributed to the Hystricidae (listed by Sulimski 1960 and van Weers and Rook 2003), and although they might belong to the new species, they will not be further discussed here as they lack the recognized diagnostic features of *H. velunensis* sp. nov.

The specimen ZPAL VIII/I-140/1 (Zakład Paleozoologii, i.e., the Department of Palaeozoology, being the previous name of the Institute of Paleobiology, PAS) is a right mandible with m1–m3 (Fig. 3) belonging to *Hystrix refossa*. It was handpicked during the excavations conducted at the nearby Węże 2 site in the early 1960s (Sulimski 1960a). The specimen is housed in the collection of the Institute of Paleobiology, PAS in Warsaw.

Illustrated cranial, maxillary, mandibular and isolated dental specimens of *H. primigenia* (Wagner, 1848), *H. refossa* and *H. depereti* Sen, 2001 were used to compare them with the Węże material. These include the IPGM ASII144 skull of *H. primigenia* from the type locality of Pikermi, Greece (van Weers and Rook 2003), two P4 specimens (Pp-58d and PE-1a) indicated as paratypes of *H. depereti* from Perpignan, France (Sen 2001), the holotype specimen of *H. refossa* from Les Etouaires, Perrier, France (Gervais 1852a, b, c, van Weers 1994), and two mandibles (PN11/nn and DE1/nn) of *H. refossa* from Pirro Nord, Italy (Rook and Sardella 2005). Cranial and mandibular specimens of extant *Hystrix cristata* Linnæus, 1758 and *Hystrix indica* Kerr, 1792 (from the collections of the Museum of Natural History, University of Wrocław and the Municipal Zoological Garden in Warsaw) were also examined.

For the purpose of this study, microcomputed tomography (microCT) was conducted on the Węże specimens, an imaging technique which detects differences in the attenuation of an X-ray beam propagating through a solid object (e.g, Błażejowski et al. 2013, 2015). This data allows one to visualize the internal structure of the specimens and, after computer processing, to render 3-D models.

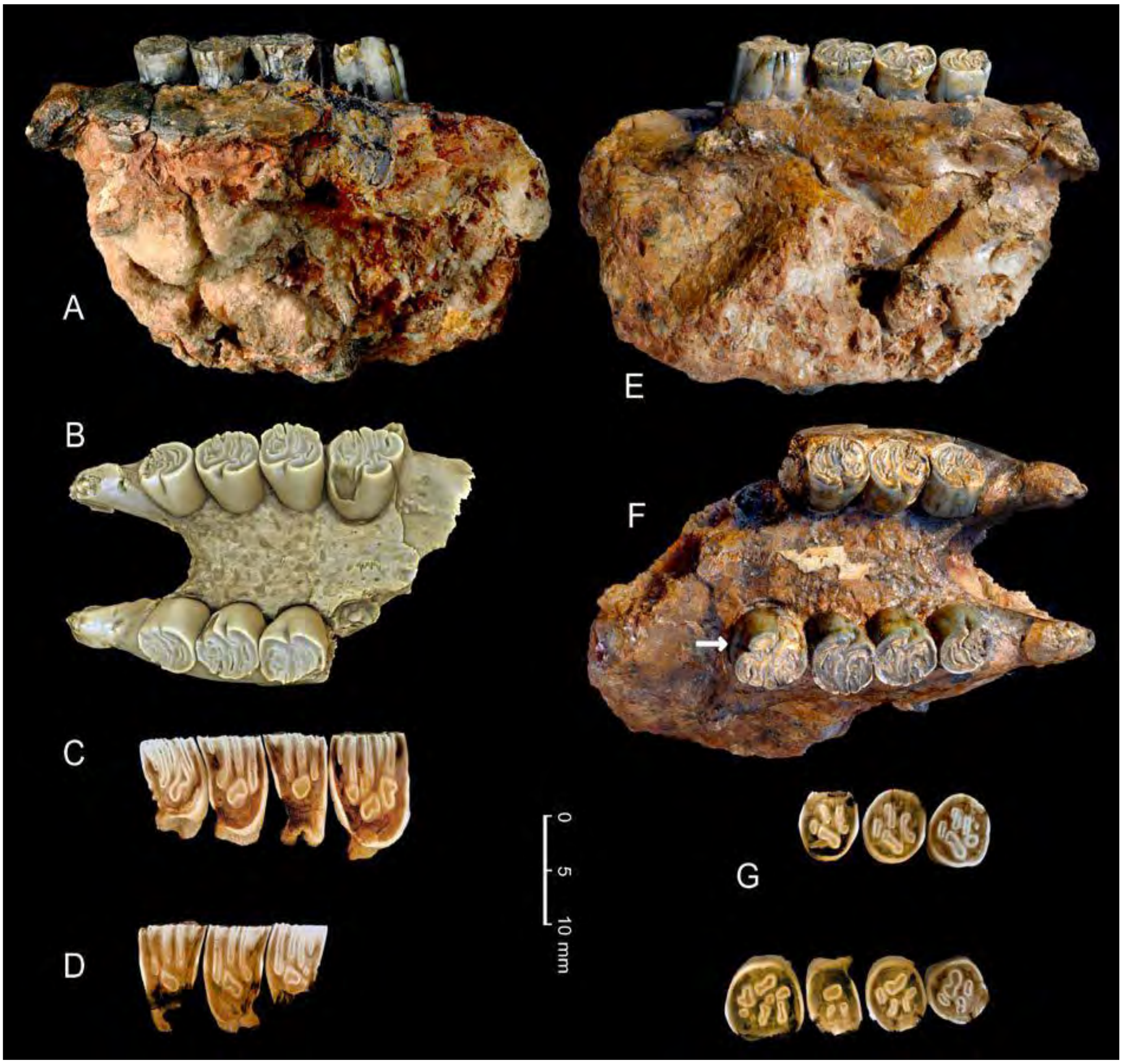

Fig. 2. *Hystrix velunensis* sp. nov. from Węże 1, Wieluń Upland; MZ VIII-Vm/731-1 (holotype), palate and maxilla with right P4– M3 and left M1–M3. A – left lingual view; B – palatal view, 3D CT model; C – right tooth row, CT scan; D – left tooth row, CT scan; E – right buccal view; F – palatal view (anterior sulcus marked with arrow); G – occlusal view of the tooth rows, CT scan.

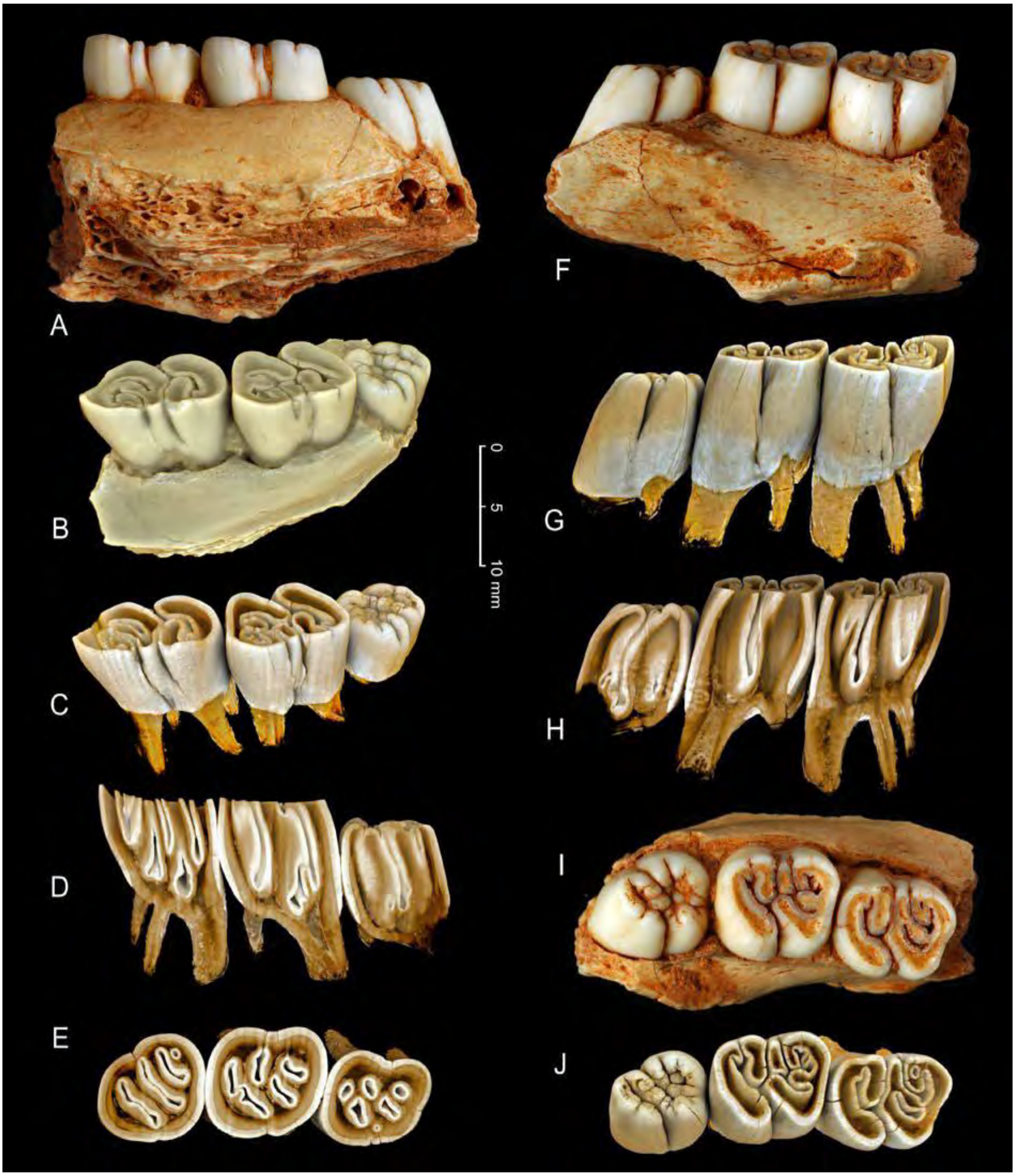

Fig. 3. *Hystrix refossa* Gervais, 1852b from Węże 2, Wieluń Upland; ZPAL VIII/I-140/1, right mandible fragment with m1–m3. A – lingual view; B – mesio-lingual oblique view, 3D CT model; C – mesio-lingual right oblique view of the tooth row, 3D CT model; D – lingual view, CT scan; E – occlusal view, CT scan; F – buccal view; G – buccal view of the tooth row, 3D CT model; H – buccal view, CT scan; I – occlusal view; J – occlusal view, 3D CT model.

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Hystricidae Fischer, 1817

Genus *Hystrix* Linnæus, 1758

Hystrix velunensis sp. nov.

(Figs 2 and 4B)

v1960. *Hystrix primigenia* (Wagner); Sulimski, pp. 320–324, figs 1–2, pl. 1.

v1964. *Hystrix primigenia* (Wagner); Sulimski, pp. 233–234.

v1986. *Hystrix primigenia* (Wagner); Shevyreva, pp. 120, 123, 130, fig. 4.

v2003. *Hystrix* sp.; Lopatin et al., p. 31.

v2003. *Hystrix depereti* Sen; van Weers and Rook, p. 97.

Holotype: MZ VIII-Vm/731-1, referred to as Rod. 1 in Sulimski (1960), a fragment of the upper-middle part of the skull, showing portions of the palate, a partial outline of the mesopterygoid fossa, and incompletely preserved maxillary bones with right P4–M3 and left M1–M3 *in situ*.

Type horizon: Beds of Węże 1 (Samsonowicz's Cave), Pliocene, MN15b (according to Stefaniak et al. 2020).

Type locality: Węże 1 (Samsonowicz's Cave), Wieluń Upland, Pajęczno County, southern Poland [51°05′45.8″N, 18°17′21.94″E].

Derivation of the name: Latin for "of Wieluń", after the town of Wieluń, giving its name to the Wieluń Upland and the Wieluń Land (*Terra Velunensis*) where the type locality is situated.

Diagnosis: A large porcupine with occlusal morphology similar to that of *Hystrix primigenia* (Wagner, 1848) and *Hystrix depereti* Sen, 2001; P4 posteriorly narrowed; the anteroloph of P4 dissected by a flexus on the anterolingual side; five grooves (flexus) on the labial side of P4.

Description: Specimen MZ VIII-Vm/731-1 displays a large portion of the palate and incomplete maxillary bones, with the right P4–M3 and the left M1–M3 *in situ*. A partial outline of the mesopterygoid fossa (the internal choana) is discernible. The right side of the specimen is significantly better preserved than the left side. The specimen was described in detail by Sulimski (1960), and the following measurements are given there. The length of the palate is approximately 55.0 mm; its average width (measured between the lingual borders of the molars) is approximately 15.0 mm. The length of the right tooth row is 45.5 mm. The length/width of particular teeth of the right tooth row is as follows – P4: 13.2/11.8 mm; M1: 11.0/10.0 mm; M2: 11.0/10.0 mm; M3: 10.0/9.0 mm. The crown heights of the right tooth row measured on the lingual side (which were not given in Sulimski 1960) are c. 13 mm (P4), 11 mm (M1), 10 mm (M2) and 10 mm (M3). The left tooth row is incomplete, lacking the P4. REMARKS: Specimen MZ VIII-Vm/731-1 represents an adult animal, probably a young adult judging by the low tooth surface loss. The teeth were described by Sulimski as "slightly worn" (which, according to him, suggested that the animal was a young adult), and as "highly hypsodont" (Sulimski 1960, p. 321). The latter feature was discussed by van Weers and Rook (2003, p. 98), who reassigned the *Hystrix* material from Węże 1 to the slightly more high-crowned *H. depereti* instead of *H. primigenia*. As already observed by Sulimski (1960, pp. 321–322, 330), the specimen differs from *H. primigenia* from the type locality of Pikermi (Wagner 1848) and from *H. depereti* of Roussillon (Depéret 1890, Sen 2001) by the distinct occlusal morphology of P4, particularly by the presence of the "anterior sulcus", which is an additional flexus dissecting the anteroloph on the anterolingual side of the tooth. Moreover, five well developed grooves are present on the labial side of P4 instead of the typical four of *H. primigenia* and *H. depereti* (Sulimski 1960, pp. 321–322, 330; Fig. 4).

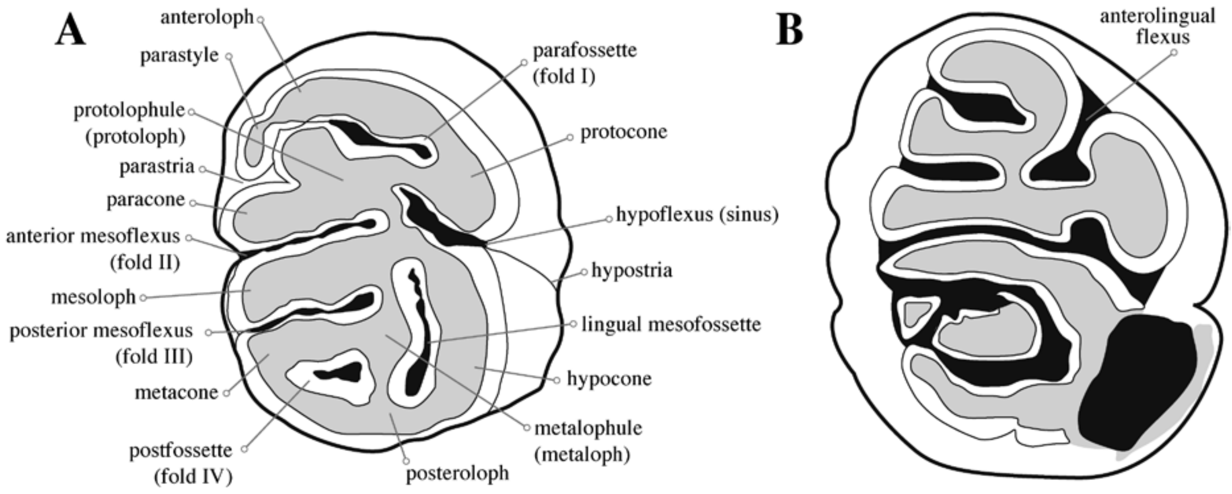

Fig. 4. Comparison of P4 occlusal morphology of *Hystrix primigenia* (Wagner, 1848) and *H. velunensis* sp. nov. A – right P4 of *H. primigenia* from Morskaya 2 locality (after Lopatin et al. 2003). B – right P4 of *H. velunensis* sp. nov. from Węże 1 (MZ VIII-Vm/731-1, after Sulimski 1960).

Hystrix refossa Gervais, 1852b

(Fig. 3)

1852b. *Hystrix refossa*; Gervais, pp. 6, 7.

1852c. *Hystrix refossa*; Gervais, pl. 48, fig. 11.

1859. *Hystrix major*; Gervais, p. 512.

1898. *Hystrix etrusca*; Bosco, p. 142, pl. 1, figs 1–9.

1955. *Hystrix major*; Greenwood, pp. 78, 79, fig. 27.

1958. *Hystrix makapensis*; Greenwood, p. 365.

1970. *Hystrix angressi*; Frenkel, p. 53, pl. 5, fig. 6.

Holotype: Fragment of a right mandible with p4 *in situ*, housed in Muséum National, Laboratoire de Paléontologie, Paris.

Type locality: Les Etouaires, Perrier, Puy-de-Dôme, central France.

Description: The specimen from Węże 2, ZPAL VIII/I-140/1 (Fig. 3), is a fragmentary right mandible with m1–m3 *in situ*, with the m3 freshly erupted and not yet well developed. The length/width of the occlusal surfaces of particular teeth is as follows – m1: 10.8/7.8 mm; m2: 10.8/8.1 mm; m3: 8.4/6.9 mm.

Remarks: The specimen belongs apparently to an immature individual. Morphologically it strongly resembles the material of the high-crowned, large porcupine *H. refossa* from the lower Pleistocene locality of Pirro Nord in southern Italy (Rook and Sardella 2005).

Discussion

The oldest fossil representative of the genus *Hystrix* may be the European *H. parvae* (Kretzoi, 1951) known from several upper Miocene (Tortonian, MN 10–MN 11) sites. It is however not clear if the genus is actually of European origin (van Weers and Montoya 1996, van Weers 2005, Lazaridis et al. 2019). It was already widespread through the Old World in the late Miocene, with *Hystrix* specimens of that age being known e.g. from the famous hominid sites of Toros-Menalla in Chad (Vignaud et al. 2002), Lothagam in Kenya (Winkler 2003), Middle Awash in Ethiopia (Haile-Selassie et al. 2004) and Lufeng in China (Wang and Qi 2005). Apart from *H. parvae*, several *Hystrix* species, i.e., *H. primigenia*, *H. depereti*, *H. caucasica* (Argyropulo, 1939) and *H. refossa*, were present in Europe during different time-spans from the late Miocene until the late Pleistocene (van Weers 1994, Sen 2001, Lopatin et al. 2003, van Weers and Rook 2003, van Weers 2005, Lazaridis et al. 2019). It is probable that different species spread across Europe in separate waves of migrations from Asia Minor with little speciation taking place in Europe (Lazaridis et al. 2019). After several thousand years of absence from the European fossil record, porcupines re-emerged in Europe inhistorical times when the extant species *H. cristata* made its appearance in the Italian Peninsula, supposedly introduced by the Romans or, more probably, shortly after the fall of Rome (Masseti et al. 2010, Mori et al. 2013). Fossil sites of extinct European porcupines are known mainly from Western Europe, the Balkans, the Carpathian Basin and south European Russia, and findings outside these areas are relatively rare (van Weers 1994, 2005, van Weers and Montoya 1996, Sen 2001, Lopatin et al. 2003, van Weers and Rook 2003, Lazaridis et al. 2019).

Throughout the evolution of the clade, the Hystricidae displayed markedly conservative occlusal morphology; at the same time, however, they show high intraspecific variability due to toothwear which makes it difficult to distinguish between particular species based solely on the morphology of the occlusal surfaces. Thus, additional features have been used, including the outlines of specific teeth (especially the third molar), the levels of hypsodonty, and morphometric traits of the occlusal surfaces. Distinguishing species on morphometric grounds may be especially problematic due to the relatively small sizes of available samples (van Weers 1994, 2005, van Weers and Montoya 1996, Sen 2001, Lopatin et al. 2003, van Weers and Rook 2003, Lazaridis et al. 2019). However, *H. velunensis* sp. nov. can be clearly distinguished from other fossil hystricids by the distinct anterolingual flexus dissecting the anteroloph of P4. It is possible that the newly described species was immediately related to *H. primigenia* or *H. depereti*. It also shares some important dental features with modern taxa (*H. cristata*, *H. indica*, *H. africaeaustralis* Peters, 1852), including the enlarged P4 and the typical *Hystrix*-like enamel pattern. Such dental morphology is suggestive of a herbivorous animal, adapted to crushing hard plant materials (van Jaarsveld and Knight-Eloff 1984).

The mandible ZPAL VIII/I-140/1 belongs to a young individual with one of the molars not yet fully formed and erupted, and most probably represents an immature specimen of *Hystrix refossa* (Rook and Sardella 2005). This species became widespread in East-Central Europe (especially the Carpathian Basin) in the early Pleistocene. If the assignment of the Węże 2 site to MN 16b is to be upheld, the ZPAL VIII/I-140/1 specimen becomes one of the oldest records of *H. refossa*, with other MN16 occurrences known only from Milia in mainland Greece, Damatria in the island of Rhodes, Gundersheim in western Germany, and the sites of Le Coupet and Les Etouaires in France. *Hystrix refossa* became a relatively commonplace species in East-Central Europe (especially the Carpathian Basin) only in the early Pleistocene (Lazaridis et al. 2019).

Conclusions

A new species of fossil porcupine, *Hystrix velunensis* sp. nov. has been recognized based on the specimen MZ VIII-Vm/731-1 from Węże 1, which displays a distinctive occlusal morphology of P4. The newly recognized species was probably immediately related to either *H. primigenia* or *H. depereti*. The presence of *Hystrix refossa* in Węże 2 is supported by the fragmentary mandible ZPAL VIII/I-140/1. The discovery shows that the late Pliocene range of this species was wider than previously indicated and that it started to spread across East-Central Europe before the onset of the early Pleistocene. The finding of a *Hystrix* specimen at Węże 2 makes this site (along with Węże 1) one of the northernmost occurrences of fossil porcupines in Europe.

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Chapter 4: New data on the Sciuridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland[1]

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Abstract

In addition to specimens attributable to *Pliopetaurista dehneli* (Petauristini), already described by Sulimski (1964), the fossil dental material collected at the Upper Pliocene (MN 16b) site of Węże 2 in southern Poland comprises specimens assignable to other representatives of the Sciuridae. These include *Tamias orlovi* (Marmotini), *Blackia miocaenica* (Petauristini) 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, Węże 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 used also more open wooded environments.

Key words: Villafranchian; Pliocene; rodents; squirrels; Węże

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 Sciuridae are, 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 is not resolved if the Sciuridae originated in North America or in Eurasia. The earliest known fossil sciurid may be *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, *Junngarisciurus jeminaiensis* and *Eopetes irtyshensis* have been described based on dental material from the Upper Eocene of northwestern China. They represent respectively a “tree-squirrel” and a “flying squirrel” morphotypes and make a strong case for Asiatic origin of the family (Li et al. 2023). The oldest fossil representatives of the Sciuridae in Europe, dated at 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 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 in the Late Pliocene ~3.1 Ma (Mercer and Roth 2003, Steppan et al. 2004, Li et al. 2023).

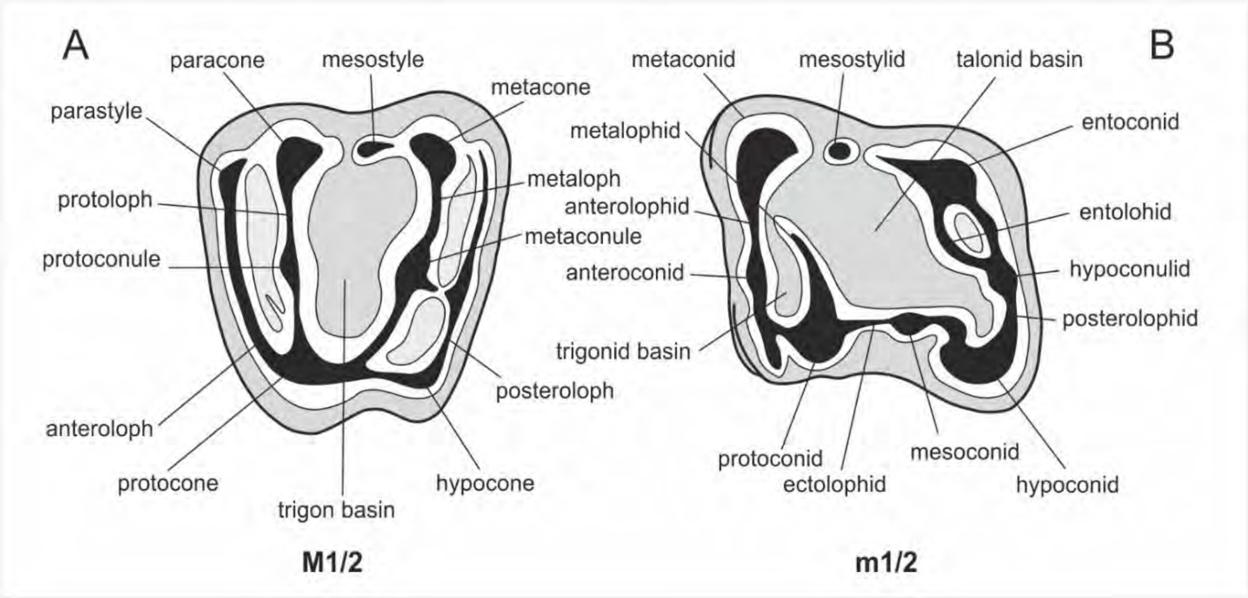

Fig. 1. Idealized occlusal morphology of sciurid cheek teeth
(after Qiu 1996, 2019, Li et al. 2023)

Early occurrences of squirrels in Poland include the presence of Sciuridae indet. at the Early/Middle Miocene (MN 4/5) assemblage of Bełchatów C, Early/Middle Miocene (MN 5/6) of Bełchatów B, and Middle/Late 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?) 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 as a junior synonym of *B. miocaenica* which is followed in this study. Other sciurids present at that site included *Pliopetaurista* sp. (Pteromyini), *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 respectively Węże 1 (MN 15) and Węże 2 (MN 16b), *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, the presence of *Blackia polonica* and *Pliopetes* cf.

hungaricus was also attested at that site (Sulimski 1964), however *B. polonica* is here treated as a junior synonym of *B. miocaenica* and the species *Pliopetes hungaricus* has been 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 summed up in Table 1.

The purpose of this paper is to present previously undescribed dental fossil 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). Węże 2 is then virtually identical in terms of sciurid diversity to the roughly contemporaneous and proximate site of Rębielice Królewskie 2 (Table 1). All the sciurid species present at Węże 2 are indicative of a woodland habitat.

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	*Pliopetaurista dehneli*, *Tamias orlovi*	Late Pliocene, MN 16b	Sulimski 1964, Stefaniak et al. 2020
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

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), Hellmund and Ziegler (2012), Hordijk and de Bruijn (2009).

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 2. Measurements (mm) of isolated sciurid teeth from Węże 2

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*

Table 3. Sciurids present at Węże 2 according to stratigraphic units

Geological setting and age of the fauna

The locality of Węże 2 is situated in the Wieluń Upland (southern Poland), on a slope of the Zelce Hill, in proximity of the town of Działoszyn (Pajęczno County, Łódź Voivodeship). Originally it comprised an 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 the Late Pliocene age were collected during field work 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 Department of Paleozoology of the Wrocław University. Four, and later five clayey strata containing fossils were distinguished that differed slightly in lithology, nevertheless 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 (Sulimski 1962, Szynkiewicz 2015).

The faunal composition of the Węże 2 fossil assemblage is currently dated at the Late Pliocene (Lower Villafranchian) and is 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), artiodactylan (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 at 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 is suggestive of an arboreal environment, proximity of a constant freshwater source, and 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 collected by handpicking during the fieldwork conducted in the early sixties 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 with 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: Fig. 6c, 7, 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 in regard to occlusal morphology. The protoloph, the metaloph, the paracone and the metacone are all 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 Węże 2 specimens 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 sunken 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: Fig. 5, 6). The length/width measurements are 1.6/1.4 for m1 and 1.8/1.5 for m2.

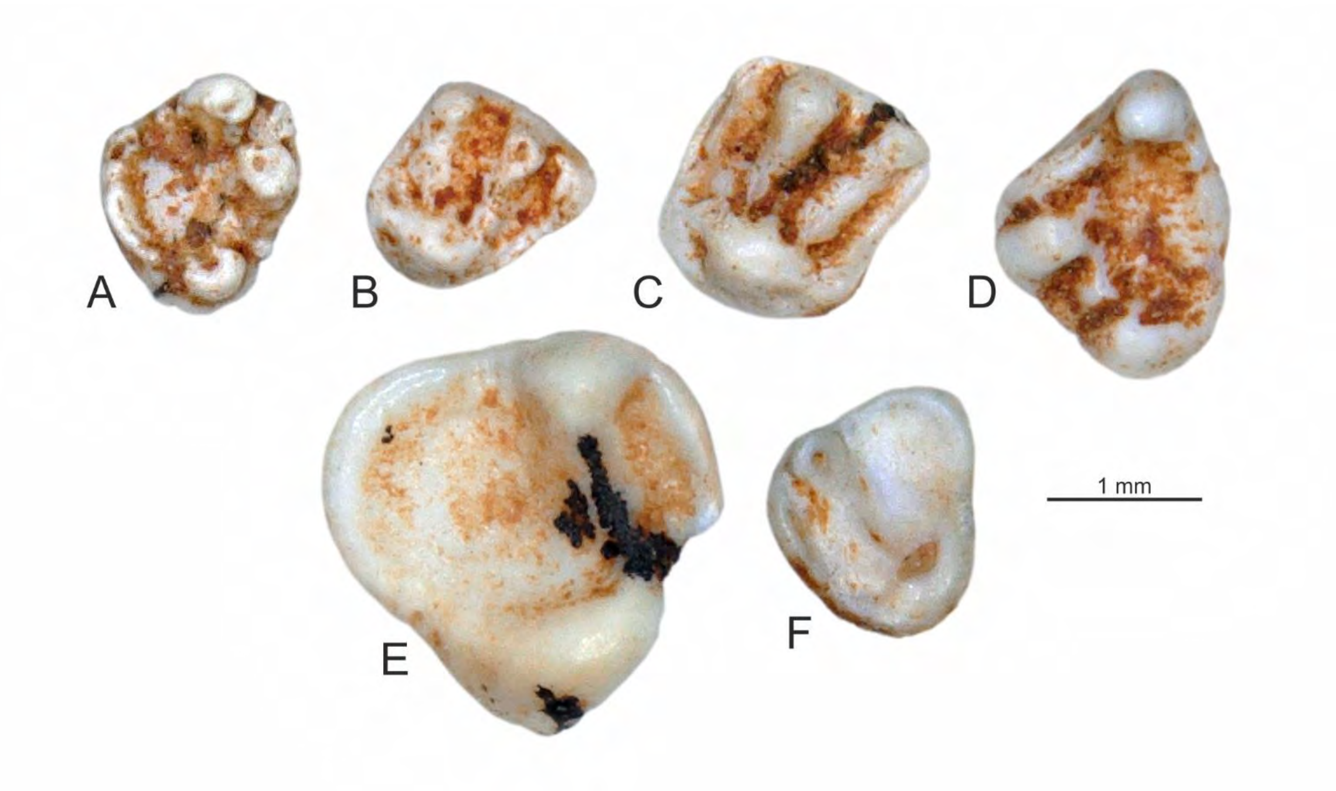

Fig. 2. Isolated sciurid teeth from Węże 2. A – *Tamias orlovi*, right p4 (ZPAL M. VIII/b/S1/29). B – *Tamias orlovi*, right P4 (ZPAL M. VIII/b/S1/25). C – *Tamias orlovi*, right M1/2 (ZPAL M. VIII/b/S1/8). D – *Tamias orlovi*, left m3 (ZPAL M. VIII/b/S1/23). E – *Sciurus warthae*, right M3 (ZPAL M.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

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

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 the large, deep trigon basin and the 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, 79) as well as the *B. miocaenica* specimen from Hambach 11C illustrated and described by Van Laere and Mörs (2023, Fig. 8 A).

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.

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 the craterlike trigon basin and the 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. The only specimen from Węże 2 is slightly damaged, with part of the anterior valley broken off. This is also the largest tooth out of all the studied specimens. The morphology of the occlusal surface is very similar to 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 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 the MN 4 of the Greek island of Evia (de Bruijn et al. 1980) and *Eutamias sihongensis* from the MN 4? of the Chinese province of Jiangsu located on the Pacific coast (Qiu and Liu 1986), which shows that the lineage was widespread in Eurasia already in 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 (Danukalova et al. 2009). The *Tamias* dental specimens from Węże 2 are very similar to the material uncovered at the *Tamias orlovi* type site of Węże 1 and are considered here to belong to the same species.

Blackia 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 department of Isère, south-western France (MN 7/8). Another species, *B. woelfersheimensis*, was recognized in the same study, the type site being 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 the 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 for *B. miocaenica*. Especially, Hellmund and Ziegler (2012) make the case for synonymity between *B. miocaenica* and *B. polonica*, 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 was reported from the Upper Pliocene of Rębielice Królewskie 1A and Rębielice Królewskie 2, the other reported Polish occurrences being 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 *Blackia miocaenica* and *Blackia* sp. specimens described and illustrated by Mein (1970) as well as to the singular *B. miocaenica* tooth illustrated and described by Van Laere and Mörs (2023). Thus, along with another 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 species (Lu et al. 2013, Van Laere and Mörs 2023).

Sciurus 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 Sciuruni, 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 were assigned to *Sciurus* cf. *warthae* (Table 1.). Later, *S. warthae* was reported at the Lower Pliocene locality of Wölfersheim in central Germany (Dahlmann, 2001), as well as at the Pleistocene site of Monte la Mesa (Marchetti et al. 2000), while the Late Miocene (Turolian, MN 13) occurrence of *S. warthae* at 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 *Pliopetaurista dehneli*, *Blackia miocaenica* and *Sciurus warthae*, while the latter by *Tamias 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 *Pliopetaurista dehneli*, *Tamias orlovi*, *Blackia miocaenica* and *Sciurus warthae*. All these species are considered to be typical for 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 at the Late Pliocene, it is also one of the younger occurrences of *T. orlovi*. The composition of the sciurid fauna is apparently identical to the site of Rębielice Królewskie 2. The sciurid species of Węże 2 represent both main ecological types evolved among squirrels, i.e. the arboreal and terrestrial modes of life.

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Chapter 5. Prospalax priscus jaw from the site of Węże 2 (Southern Poland, Pliocene)[1]

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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.

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 and Weksler 2004, Steppan et al. 2004, Musser and 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 and 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 and 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 and de Bruijn 2009, Nesin and 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 and 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 and 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

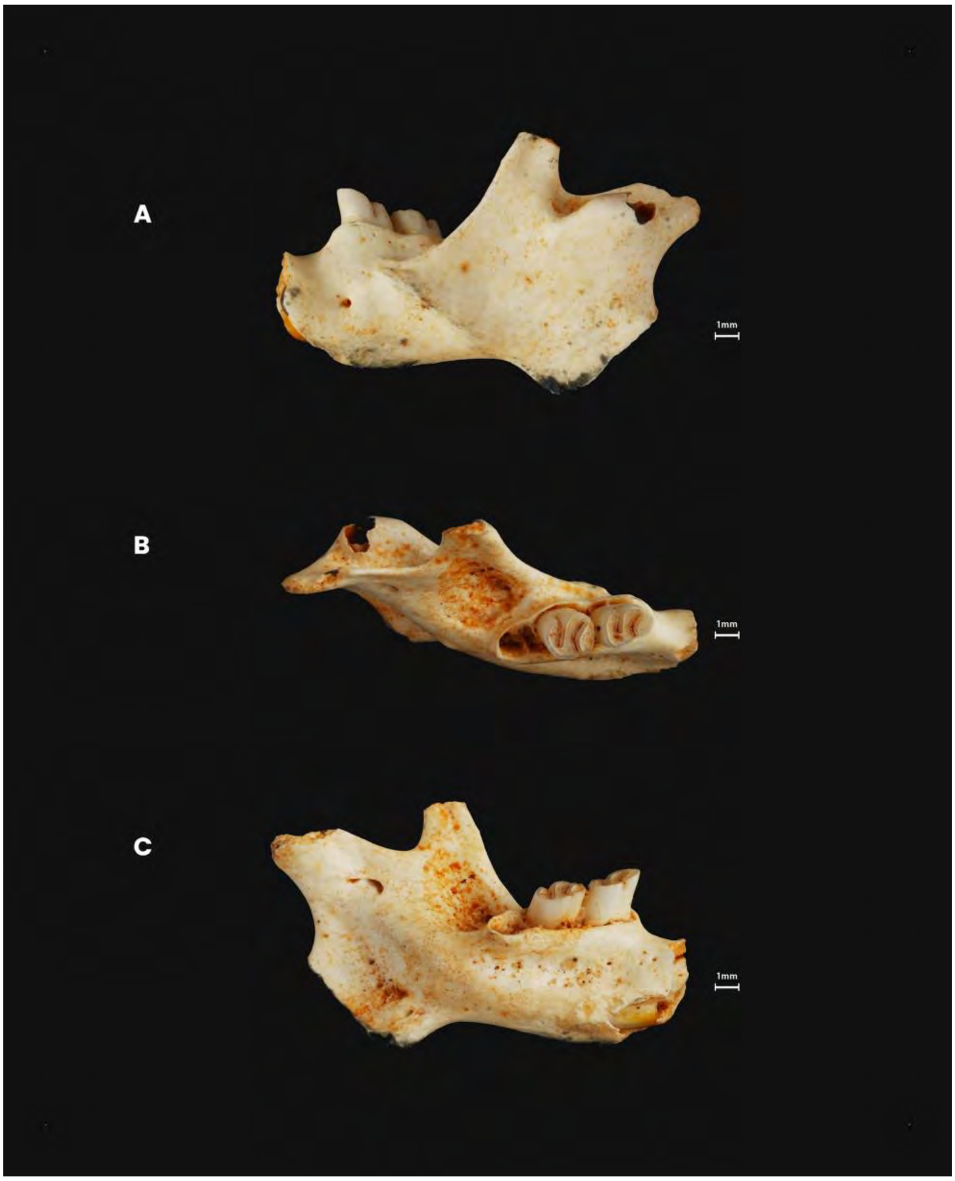

Fig. 1. Left mandible of *Prospalax priscus* (ZPAL M. VIII/b/P1/1) in labial (A), occlusal (B) and lingual (C) views

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 he 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 m_1–m_2 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).

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.

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

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

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

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 and 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 and Wilson 1978, Kordos 1985, Hugueney and Mein 1993, Bolliger 1999, Jansa and Weksler 2004, Musser and Carleton 2005, Nesin and 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 and Kovalchuk 2020). The evolutionary lineage *Anomalomys – Prospalax* has been inferred from the fossil record (Bachmayer and Wilson 1970, Nesin and 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 Wężе 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 and 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 and 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 and 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 and de Bruijn 2009, Nesin and Kovalchuk 2020). Such a shift has been caused by findings of anomalomyid remains within faunal assemblages otherwise typical for forest habitats (Hordijk and de Bruijn 2009, Nesin and Kovalchuk 2020) as well as by the reinterpretation of the anomalomyid incisors as not being proficient digging tools (Kalthoff 2000, Nesin and 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 and 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 and de Bruijn 2009, Marković and 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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Chapter 6. Fossil caries in a Pliocene rodent with a plausible case of in situ preservation of bacterial remains[1]

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Abstract

An extraordinary case of a caries-affected area where bacterial remains were plausibly preserved in situ was found in an isolated tooth of the Plio-Pleistocene dormouse *Glis sackdillingensis* (Rodentia, Gliridae). The sample is 2.9–2.6 million years old, and may be the only described case of a dental pathological condition preserved in a fossil together with the microbial pathogen responsible for its development. The tooth was investigated using various complementary techniques such as Scanning Electron Microscopy with Energy Dispersive Spectroscopy, Microtomography, and Light Microscopy. Available data on dietary habits and lifestyle of modern dormice are extrapolated to explain the origin of the infection. The results of the investigation are presented within the wider context of the fossil record of dental infections and other microbe-related diseases in vertebrates. Possible methodological reasons for the lack of similar reports are also discussed.

Key words: Rodentia, Gliridae, Plio-Pleistocene, enamel caries, bacterial infection

Introduction

Dental infections are thought to have been present in vertebrates since the Palaeozoic era (538.8–251.9 Mya), the earliest examples including cases of caries described in Devonian (419.2–358.9 Mya) lungfish (Kemp 2003, Reisz et al. 2011). In spite of that, relatively few pre-Holocene (older than ca. 12 kya) fossil specimens of bacteria-related tooth decay have been reported in scientific literature. Examples regarding occurrences of caries found in fossil hominids may be considered an exception (e.g. Grine et al. 1990, Tillier et al. 1995, Trinkaus et al. 2000, Humphrey et al. 2014, Fuss et al. 2018, Towle et al. 2021). The reason for that may be that hominid dental samples are studied more extensively with regard to caries due to their perceived immediate relevance to the topic of tooth decay in modern humans. Other pre-Holocene examples of conditions suspected to have resulted from dental infections were discovered in a Permian captorhinid reptile (Reisz et al. 2011), a Cretaceous ichthyosaur (Kear 2001), an early Eocene plesiadapiform primate (Selig and Silcox 2021), Miocene lungfishes (Kemp 2003), a Miocene artiodactyl (Sala Burgos et al. 2007) and a Pleistocene short-faced bear (Figueirido et al. 2017). Such studies are usually focused on recognizing and interpreting indirect evidence for the involvement of bacteria, i.e., pathological changes that are presumed to have been caused by bacteria because of their similarity to bacteria-induced conditions occurring in extant animals. This is also true for microbial infections which leave marks on bones (e.g. Wolff et al. 2009, Surmik et al. 2018, Moncunill-Solé et al. 2019).

More direct associations between bacteria and teeth do occur in the fossil record in the form of calcified dental plaque (also known as dental calculus), which is occasionally present in subfossil and fossil humans. It is known to preserve not only bacterial morphology but sometimes also a genetic information of the microbes responsible for the formation of the plaque (e.g. Preus et al. 2011, Adler et al. 2013, Weyrich et al. 2017). Bacterial body fossils preserved this way have also been recognized in the Miocene hominid *Sivapithecus* from Pakistan (Hershkovitz et al. 1997). However, what has been lacking in the fossil record is a clear instance of an association between a pathological condition and the microbial pathogen responsible for its development. To our knowledge, no such case has yet been convincingly documented.

In this paper we report a discovery of carious tooth damage of an isolated tooth of a Plio-Pleistocene dormouse with bacteria-like microstructures. We identified the microstructures as fossilized bacterial microflora associated with the enamel demineralization and dentine inflammation observed. The finding may represent an in situ preservation of cariogenic microbes that were causing the pathological condition during the animal's life. The species in question, *Glis sackdillingensis* (Rodentia, Gliridae), is considered to be the direct ancestor of the modern European edible dormouse, *Glis glis*. The investigated tooth is ca. 2.9–2.6 My old and, to our knowledge, it is the only thus far described caries-affected fossil dental specimen with bacterial microflora preserved in clear association with the affected area. It is apparently the first described case of fossil caries in a rodent.

Institutional abbreviations – ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations – EDS, Energy Dispersive Spectroscopy; LM, Light Microscopy; micro-CT, X-ray Microcomputed Tomography; SEM, Scanning Electron Microscopy.

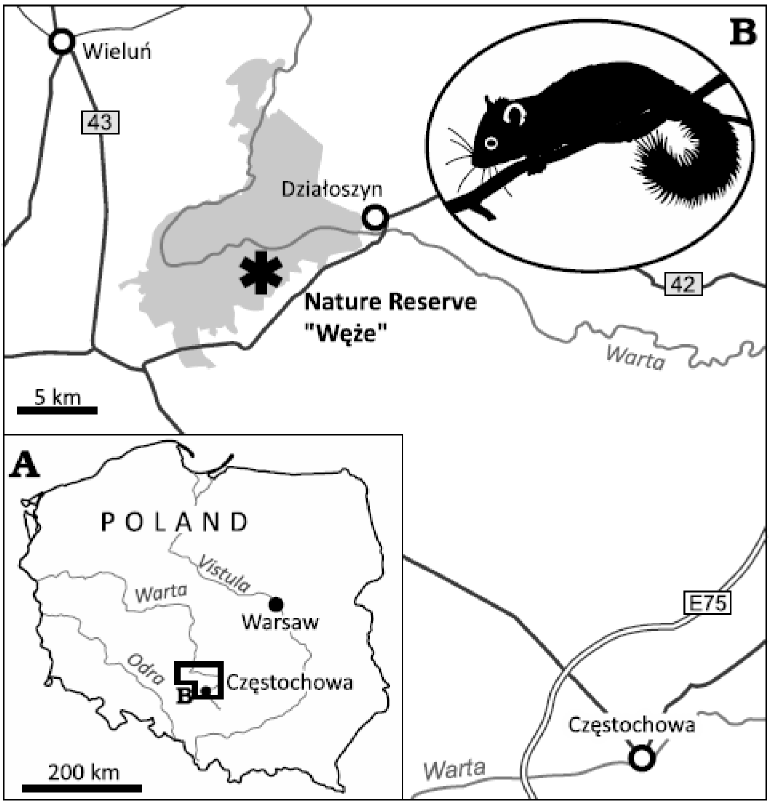

Fig. 1. Road map (A) with the location of the Nature Reserve “Węże” in the proximity to Wieluń in Central Poland (B). A silhouette of modern dormouse is given as an inset.

Material and methods

The tooth specimen, ZPAL M. VIII/b/G2/1, is part of the fossil assemblage of Węże 2, a paleontological site located in the Wieluń Upland, southern Poland (Fig. 1). The described tooth is an isolated permanent left lower first molar representing an adult individual of the species *Glis sackdillingensis* (Fig. 2A1, B1). One of the roots of the tooth is missing (partly broken off) (SOM: fig. S1, Supplementary Online Material available at http://app.pan.pl/SOM/app69-Czernielewski_etal_SOM.pdf). It was recovered from the fossiliferous terra rossa sediments that were collected in a karst crevice during field surveys to the location organized in the late 50s and early 60s of the XX century. Based on its faunal composition, the age of the fossil assemblage is currently dated at the late Pliocene (2.9–2.6 Mya) (Sulimski 1962, Stefaniak et al. 2020). The specimen is housed at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw.

To reveal the enamel structure the tooth was embedded in epoxy resin, polished perpendicularly to the vertical axis, treated with dilute (1%) orthophosphoric acid for ca. 60 seconds and dried. Subsequently, the internal structure of the enamel and dentin was examined using the Quattro S (Thermo Fisher) SEM apparatus. Energy dispersive X-ray spectroscopy (EDS) analyses were conducted using the Octane Elect (EDAX) detector. The procedure of both mechanical and chemical polishing was once repeated to enable observation of deeper parts of the tooth.

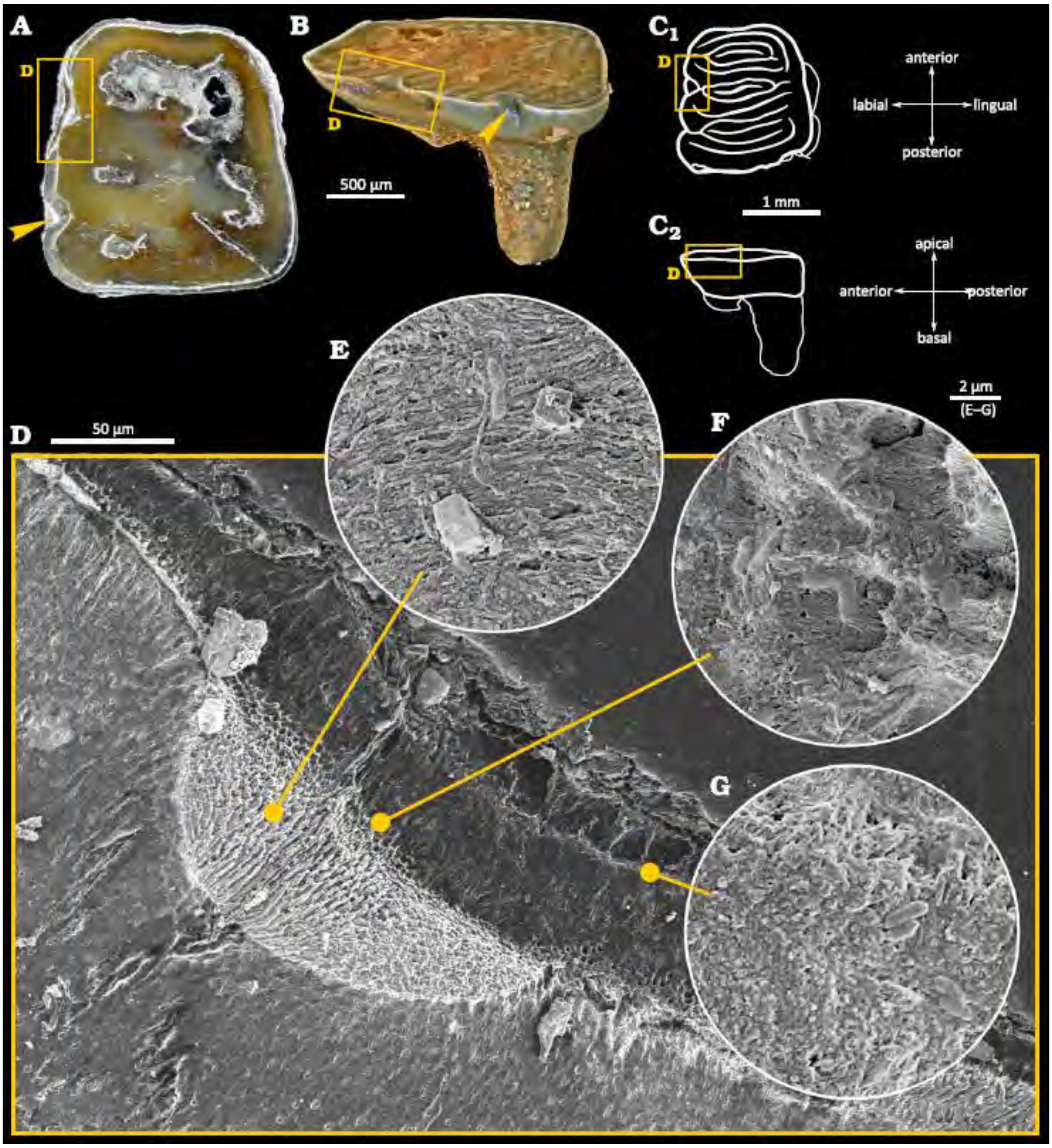

Fig. 2. Tooth of *Glis sackdillingensis* (Heller, 1930) (ZPAL M. VIII/b/G2/1) from Węże 2 (2.9–2.6 Mya), late Pliocene. A. Photography with the overview of the occlusal surface. The cavity area is indicated by yellow box. B. 3D CT model showing the cavity area. C. Drawings of occlusal (C1) and left lateral (C2) view, the upper surfaces created after each polishing marked with horizontal lines, the cavity area highlighted. Interpretation of the occlusal surface after Striczky and Pazonyi 2014. D. SEM photograph of the cavity area with the damage to the enamel and the dentin layers visible. E–G. SEM photographs showing fossilized bacteria-like microstructures.

To visualize the affected area and build 3D models, X-ray microcomputed tomography (micro-CT) was performed. The digital processing and analysis of the tomographic data enabled the construction of isosurface-based and volume-based 3D “virtual fossils”, which can be manipulated and dissected interactively (Błażejowski et al. 2011, Zapalski et al. 2021). Micro-CT data were collected with the XRadia MicroXCT-200 (ZEISS) system in the Laboratory of Microtomography, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland. The reconstructed computed tomography (CT) data were converted into TIFF image stacks that were subsequently imported and segmented in VGStudio MAX version 3.0 (Volume Graphics Inc.).

Results

Light and Scanning Electron Microscopy (LM, SEM).— Despite the small size of the sample (ca. 2×1×2 mm), physical damage to the enamel layer is visible at low magnification on the buccal side of the tooth (Fig. 2C). However, it can be distinguished from surrounding material only in cross-section and is not visible upon the investigation of the tooth's surface. The damage is generally superficial and limited to the enamel tissue, but locally an indentation is visible, wedging into the dentine layer (Fig. 2D). We interpreted this damage as a cavity caused by an early stage of tooth decay, and the spot concerned as a caries-affected area. This area has become the focus of subsequent examinations. Detailed SEM inspections revealed that the dentine layer within the area was also damaged, which we consider to be caused by bacteria-inflicted inflammation and demineralization.

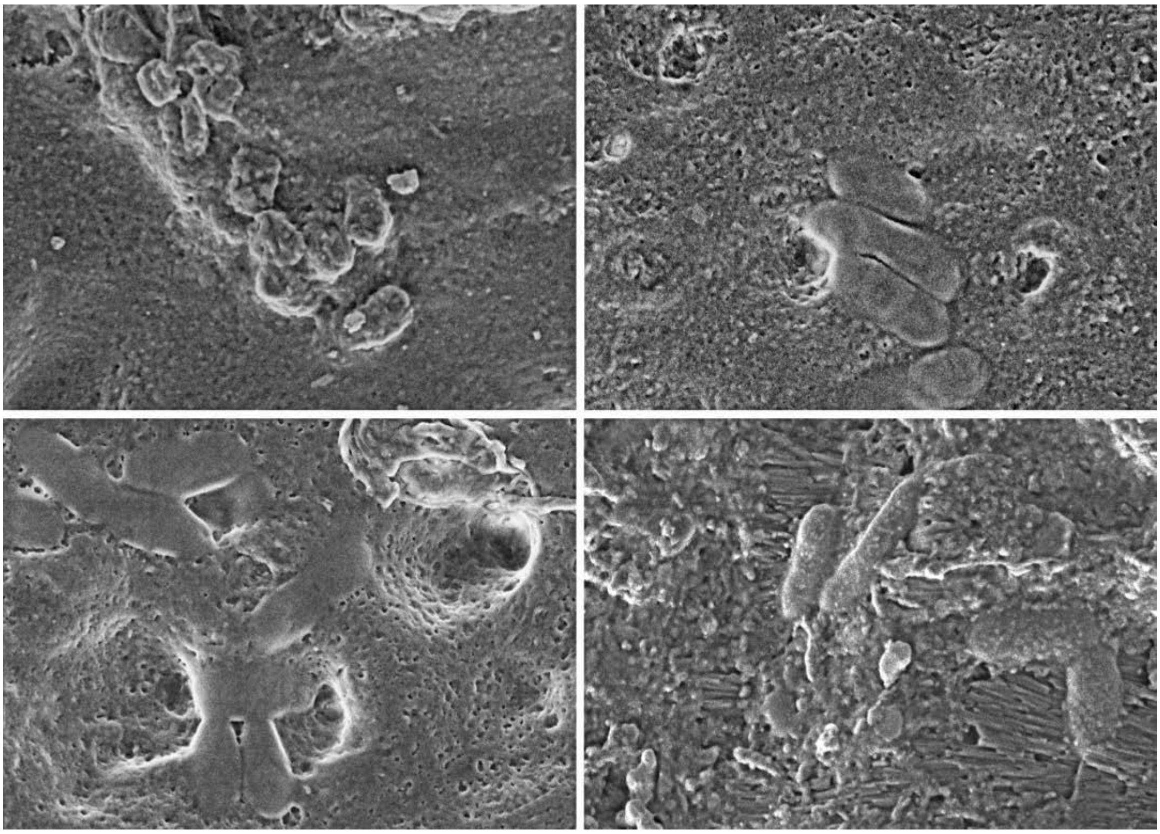

Fig. 3. Tooth of *Glis sackdillingensis* (Heller, 1930) (ZPAL M. VIII/b/G2/1) from Węże 2 (2.9–2.6 Mya), late Pliocene. SEM photographs showing various morphologies of probable bacterial fossils found in the tooth cavity. A. Cocci-like objects. B–D. Bacilli-like objects.

Within the cavity area, cocci-like objects and bacilli-like objects were found. A compilation of SEM photographs showing examples of those various morphologies of plausible bacterial fossils is presented in Fig. 3A–D. Their presence in the tooth sample is limited to the tooth area with damaged enamel and near to the surface area of dentine as shown in Fig. 2D–G. Cocci-like structures (Figs. 2G, 3A) are c.a. 0.6 μm in diameter. Bacilli-like objects (Figs. 2D, G, 3B–D) are elongated with dimensions of c.a. 0.6–0.7 μm in width and up to 2 μm in length, with typical 1:2.5 aspect ratio. Structures resembling shapes like: diplococci (Fig. 3A), coccobacilli or diplobacilli (Figs. 2F, 3C), pali-sades (Fig. 3B) can be seen, however this organization can be illusory, and related to taphonomy issues. All mentioned bacteria-like structures were found in a wide range of morphologies from to being semi-flat to almost round in cross section, which can be related to different bacteria or results from the preservation processes.

Energy Dispersive Spectroscopy.—Elemental distribution mapping was performed by the means of EDS (Fig. 4, SOM: fig. S2, S3). Elemental mapping revealed that the content of carbon is relatively higher in the cavity, which is most likely caused by contamination with the epoxy resin used for fixing the sample (Fig. 4B, SOM: fig. S3B). At the same time, a slight decrease in the content of phosphorus and calcium was observed in the cavity area (Fig. 4C, D, SOM: fig. S3C, D). Contrarily, the content of fluorine was practically identical in the damaged area and in the non-affected enamel tissue (SOM: fig. S2H). Between the tooth (the cavity area) and the epoxy resin we detected clear indications of the presence of magnesium, chlorine, sulfur, sodium, oxygen, silicon, and aluminum (SOM: fig. S2B–G). This is indicative of residual soil, inorganic salts or the polishing agent, or a combination thereof. These elements are generally present neither in the section through the enamel, nor in the main mass of the tooth. Therefore, the observed elemental distribution within the caries-affected area should be interpreted as a filling of semi-porous material, i.e., enamel depleted in P and Ca (in vivo), by C-rich modern epoxy. The phosphorus and calcium contents within the cavity are lower than in other parts of the tooth where hydroxyapatite, the building material of enamel, remained uninfected (Fig. 4, SOM: fig. S3).

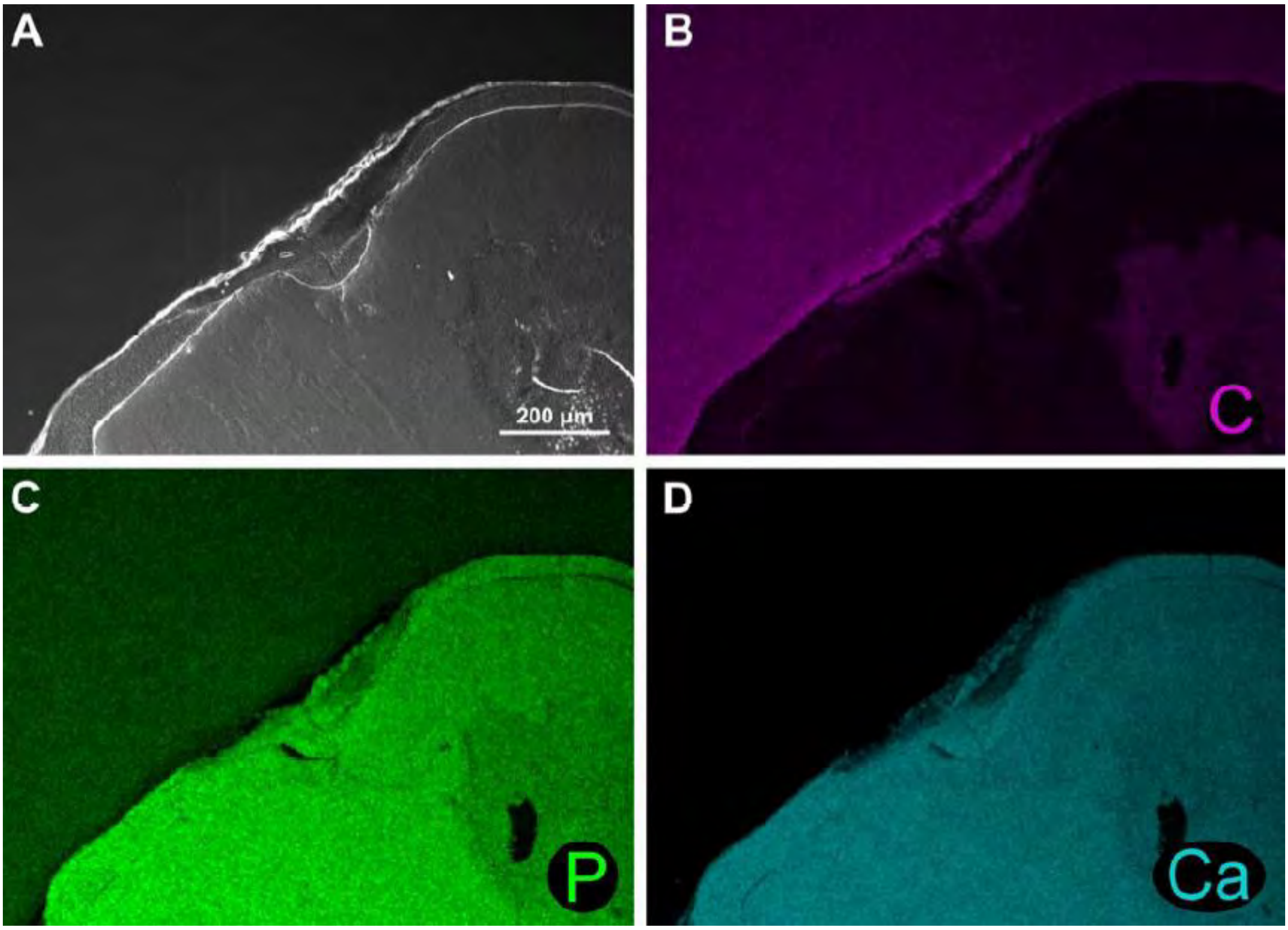

Fig. 4. Tooth of *Glis sackdillingensis* (Heller, 1930) (ZPAL M. VIII/b/G2/1) from Węże 2 (2.9–2.6 Mya), late Pliocene. SEM photograph (**A**) and EDS maps of distributions of carbon (**B**), phosphorus (**C**), and calcium (**D**) within the tooth and in the cavity area.

Microtomography.—Visualization of the 3D structure of the specimen was done using microtomography, which allowed to locate the caries within the tooth in respect to its morphological details (SOM: fig. S1). The caries-affected area was situated in one of the tooth's sinuses (Fig. 2A–D). Considering that, as well as the elongated shape of the lesion, we deduce that we found an early stage of enamel caries where no hollow structure had been created yet, but instead there was a straight, sharp breakage formed in vivo in the enamel tissue, surrounded by partially demineralized (and therefore porous) enamel that was colonized by pathogens. Although we chose to apply the term "cavity", generally accepted when dealing with caries-induced dental traumas, this structure is not a hollow or a gap, and should rather be imagined as demineralized porous material contrasting with the surrounding enamel. The changes in the dentin structure may be interpreted as tertiary dentin. Such tissue is formed by odontoblasts or odontoblast-like cells as a reaction against physical damage or development of caries (Goldberg et al. 2011).

Other samples.—Other dental specimens belonging to the dormouse assemblage of Węże 2 were studied using the same methodology and techniques to determine whether more cases of bacterial fossilization could be found. No other cases of caries with remains of fossilized bacteria were discovered.

Discussion

Caries are caused by cariogenic bacteria (most notably *Streptococcus mutans*) that metabolize carbohydrates and create acidic conditions in the mouth, which leads to enamel demineralization and favors their further growth at the expense of microorganisms neutral to oral health. The relatively recent global dispersal of *S. mutans* was apparently facilitated by evolutionary changes caused by positive selection of genes involved in acid tolerance and sugar metabolism. Such genetic transformations accompanied the spread of agriculture (and thus the worldwide shift towards carbohydrate-rich diets) which resulted in caries becoming almost ubiquitous in human populations (Burne 1998, Ajdić et al. 2002, Cornejo et al. 2013, Adler et al. 2017, Larsen et al. 2019). However, dental caries or, more broadly speaking, dental infections, are not confined to modern-day humans, but have been present also in many other toothed animals. Despite this fact, earlier evolutionary history of the parasitic relationship between cariogenic pathogens and their hosts remains unclear (Bowen 2013, Poinar 2014).

As a result of the analyses of bacteria-like objects found during the SEM examination of the internal structure in the described dental specimen, we suggest that they are in fact cariogenic bacteria due to their morphology, dimensions, and the context in which they were found (Watanabe et al. 2013, You et al. 2017, Ortega-Cuadros et al. 2018). Unfortunately, the methods commonly used to determine taxonomic identity of extant bacteria (such as comparative analysis of 16S rRNA sequences, DNA-DNA hybridization or chemotaxonomic methods) are obviously not available for such ancient fossil-ized bacterial specimens (Neefs et al. 1990, Raina et al. 2019). Therefore, when dealing with such material we are forced to rely only on the shape and size of bacterial structures.

Although we consider the case here described as themost compelling instance of a possible in situ preservation of a pathogen-host association in a fossil, some kind of contamination cannot be completely ruled out. While the bacteria are spatially associated with the caries-affected area, their incorporation into plaque would make a stronger case against in vivo or postmortem contamination (Bruce M. Rothschild, personal communication 2024). It is also worth noting that even though in our opinion *Streptococcus*like bacteria are clearly present in the affected area, at last two, if not three, distinctive bacterial morphotypes may be distinguished, which may suggest contamination of the wound by different organisms ("in vivo contamination") or post-portem contamination (Bruce M. Rothschild, personal communication 2024). However, such “in vivo contamination” of a mechanically injured tooth is one of several scenarios that we consider plausible (see below) and, in itself, it does not undermine our interpretation of the fossilized microbes as representing pathogenic flora that was causing enamel demineralization and defense reaction of the dentin. On the contrary, we still deem it to be perhaps the most parsimonious explanation for the spatial association between the observed non-mechanical damage to the enamel and dentin and the fossilized microbes. Although bacteria colonizing cracks in teeth are indeed supposed to create a biofilm structure, described instances of in vivo and in vitro contamination of damaged teeth demonstrate that such structure is not always present, with some samples showing only few microorganisms or small clusters of them (Michelich 1980, Kahler et al. 2000, Love and Jenkinson 2002, Ricucci et al. 2015). The supposed taxonomic diversity of the bacteria-like organisms present in the sample does not necessarily weaken our interpretation either as not only *S. mutan*s but also several other species of microorganisms are often found in caries-affected dentin and are supposed to induce caries as well as contribute to its progression. These include species of the genera *Lactobacillus*, *Propionibacterium*, *Bifidobacterium*, *Veillonella*, *Actinomyces*, *Atopobium* (Aas et al. 2008), *Candida* (Klinke et al. 2011), and *Scardovia* (Fakhruddin et al. 2019).

Although there seems to be no systematic research on the incidence of caries in extant dormice, one can suspect that they may be prone to dental infections owing to their low-cellulose diet with a relatively high sugar intake connected to the regular consumption of fruit. The low tolerance for dietary fiber exhibited by modern glirids is caused by their lack of a caecum, which is a seemingly unique feature among rodents. The loss of the caecum has been hypothesized to have occurred during the middle Miocene, as a consequence of increasing specialization. Another factor potentially contributing to the onset of caries in dormice is the presence of hard-shelled fruits in their diet, including beechnuts (*Fagus* spp.), acorns (*Quercus* spp.) and hazelnuts (*Corylus* spp.). (Daams and de Bruijn 1994; Freudenthal and Martín-Suárez 2013; Jurczyszyn 2018). This increases the chances of mechanical damage to the enamel (e.g., cracks and breaks) which would then make the colonization of the tooth by cariogenic pathogens easier. Moreover, the complicated enamel patterns of the occlusal surfaces of the teeth (Daoud 1993, Daams and de Bruijn 1994, Lu et al. 2021) may facilitate the accumulation of food material and the growth of bacterial biofilm. These patterns may represent an adaptation driven by consumption of hard-shelled fruits. Although the earliest known dormouse, *Eogliravus wildi* (known from the lower and middle Eocene of Europe), had a simpler occlusal morphology (Storch and Seiffert 2007), more complicated enamel patterns appeared already in late Eocene forms and resembled those discernible in modern dormice (Freudenthal 2004). The fact that dormice are hibernating animals (an ability that could have been acquired as early as in the early Oligocene) (Bieber and Ruf 2009, Lu et al. 2021) can also be of significance as, according to some studies, hibernation may have an adverse effect on dental and peridental tissues (Richardson et al. 1961, Mayer and Bernick 1963). It is however also worth noting that the average lifespan of the extant edible dormouse *Glis glis* may be as much as nine (or even 12) years in wild populations. This is remarkably long for a small rodent but still relatively short for a mammal and thus a high incidence of diseases which require a longer time to develop is not to be expected owing to this factor alone (Hoelzl et al. 2016, Lemaître et al. 2020).

As far as we know, the described tooth is to date the only recognized pre-Holocene specimen which possibly provides direct evidence of bacterial involvement in the formation of a pathological condition. Potentially pathogenic actinomycetous bacteria (which are present in soil and are normal part of oral microbiomes) (Könönen and Wade 2015, Gajdács and Urbán 2020) have been discovered fossilized within the dental tissue of the Eocene lagomorph *Megalagus brachyodon* from the United States (Fostowicz-Frelik and Frelik 2010), but unlike the case here reported, no mutual association between the bacteria and any tissue damage could be demonstrated. Similarly, the report on the Pleistocene australopithecine *Paranthropus boisei* (involving a microbe reminiscent of *Clostridium*) most probably describes a postmortem colonization (Furseth Klinge et al. 2009).

In the case of the described *Glis sackdillingensis* specimen ZPAL M. VIII/b/G2/1 the bacteria are spatially associated with damaged tissue (enamel and dentine) and are not found anywhere else in any of the studied samples. We consider it unlikely that the fossilized microflora represents a subsequent postmortem colonization of caries-affected tissue by bacteria but with the original pathogens having left no trace. Therefore, we tentatively deduce the specimen to be a unique example of an in situ fossil preservation of the actual pathogens that were causing damage to a tissue during the animal's life. The enamel had supposedly been physically/mechanically injured before the infection developed, facilitating the colonization by cariogenic bacteria which, in turn, worsened the condition. We assume this based on the shape of the cavity, which makes us suspect that the most plausible scenario of caries development in this case was that the tooth had been subjected to a mechanical trauma and that a resulting longitudinal crack in the enamel initiated the process of cariogenesis. According to a less probable scenario, initial damage to the enamel had been caused by the microbes themselves (that could be driven by especially cariogenic diet based on fruits).

Such fossil pathogen-host associations as the one documented here have not yet been reported in the literature. This can be explained by the fact that bacteria are rarely fossilized (however in some settings bacterial remains may undergo rapid biomineralization) or fossilize in far different conditions (Westall 1999, Ushatinskaya 2009). Another factor contributing to the lack of such reports and the relative scarcity of the described cases of caries in fossil assemblages is that teeth that have already been affected by caries, and thus are partially demineralized, may be more prone to degradation due to diagenetic processes after the deposition in the soil. Furthermore, it is possible that the same bacteria that were causing caries during the animal's life continue to feed on the affected tooth after the death ofthe animal, thereby reducing the chances of fossilization of such a specimen. In addition, fossilized carious changes may be inconspicuous, especially those present in the teeth of small animals.

Nevertheless, even if these changes are observed and subjected to an examination, the actual bacterial body fossils may be hard to detect or interpret. In laboratory conditions, the preparation of bacterial samples for SEM investigation consists of several steps, usually including fixing (e.g. with glutaraladehyde), staining and finally drying (dehydration of the bacteria). These procedures promote the maintenance of cell shapes and their three-dimensional organization within a bacterial biofilm and permit to achieve satisfactory material contrast. Obviously, these steps do not occur during natural preservation of bacterial specimens. Therefore, the observed bacteria may differ significantly from the samples prepared in laboratory conditions. We found that when investigating such naturally prepared bacterial samples it is a good strategy to ensure that the surface of the cross-section is coated with a conductive layer (e.g. carbon, platinum) as thinly as possible, or non-sputtered at all. This is because the thin bacterial remains can be flattened and therefore easily covered even with thin coating, becoming indistinguishable from their surroundings. Besides, the observed bacterial structures were found to have merely little to no material contrast vs. the surrounding material. Moreover, as such bacteria are thin and rather flat, the applied high tension of the SEM beam should be kept low so that the volume interaction of the incident electron beam is as little as possible. Perhaps the factors mentioned above may be the reason why such bacterial traces have often been overlooked and therefore not yet properly described in the literature.

Conclusions

The described dental specimen belonging to a fossil dormouse may document a case of bacterial infection that was developing in vivo in a rodent living around 2.9–2.6 Mya. Discovering fossil examples of bacterial microflora linked to specific pathological conditions may prove indispensable in deciphering the profound evolutionary origins of pathogen-host associations and provide the means to better comprehend the dynamics behind their formation. In turn, we can acquire a more in depth understanding of pathogens immediately relevant to human health and economy, and of the diseases caused by them. The described case of a plausible bacterial dental infection preserved in a fossil is also exceptional when considered in the wider context of the paleopathological record of hard-tissue infections in general, as we are also not aware of any examples of fossilized bacteria associated with signs of bone disease. Although it can very well be caused by objective reasons (both bacteria themselves and the affected tissues may not be sufficiently prone to fossilization), methodological issues, such as the difficulty of working with minute samples, may also play an important role.

Regardless to the provenance of the fossilized bacteria, the specimen here discussed is apparently the first case of fossil caries described in a rodent. Whether there is a correlation between the diet and lifestyle of the Plio-Pleistocene dormouse *Glis sackdillingensis* and the chances of dental pathologies occurring in this species remains an open question. It is conceivable that the low-fiber and carbohydrate-rich diet, the consumption of hard-shelled fruits, the ability to hibernate, as well as an extremely long lifespan (for an animal of this size) contributed to a relatively high risk of dental trauma and bacterial dental infections as exemplified by the specimen described in this paper.

Authors’ contributions

PB and MC are equal contributors to this work and designated as co-first authors.

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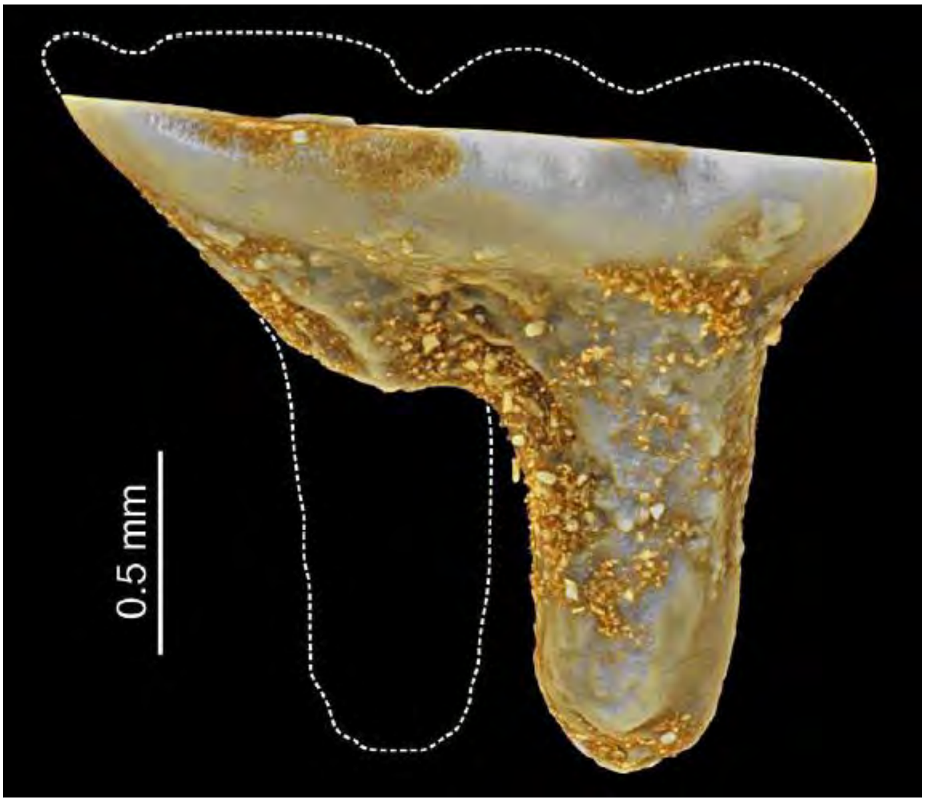
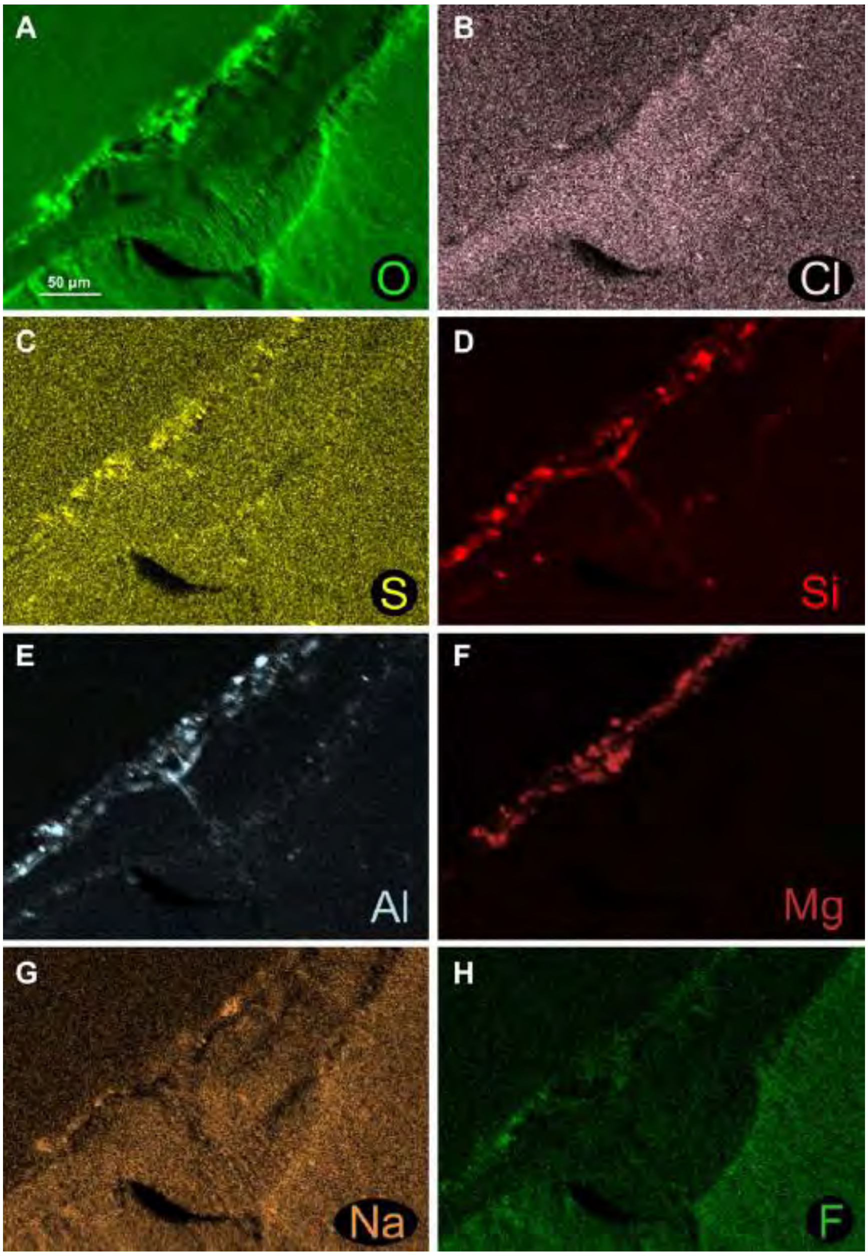
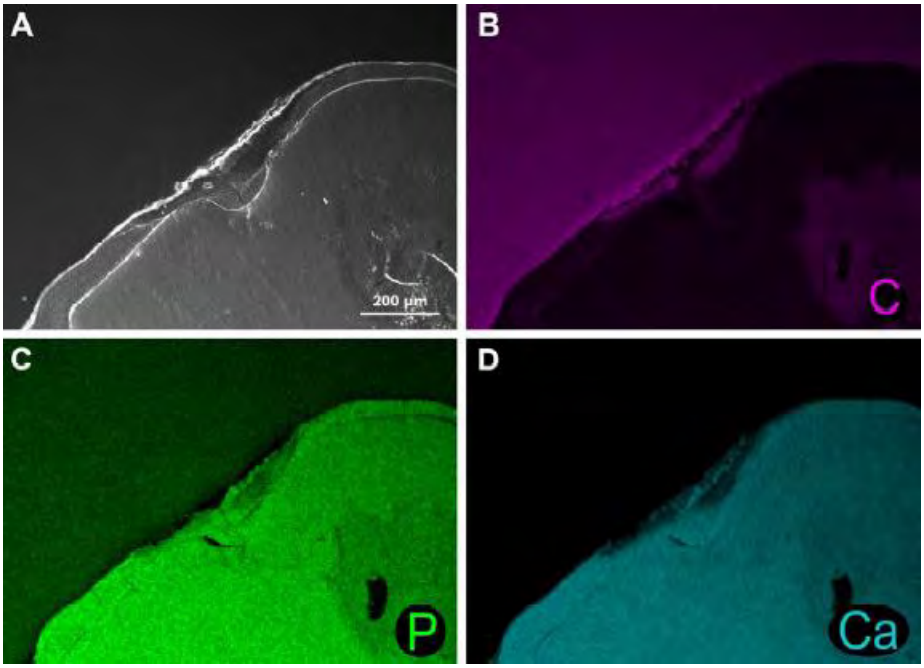
Supplementary Online Material



SOM: fig. S1. 3D-CT model of tooth with the cavity *Glis sackdillingensis* (Heller, 1930) (ZPAL M. VIII/b/G2/1) from Węże 2 (2.9-2.6 Mya), late Pliocene. Shapes of missing parts of the tooth, namely root and part of crown, are sketched in white dashed line.



SOM: fig. S2. Tooth of *Glis sackdillingensis* (Heller, 1930) (ZPAL M. VIII/b/G2/1) from Węże 2 (2.9-2.6 Mya), late Pliocene. EDS maps of distributions of oxygen (A), chlorine **(**B), sulphur (C), silica (D), alumina (E), magnesium (F), sodium (G), and fluorine (H). Location and distribution (i.e., on the boundary of tooth and resin) of Cl, S, Si, Al, Mg and Na suggest that those elements are soil residues. Presented data are complementary to results depicted in Fig. 3 in the main text.



SOM: fig. S3. Tooth of *Glis sackdillingensis* (Heller, 1930) (ZPAL M. VIII/b/G2/1) from Węże 2 (2.9-2.6 Mya), late Pliocene. SEM image (A) and EDS maps of distributions of carbon (B), phosphorus (C), and calcium (D) depicting change in composition of enamel in the cavity area.

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Chapter 7. Orzesznice (*Muscardinus* spp.) i popieliczka Glirulus pusillus z późnoplioceńskiego stanowiska Węże 2 (Wyżyna Wieluńska) / Dormice *Muscardinus* spp. and *Glirulus pusillus* from the late Pliocene site of Węże 2 (Wieluń Upland)[1]

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[1] Accepted manuscript: Czernielewski M. 202X. Orzesznice (*Muscardinus* spp.) i popieliczka *Glirulus pusillus* z późnoplioceńskiego stanowiska Węże 2 (Wyżyna Wieluńska). *Kosmos* XX: XXX–XXX, doi: 10.36921/kos.2024_2981

Abstrakt

Oprócz *Glis minor* i *G. sackdillingensis* (których szczątki zostały już opisane) trzy kolejne gatunki popielicowatych (Gliridae) zostały stwierdzone w materiale kopalnym ze stanowiska Węże 2 (2,9–2,6 mln lat temu, późny pliocen). Należą do nich *Muscardinus pliocaenicus*, *M. dacicus* oraz *Glirulus pusillus*. Fakt obecności na tym stanowisku *M. pliocaenicus* był już wstępnie poświadczany, niemniej pochodzący z Wężów 2 materiał należący do tego gatunku nie został wcześniej dokładnie opisany. Wystąpienia *M. dacicus* i *G. pusillus* w Wężach 2 najwyraźniej nie zostały do tej pory odnotowane. *M. pliocaenicus* jest uważany za bezpośredniego przodka współczesnej orzesznicy leszczynowej (*M. avellanarius*). Okazy przypisywane *M. dacicus* mogą reprezentować ten sam gatunek, co *M. avellanarius*, lub też siostrzaną dla *M. pliocaenicus – M. avellanarius* linię ewolucyjną.

Słowa kluczowe: gryzonie, popielice, stanowisko Węże, pliocen, paleontologia

Abstract

In addition to *Glis minor* and *G. sackdillingensis* (the remains of which have been already described), three more species belonging to the Gliridae family have been found in the fossil assemblage of the Węże 2 site (2.9–2.6 Ma, Late Pliocene). These include *Muscardinus pliocaenicus*, *M. dacicus* and *Glirulus pusillus*. The presence of *M. pliocaenicus* at the site has been already preliminary noted, although the material from Węże 2 belonging to this species has not yet been scrupulously described. It seems that the occurrences of *M. dacicus* and *G. pusillus* in Węże 2 have not yet been recorded. *M. pliocaenicus* is considered to be the direct ancestor of the extant hazel dormouse (*M. avellanarius*). Specimens assigned to *M. dacicus* may be conspecific with *M. avellanarius* or represent a sister taxon to the *M. pliocaenicus – M. avellanarius* evolutionary lineage.

Keywords: rodents, dormice, Węże site, Pliocene, paleontology

Wstęp

Należący do rodziny popielicowatych (Gliridae) rodzaj *Muscardinus* jest we współczesnej faunie reprezentowany przez jeden gatunek, *M. avellanarius*, czyli orzesznicę leszczynową (Wilson i Reeder 2005). Gryzoń ten zamieszkuje znaczną część Europy, z wyjątkiem m.in. Półwyspu Iberyjskiego, większości Fennoskandii, dużych obszarów południowo-wschodniej Ukrainy oraz większej części europejskiej Rosji. Stwierdzany jest ponadto w północnej Anatolii. Występuje głównie w środowiskach leśnych, niemniej może zasiedlać także krzewiaste zarośla (Hutterer i współaut. 2021). Ewolucyjne pochodzenie rodzaju *Muscardinus* jest niejasne. Daams i de Bruijn (1995) uważają, że wywodzi się z rodzaju *Glirudinus*, natomiast Freudenthal i Martínez-Suárez (2013), iż od *Microdyromys*.

Zaliczany do popielicowatych rodzaj *Glirulus* również obejmuje tylko jeden współczesny gatunek – *G. japonicus* (popieliczka japońska) (Wilson i Reeder 2005), endemiczny dla Wysp Japońskich. Podobnie jak *M. avellanarius*, gatunek ten związany jest ze środowiskami leśnymi (Cassola 2016). Zarówno Daams i de Bruijn (1995), jak i Freudenthal i Martínez-Suárez (2013) uważają *Glirulus* za potomka *Microdyromys*.

W niniejszej pracy opisuję pozyskany z późnoplioceńskiego stanowiska Węże 2 materiał kopalny należący do wymarłych przedstawicieli rodzajów *Muscardinus* i *Glirulus*, mianowicie *Muscardinus pliocaenicus*, *M. dacicus* oraz *Glirulus pusillus*. O ile fakt obecności *M. pliocaenicus* w faunie kopalnej tego stanowiska był już wstępnie poświadczony (Nadachowski 1989, Nadachowski i współaut. 2015), wydaje się, że występowanie *M. dacicus* i *Glirulus pusillus* w Wężach 2 nie zostało do tej pory odnotowane.

Wszystkie te trzy gatunki rozpoznawane są w materiale kopalnym na podstawie izolowanych zębów oraz fragmentów szczęk, co ze względu na szczególną wartość diagnostyczną i trwałość takich okazów jest normą dla gryzoni i innych drobnych ssaków. Taki też charakter ma materiał opisany w niniejszej pracy. Zbadane okazy znajdują się w zbiorach Instytutu Paleobiologii Polskiej Akademii Nauk.

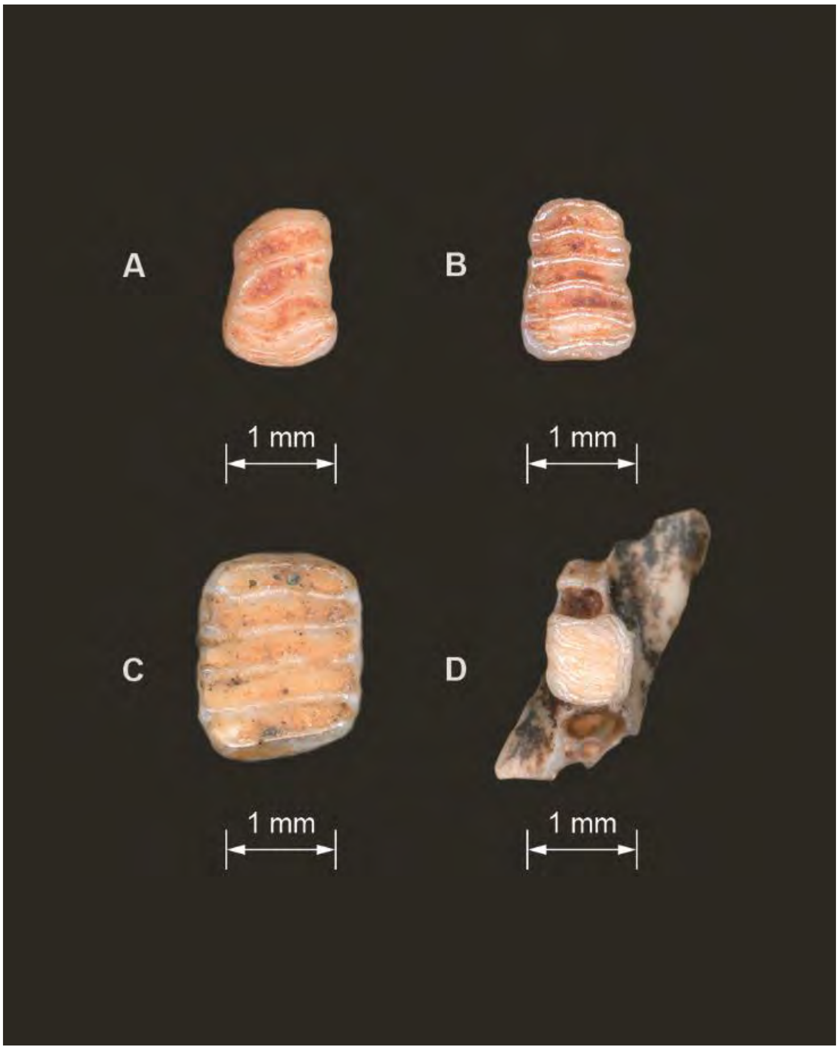
Ryc. 1. Położenie rezerwatu przyrody Węże na obszarze Polski

Lokalizacja stanowiska i wiek fauny

Stanowisko Węże 2 znajduje się na zboczu wapiennego ostańca zwanego górą Zelce (Wyżyna Wieluńska), niedaleko Działoszyna w województwie łódzkim, na obszarze rezerwatu przyrody Węże, który jest częścią Załęczańskiego Parku Krajobrazowego (Ryc. 1). Teren stanowiska obejmuje szczelinę krasową, pierwotnie wypełnioną kościonośnym sedymentem typu *terra rossa* (Sulimski 1962, Szynkiewicz 2015). Pozyskany z tego miejsca materiał kopalny datowany jest na 2,9–2,6 mln lat temu (późny pliocen) (Nadachowski i współaut. 2015, Stefaniak i współaut. 2020).

Węże 2 są lokalizacją typową dla polatuchy („latającej wiewiórki") *Pliopetaurista dehneli* (Sulimski 1964, Hordijk i de Bruijn 2009) oraz kretowatego *Rzebikia skoczeni* (Sansalone i współaut. 2016). Inne lepiej poznane gatunki ssaków poświadczonych w Wężach 2 to m.in. jeleniowate *Croizetoceros ramosus, Matacervocerus pardinensis, Procapreolus moldavicus* oraz *Arvenoceros* cf. *ardei* (Stefaniak 1995, Stefaniak i współaut. 2020), zajęczak *Hypolagus beremendensis* (Fostowicz-Frelik 2007) czy jeżozwierz *Hystrix refossa* (Czernielewski 2023). W materiale z Wężów 2 stwierdzono też prawdopodobnie jedyne znane do tej pory w Polsce wystąpienia bobrowatych z rodzaju *Dipoides* i gatunku *Trogontherium minus* (Czernielewski 2022). Również znaczna część szczątków popielicowatych z tego stanowiska została już opisana i zaliczona do dwóch gatunków – *Glis minor* oraz *G. sackdillingensis* – z których ten drugi jest uważany za bezpośredniego potomka pierwszego (Czernielewski 2021). Z kolei niewielkie gryzonie naziemne reprezentowane były m.in. przez różne gatunki chomikowatych, w tym bardzo licznie występujące karczowniki (Nadachowski i współaut. 2015). Ponadto odnotowano wystąpienia niezidentyfikowanego bliżej przedstawiciela nosorożcowatych oraz trąbowca przypuszczalnie należącego do rodzaju *Anancus* (Stefaniak i współaut. 2020). Stwierdzono także szczątki gadów, płazów (Młynarski i współaut. 1984, Młynarski i Szyndlar 1989), ptaków (Bocheński i współaut. 2012) oraz ryb (Nadachowski i współaut. 2015).

Fauna Wężów 2 jest opisywana jako mozaikowa, zawierająca zarówno elementy typowo plioceńskie, jak i formy właściwe dla wczesnego plejstocenu. Jest ona charakterystyczna dla środowiska w dużej mierze lesistego, położonego wokół stałego źródła słodkiej wody (Nadachowski i współaut. 2015, Stefaniak i współaut. 2020).



Ryc. 2. *Muscardinus* spp. i *Glirulus pusillus* ze stanowiska Węże 2. Przednia krawędź zęba zawsze u góry. A – *M. pliocaenicus*, lewy górny pierwszy trzonowiec (M1) (ZPAL M.VIII/b/G3/1). Powierzchnia wargowa zęba z prawej strony. B – *M. pliocaenicus*, prawy dolny pierwszy trzonowiec (m1) (ZPAL M.VIII/b/G3/4). Powierzchnia wargowa zęba z prawej strony. C – *M. dacicus*, prawy dolny drugi trzonowiec (m2) (ZPAL M.VIII/b/G4/1). Powierzchnia wargowa zęba z prawej strony. D – *G. pusillus*, fragment lewej żuchwy z pierwszym dolnym trzonowcem (m1) *in situ* (ZPAL M.VIII/b/G5/1). Powierzchnia wargowa zęba z lewej strony.

Paleontologia systematyczna

Rząd Rodentia Bowdich, 1821

Podrząd Sciuromorpha Brandt, 1855

Rodzina Gliridae Muirhead, 1819

Rodzaj *Muscardinus* Kaup, 1829

Muscardinus pliocaenicus Kowalski, 1963

Materiał

ZPAL M.VIII/b/G3/1–3 – izolowane górne pierwsze trzonowce (Ryc. 2A)

ZPAL M.VIII/b/G3/4–8 – izolowane dolne pierwsze trzonowce (Ryc. 2B)

Opis materiału

Górne pierwsze trzonowce (M1) odznaczają się charakterystycznym dla rodzaju *Muscardinus* wydłużonym, lekko „klepsydrowatym” kształtem powierzchni zgryzowej, z niewielkim przewężeniem w środkowej części korony. Na powierzchni zgryzowej widocznych jest pięć grzbiecików. Pierwszy i drugi są delikatnie łukowato wygięte w kierunku przednim, piąty w kierunku tylnym, a trzeci i czwarty mają kształt mniej lub bardziej esowaty (Ryc. 2A). Wymiary powierzchni zgryzowych to odpowiednio 1,46/1,00 mm (ZPAL M.VIII/b/G3/1), 1,45/1,00 mm (ZPAL M.VIII/b/G3/2) oraz 1,60/1,07 mm (ZPAL M.VIII/b/G3/3). ZPAL M.VIII/b/G3/1 ma cztery korzenie, dwa przednie i dwa tylne. U ZPAL M.VIII/b/G3/2 występuje dodatkowy, niewielki piąty korzeń, przylegający do jednego z normalnie rozwiniętych korzeni przednich. ZPAL M.VIII/b/G3/3 miał również cztery korzenie. Kształtem i morfologią powierzchni zgryzowej okazy te uderzająco przypominają materiał *M. pliocaenicus* z typowej dla tego gatunku lokalizacji Węże 1 (zob. Ryc. 4D w Kowalski 1963), a także z Podlesic (zob. Ryc. 3D w Kowalski 1963) i Rębielic Królewskich (zob. Ryc. 5A w Kowalski 1963). Również rozmiary zębów z Węży 2 są podobne do rozmiarów górnych pierwszych trzonowców *M. pliocaenicus* z wymienionych stanowisk (Kowalski 1963).

Dolne pierwsze trzonowce (m1) także odznaczają się delikatnie „klepsydrowatym" kształtem. Na powierzchni zgryzowej widocznych jest sześć z grubsza równolegle ułożonych grzbiecików, położonych w mniej więcej jednakowych odległościach. Pierwszych pięć jest lekko łukowato wygiętych w kierunku przednim (Ryc. 2B). Powierzchnie zgryzowe okazów mają wymiary odpowiednio 1,48/1,05 mm (ZPAL M.VIII/b/G3/4), 1,42/1,07 mm (ZPAL M.VIII/b/G3/5), 1,52/1,07 mm (ZPAL M.VIII/b/G3/6), 1,47/1,05 mm (ZPAL M.VIII/b/G3/7) oraz 1,52/1,05 mm (ZPAL M.VIII/b/G3/8). ZPAL M.VIII/b/G3/4–7 mają po trzy zwyczajnie rozwinięte korzenie – jeden przedni i dwa tylne. U ZPAL M.VIII/b/G3/8 przedni korzeń jest natomiast wyraźnie rozdwojony. Kształtem, wielkością oraz morfologią powierzchni zgryzowej okazy te odpowiadają materiałowi *Muscardinus pliocaenicus* z Wężów 1 (zob. Ryc. 4A w Kowalski 1963), Podlesic (zob. Ryc. 3A w Kowalski 1963) i Rębielic Królewskich (zob. Ryc. 5B w Kowalski 1963). Wielkością najbardziej zbliżone są do materiału z Rębielic Królewskich (Kowalski 1963).

Rząd Rodentia Bowdich, 1821

Podrząd Sciuromorpha Brandt, 1855

Rodzina Gliridae Muirhead, 1819

Rodzaj *Muscardinus* Kaup, 1829

Muscardinus dacicus Kormos, 1930

Materiał

ZPAL M.VIII/b/G4/1 – izolowany prawy dolny drugi trzonowiec (Ryc. 2C)

Opis materiału

Dolny drugi trzonowiec *Muscardinus* z Wężów 2 kształtem powierzchni zgryzowej przypomina prostokąt o zaokrąglonych kątach. Ma ona rozmiary 1,76/1,51 mm. Widocznych jest sześć grzbiecików, położonych w mniej więcej jednakowych odległościach od siebie (Ryc. 2C). Ząb miał cztery korzenie – dwa przednie i dwa tylne. Kształtem powierzchni zgryzowej i jej morfologią oraz rozmiarami okaz ten najbardziej przypomina opisany do tej pory materiał *M. dacicus* (Kowalski 1963, Daoud 1993). Podobny okaz pochodzący z Podlesic zilustrował Kowalski (zob. Ryc. 6A w Kowalski 1963). Okaz z Wężów 2 różni się od m2 typowych dla *M. avellanarius* innym kształtem grzbiecików (u *M. avellanarius* są one łukowato wygięte w kierunku przednim) oraz wyraźnie większymi rozmiarami (Daoud 1993, Wahlert i współaut. 1993).

Rząd Rodentia Bowdich, 1821

Podrząd Sciuromorpha Brandt, 1855

Rodzina Gliridae Muirhead, 1819

Rodzaj *Glirulus* Thomas, 1906

Glirulus pusillus (Heller, 1936)

Materiał

ZPAL M.VIII/b/G5/1 – fragment lewej żuchwy z pierwszym trzonowcem zachowanym *in situ* (Ryc. 2D).

Opis materiału

Charakterystyczny kształt powierzchni zgryzowej tkwiącego we fragmencie żuchwy m1 jest typowy dla rodzaju *Glirulus* (Kowalski 1963, Daoud 1993, Wahlert i współaut. 1993). Po stronie językowej zęba znajduje się dobrze rozwinięty grzbiecik, endolofid, stanowiący najwyraźniej odznaczającą się strukturę na powierzchni zgryzowej (Ryc. 2D). Pozostałe grzbieciki są dużo słabiej zaznaczone, niemniej da się wyróżnić pięć głównych grzbiecików występujących na dolnych przedtrzonowcach i trzonowcach u rodzajów *Glis* i *Glirulus*. Są to: pierwszy (anterolofid) i ostatni (posterolofid), pomiędzy nimi stosunkowo jeszcze wyraźne metalofid i mezolofid (najlepiej widoczne przy stronie językowej zęba), a także szczątkowy centrolofid pomiędzy metalofidem i mezolofidem (cf. Czernielewski 2021). Kształtem i morfologią powierzchni zgryzowej okaz z Wężów 2 odpowiada m1 *Glirulus pusillus*, przy czym wymiary powierzchni zgryzowej, 0,85/0,81 mm, są bardzo podobne do okazu z Podlesic (Kowalski 1963).

Dyskusja

Gatunek *Muscardinus pliocaenicus* (orzesznica plioceńska) opisany został przez Kowalskiego (1963) na podstawie niekompletnej żuchwy z dwoma dolnymi trzonowcami (m1 i m2) zachowanymi *in situ*. Okaz ten pochodził z datowanego na 4–3,3 mln lat temu poziomu z Wężów 1, innego znanego plioceńskiego stanowiska położonego na górze Zelce (Stefaniak i współaut. 2020). *M. pliocaenicus* różni się od *M. avellanarius* mniejszymi rozmiarami zębów oraz nieco innym kształtem m1 (który u *M. avellanarius* bardziej zwęża się ku przodowi) i m2 (który u *M. avellanarius* zwęża się wyraźniej ku tyłowi) (Kowalski 1963). Występowanie *M. pliocaenicus* stwierdzono na co najmniej około dwudziestu plioceńskich i wczesnoplejstoceńskich stanowiskach położonych w Polsce, Niemczech, Austrii, Francji, Holandii, na Węgrzech i we Włoszech (Kowalski 1963 i 2001, Daoud 1993, van den Hoek Ostende 2003, Garcia-Ibaibarriaga i współaut. 2015). Gatunek ten uważany jest za bezpośredniego przodka *M. avellanarius* (Daoud 1993, van den Hoek Ostende 2003).

M. dacicus (orzesznica dacka) opisany został przez Kormosa (1930) na podstawie późnoplioceńskiego materiału ze stanowiska Betfia 2 w Rumunii (Kormos 1930, Kowalski 2001). Gatunek ten stwierdzony został również na kilku innych plioceńskich i wczesnoplejstoceńskich stanowiskach położonych w Polsce, Austrii, Rumunii i na Węgrzech (Daoud 1993, Kowalski 2001, Garcia-Ibaibarriaga i współaut. 2015), m.in. Kowalski (zob. Ryc.

6A w Kowalski 1963) zilustrował i opisał ząb *M.* aff. *dacicus* z Podlesic, który Daoud (1993) przypisał *M. dacicus*. Kowalski (2001) następnie uznał jednak *M. dacicus* za synonim *M. avellanarius*. Obecność zarówno *M. pliocaenicus*, jak i *M. avellanarius* w Wężach 2 byłaby kolejnym (po *Glis minor* i *G. sackdillingensis*) przypadkiem współwystępowania na tym stanowisku dwóch gatunków popielicowatych, z których jeden jest uważany za bezpośredniego potomka drugiego (Czernielewski 2021).

Niemniej, uznanie całego materiału przypisywanego *M. dacicus* za reprezentujący *M. avellanarius* wydaje się nie do końca uzasadnione, biorąc pod uwagę różnice w morfologii powierzchni zgryzowych i liczbie korzeni zębów (stwierdzono występowanie sześciu korzeni u M1 *M. dacicus*), a także wyraźnie większe rozmiary okazów zaliczanych do *M. dacicus* (Daoud 1993, Wahlert i współaut. 1993). Daoud (1993) uważa *M. dacicus* za takson siostrzany względem linii ewolucyjnej *M. pliocaenicus – M. avellanarius*. Współwystępowanie *M. pliocaenicus* i *M. dacicus* stwierdzono także w Podlesicach i Pańskiej Górze, wczesnoplioceńskich stanowiskach datowanych na 4,9–4,2 mln lat temu (Daoud 1993). *M. avellanarius* sensu stricto pojawia się w zapisie kopalnym dopiero we wczesnym plejstocenie (Daoud 1993, Kowalski 2001, Garcia-Ibaibarriaga i współaut. 2015).

Plioplejstoceński (5,333 mln lat temu – ok. 11 700 lat temu) materiał kopalny należący do *Glirulus* a pochodzący z Europy jest rutynowo przypisywany do gatunku *G. pusillus* (popieliczka malutka). Wystąpienia *G. pusillus* odnotowano w Niemczech, Polsce, Austrii, Holandii, Francji, Rumunii, we Włoszech, na Ukrainie i na Węgrzech. Regułą jest, iż szczątki należące do tego gatunku pozyskiwane są na poszczególnych stanowiskach w bardzo skromnych ilościach (Kowalski 1963 i 2001, Daoud 1993, van den Hoek Ostende 2003).

Wnioski

Oprócz *Glis minor* i *G. sackdillingensis* w kopalnej faunie z Wężów 2 (późny pliocen) pojawiają się także trzy kolejne gatunki popielicowatych (Gliridae). Do tej grupy należą: *Muscardinus pliocaenicus*, *M. dacicus* oraz *Glirulus pusillus*. Występowanie tylu gatunków gryzoni o prawdopodobnie nadrzewnym trybie życia jest zgodne z interpretacją fauny Wężów 2 jako reprezentującą środowisko zalesione. *M. dacicus* i *G. pusillus* są dość rzadkie w zapisie kopalnym, co zwiększa wagę materiału pozyskanego w Wężach 2. Prawdopodobnie *M. pliocaenicus* jest bezpośrednim przodkiem współczesnego gatunku *M. avellanarius*, podczas gdy *M. dacicus* stanowi takson siostrzany dla linii ewolucyjnej *M. pliocaenicus – M. avellanarius*. Zgodnie z alternatywną interpretacją, materiał kopalny przypisywany *M. dacicus* należy już w istocie do *M. avellanarius*.

Podziękowania

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Chapter 8. *Baranomys longidens* Kowalski, 1960 (Cricetidae: Baranomyinae) z późnoplioceńskiego stanowiska Węże 2 (Wyżyna Wieluńska) / *Baranomys longidens* Kowalski, 1960 (Cricetidae: Baranomyinae) from the Late Pliocene locality of Węże 2 (Wieluń Upland)[1]

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Abstrakt

Na stanowisku Węże 2 (2,9–2,6 mln lat temu) znaleziono fragment szczęk i izolowane zęby gryzonia *Baranomys*, należącego do chomikowatych (Cricetidae). Badania morfometryczne potwierdzają, że materiał z Wężów 2 reprezentuje ten sam gatunek, co materiał *Baranomys* z pobliskiego stanowiska Węże 1 (3,6–3,2 mln lat temu), które jest *locus typicus* gatunku *Baranomys longidens*. Ponieważ uważa się, że fauna kopalna Wężów 2 w biostratygrafii osadów lądowych neogenu odpowiada zonie MN 16, obecność *Baranomys longidens* na tym stanowisku stoi w sprzeczności z pojawiającą się w literaturze tezą, iż gatunek ten jest ograniczony stratygraficznie do zony MN 15 (4,2–3,2 mln lat temu). Kwestią otwartą pozostaje, czy *Baranomys longidens* nie jest młodszym synonimem *Baranomys loczyi* Kormos, 1933 oraz czy sama nazwa *Baranomys* Kormos, 1933 nie jest młodszym synonimem nazwy rodzajowej *Microtodon* Miller 1928.

Słowa kluczowe: gryzonie, chomikowate, Węże 2, pliocen, paleontologia

Abstract

At the Węże 2 site (2.9–2.6 million years ago) fragments of jaws and isolated teeth of the rodent *Baranomys*, a member of the Cricetidae family, were found. Morphometric studies confirm that the material from Węże 2 represents the same species as the *Baranomys* material from the nearby Węże 1 site (3.6–3.2 million years ago), which is the locus typicus of the species *Baranomys longidens*. Since the fossil fauna of Węże 2 in the biostratigraphy of Neogene terrestrial sediments is believed to correspond to the MN 16 zone, the presence of *Baranomys longidens* at this site contradicts the notion, which appears in the literature, that this species is stratigraphically limited to the MN 15 zone (4,2–3.2 million years ago). It remains an open question whether *Baranomys longidens* is not a junior synonym of *Baranomys loczyi* Kormos, 1933 and whether the name *Baranomys* Kormos, 1933 itself is not a junior synonym of the genus name *Microtodon* Miller, 1928.

Key words: rodents, hamster-like rodents, Węże 2, Pliocene, paleontology

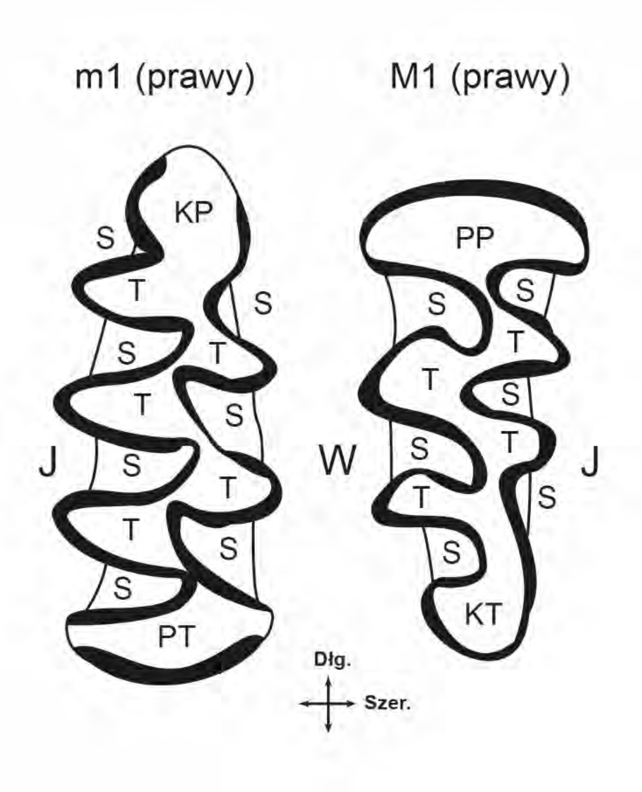
Wstęp

Chomikowate, Cricetidae Fischer, 1817, są liczącą około 600 gatunków rodziną gryzoni, Rodentia Bowdich, 1821, w obrębie kladu myszowych, Muroidea Illiger, 1811. Współczesnych przedstawicieli chomikowatych podzielić można na chomiki, Cricetinae Fischer, 1817; karczowniki, Arvicolinae Gray, 1821; nowiki, Neotominae Merriam, 1894; bawełniaki, Sigmodontinae Wagner, 1843 oraz gałęziaki, Tylomyinae Reig, 1984 (Jansa i Weksler 2004, Musser i Carleton 2005). Chomikowate występują w Eurazji (gdzie odkryto ich najstarsze szczątki) oraz Ameryce Północnej, a ich historia ewolucyjna sięga przynajmniej wczesnego oligocenu (33,9–27,82 mln lat temu) (Freudenthal 1996, Gomes Rodrigues i współaut. 2012, Li i współaut. 2016). Uważa się, że – reprezentujący wymarłą podrodzinę Baranomyinae Kretzoi, 1955 – rodzaj *Baranomys* Kormos, 1933 jest relatywnie blisko spokrewniony z bezpośrednim przodkiem karczowników (Repenning 1968, Fejfar i Repenning 1998, Fejfar i współaut. 2011).

Celem niniejszej pracy jest opis szczątków *Baranomys longidens* ze stanowiska Węże 2 (późny pliocen) na Wyżynie Wieluńskiej. *B. longidens* (Kowalski, 1960) został opisany jako *Microtodon longidens* na podstawie materiału z pobliskiego stanowiska Węże 1, który datowany jest na 3,6–3,2 mln lat temu (MN 15b) (Stefaniak i współaut. 2020). Następnie Sulimski (1964) przypisał ten gatunek do rodzaju *Baranomys*. Kowalski (1960) zdefiniował *B. longidens* jako gatunek posiadający trzonowce (zwłaszcza trzecie) bardziej wydłużone niż u pokrewnego *B. loczyi* (którą to formę w tamtym momencie Kowalski również uważał za przedstawiciela rodzaju *Microtodon* Miller, 1928). Warto przy tym zwrócić uwagę, iż w badaniach porównawczych Kowalski (1960) opierał się nie tylko na nieopublikowanym materiale *B. loczyi* z Węgier, ale także na badanym przez siebie materiale *Baranomys* z Podlesic (Kowalski 1956), który następnie Kretzoi (1962) przypisał do innego gatunku (*B. kowalskii*).

Obecność *B. longidens* w materiale z Wężów 2 była już uprzednio wzmiankowana (Nadachowski i współaut. 2015), niemniej materiał ten nie został do tej pory dokładniej opisany ani poddany badaniom morfometrycznym. Gatunek był natomiast interpretowany jako ograniczony do biozony MN 15 (4,2–3,2 mln lat temu) w biostratygrafii lądowych osadów neogenu (Fejfar i współaut. 2011, Hellmund i Ziegler 2012). Ponieważ stanowisko Węże 2 jest obecnie datowane na zonę MN 16b (2,9–2,6 mln lat temu) (Nadachowski i współaut. 2015, Stefaniak i współaut. 2020, Marciszak i współaut. 2023), odkrycie na nim szczątków *B. longidens* podważałoby taką interpretację.

Na potrzeby niniejszego opracowania okazy z Wężów 2 zostały poddane oględzinom, zmierzone i sfotografowane za pomocą Keyence VHX 900-F Digital Microscope System w Instytucie Paleobiologii Polskiej Akademii Nauk w Warszawie. Korony zębów *Baranomy*s są zbudowane zasadniczo tak jak korony zębów karczowników i zostały tutaj opisane za pomocą tych samych pojęć (Ryc. 1).



Ryc. 1. Nomenklatura używana do opisu morfologii powierzchni zgryzowych zębów karczowników (za: Piñero i współaut. 2015).

M1 – górny pierwszy trzonowiec,

m1 – dolny pierwszy trzonowiec,

J – strona językowa,

W – strona wargowa,

KP – kompleks przedni,

PT – pętla tylna,

PP – pętla przednia,

KT – kompleks tylny,

T – trójkąt,

S – synklina,

Dłg. – długość,

Szer. – szerokość.

Lokalizacja stanowiska i wiek fauny

Stanowisko Węże 2 znajduje się na Wyżynie Wieluńskiej, niedaleko miasta Działoszyn (powiat pajęczański), na zboczu wzgórza Zelce. Jest to szczelina krasowa długości 10 m, szerokości 4 m oraz głębokości ok. 3–5 m, pierwotnie wypełniona sedymentem typu *terra rossa*. Pozyskany z tego miejsca zespół kopalny jest datowany na biozonę MN 16b (2,9–2,6 mln lat temu, późny pliocen) (Sulimski 1962, Nadachowski i współaut. 2015, Szynkiewicz 2015, Stefaniak i współaut. 2020, Marciszak i współaut. 2023).

Spośród fauny ssaków z Wężów 2 lepiej opisane zostały szczątki wiewiórkowatych *Pliopetaurista dehneli* (Sulimski, 1964) (Sulimski 1964, Hordijk i de Bruijn 2009), *Sciurus warthae* Sulimski, 1964, *Tamias orlovi* (Sulimski, 1964) (Sulimski 1964, Black i Kowalski 1974) i *Blackia miocaenica* Mein 1970 (Czernielewski 2023); kretowatych *Condylura kowalskii* Skoczeń, 1976 i *Rzebikia skoczeni* (Zijlstra, 2010) (Skoczeń 1993, Zijlstra 2010, Sansalone i współaut. 2016); jeleniowatych *Croizetoceros ramosus* Croizet i Jobert, 1828, *Metacervocerus pardinensis* Croizet i Jobert, 1828, *Procapreolus moldavicus* (Janovskaya, 1954) oraz *Arvenoceros* cf. *ardei* (Croizet i Jobert, 1828) (Stefaniak 1995, Stefaniak i współaut. 2020); popielic *Glis minor* Kowalski, 1956 i *Glis sackdillingensis* Heller, 1930 (Czernielewski 2021) oraz bobrów *Trogontherium minus* Newton, 1890 i *Dipoides* ex gr. *problematicus-sigmodus* (Czernielewski 2022). Obecność wielu gatunków (m.in. różnych przedstawicieli chomikowatych) była odnotowywana na listach faunistycznych (Sulimski 1962, Nadachowski 1989, Nadachowski i współaut. 2015), jednak ich szczątki nie były dokładniej opisywane i ilustrowane ani też nie zostały poddane badaniom morfometrycznym.

Paleontologia systematyczna

Rząd Rodentia Bowdich, 1821

Nadrodzina Muroidea Illiger, 1811

Rodzina Cricetidae Fischer, 1817

Podrodzina Baranomyinae Kretzoi, 1955

Rodzaj *Baranomys* Kormos, 1933

Baranomys longidens (Kowalski, 1960)

Materiał

ZPAL M. VIII/b/C1/1 – niekompletna żuchwa z m1–m2 *in situ* (Ryc. 2)

ZPAL M. VIII/b/C1/2–3 – niekompletne żuchwy z m1 *in situ*

ZPAL M. VIII/b/C1/4 – 251 izolowanych m1

ZPAL M. VIII/b/C1/5 – 52 izolowane m2

ZPAL M. VIII/b/C1/6 – 16 izolowanych m3 (Ryc 3A)

ZPAL M. VIII/b/C1/7 – 194 izolowane M1 (Ryc 3B)

ZPAL M. VIII/b/C1/8 – 28 izolowanych M2 (Ryc 3C)

ZPAL M. VIII/b/C1/9 – 14 izolowanych M3 (Ryc 3D)

ZPAL M. VIII/b/C1/10–12 – niekompletne żuchwy z m1–m2 *in situ*

ZPAL M. VIII/b/C1/13 – fragment żuchwy z m1–m2 *in situ*

ZPAL M. VIII/b/C1/14–19 niekompletne żuchwy z m1 *in situ*

ZPAL M. VIII/b/C1/20 – fragment żuchwy z m1 *in situ*

ZPAL M. VIII/b/C1/21 – niekompletna żuchwa z m2 *in situ*

Opis materiału

Trzonowce *B. longidens* ze względu na relatywnie średnią wysokość korony mogą być opisane jako „mezodontyczne”. Środkowe części koron zbudowane są z naprzemiennie ułożonych trójkątów zębinowych, które stanowią cechę występującą u karczowników (Arvicolinae) (Ryc. 1). Powstałe w ten sposób na powierzchni policzkowej i wargowej zębów synkliny (wcięcia) u *B. longidens* nie zawierają kostniwa (cementu) (Fejfar i współaut. 2011). Morfologia powierzchni zgryzowych okazów z Wężów 2 bardzo przypomina materiał *B. longidens* z Wężów 1 (zob. Ryc. 1 w Kowalski 1960, Tabl. VIII w Sulimski 1964), w tym holotyp tego gatunku (zob. Ryc. 1A w Kowalski 1960). Jest także morfologicznie zbliżony do sklasyfikowanego jako *B. longidens* materiału ze stanowisk Osztramos 7 (zob. Ryc. 5 w Fejfar i współaut. 2011) i Wölfersheim (zob. Ryc. 6 w Fejfar i Repenning 1998).

m1 (Ryc. 2B) – ząb ma wydłużony kształt i zwęża się ku przodowi. Powierzchnia zgryzowa może być podzielona na „kompleks przedni”, trzy trójkąty oraz „pętlę tylną” (Sulimski 1964, Piñero i współaut. 2015). Na stronie językowej zęba znajdują się dwa trójkąty i trzy synkliny, na stronie wargowej natomiast jeden trójkąt i dwie synkliny. Kompleks przedni ma „kształt hełmu” (Fejfar i współaut. 2011), a jego relatywne rozmiary oraz głębokość przedniowargowej synkliny różnią się w zależności od okazu. Wysepka szkliwa, niekiedy obecna na kompleksie przednim u *B. longidens* z innych stanowisk (Sulimski 1964, Fejfar i współaut. 2011), jest bardzo rzadko widoczna u okazów z Wężów 2. Ząb ten ma dwa korzenie.

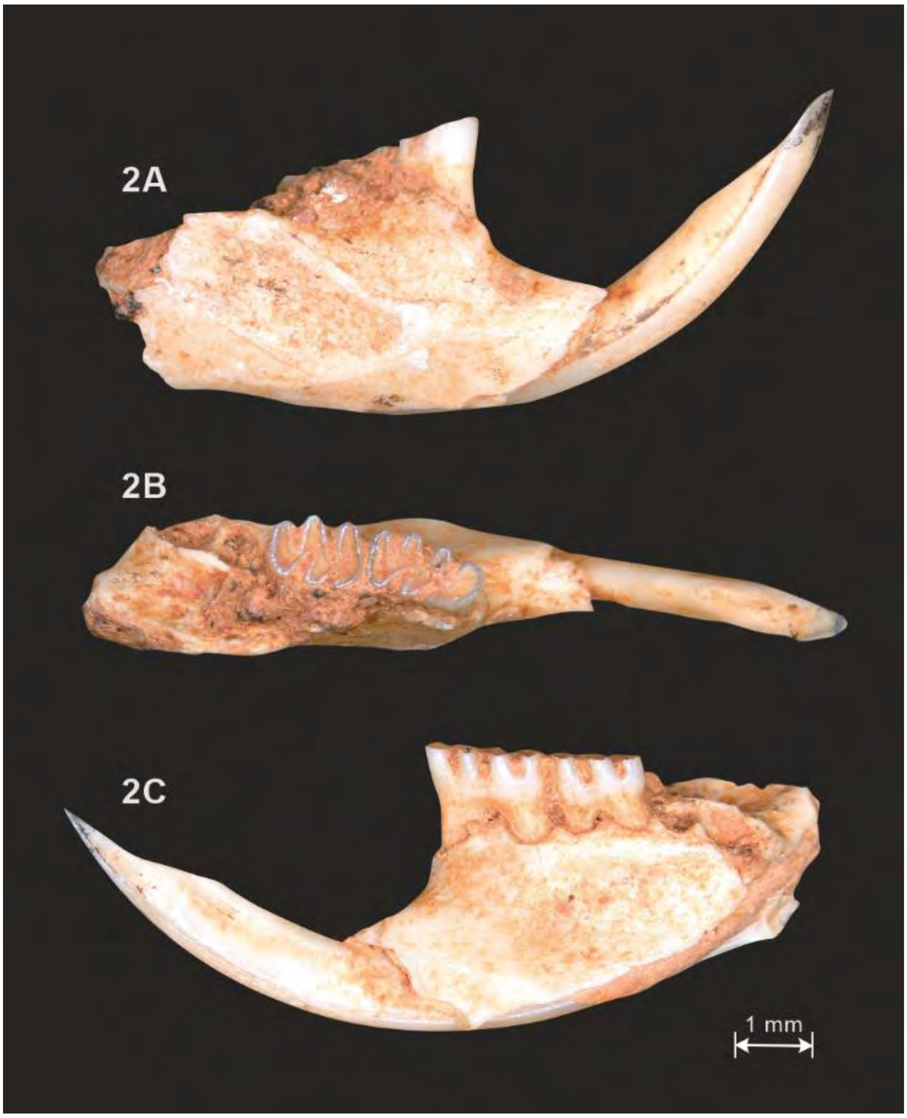
m2 (Ryc, 2B) – korona ma kształt zbliżony do owalnego. Kompleks przedni i pętla tylna są dobrze rozwinięte. Jedynie dwa trójkąty są widoczne, jeden na stronie językowej i jeden na wargowej. Zarówno na stronie językowej, jak i wargowej są widoczne dwie synkliny. Ząb ten ma również dwa korzenie.

m3 (Ryc. 3A) – morfologia powierzchni zgryzowej jest prawie taka sama jak u m2, jednak m3 wyraźniej zwęża się w kierunku tylnym, co nadaje zębowi kształt bardziej zbliżony do trójkąta. Okazy z Wężów 2 morfologią powierzchni zgryzowej przypominają materiał *B. longidens* z Wężów 1 (zob. Ryc. 1 w Kowalski 1960, Tabl. VIII: Ryc. 1 w Sulimski 1964), w tym ząb należący do holotypu (zob. Ryc. 1A w Kowalski 1960), jak również przypisywane temu gatunkowi okazy m3 ze stanowisk Osztramos 7 (zob. Ryc. 5: 21 w Fejfar i współaut. 2011) i Wölfersheim (zob. Ryc. 6: 14 w Fejfar i Repenning 1998). Różnią się natomiast od okazów *Baranomys* z Podlesic (zob. Ryc. 2: I, J, N w Kowalski 1956), które mają uproszczoną budowę (brak pętli tylnej). Występują dwa korzenie.

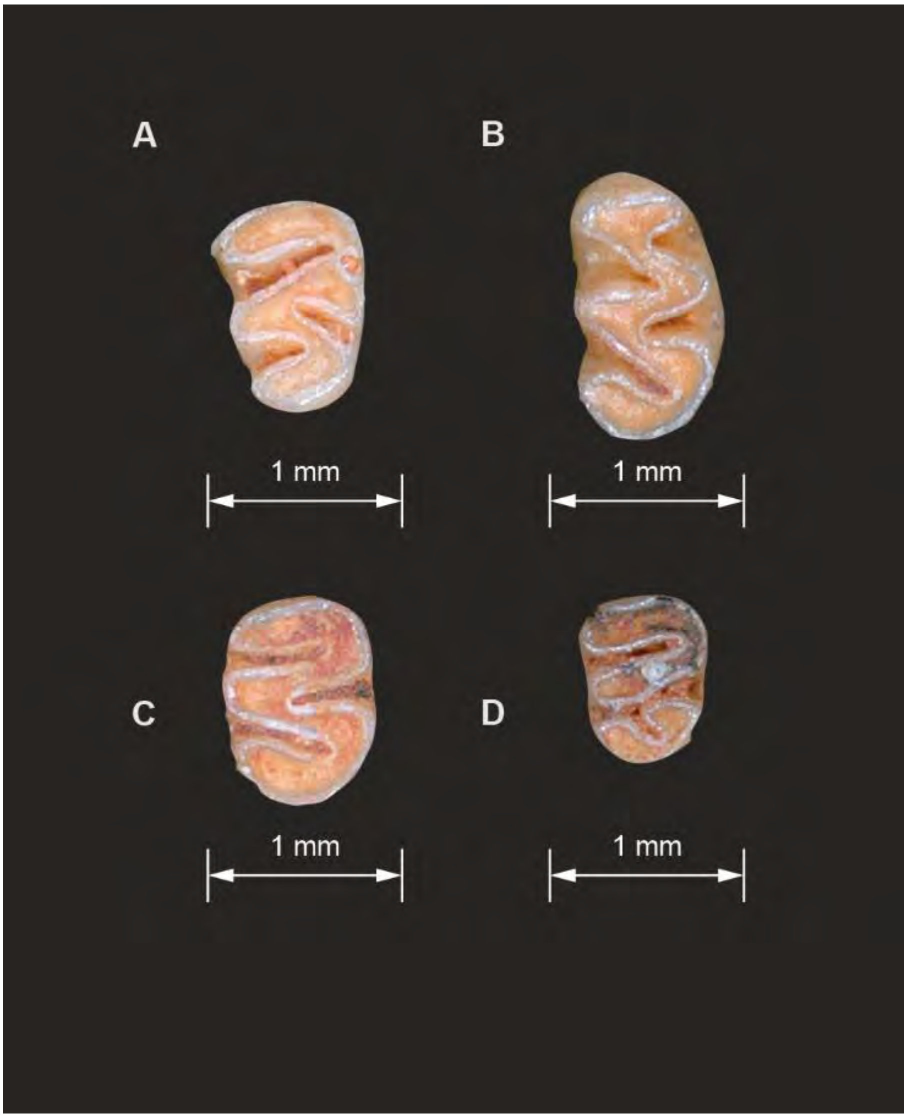
M1 (Ryc. 3B) – korona ma kształt zbliżony do owalnego, lecz nieco zwężający się ku tyłowi. Powierzchnię zgryzową można podzielić na „pętlę przednią”, trzy trójkąty oraz „kompleks tylny” (Sulimski 1964, Piñero i współaut. 2015). Na stronie językowej zęba znajdują się dwa trójkąty i dwie synkliny, a na stronie wargowej jeden trójkąt i dwie synkliny. Występują trzy korzenie – przedni i tylny, a także dodatkowy, mniejszy trzeci korzeń, położony bądź wyraźnie bliżej korzenia tylnego, bądź też bardziej centralnie pomiędzy dwoma głównymi korzeniami.

M2 (Ryc. 3C) – korona ma kształt z grubsza owalny, zwężający się lekko ku tyłowi. Wyróżnić można dwa trójkąty, jeden na stronie językowej i jeden na wargowej. Na stronie językowej jest widoczna jedna synklina, a na stronie wargowej dwie. Z reguły ząb ten ma trzy korzenie, jednak niekiedy trzeci korzeń jest słabo rozwinięty lub w ogóle nieobecny.

M3 (Ryc. 3D) – korona zwęża się ku tyłowi i ma kształt zbliżony do trójkąta o zaokrąglonych kątach. Morfologią powierzchni zgryzowej ząb ten przypomina M2, jednak wierzchołek trójkąta po stronie wargowej jest skierowany ku tyłowi, a nie ku przodowi jak w przypadku M2.



Ryc. 2. Niekompletna prawa żuchwa *Baranomys longidens* z Wężów 2 z m1–m2 *in situ* (ZPAL M. VIII/b/C1/1). A – widok od strony wargowej. B – widok od strony powierzchni zgryzowych. C – widok od strony językowej.



Ryc. 3. Izolowane zęby *Baranomys longidens* z Wężów 2. A – prawy m3 (ZPAL M. VIII/b/C1/6a). B – prawy M1 (ZPAL M. VIII/b/C1/7a). C – prawy M2 (ZPAL M. VIII/b/C1/8a). D – prawy M3 (ZPAL M. VIII/b/C1/9a).

Rodzaj zęba	N	Długość (mm): min.	Długość (mm): średnia	Długość (mm): maks.	Szerokość (mm): min.	Szerokość (mm): średnia	Szerokość (mm): maks.
m1	265	1,37	1,58	1,79	0,77	0,87	0,97
m2	58	1,07	1,24	1,38	0,84	0,94	1,07
m3	16	1,05	1,17	1,35	0,76	0,82	0,89
M1	194	1,36	1,51	1,70	0,81	0,94	1,06
M2	28	1,05	1,21	1,35	0,82	0,91	0,97
M3	14	0,98	1,07	1,15	0,72	0,80	0,88

Tabela 1. Pomiary zębów *Baranomys longidens* z Wężów 2, z uwzględnieniem izolowanych okazów oraz zębów zachowanych *in situ* w żuchwach

Dyskusja

Rodzaj *Baranomys* wydzielił Kormos (1933), który na podstawie materiału z późnoplioceńskiego stanowiska Csarnóta na Węgrzech opisał gatunek *B. loczyi*. Pojedynczy ząb (m1) Baranomys z Jaskini Południowej (Sudety), określony jako holotyp *Baranomys langenhani* Heller, 1937, prawdopodobnie również należy do *B. loczyi.* Kowalski (1956), który badał szczątki *Baranomys* z Podlesic (MN 14), zaliczone przez siebie do *B. loczyi*, uznał, że ząb z Jaskini Południowej reprezentuje ten sam gatunek. Jakkolwiek Kretzoi (1962) na podstawie materiału z Podlesic ustanowił gatunek *B. kowalskii*, Bieroński i współaut. (2007) opisują wspomniany okaz jako reprezentujący „prawdopodobnie *B. loczyi*". W kolejnych opracowaniach dotyczących fauny z Jaskini Południowej (Marciszak i współaut. 2016, Marciszak 2020) okaz ten jest w dalszym ciągu przypisywany *B. loczyi*.

B. kowalskii został z kolei stwierdzony na datowanym na MN 15 stanowisku Wölfersheim w Niemczech, gdzie miał prawdopodobnie koegzystować z *B. longidens*, oraz na innym niemieckim stanowisku, Gundersheim 4 (MN 15) (Fejfar i Repenning, 1998). Fejfar i współautorzy (2006) zaliczają jednak materiał z Gundersheim 4 do *B. longidens*, a w kolejnej pracy Fejfar i współaut. (2011) sugerują, iż *B. kowalskii* ograniczony jest do MN 14 i nie wymieniają żadnych jego stanowisk poza Podlesicami. Może być to zaskakujące, biorąc pod uwagę, iż m3 z Wölfersheim, który zilustrowali Fejfar i Repenning (zob. Ryc. 6: 14 w Fejfar i Repenning 1998), przypisany przez nich *B. kowalskii*, morfologią powierzchni zgryzowej odpowiada okazom z Podlesic, odznaczającym się uproszczoną budową (zob. Ryc. 2: I, J, N w Kowalski 1956), a nie okazom z Wężów 1 (zob. Ryc. 1: A–C w Kowalski 1960). Hellmund i Ziegler (2012) odnotowują obecność w Wölfersheim zarówno *B. longidens*, jak i *B. kowalskii*.

Pomiary morfometryczne zębów z Wężów 2 (Tab. 1) dały wyniki bardzo podobne do pomiarów materiału z Wężów 1 (zob. Tab. 12 w Sulimski 1964). Zakresy uzyskanych wartości są przy tym dość wyraźnie szersze w przypadku Wężów 1, co jest jednak zrozumiałe, gdyż próba z tego stanowiska była zdecydowanie większa. Niemniej zwraca uwagę, iż długość powierzchni zgryzowych m3 *Baranomys kowalskii* z Podlesic podana przez Kowalskiego (1957), tj. 1,0 mm, mieści się w zakresach otrzymanych dla m3 *Baranomys* z Wężów 1 (zob. Tab. 12 w Sulimski 1964) i Wężów 2 (niniejsza praca). Sugeruje to, iż o ile trzecie trzonowce *B. kowalskii* są istotnie średnio nieco mniejsze niż u *B. longidens*, same pomiary morfometryczne nie wystarczają do odróżnienia od siebie tych dwóch gatunków.

Sulimski (1964) uważa jednak różnice w morfologii powierzchni zgryzowych m3 za na tyle istotne, iż proponuje przesunięcie formy z Podlesic do rodzaju *Microtodon* (który charakteryzować się ma podobnym uproszczeniem budowy tego zęba) przy zachowaniu nazwy rodzajowej *Baranomys* dla formy z Wężów 1. Warto zaznaczyć, że Kretzoi (1969) zaproponował dla materiału z Podlesic osobną nazwę rodzajową *Wartamys* (która jednak nie przyjęła się w literaturze), pozostawiając formy ze stanowiska Csarnóta 1 (*B. loczyi*) i Wężów 1 (*B. longidens*) w rodzaju *Baranomys*. Materiał ze stanowiska Csarnóta 1 również Sulimski (1964) uznaje za reprezentujący rodzaj *Baranomys* na podstawie informacji ustnej (Kretzoi) o pojawianiu się w tamtejszej faunie m3 o budowie identycznej jak u *B. longidens*. Niestety brak jest w literaturze bliższych danych na temat morfologii i morfometrii m3 i M3 *B. loczyi*, co utrudnia wykluczenie lub potwierdzenie możliwości, iż *B. longidens* jest jego młodszym synonimem.

Status samego rodzaju *Baranomys* podważał nie tylko Kowalski (1960), który uznawał *B. loczyi* i materiał z Wężów 1 za reprezentujące w istocie rodzaj *Microtodon*. Po przeanalizowaniu bogatego materiału *M. atavus* z późnego miocenu i wczesnego pliocenu z terenu Mongolii Wewnętrznej Fahlbusch i Moser (2004) stwierdzili, iż „jest teraz oczywistym, że różnorodność jest bardzo duża, zwłaszcza w przypadku trzecich trzonowców, dolnych i górnych. Różnica pomiędzy *Microtodon* i *Baranomys* w redukcji m3/M3 nie istnieje”. Na tej podstawie postawili oni tezę, że nie ma już „żadnego argumentu, aby traktować *Baranomys* i *Microtodon* jako osobne rodzaje” i zaproponowali uznanie *Baranomys* za młodszy synonim *Microtodon*. Fejfar i współaut. (2011) podtrzymali jednak status rodzaju *Baranomys* oraz gatunków *B. loczyi*, *B. longidens* i *B. kowalskii* a *Microtodon* potraktowali jako osobny rodzaj, ograniczony do Azji. Zaznaczają przy tym, że status *Baranomys* jest przedmiotem dyskusji.

Na koniec warto odnotować, iż pewną różnicą pomiędzy materiałem z Wężów 2 i Wężów 1 jest regularne występowanie jedynie dwóch a nie trzech korzeni u M3 w przypadku okazów z Wężów 2. W materiale *B. longidens* z Wężów 1 Sulimski (1964) zaobserwował bowiem tylko okazjonalne zlewanie się dwóch przednich korzeni u w większości trójkorzeniowych M2 i M3. Brak w próbie pochodzącej z Wężów 2 okazów M3 z trzema korzeniami nie wydaje się jednak wystarczającą przesłanką, aby podważyć przynależność do tego samego gatunku, co materiał z Wężów 1.

Wnioski

Szczątki *Baranomys* ze stanowiska Węże 2 reprezentują ten sam gatunek, co forma z Wężów 1 opisana jako *Microtodon longidens*. Interpretacja taka wsparta jest podobieństwem powierzchni zgryzowych okazów z Wężów 2 do okazów z Wężów 1, w tym holotypu, a także pomiarami morfometrycznymi. Ponieważ fauna kopalna Wężów 2 jest obecnie datowana na biozonę MN 16b, potwierdzenie obecności *B. longidens* na tym stanowisku podważałoby tezę o tym, iż gatunek ten jest ograniczony do biozony MN 15.

Pojawienie się nowego materiału *Baranomys* z innych stanowisk, w tym nowych informacji na temat różnorodności trzecich trzonowców u poszczególnych przedstawicieli tego rodzaju, pozwoli na lepsze zrozumienie różnic gatunkowych pomiędzy *B. loczyi*, *B. longidens* i *B. kowalskii* bądź też na podważenie istnienia tych różnic. Kwestią otwartą pozostaje też status samej nazwy rodzajowej *Baranomys*, która może w istocie stanowić młodszy synonim nazwy *Microtodon*.

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Conclusions

The data on the Węże 2 rodent assemblage acquired in recent years and summed up in this thesis are coherent with the notion of this site belonging to the MN 16b zone in Mammal Neogene Zonation (2.9–2.6 Ma) and representing a woodland environment. However, closer examination of the material led to better understanding of its taxonomic diversity. In addition to species that have been previously appearing on the published faunal lists for the site (*Glis* ex gr. *minor-sackdillingensis*, *Muscardinus pliocaenicus*, *Tamias orlovi*, *Blackia miocaenica*, *Sciurus warthae*, *Prospalax priscus*, *Baranomys longidens*), the presence of *Muscardinus dacicus*, *Glirulus pusillus*, *Trogontherium minus, Dipoides* ex gr. *problematicus-sigmodus* and *Hystrix refossa* was demonstrated, expanding their known ranges. New light was shed on the ecology of rare and enigmatic species, including *Trogontherium minus*, *Dipoides* ex gr. *problematicus-sigmodus* and *Prospalax priscus*. Moreover, a comparison of porcupine fossil material from different sites made as a part of this work led to a formal description of a new species of porcupine, present at the site of Węże 1, which was given the name *Hystrix velunensis*. New information was gathered on the enamel structure of *Glis* ex gr. *minor-sackdillingensis* and a remarkable caries-affected specimen was recognized and studied in detail, revealing a probable instance of in situ preservation of cariogenic bacteria.

Future perspectives

The Węże 2 fossil material belonging to Arvicolinae remains undescribed and is currently under study. It consists of hundreds of detached teeth and dozens of toothed jaws for the most part assignable to *Mimomys*, a genus comprising a multitude of species, and taxonomy of which has been highly debated. The specific composition of this assemblage is to be determined. The ongoing study on this abundant material will hopefully result in shedding new light on inter-specific differences within *Mimomys*. Moreover, some specimens belonging to the genera *Germanomys* and *Trilophomys* (Arvicolinae), as well as some Cricetinae and Muridae specimens were found at Węże 2 and as for now still await detailed description.

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