

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

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ABSTRACT:

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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; Text-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



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

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 (Text-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; Szykiewicz 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; Szykiewicz, 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, *Petenya hungarica* Kormos, 1934, *Crocidura* sp. and *Paenelimoecus 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), *Arvernoceus* 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), *Plioselinia 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).

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; Szyrkiewicz 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

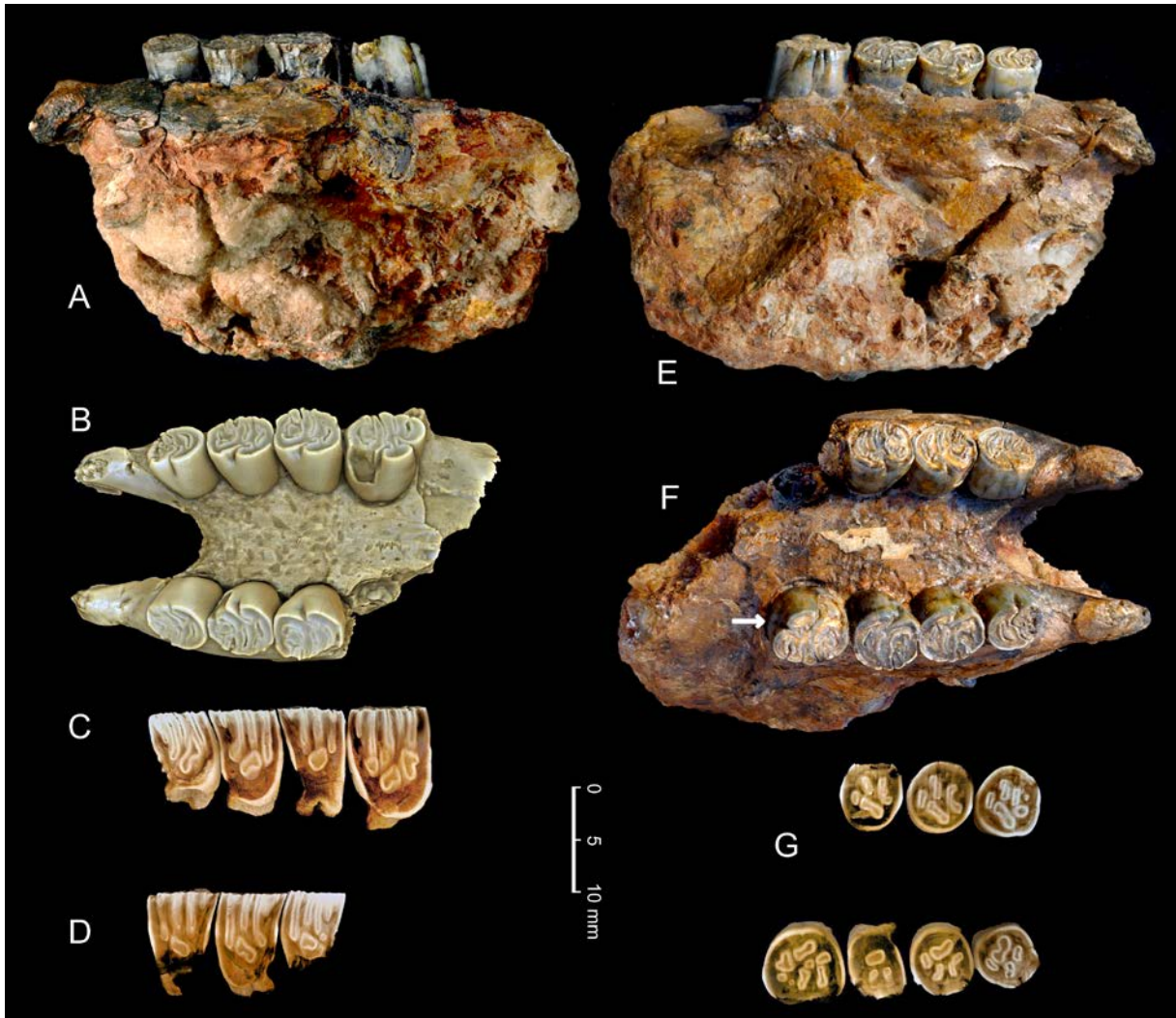
cervids *Croizetoceros ramosus* (Croizet and Jobert, 1828) and *Metacervoceros pardinensis* (Croizet and Jobert, 1828), an unidentified rhinocerotid, an elephantid probably assignable to the genus *Anancus* Aymard, 1855 (Stefaniak *et al.* 2020), the talpids *Rzebikia polonica* and *R. skoczni* (Rzebik-Kowalska 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).

MATERIAL AND METHODS

The specimen MZ VIII-Vm/731-1 (a fragmentary palate, Text-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 (Text-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



Text-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.

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.

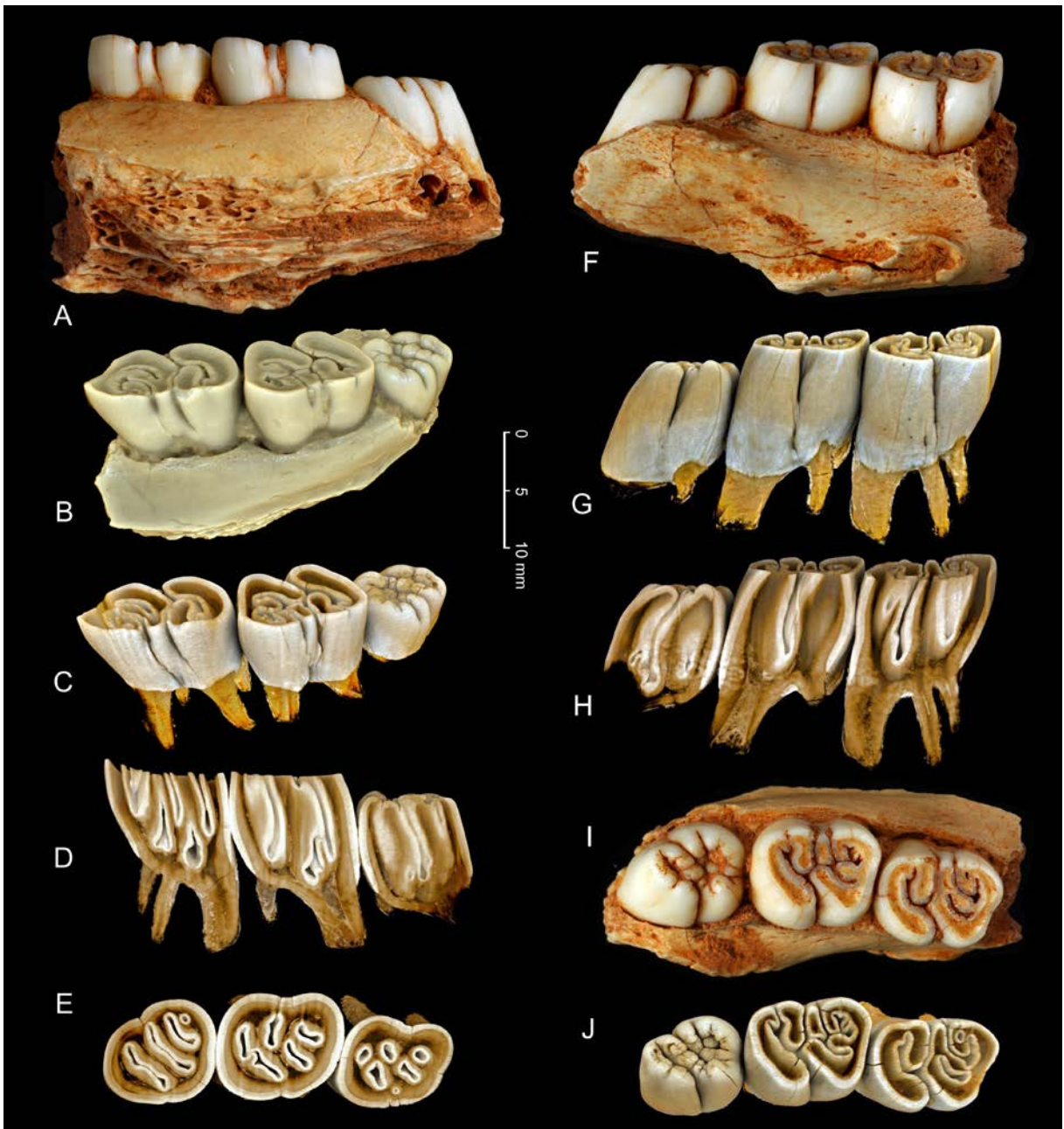
For the purpose of this study, microcomputed tomography (microCT) was conducted on the Węże specimens, an imaging technique which detects differences in the attenuation of an X-ray beam propagating through a solid object (e.g., Błażejowski *et al.*

2013, 2015). This data allows one to visualize the internal structure of the specimens and, after computer processing, to render 3-D models.

SYSTEMATIC PALAEOLOGY

Order Rodentia Bowdich, 1821
 Family Hystricidae Fischer, 1817
 Genus *Hystrix* Linnæus, 1758
Hystrix velunensis sp. nov.
 (Text-figs 2 and 4B)

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



Text-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 of the tooth row, 3D CT model; G – buccal view, CT scan; H – buccal view, CT scan; I – occlusal view; J – occlusal view, 3D CT model.

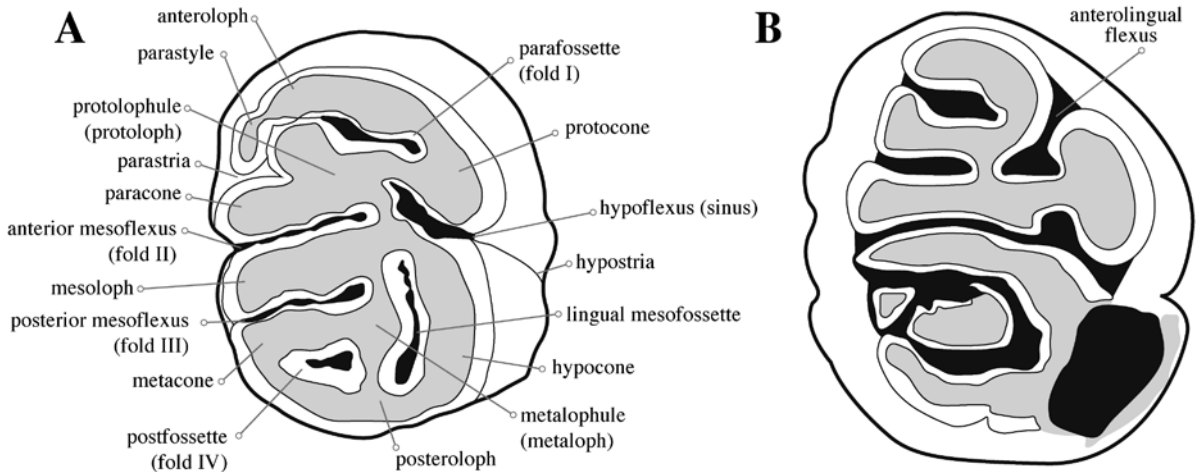
v1964. *Hystrix primigenia* (Wagner); Sulimski, pp. 233–234.

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*.



Text-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).

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; Text-fig. 4).

Hystrix refossa Gervais, 1852b
(Text-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 (Text-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 in historical 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 tooth-wear 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. africae australis* 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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