# First record of *Trogontherium cuvieri* (Mammalia, Rodentia) from the middle Pleistocene of Poland and review of the species

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Fostowicz-Frelik Ł. 2008. — First record of *Trogontherium cuvieri* (Mammalia, Rodentia) from the middle Pleistocene of Poland and review of the species. *Geodiversitas* 30 (4): 765-778.

## ABSTRACT

The fossil record of the family Castoridae in Poland is rather poor. It consists mainly of small Miocene species, *Chalicomys jaegeri* Kaup, 1832, *Steneofiber eseri* (Meyer, 1846), and *S. minutus* Meyer, 1838, as well as Pliocene *Boreofiber wenzensis* (Sulimski, 1964) and more abundant remains of *Castor fiber* Linnaeus, 1758, from the late Pleistocene. Herein, the first discovery of *Trogontherium cuvieri* Fischer de Waldheim, 1809, a large Eurasian beaver from the early middle Pleistocene site of Kozi Grzbiet (Central Poland) is reported. This species was widespread in Eurasia during the late Pliocene and early Pleistocene, when it reached its maximum dispersal, ranging from France eastwards to China and from northern Siberia (the Kolyma region) southwards to the Sea of Azov. It became extinct in the middle Pleistocene (Saalian). The taxonomic history and complex nomenclature of this beaver are reviewed and discussed. The European fossil record of this species and some evolutionary trends in its dentition are summarized. Also, a brief review of the postcranial characters and possible mode of life of the animal are presented. In general, its adaptations confirm a more terrestrial lifestyle than that of the modern *Castor*.

KEY WORDS
Mammalia,
Rodentia,
Castoridae,
adaptations,
distribution,
systematics,
Kozi Grzbiet,
Pleistocene.

**RÉSUMÉ**

*Première récolte de* Trogontherium cuvieri *(Mammalia, Rodentia) du Pléistocène moyen de Pologne et révision de l'espèce.*

Les restes fossiles de Castoridae sont relativement rares en Pologne. Il s'agit essentiellement de petites espèces miocènes, comme *Chalicomys jaegeri* Kaup, 1832, *Steneofiber eseri* (Meyer, 1846) et *S. minutus* Meyer, 1838, ainsi que *Boreofiber wenzensis* (Sulimski, 1964) du Pliocène et de l'espèce contemporaine *Castor fiber* Linnaeus, 1758 connue en abondance dans le Pléistocène supérieur. On décrit ici la récolte de *Trogontherium cuvieri* Fischer de Waldheim, 1809, un grand Castoridae eurasiatique dans le site Kozi Grzbiet (centre de la Pologne) daté du début du Pléistocène moyen ; il s'agit de la première récolte de cette espèce en Pologne. L'aire de répartition de cette espèce au Pliocène supérieur et au Pléistocène inférieur (où il a atteint son maximum) englobait l'Eurasie depuis la France jusqu'à la Chine à l'est et depuis la Sibérie du nord (région de la Kolyma) jusqu'à la Mer d'Azov au sud. *Trogontherium cuvieri* s'est éteint à la fin du Pléistocène moyen (Saalien). L'histoire taxonomique et les problèmes complexes de nomenclature de cette espèce sont présentés. On présente également la répartition des restes fossiles de cette espèce et quelques changements évolutifs concernant la dentition, ainsi qu'un bref résumé des caractères du squelette postcrânien. De façon générale, le mode de vie de cet animal était plus lié à l'habitat terrestre que celui du *Castor* contemporain.

**MOTS CLÉS**
Mammalia,
Rodentia,
Castoridae,
adaptations,
répartition,
systématique,
Kozi Grzbiet,
Pléistocène.

## INTRODUCTION

Although Poland is one of the few European countries where beavers, members of the rodent family Castoridae, have survived until today, the Polish fossil record of this family is rather poor. It includes remains of *Chalicomys jaegeri* Kaup, 1832, collected in the localities Przeworno 1 (Kubiak & Wolsan 1986), Opole 1 (Oppeln; Wegner 1913; Kowalski 1967), and Opole 2 (Kowalski 1967), *Steneofiber eseri* (Meyer, 1846) and *S. minutus* Meyer, 1838, from Opole 2 (Kowalski 1967), all middle Miocene in age, also the Pliocene *Boreofiber wenzensis* (Sulimski, 1964) from Węże 1 (Radulescu & Samson 1972), as well as more numerous finds of the extant *Castor fiber* Linnaeus, 1758, from the late Pleistocene and Holocene deposits (Sommer & Nadachowski 2006). Here the first Polish record of the Plio-Pleistocene Eurasian *Trogontherium cuvieri* Fischer de Waldheim, 1809, is reported. The paper also reviews and updates information on this extinct species, with emphasis on its taxonomic history, chronobiogeography, and lifestyle.

*Trogontherium cuvieri* is known from many Plio-Pleistocene fossil sites in Europe and China (Maul 1990; Xu 1994). It is sometimes called the "giant beaver", but this usage could be misleading because it was also applied to the North American extinct beaver *Castoroides* Foster, 1838, which was significantly larger than any other beaver as its skull attained 242-397 mm in lenght (Xu 1994). Among other Eurasian beavers also *Youngofiber* Chow & Li, 1978, exceeded *Trogontherium* by 5-10% in the skull dimensions, and *Anchitheriomys* Roger, 1898, matched it in size (Xu 1994). Therefore, the term "giant beaver" should be restricted to *Castoroides* only (Schreuder 1931; Mayhew 1978) and the term "Eurasian Giant Beaver", being ambiguous, should be avoided.

## MATERIAL AND METHODS

The terminology used for the folds in the cheek teeth follows Stirton (1935). The length (greatest mesio-distal dimension) and width (greatest bucco-lingual dimension) of the P4 crown were measured at the occlusal surface. The specimen examined is housed in ISEZ.

Comparative material: *Castor canadensis* Kuhl, 1820 (CM 1217, 25282, 31618), *C. fiber* (CM 1793), *Myocastor coypus* (Molina, 1782) (CM 1776), and *Ondatra zibethicus* (Linnaeus, 1766) (CM 2081).

ABBREVIATIONS

| | |
|---|---|
| CM | Carnegie Museum of Natural History, Pittsburgh; |
| ISEZ | Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow; |
| PIN | Paleontological Institute, Russian Academy of Sciences, Moscow. |

## SYSTEMATICS

### Order RODENTIA Bowdich, 1821
### Family CASTORIDAE Hemprich, 1820
### Genus *Trogontherium* Fischer de Waldheim, 1809

### ***Trogontherium cuvieri*** Fischer de Waldheim, 1809

*Castor trogontherium* Cuvier, 1812: pt. IV, chap. V, a. I: 4.

"*Diabroticus schmerlingi*" Pomel, 1848: 167, *nomen nudum*.

*Conodontes boisvilletti* Laugel, 1862: 715-717.

*Dipoides lydekkeri* Schlosser, 1902: 117.

*Trogontherium Soergeli* Rüger, 1928: 224, pl. 11, figs 5, 6.

*Sinocastor andersoni* Teilhard de Chardin, 1942: 5, fig. 7.

HOLOTYPE. — PIN 2422/1, an incomplete skull (Fischer de Waldheim 1809a: pl. I).

TYPE LOCALITY. — Taganrog, Azov seashore, Russia; the horizon unknown.

DISTRIBUTION. — Late Pliocene to middle Pleistocene in Europe, and late Pliocene to Pleistocene in Asia.

MATERIAL EXAMINED. — ISEZ MF/2314, a right P4.

LOCALITY AND HORIZON OF THE REFERRED SPECIMEN. — Unit 2, layers 2a-c, of a partly destroyed cave etched in a Devonian limestone hill, Kozi Grzbiet, 50°51'N, 20°21'E, at Zajączków near Kielce, Świętokrzyskie Mts, southeastern Poland (Głazek *et al.* 1976, 1977a, b). Unit 2 is composed principally of yellowish-brown to dark brown sandy loams and contains abundant fossils. These represent more than 100 species of mammals, including lipotyphlans (Rzebik-Kowalska 1994), bats (Wołoszyn 1988), lagomorphs (Sych 1980; Fostowicz-Frelik 2008), rodents (Kowalski 2001, and references therein), carnivorans (Wiszniowska 1989), and artiodactyls (Stefaniak 2007).

The deposition period of the bone bearing layers of Kozi Grzbiet (Fig. 1) was established on the basis of the fluoro-chloro-apatite (FCL/P) and collagene methods at *c.* 700-550 ka (Głazek *et al.* 1976). It is assigned to an interstadial warming, correlated with the Cromerian II (Małopolanian Interglacial according to Ber 2005). Paleomagnetic investigation of the sediment revealed positive magnetic polarity referred to Brunhes normal magnetic epoch (Głazek *et al.* 1977b; Lindner 1982). The composition of the rodent fauna indicates the uppermost Biharian of the Templomhegy phase (Nadachowski 1990). *Mimomys savini* Hinton, 1910, the index species for the upper Biharian in Central Europe, is quite abundant and shows some advanced morphological features similar to *Arvicola* Lacépède, 1799, believed to be its descendant (Nadachowski 1985). The presence of the other Biharian species, such as *Pliomys episcopalis* Méhely, 1914, *P. lenki* (Heller, 1930), *Allocricetus bursae* Schaub, 1930, and *A. ehiki* Schaub, 1930, as well as the late Villanyian and Biharian glirid species, *Glis* cf. *sackdillingensis* and, on the other hand, the lack of *Allophaiomys* Kormos, 1933, confirm the late Biharian dating. Presence of *Microtus* (*Pitymys*) *arvalidens* Kretzoi, 1958, *M.* (*Stenocranius*) *gregaloides* (Schrank, 1798), and *Clethrionomys glareolus* (Schreber, 1780) narrows this period to the latest part of the Biharian (Nadachowski 1990).

The composition of the vertebrate fauna suggests a moist and sylvan environment (Lindner 1982), at least for the greater part of the time of deposition. The presence of typical forest rodents such as *Petauria* sp., *Clethrionomys glareolus*, *Eliomys* cf. *quercinus*, *Sicista praeloliger* Kormos, 1930, and *Glis* cf. *sackdillingensis*, as well as birds such as *Tetrao* sp. and *Tetrastes* sp., indicates a woodland habitat of taiga type (Bocheński 1984).

REVISED DIAGNOSIS. — Large beaver but smaller than *Castoroides* and *Youngofiber*, maximal skull length 210 mm; sagittal suture of skull distinct, flanked by two deep depressions. Incisors with convex enamel face, lower pair pear-shaped in cross section. The enamel surface of the incisors covered with subtle longitudinal grooves.

Cheek teeth high-crowned with weak roots. P4 larger than any other upper cheek tooth. M1 and M2 about equal in size, each shorter than M3. M3 considerably elongated anteroposteriorly. Shallow striae of upper cheek teeth, reaching no further than a half of the crown height (hypostria is the deepest one), differentiate *Trogontherium*

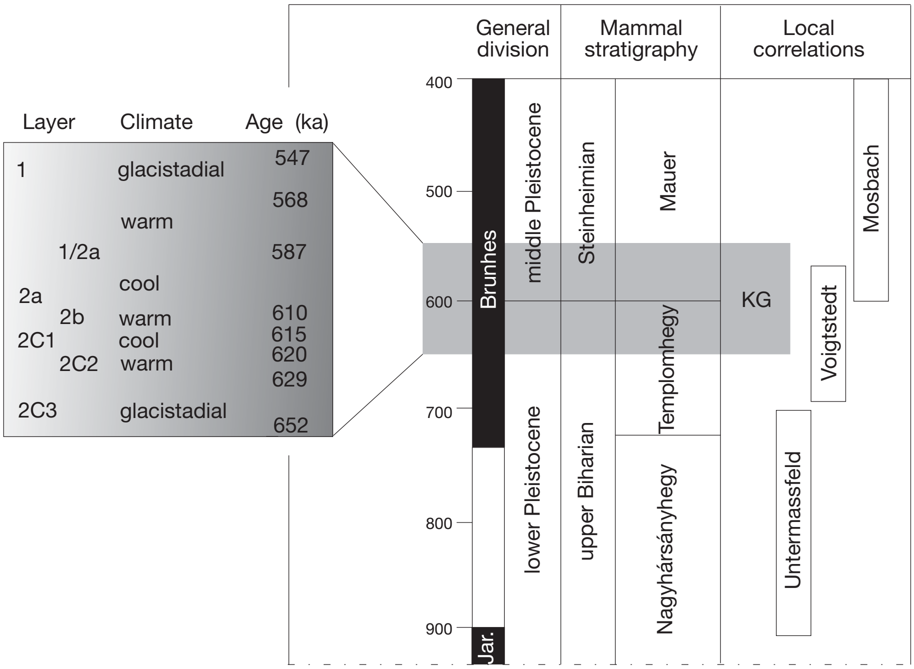

FIG. 1. — Stratigraphy of bone bearing sediments of Kozi Grzbiet, KG (from Głazek *et al.* 1976, modified). Abbreviation: **Jar.**, Jaramillo.

*cuvieri* from *Castor* Linnaeus, 1758, which has very deep striae and striids (sometimes covered by cement), reaching the base of the tooth. Early wear stages of P4 and M3 with small flexus or fossette posterior to metaflexus. Metaflexus closes early in ontogeny, *T. cuvieri* differs from *Castor* which has most of the folds open even in strongly worn teeth. Lower cheek teeth with hypoflexid extending between mesoflexid and metaflexid, nearly straight (in occlusal view) flexids, and striids reaching half of crown height. Differs from *Euroxenomys* in larger size, ridged incisor enamel, lower-crowned cheek teeth, and M3 longer anteroposteriorly relative to length of either M1 or M2.

### DESCRIPTION OF THE REFERRED SPECIMEN

Isolated, right P4 of an adult but relatively young animal. The crown is 12.4 mm wide and 10.0 mm long (Fig. 2). The wear surface shows only one closed fold, transformed into isolated fosset (here metafosset, 5.0 mm width), which indicates age class 2 (Mayhew 1978). There are two open folds on the buccal side, paraflexus (5.2 mm width) and mesoflexus (8.7 mm width), and one on the lingual side, hypoflexus, 4.6 mm width. Hypoflexus does not significantly overlap paraflexus anteriorly, but at its most lingual end it delicately bends anteriorward. Mesoflexus is very deep and cut across the whole width of the tooth, ending at the lingual layer of enamel surrounding the tooth. The vertical depth of hypostria and mesostria is 5.7 and 1.7 mm respectively, measured at the buccal side. The wear stage of the tooth almost reached the bottom of the buccal incision of the paraflexus but a fault is still open. The tooth exhibits the partial hypsodonty revealed by the presence of an elongated, broad main root, placed anteriorly and in equal breadth with the crown of the tooth, and a small posterior rootlet. Consequently, the enamel margin is reaching deeper into tooth base at the anterior margin. Both roots are compressed anteroposteriorly, beginning to close, which is a characteristic feature in mature beavers (Xu 1994).

### REMARKS

The tooth of *Trogontherium cuvieri* from Kozi Grzbiet is the first and only Polish discovery of

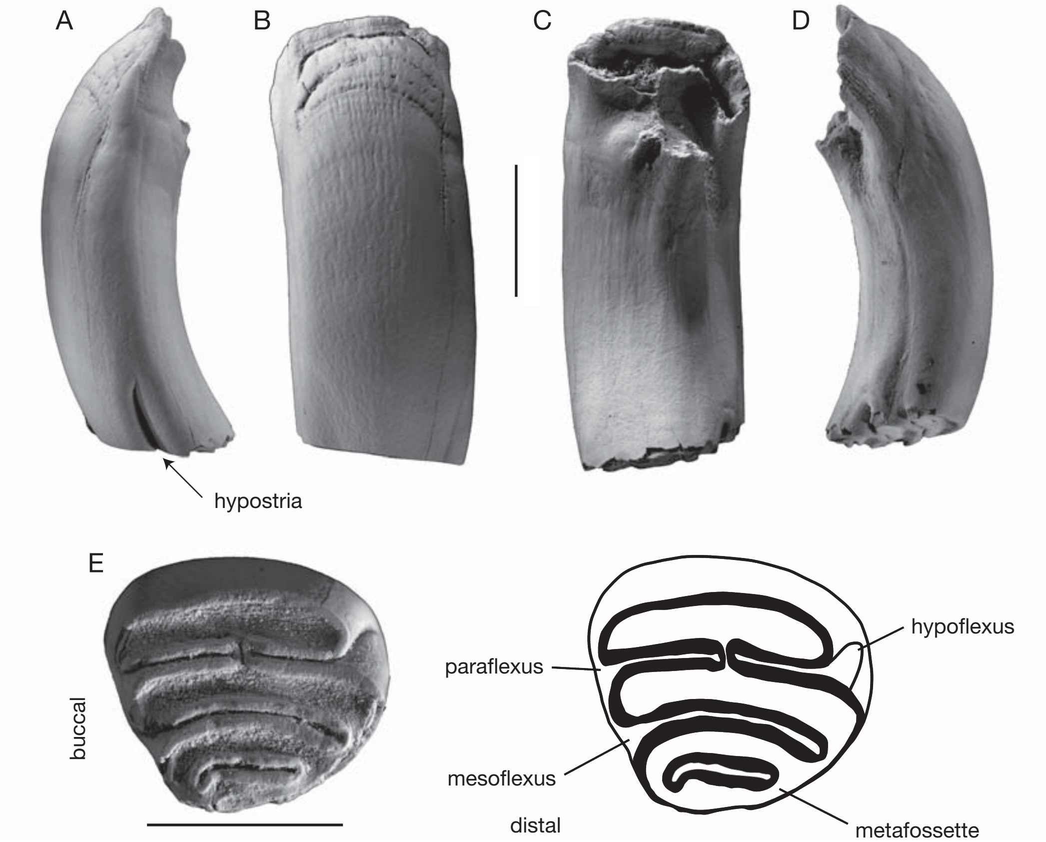

FIG. 2. — Right P4 of *Trogontherium cuvieri* Fischer de Waldheim, 1809 from the early middle Pleistocene of Kozi Grzbiet (ISEZ MF/2314): **A**, lingual view; **B**, mesial view; **C**, distal view; **D**, buccal view; **E**, occlusal view. Scale bars: 10 mm.

this species. It is the most northern occurrence of *T. cuvieri* in Central Europe and one of the few specimens found in cave sediments. The specimen ISEZ MF/2314 was previously ascribed to *Castor fiber* (Bartolomei *et al.* 1975: 423; Głazek *et al.* 1976, 1977a, b) and subsequently recognized as *T. cuvieri* by Mieczysław Wolsan; however, it was listed only (e.g., Nadachowski 1990; Kowalski 2001), and presented briefly in the volume of abstracts by Fostowicz-Frelik & Wolsan (2004).

The morphology of the specimen is typical for *T. cuvieri*. The striae are relatively shallow and presumably reached about one-third of the crown depth in the unworn stage; certainly not exceeding half of it, as noticed for this species (Xu 1994). This feature distinguishes the specimen ISEZ MF/2314 from *Castor* which has definitely deeper striae, with hypostriae reaching nearly the base of the crown (Xu 1994). Furthermore, the well separated rootlet (Fig. 2) differentiates this specimen from *Castor*, which has a higher ratio of hypsodonty and the radical part decreases in diameter, but no separate roots are observed. The described tooth differs from the holotype (PIN 2422/1) in still open paraflexus, although the tooth wear almost reaches the base of the fold (Fig. 2). In the studied specimen the metaflexus is already closed into a metafossette, while in *Castor* even heavily worn teeth have this fold still open. Morphology of all flexi is simple, they lack crenulation and do not show any kind of splitting or widening at the end. The hypoflexus does not significantly overlap the paraflexus anteriorly.

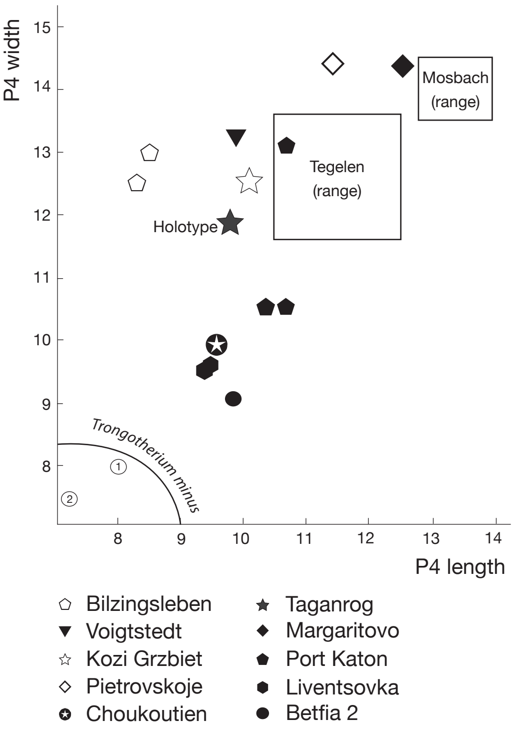

FIG. 3. — Plot of P4 measurements of *Trogontherium cuvieri* Fischer de Waldheim, 1809 from the Eurasian sites. Dimensions of the youngest remains of *T. minus* Newton, 1890, given for comparison (**1**, Red Crag; **2**, Perrier-Étouaires).

## DISCUSSION

### TAXONOMIC HISTORY OF *TROGONTHERIUM CUVIERI*

The genus *Trogontherium* was described on the basis of the skull offered by Count Alexander Sergeyevich Strogonov from his collection to Fischer de Waldheim. The specimen was collected on the coast of the Sea of Azov near Taganrog (Russia) and although the stratigraphical context of this discovery is not clear, it is supposed to be early Pleistocene (Vereshchagin 1951; Motuzko 1972), correlated with Villány 5 and Betfia phase in Central European stratigraphy (Rekovets & Krakhmalnaya 1998). In the original work describing *Trogontherium*, which was a published letter to Count Strogonov, Fischer de Waldheim (1809a) did not use any specific name. He applied the sole generic name also in the subsequent publication providing the more comprehensive description of the specimen (Fischer de Waldheim 1809b). The consistently binomial name, *Castor trogontherium*, used for the holotype specimen, appeared in the first edition of Cuvier's "Recherches sur les ossemens [*sic*] fossiles" (1812). In the following edition (1824), Cuvier cited the name as *T. cuvieri* and attributed it to Fischer de Waldheim, beginning the article III, concerning the holotype, with a title: "Des Castors des terrains meubles et notamment de la grande espèce nommée *T. cuvieri* par M. de Fischer."

Mayhew (1978) stated that the specific name should be attributed to Fischer de Waldheim, as a result of the long-lasting unquestioned usage, beginning with the second edition of the "Recherches sur les ossements fossiles" (1824).

Laugel (1862) described the remains of *Trogontherium* from St. Prest (France) under a new name, *Conodontes boisvilletti* giving rise to a lengthy discussion about the evolution and species diversity of West European *Trogontherium*. *Conodontes boisvilletti* was classified as a junior synonym of *T. cuvieri* by Newton (1882, 1892), who pointed out that in describing a new species, Laugel had neglected wear stages observed in the enamel pattern of *Trogontherium* teeth. Newton's argument was not universally accepted and Laugel's species was referred to in the description of the remains from Tegelen (Schreuder 1929). However, in her later works Schreuder (1931, 1951) reverted to the generic name and suggested existence of two species divided by the Rhine river system, the less specialized *T. boisvilletti* inhabiting Europe west of the Rhine and *T. cuvieri*, the larger and more specialized species, occupying areas east of the Rhine.

Schreuder (1929, 1931, 1951) based this distinction on crucial, in her opinion, differences in skull structure, giving the detailed morphological description of *Trogontherium*. On the other hand, Mayhew (1978) noticed no significant differences in the skull structure of the two forms proposed by Schreuder. He provided a new reconstruction of some cranial structures and stated that these two species of *Trogontherium* form a monophyletic lineage as chronosubspecies, with the earlier (Tiglian-Eburonian-early Cromerian) *T. cuvieri boisvilletti* and the later (Elsterian-Holsteinian) *T. cuvieri cuvieri*.

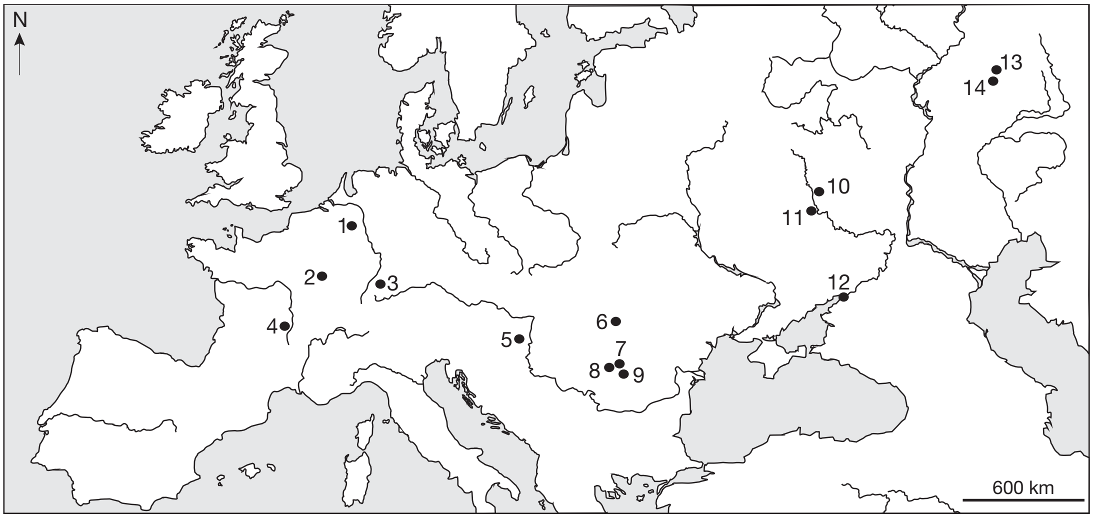

FIG. 4. — Distribution of *Trogontherium cuvieri* Fischer de Waldheim, 1809 in late Pliocene European sites: **1**, Tegelen; **2**, Commenailles; **3**, Erpfingen-2; **4**, Perrier-Étouaires; **5**, Kislang; **6**, Betfia XIII; **7**, Otlet-Valley 1 and 2; **8**, Izvoru-2; **9**, Slatina-3; **10**, Korotoak-1; **11**, Uryv 1 and 2; **12**, Liventsovka; **13**, Simbugino; **14**, Akkulaevo.

The morphology of *T. cuvieri* is generally uniform in all Eurasian specimens but the Pleistocene specimens are usually larger than the Pliocene ones (Fig. 3). The slight tendency towards an increase in size was sometimes observed within the Pleistocene samples (Schreuder 1951; Mayhew 1978; Heinrich 1998; Mol *et al.* 1998). Also, the enlargement, presumably in line with the Bergmann's rule, is mentioned for the Siberian specimen from the Kolyma River sediments (Motuzko 1972). The dimensions of P4 of *T. cuvieri* from Pleistocene Eurasian sites (Fig. 3), and the holotype in particular, are very close to the Tegelen "*boisvilletti*" sample, which weakens the argument of Schreuder (1931, 1951) on the two distinct subspecies.

*Trogontherium cuvieri* is the largest, best known, and the last member of the genus (Mol *et al.* 1998; Hugueney 1999). *Trogontherium minus* Newton, 1890, known from the Pliocene and earliest Pleistocene (Hugueney *et al.* 1989; Hugueney 1999; Stefen & Rummel 2003) of Europe, is a distinctly smaller species. Mayhew (1978) regarded it as a direct ancestor of *T. cuvieri*, but Hugueney *et al.* (1989) demonstrated that these two species coexisted during the latest Pliocene to the earliest Pleistocene interval and the disparity in size was too significant to make Mayhew's conjecture plausible.

### GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION OF THE SPECIES

*Trogontherium cuvieri* apparently never was a particularly abundant species. Nevertheless, there are numerous remains from the Palearctic ranging from the late Pliocene to middle Pleistocene interval (Figs 4-6), especially in fossil sites near large river systems (e.g., Don and Rhine) or areas adjacent to river mouths (Schreuder 1929, 1931, 1951; Motuzko 1972; Mayhew 1978; Jánossy 1986; Van Kolfschoten 1990). Most specimens come from water lain sediments (Mayhew 1978) and only a handful were found in caves, such as Erpfingen (Lehmann 1953), Vértesszölöss (Kretzoi & Vértes 1965), Choukoutien (Young 1934), and the specimen from Kozi Grzbiet described here.

*Trogontherium cuvieri* was known in the European fossil record from France (Hugueney *et al.* 1989; Guérin *et al.* 2003) in the west to the Black Sea and Sea of Azov regions (Maul 1990; see Figs 4; 5) in the east. It has not been reported south of the Alps (Rook & Kotsakis 1994), and is not known from Spain.

Apart from Europe, *T. cuvieri* is also an important faunal element in the Pleistocene of China, where it has been described from the Haiyan Formation

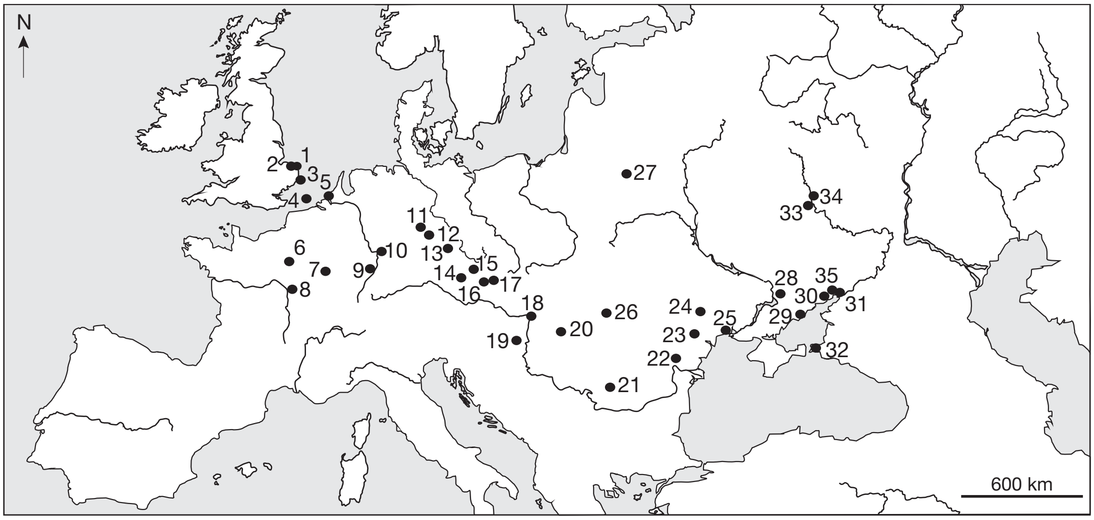

FIG. 5. — Distribution of *Trogontherium cuvieri* Fischer de Waldheim, 1809 in early Pleistocene European sites: **1**, East Runton; **2**, West Runton; **3**, Easton Bavents; **4**, Deep Water Channel; **5**, Maasvlakte; **6**, Saint-Prest; **7**, Chagny 1; **8**, Courterolles; **9**, Jockgrim; **10**, Mosbach 1; **11**, Voigtstedt; **12**, Süssenborn; **13**, Untermassfeld; **14**, Chlum; **15**, Přezletice; **16**, Stránská Skála; **17**, Gombasek; **18**, Üromhegy; **19**, Somssich-hegy 2; **20**, Szeged; **21**, Otlet Valley 3; **22**, Chismikioi; **23**, Tiraspol; **24**, Dolinskoe; **25**, Cherevichnoe; **26**, Betfia 2; **27**, Korcevo; **28**, Kairy; **29**; Primorsk; **30**, Taganrog; **31**, Port Katon; **32**, Taman Peninsula; **33**, Uryv 3; **34**, Bogdanovka; **35**, Margaritovo.

(Yushe Basin, Shanxi Province), Choukoutien near Beijing, Tangshan (Hebei), Hexian (Anhui Province) and from Palaeolithic sites in Liaoning Province (Young 1934; Teilhard de Chardin 1942; Xu 1994; Flynn *et al.* 1997). The earliest known remains of *T. cuvieri* in China are from the latest Pliocene-early Pleistocene Haiyan Formation (Xu 1994). The presence of *T. cuvieri* in China is the result of immigration from the West, most probably from Kazakhstan, where the remains of both species of the genus were found in Pliocene sediments (Motuzko 1972; Xu 1994). Late Pliocene remains of *T. cuvieri* were also found in Siberia in the valley of the Kolyma River and in the lower course of the Aldan River (Motuzko 1972). The present record suggests that this species reached its maximum dispersal in Eurasia during the late Pliocene and earliest Pleistocene interval.

Nonetheless, the richest fossil record of *T. cuvieri* comes from Europe and the Sea of Azov region, the Netherlands (Tegelen), Germany (Mosbach, Voigtstedt), and England (Cromerian Forest-Bed Series) yielded relatively abundant remains of this species.

The earliest European appearance of *T. cuvieri* dates to the late Pliocene, Villanyian, MN 16 (Fig. 4) from Commenailles and Vialette in France (Hugueney *et al.* 1989). The species became extinct in Europe during the middle Pleistocene (Mayhew 1978; Van Kolfschoten 1990). Holsteinian discoveries of *T. cuvieri* are known from Bilzingsleben and Reilingen in Germany (Mol *et al.* 1998; Ziegler & Dean 1998), Neede and Rhenen in the Netherlands, and from Medzhybozh in Ukraine (Rekovets *et al.* 2007). The youngest specimens known so far (Fig. 6) come from Schöningen 12 (Germany), dated to the earliest Saalian Reinsdorf Interglacial (Mol *et al.* 1998).

## LIFESTYLE, BIOMECHANICS, AND ENVIRONMENTAL PREFERENCES OF *TROGONTHERIUM CUVIERI*

*Trogontherium cuvieri* has generated considerable speculations about its swimming abilities, food preferences and lifestyle. Two main views, partly contradictory, were presented by Schreuder (1929, 1951) and Motuzko (1972). This paper presents a summary of these opinions and discusses the functional adaptations in *Trogontherium* and the possible lifestyle of this extinct species.

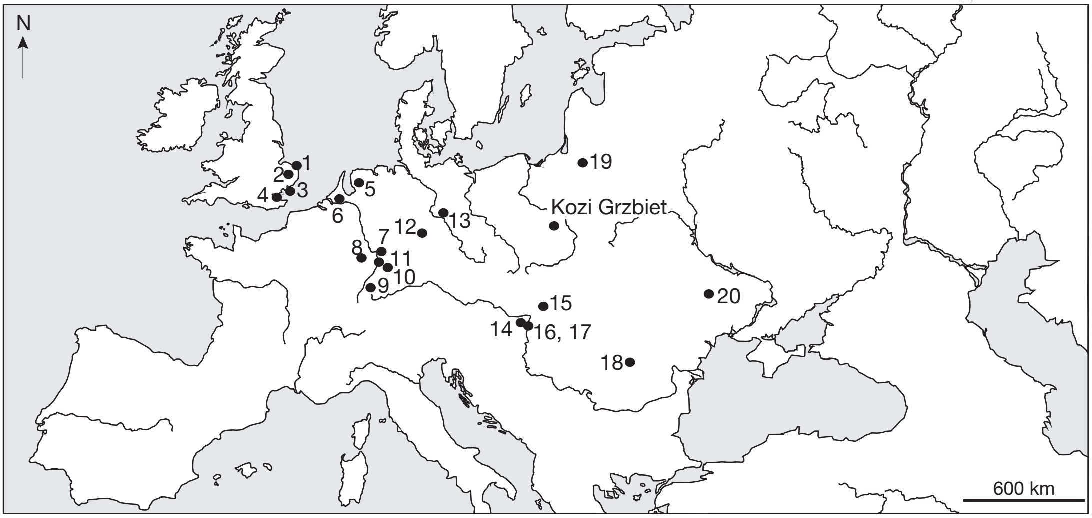

FIG. 6. — Distribution of *Trogontherium cuvieri* Fischer de Waldheim, 1809 in middle Pleistocene European sites: **1**, Ostend; **2**, Hoxne; **3**, Clacton; **4**, Swanscombe; **5**, Neede; **6**, Rhenen; **7**, Mosbach 2; **8**, Miessenheim-I; **9**, Reilingen; **10**, Mauer; **11**, Pilgerhaus; **12**, Bilzingsleben; **13**, Schöningen 12; **14**, Vertesszölös 1 and 2; **15**, Tarkő; **16**, 25 Fortuna Street; **17**, Országház Street (both Castle Hill, Budapest); **18**, Rotbav-Dealul Tiganilor; **19**, Nyaravaj-2; **20**, Medzhybozh.

It is worthy of notice that *T. cuvieri* was a relatively large rodent with the range of total skull length known as 133-210 mm (157 mm in the holotype), slightly larger than the European beaver, *Castor fiber* (skull length 114-146 mm). *Trogontherium cuvieri* (Fig. 7) had also more robust and massive skull with a flat roof (not gently bent, as in *Castor*), and more powerful incisors with striated enamel (Newton 1892; Schreuder 1951; Mayhew 1978). These facts narrow considerably the number of extant species, which can be studied as a possible analog for *Trogontherium*.

### *Food preference and gnawing ability*

Schreuder (1951) stated that *Trogontherium* was a "more vigorous gnawer" than *Castor* and was able to do tree-cutting, especially in wintertime, but she also suggested that animal fed on floating water plants, gathered by means of strong mobile lips. This concept was supported by the morphology of the anterior part of the premaxillae, where two tubercles, strongly impressed by the muscle attachments were found, placed symmetrically above the alveoli of the upper incisors (Newton 1892; Schreuder 1929), similarly to *Castoroides* (Mayhew 1978). Schreuder (1951) compared this feature to the condition found in *Myocastor* Kerr, 1792. It possesses a distinctive crest in the suture of the premaxillae, extending vertically between the alveoli of the upper incisors and the nasal openings, where *Trogontherium* possessed the mentioned tubercles and insertions for the powerful muscles possibly moving the lips.

In beavers the ability to cut relatively large trees is associated with the morphology of the incisors, particularly the lower pair. Two forms of lower incisors are encountered in Castoridae and this difference is also reflected in the enamel structure of the incisors: the typical wood-cutters have more strongly inclined internal enamel layer (PI – portio interna), occupied by the uniserial Hunter-Schreger band, HSB (Koenigswald & Mörs 2001). The incisor of this first type is semi-flattened with a straight anterior margin, known in *Castor*, *Chalicomys* Kaup, 1832, *Palaeocastor* Leidy, 1869, and *Steneofiber depereti* Mayet, 1908. These representatives are supposed to be the best wood-gnawers. In the case of extinct forms, they are regarded as being able to do wood-cutting with the similar efficiency as the extant beaver. It is also noteworthy that this group includes *Paleocastor fossor* (Peterson, 1905), which was a burrowing animal (Stirton 1935). This beaver was recognized as a builder of deep spiral burrows, the *Daimonelix* ichnotaxon, and the reconstruction of its burrowing behavior included digging with incisors (Martin & Bennet 1977). The incisors of the second type are convex-faced, recognized in *Agnotocastor* Stirton, 1935, *Amblycastor* Matthew, 1918, *Anchitheriomys* Roger, 1898, *Dipoides* Schlosser, 1902, *Eucastor* Leidy, 1858, *Monosaulax* Stirton, 1935, *Steneofiber eseri*, and *Trogontherium* (Stirton 1935; Crusafont Pairo & Villalta 1948; Hugueney 1999; Rybczynski 2007). These animals could also gnaw on hard vegetation, but their efforts were less productive because of the relatively shorter and curved cutting edge. The efficiency of the process becomes obvious in analyzing the shape of the chips produced. The convex-faced incisors cut deeper than the flatter ones, but the cutting edge is definitely narrower. They act more like a gouge than a chisel, being suited rather for carving than cutting, thus the chips are narrow and semi-round in cross section. On the other hand, *Castor* and other genera with flattened incisors gnaw in a chisel-like mode, chipping the flat, definitely wider and shallower shavings, which makes the whole process more efficient. Thus, Schreuder's (1951) view on the cutting ability of *T. cuvieri* is unsupported on the basis of comparison with extant species. This does not exclude the ability of *T. cuvieri* to gnaw seedlings, deciduous trees or bushes and to feed on the outer layers of trunks as, e.g., *Myocastor* does (Woods *et al.* 1992).

Different interpretation of the gnawing behavior of *Trogontherium* was proposed by Motuzko (1972), who pointed out that the incisors of *T. cuvieri* protruded slightly more anteriorly than in *Castor*. He pointed to the similarity, in that respect, to some extant burrowing rodents (*Lagurus*, *Spalax*, and *Citellus*) that gnaw on roots and make their burrows with the help of incisors. In the mentioned genera, the upper and lower incisors are inclined anteriorly (much more than in *Trogontherium*), forming a sharp angle between their distal surfaces. Such an arrangement makes the force applied at the cutting edge weaker, but these animals are able to bite substrate placed just in front of them and scrape it off, in a pincers-like manner. According to Motuzko (1972), the similarity of *Trogontherium* with burrowing rodents could be also confirmed by the greater length of the diastema compared to *Castor*. This allows burrowing rodents to separate completely the two functionally distinctive compartments of the muzzle: the incisors, which gnaw and dig both food and soil, and the cheek teeth, which mill the food. However, this separation is observed also in *Myocastor*, in which it prevents the animal from swallowing water during underwater gnawing (Woods *et al.* 1992), and in *Castor*. Although Motuzko (1972) agreed that the anterior protruding arrangement of incisors allowed a presumption that gnawed material was softer, he pointed out that the powerful incisors and thick ribbed enamel in *Trogontherium* enabled the animal to gnaw on every material, including trees, but in a different manner from that of extant beavers.

The masticatory apparatus of *T. cuvieri* shows similarities with that of *Castoroides* and differs from that of *Castor* in having a relatively larger superficial layer of the masseter and internal pterygoid muscles and weaker temporal muscle (Mayhew 1978). The superficial masseter and internal pterygoid muscles seemed to be closely related in size and their extended insertions occupied the opposite sides of the mandibular angle. The functional role of this fact remains uncertain, but it could have resulted in the relatively larger force being applied to the incisors during gnawing (the masseter brings the jaws forward and together) and increasing lateral movements of the mandible by the large internal pterygoid muscle. Rodents gnawing on hard material such as bark, roots or rhizomes (e.g., *Hystrix*), have greatly developed masseter muscles, especially the pars superficialis (Turnbull 1970). Thus, irrespective of the environment, it is possible that *Trogontherium* fed on plants with wooden trunks, gnawing on bark and outermost wood layer or lignified rhizomes. A similar type of diet, consisting of roots, was suggested for some extinct American beavers (Hugueney 1999).

FIG. 7. — Reconstructed life appearance of *Trogontherium cuvieri* Fischer de Waldheim, 1809 (drawing by A. Hołda-Michalska).

### *Locomotor adaptations*

The behavior of *T. cuvieri* was another subject of speculation. *Trogontherium* was an animal connected with an aquatic environment (Schreuder 1951; Motuzko 1972; Mayhew 1978; Mol *et al.* 1998). Schreuder (1951) stated that it was an excellent swimmer with long webbed feet and agile forelimb. Motuzko (1972) argued that it was much more terrestrial, based on, apart the incisor structure, some characters of the hind limb skeleton, clearly indicating more cursorial adaptations. The postcranial skeleton of *T. cuvieri* is characterized by shortening of the humerus and femur and elongation of radio-ulnar and tibio-fibular bones in comparison with *Castor* (Schreuder 1929, 1951; Guenther 1965; Motuzko 1972; Mayhew 1978). The shortening of the upper arm and thigh with simultaneous elongation of the forearm and shank, as well as foot is commonly observed in cursorially adapted mammals (e.g., Hildebrand 1974; Fostowicz-Frelik 2007), whereas in more aquatic ones, the shortening occurs in both upper arm/thigh and forearm/shank segments, whereas the relative elongation of the foot is generally not so pronounced. The ratio of femur to tibia length is lowest in *T. cuvieri* (68%) in comparison with other swimming rodents: *Ondatra* Link, 1795 (76%), *Castor* (78%), and *Myocastor* (82%). An even more clear picture can be seen in the ratio of the humerus to radius length: *Trogontherium* (77%), *Castor* (92%), *Myocastor* (96%), and *Ondatra* (99%). In most animals (excluding ricochetal and exclusively bipedal ones), cursoriality increases due to the elongation of the forelimb rather than the elongation of the hind limb (Hildebrand 1974). Thus, *c.* 15% elongation of the forelimb in *Trogontherium* in comparison with *Castor* and other swimming rodents indicates more cursorial locomotion in the former species.

Moreover, in comparison with *Castor* the metatarsals and the hind limb phalanges were more slender, elongated, and compressed medio-laterally, and not flattened dorso-plantary as in *Castor* (Motuzko 1972). Again, the slenderness of the metatarsals and phalanges also points to the more advanced cursoriality (Fostowicz-Frelik 2007). Furthermore, the medio-lateral compression of phalanges puts in doubt the presence of a well-developed web (observed in *Castor*) and suggests that the external appearance of the hind foot was more similar to that of *Ondatra*, contributing to the overall picture of *Trogontherium* as an agile animal capable of running. Its cursorial abilities are also visible in specific structures of the ankle joint having a limited, but functional, calcaneo-fibular connection (Schreuder 1931), unknown from any other rodents, but present in lagomorphs and ungulates. This structure stabilizes the ankle joint, allowing for more efficient movements during locomotion.

According to Schreuder (1931, 1951) the fore paws of *Trogontherium* were smaller and more delicate in comparison to those of *Castor*, but indicated agility and supported relatively strong claws. The two last features characterize also fore paws of beaver, which uses them to manipulate with food and do the grooming, so in this regard similar behavior could be suspected in *Trogontherium*.

In conclusion, the anatomy of the limbs indicates a more cursorial way of life for *Trogontherium*. In comparison with modern beavers the animal spent more time browsing on land than swimming. In addition, the structure of the caudal vertebrae does not show any trace of the dorso-ventral flattening of a tail (Schreuder 1929, 1931).

**Acknowledgements**
I would like to thank Mieczysław Wolsan (Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw) for attracting the attention to the specimen examined and encouragement at the earlier stages of this work. I am indebted to Zoya Bessudnova (Vernadsky State Geological Museum, Moscow) and Caroline Pepermans (National Museum of Natural History, Leiden) who helped in obtaining some publications. I am grateful to Thomas Mörs (Swedish Museum of Natural History, Stockholm) for the discussion on stratigraphic and geographic dispersal of *Trogontherium*, held during the Colloquium in Weimar (2004), and to Suzanne B. McLaren and John R. Wible (both CM) for making comparative material available for study.

Thanks are directed to the reviewers, Marguerite Hugueney (Université Claude-Bernard, Lyon), Sevket Sen, and Annemarie Ohler (both Muséum national d'Histoire naturelle, Paris) for their valuable comments. I am also indebted to Mary R. Dawson (CM) who read critically the revised version and corrected English. Grażyna Dziewińska and Aleksandra Hołda-Michalska (both from the Institute of Paleobiology, Polish Academy of Sciences, Warsaw) made the photographs and the reconstruction of external appearance of the beaver, respectively. Adam Halamski (Institute of Paleobiology, Polish Academy of Sciences, Warsaw) kindly provided the French translation of the abstract. This work was supported by the Foundation for Polish Science.

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*Submitted on 16 November 2007;*
*accepted on 19 June 2008.*