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THE YOUNGEST PANGOLIN (MAMMALIA, PHOLIDOTA) FROM EUROPE

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ABSTRACT—The fossil record for pangolins is sparse. Current biogeographic data suggest this clade originated in Europe, though pangolins seem to have disappeared from the European paleontological record during the middle Miocene, when they were hypothesized to have been pushed toward more tropical and sub-tropical equatorial environments due to global cooling trends. Here we report on a nearly complete humerus of a pangolin from the early Pleistocene (~2.2–1.9 Ma) site of Grăunceanu, Romania. This fossil revises this previous understanding of pangolin evolution and biogeography and represents both the youngest fossil pangolin from Europe and the only fossil from Pleistocene Europe. The new species described here, *Smutsia oteniensis*, sp. nov., shares several synapomorphic traits with other *Smutsia* species, which are currently found only in Africa. However, relative to extant *Smutsia*, it has several unique traits that set it apart, including a longer and narrower entepicondyle, an enlarged supinator crest, and an enlarged greater tubercle. Together this unique suite of features justifies the description of a new species. This specimen definitively demonstrates that pangolins were present in Europe during the Pleistocene. Further, *Smutsia* has previously been thought to be an African taxon, with the oldest specimen from South Africa at ~5 Ma and living species found across Africa. This specimen now demonstrates that *Smutsia* previously had a far larger biogeographic range. Finally, Grăunceanu has been reconstructed to have consisted of relatively open grasslands and woodlands, which is an unusual habitat for most pangolins.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP.

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INTRODUCTION

The evolutionary history of pangolins (order Pholidota) is not well understood. This is in large part due to the fragmentary fossil record of this clade, which results from multiple factors, including the fact that members of this order lack dentition, that they likely existed in low population densities (as inferred from extant taxa), and that pangolins tend to inhabit tropical and subtropical forest ecosystems, making fossil preservation less likely (e.g., Gaudin et al., 2009, 2020). The taxonomy of pangolins and their relationship to other placental mammals have been debated extensively, though a range of molecular and combined morphological and molecular phylogenetic studies over the past several decades (e.g., Shoshani et al., 1985; Murphy et al., 2001a, b; O’Leary et al., 2013; du Toit et al., 2014; Hassanin et al., 2015; Gaubert et al., 2016, 2018, 2020) have helped establish Pholidota as the sister taxon to Carnivora and attribute extant pangolins to a single monophyletic family, Manidae. Though no morphological characters currently unite Pholidota and Carnivora (Gaudin et al., 2020), morphological and molecular phylogenetic analyses within Pholidota reach largely congruent results (e.g., Gaudin et al., 2009; Ferreira-Cardosa et al., 2020).

At present the most commonly accepted taxonomy for Pholidota (e.g., Gaudin et al., 2020; Gaubert et al., 2020) identifies

three extant genera with a total of eight species. Members of one of these genera (*Manis*) are found distributed throughout southern Asia, whereas the other two genera (*Phataginus* and *Smutsia*, the African tree and African ground pangolins, respectively) are restricted to Sub-Saharan Africa. All pangolins are covered in keratinous scales and are myrmecophagous, subsisting almost entirely on ants and termites (e.g., Pieterse et al., 2014; Chao et al., 2020). A variety of cranial and postcranial adaptations found in pangolins that unite this clade are linked to their diet, including (among others) complete loss of the teeth, an extremely long tongue, and forelimbs with large claws adapted to digging and burrowing (Gaudin et al., 2020). Members of this clade may be arboreal, semi-arboreal, or terrestrial, and range in body size from 1–3 kg (*Phataginus tricuspis*) to upwards of 30 kg (*Smutsia gigantea*) (Challender et al., 2020). Nearly all species exhibit some degree of body size dimorphism with males being larger and longer than females, though the degree of size dimorphism varies considerably across species (Challender et al., 2020).

The oldest members of Pholidota are recorded from the Eocene Messel fauna of Germany (Storch, 2003; Gaudin et al., 2009), with additional late Eocene species recovered from northern China (Gaudin et al., 2006) and North America (Gaudin et al., 2016). Most authors now agree that this order is Laurasian or even more specifically, European in origin (e.g., Storch, 2003; Gaudin et al., 2006, 2009, 2020). With the possible exception of an enigmatic and questionable pangolin report from the Fayum of Egypt (Gebo and Rasmussen, 1985), the Oligocene–Miocene fossil record of pangolins is entirely restricted to

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Europe (von Koenigswald, 1999; Gaudin et al., 2009), as represented by the genus *Necromanis*, multiple species of which are known from Spain, France, and Germany (e.g., von Koenigswald, 1999; Crochet et al., 2015; Alba et al., 2018a).

Only a single report by Kormos (1934) purports to establish the presence of pangolins in Plio-Pleistocene Europe. The species erected by Kormos (1934), *Manis hungarica*, was based on a single ungual phalanx recovered from the Villány–Kalkberg fissure fill deposits in southern Hungary. Wagner et al. (2012) suggested this fossil was most likely recovered from the site of Villány 3 (though they noted Kretzoi [1956] questions this), which they estimated to date to MN 17 (~2.5–2.0 Ma) of the early Pleistocene. Kormos (1934) compared the morphology of this specimen favorably to that of *Manis pentadactyla*, but acknowledged that the Villány fossil was considerably larger than the phalanges of this extant species. Unfortunately, the likely loss of this specimen in a museum fire during the Hungarian uprising in October 1956 (Pálffy et al., 2008) makes it impossible to verify the taxonomic attribution of this specimen at present. As a result, von Koenigswald (1999) subsequently cast doubt on the authenticity of this record, calling *Manis hungarica* a nomen nudum, though he did not specify why. Furthermore, recent faunal lists (Jánossov, 1986) do not mention the presence of this species at Villány 3. Thus, even if *Manis hungarica* is not technically a nomen nudum, the fossil itself has been lost and its current attribution is impossible to fully assess. As a result, the only verifiable records of fossil pangolins in the Plio-Pleistocene are restricted to Africa (i.e., *Smutsia gigantea* at 5.1 Ma from Langebaanweg [Botha and Gaudin, 2007] and at ~3 Ma from NK 69 in Uganda [Pickford and Senut, 1991]) and Asia (i.e., *Manis paleojavanica* from the Late Pleistocene of Java and Malaysia [Dubois, 1907, 1926; Hooijer, 1947] and *M. lydekkeri* from the Pleistocene of India [Dubois 1908]). Some authors suggest that a global cooling trend following the mid-Miocene climatic optimum resulted in the restriction of pangolins' geographic range to more tropical climates, including their present-day distribution (e.g., Gaubert et al., 2018, 2020).

Here we report and describe the presence of a fossil pangolin from the early Pleistocene of Romania. The fossil in question was recovered in the 1960s from the fossil locality of Grăunceanu (= Valea Grăunceanului). Previous site reports and publications mentioned the presence of either *Manis* sp. (Rădulescu and Samson, 1990, 1991; Rădulescu et al., 1998) or *Manis* cf. *hungarica* (Rădulescu et al., 2003) in passing, but did not describe the fossil (s) representing this taxon. Recent reanalysis of the Grăunceanu assemblage by our research team (Terhune et al., 2020; Curran et al., 2021) has provided a more comprehensive picture of the fauna from Grăunceanu and multiple other fossil localities in the surrounding Olteț River Valley, including the identification of previously unknown fossil species in this area (e.g., *Pachystruthio* cf. *pannonicus*, *Puma pardoides*). Given the current biogeographic data and the lack of verification of the fossil described by Kormos (1934) from Hungary, the humerus described here would thus represent the first indisputable record of pangolins from the Plio-Pleistocene of Europe.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **ISER**, “Emil Racovita” Institute of Speleology, Bucharest, Romania; **M**, Iziko: South African Museum of Cape Town (Mammalogy), Cape Town, South Africa; **MNHN**, Muséum National d’Histoire Naturelle, Paris, France; **NMB**, National Museum, Bloemfontein, South Africa; **PFY**, Pech du Frayssse, Université de Montpellier, Montpellier, France; **SAM-PQL**, Iziko: South African Museum of Cape Town (Paleontology Quaternary Langebaanweg); **SMF**, Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany; **USNM**,

National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Anatomical Abbreviations—**ca**, capitulum; **def**, distal entepicondylar foramen; **dpc**, deltopectoral crest; **dt**, deltoid tubercle; **ec**, entepicondyle; **ecb**, entepicondylar bridge; **ecn**, entepicondylar notch; **gtu**, greater tubercle; **h**, humeral head; **ltu**, lesser tubercle; **pef**, proximal entepicondylar foramen; **sc**, supinator crest; **tc**, teres crest; **tr**, trochlea.

Other Abbreviations—**MN**, Mammal Neogene zones; **ORV**, Olteț River Valley; **VGr**, Valea Grăunceanului.

GEOLOGICAL SETTING AND AGE

The site of Grăunceanu is situated in the Olteț River Valley (ORV) of Romania (Fig. 1), approximately 175 km west-northwest of Bucharest. Geologically, Grăunceanu is located in the Dacian Basin, which is delimited to the north and west by the Carpathian Mountains and to the south and east by the Danube Valley and Dobrogea Plateau. Deposits in the ORV are attributed to the Tetoiu Formation (Andreescu et al., 2011), sediments from which are primarily sandy-pebbly facies that are fluvio-lacustrine in origin. This formation extends from the base of the Pleistocene (2.588 Ma) to as young as ~1 Ma (Andreescu et al., 2011). The Olteț River, a tributary of the Danube River (via the Olt River) crosscuts the valley. During the Villafranchian (~3.5–1.0 Ma; Rook and Martínez-Navarro, 2010) this region was dominated by the presence of the Dacian Lake, which was interconnected to the Pannonian and Euxinic lakes to the northwest and east, respectively.

Exploration of this region in the 1960s identified multiple fossil localities in the vicinity of the village of Tetoiu (Fig. 1), including Grăunceanu, which remains one of the most fossiliferous early Pleistocene sites from eastern Europe. Fossil deposits at Grăunceanu were described by Bolomey (1965) and Rădulescu and Samson (1990) as being densely concentrated in a ~0.75 m thick layer spread across at least 90 m². This fossil layer was described as being situated at the base of a silty sand layer that was ~1.5 m thick. There was no mention of any stratification within the fossil horizon, potentially suggesting the site assemblage was deposited in a relatively short period of time, which is further supported by consistent taphonomic preservation across specimens as observed by our research team.

The entire fossil collection from Grăunceanu is estimated to be ~5000–6000 specimens and is split between the ISER (Bucharest) and the Museum of Oltenia (Craiova). To date, our team has accessioned 3132 specimens from Grăunceanu and identified at least 30 separate taxa from this site (Terhune et al., 2020), including a wide range of ungulate, carnivoran, rodent, primate, and avian species. Biochronological estimates of the age of Grăunceanu consistently place this site in the late Villafranchian (MN17/MmQ1), possibly dating to as old as 2.2 Ma and as young as ~1.8–1.9 Ma (Bolomey, 1965; Rădulescu and Samson, 1990; Rădulescu et al., 2003; Terhune et al., 2020). The Grăunceanu faunal assemblage is most similar in character to the sites of Saint-Vallier and Senèze (France), Vatera (Greece), and with some affinities to the Khapry Faunal Unit of Russia (Terhune et al., 2020). Grăunceanu has been reconstructed as a fairly open habitat with woodlands nearby and located near a significant water source (Curran et al., 2021).

MATERIALS AND METHODS

The described specimen (VGr.2362; Fig. 2), a right humerus, is housed at the ISER in Bucharest. As part of our team's ongoing reinventory of the ORV collections, the specimen was accessioned, cataloged, and photographed. Prior work by Samson and Rădulescu may have previously inventoried this specimen (as evidenced by markings on the specimen itself), but

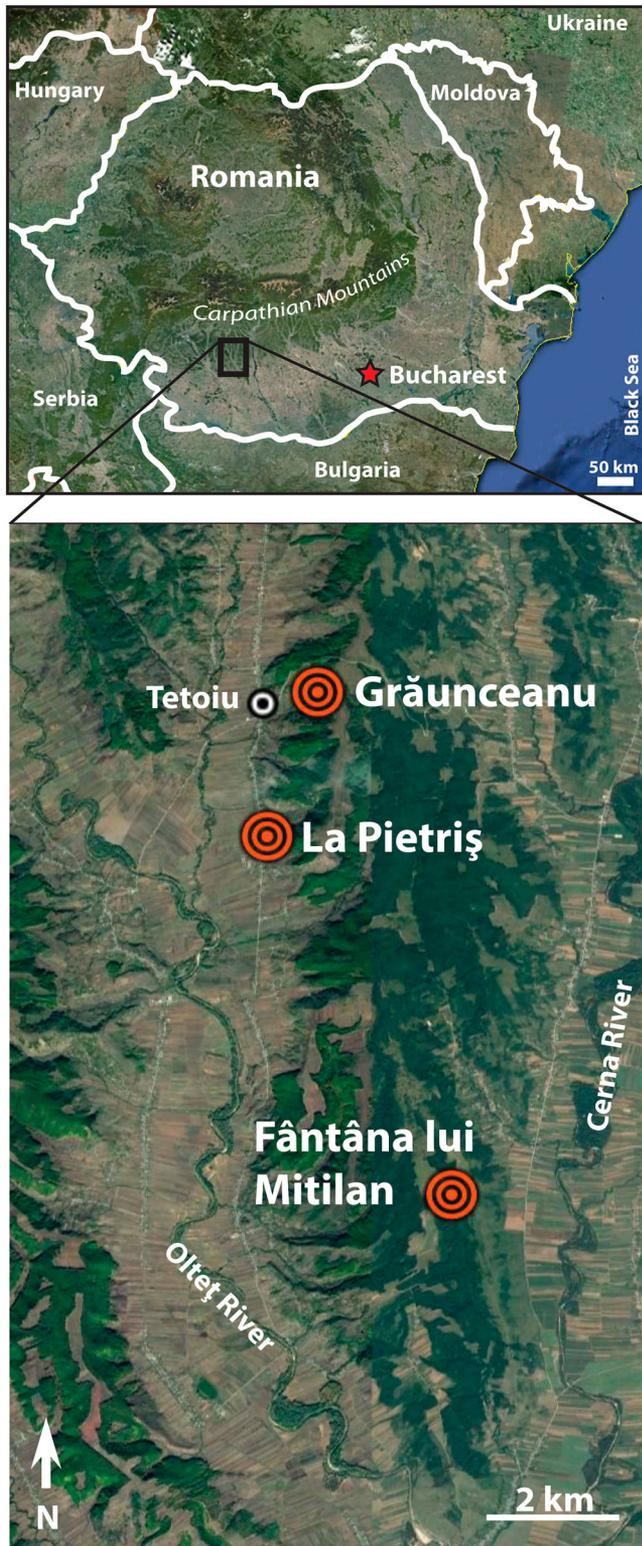


FIGURE 1. Top: map of Romania showing the location of the Olteț River Valley (ORV) project area. Bottom: overview of the ORV project area including relevant landmarks and fossil localities.

unfortunately all records or inventories of the original excavations have been lost. This specimen was further imaged using an HDI 120 Blue LED scanner (LMI Industries) which allowed us to generate a 3D model of the specimen (Fig. 3;

models available for download via Morphosource.org under the project “Olteț River Valley”, ark:/87602/m4/346059 (reconstructed model), ark:/87602/m4/346063 (proximal epiphysis and shaft), and ark:/87602/m4/346067 (distal epiphysis)). We also performed a taphonomic analysis of the specimen to evaluate surface modifications (Behrensmeier, 1978; Behrensmeier et al., 1986; Domínguez-Rodrigo, 2009, 2010; Kaiser, 2000; Pickering and Egeland, 2006) and breakage patterns (Villa and Mahieu, 1991).

Here, we compare this specimen to published data from fossil and extant pangolin specimens (Gaudin et al. 2006, 2009, 2016; Botha and Gaudin, 2007) and unpublished measurements and images by TJG. We have focused in particular on extant pangolins from the genus *Smutsia*, which most closely resemble the new fossil material, as well as a Pliocene humerus of *S. gigantea* from Langebaanweg, South Africa, reported by Botha and Gaudin (2007). Additionally, we specifically evaluate humerus characters described in Gaudin et al. (2009) (Table 1), which are diagnostic for pangolins at various taxonomic ranks.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Order PHOLIDOTA Weber, 1904
 Suborder EUPHOLIDOTA Gaudin, Emry, and Wible, 2009
 Family MANIDAE Gray, 1821
 Subfamily SMUTSIINAE Gray, 1873
 Genus *SMUTSIA* Gray, 1865
 Species *SMUTSIA OLTENIENSIS*, sp. nov.

Holotype—A nearly complete right humerus, VGr.2362 (Fig. 2).

Etymology—The species name recognizes the origin of this fossil in the geographic region of Oltenia, Romania.

Type Locality—Grăunceanu, Olteț River Valley, Romania.

Description—The fossil VGr.2362 is in two pieces, broken near the distal epiphysis, but the specimen is nonetheless nearly complete (Fig. 2). Connection between the two pieces is tenuous and therefore we made no attempt to reunite the pieces except digitally (i.e., Fig. 3). The fossil is in very good taphonomic condition with no surface weathering and only slight indications of root etching. It appears to have suffered some post-depositional damage primarily to the caudal side with cracks that may be due to excavation damage. Some of these post-depositional breaks to the specimen were repaired by previous researchers. The specimen has an estimated maximum length of 104.2 mm, with a midshaft width of 17.4 mm, and distal width at the epicondyles of 51.9 mm. Other relevant metrics and comparisons to other fossil and extant taxa are provided in Table 2 and Fig. 4.

Diagnosis—The new species shares with all eupholidotan pangolins: long axis of the humeral head oriented distomedially in posterior view; posterior distal surface of the humeral shaft marked by a concavity between the supinator crest and the posterior edge of the entepicondylar canal. It shares with manoidean pholidotans: pulley for the m. biceps brachii at the distal end of the deltopectoral crest; entepicondylar notch present; moderately developed supinator crest extending proximal to the proximal opening of the entepicondylar canal. With all Manidae it shares: shallow bicipital groove between greater and lesser tubercles for the head of m. biceps brachii; small olecranon fossa (narrower in width than the trochlea); greater and lesser tubercles equal in proximal extent. With other members of the genus *Smutsia* it shares: elongate lesser tubercle and strong teres crest; supinator crest that extends straight distally bordered medially by an elongated shallow concavity; loss of connection between the bicipital groove and the fossa anteromedial to the greater tubercle. Unique features include a larger greater tubercle and longer and narrower entepicondyle relative to *S. gigantea*

TABLE 1. Humeral characters from Gaudin et al. (2009) showing state in VGr.2368. Symbols: * = multistate character, ** = multistate and ordered character.

Character	Description	VGr.2368
205	Orientation of long axis of humeral head in posterior view: oriented proximodistally, or somewhat distolateral (0), or oriented distomedially (1).	1
206**	Orientation of deltopectoral crest of humerus: canted medially at its distal end (0), extends straight down shaft (1), or canted laterally at its distal end (2).	0
207**	Length of deltopectoral crest: extends >75% of the length of the humerus (0), extends >65, ≤75% of the length of the humerus (1), extends >55, ≤65% of the length of the humerus (2), or extends ≤55% of the length of the humerus (3).	1
208	Pulley form. biceps brachii at distal termination of deltopectoral crest: present (0), or absent (1).	0
209	Deep anterior groove between greater tubercle and lesser tubercle of humerus for head of m. biceps brachii: present (0), or groove shallow or absent altogether (1).	1
210	Large distinct deltoid crest extends across lateral surface of humerus: present (0), or absent (1).	0
211	Distinct fossa for mm. infraspinatus and teres minor on lateral surface of humerus: absent (0), or present (1).	0
212**	Width across humeral epicondyles: relatively narrow, <40% of length of humerus (0), intermediate width, 40–50% of length of humerus (1), or wide, >50% of length of humerus (2).	1
213**	Length of entepicondyle: short, <30% of epicondylar width of humerus (0), intermediate length, 30–40% of epicondylar width of humerus (1), or elongated, >40% of epicondylar width of humerus (2).	2
214	Position of proximal entepicondylar foramen: visible in anterior view (0), or visible in posterior view (1).	0
215*	Entepicondylar notch: absent (0), weak (1), or present (2).	2
216**	Size and proximal extent of supinator crest: greatly enlarged, with free-standing proximal extension reaching to middle region of humeral shaft (0), well developed but lacking freestanding proximal extension, extends proximal to proximal opening of entepicondylar foramen and extends far lateral to humeral shaft (1), moderately developed, extends proximal to proximal opening of entepicondylar foramen but weakly flared laterally (2), or reduced, ends at level of proximal opening of entepicondylar foramen (3).	2
217	Form of supinator crest: flared laterally at its distal end, with well-developed anterior concavity (0), or extends nearly straight distally, anterior concavity poorly marked or absent (1).	1
218	Posterior surface of distal humerus between supinator crest and posterior edge of entepicondyle/entepicondylar foramen, proximal to olecranon fossa: flat (0), or concave (1).	1
219	Distal edge of trochlea of humerus in anterior view: straight or slightly concave (0), or convex (1).	0
220	Medial lappet of trochlea of humerus extending underneath entepicondyle in distal view: present (0), or absent (1).	1
221	Medial extent of radial fossa of humerus: extends over lateral half of trochlea (0), or situated directly above capitulum, does not extend medially over trochlea (1).	0
222	Size of olecranon fossa of humerus: large, wider transversely than trochlea in posterior view (0), or small, narrower transversely than trochlea (1).	1
223	Relative proximal extent of greater and lesser tubercle of humerus: greater tubercle extends proximal to lesser (0), or proximal extent of greater and lesser tubercle roughly equivalent (1).	1
224	Position of proximal portion of lesser tubercle of humerus: extends anterolaterally, overlaps head in anterior view (0), or does not extend anterolaterally, remains medial to head in anterior view (1).	0
225	Bicipital groove of humerus continuous with well-developed fossa anteromedial to greater tubercle: present (0), or absent (1).	1
226	Orientation of greater tubercle of humerus relative to head in proximal view: divergent from head posterolaterally (0), or approximately parallel to lateral surface of head (1).	0

Illiger, 1815 and *S. temminckii* Smuts, 1832. The supinator crest is also enlarged relative to *S. gigantea* and *S. temminckii*, though this may represent the retention of a more primitive condition (see below).

Description and Comparison—The estimated maximum length of VGr.2362 (104.2 mm) makes it smaller than extant adult giant pangolins (*Smutsia gigantea* [Botha and Gaudin, 2007; Gaudin et al., 2016; TJG unpubl. data]; it is comparable in size to a juvenile *S. gigantea*, USNM 269706, max. length = 105.5 mm), but larger than the Pliocene specimen of *S. gigantea* reported by Botha and Gaudin (2007; max. length = 88.4 mm), and substantially larger than the humerus of the extant ground pangolin, *S. temminckii* (mean max. length = 70.8 mm [Botha and Gaudin, 2007]). The humerus possesses all of the humeral synapomorphies of Pholidotomorpha identified by Gaudin et al. (2009) that are not subsequently modified in later subgroups (i.e., an elongate deltopectoral crest canted medially at its distal end, characters (char) 206[0] and 207[1], and broad humeral epicondyles comprising >40% of humeral length, char 212[1]; Table 1). The specimen also exhibits synapomorphic humeral features of several important pholidotan subgroups (Gaudin et al., 2009 do not identify any humeral synapomorphies for Pholidota itself) including (Table 1):

- Eupholidota (*Eomanis waldi* Storch 1978 + Manoidea Gaudin et al. 2009): long axis of humeral head oriented distomedially in posterior view, char 205[1], and concave posterior distal surface between supinator crest and the posterior edge of the entepicondylar canal, char 218[1],

- Manoidea (Manidae + *Necromanis* and *Patriomanidae*): presence of pulley for m. biceps brachii at the distal end of the deltopectoral crest, char 208[0], entepicondylar notch present, char 215[2], supinator crest moderately developed, extending proximal to proximal opening of entepicondylar canal, char. 216[2],
- Manidae (clade including all extant taxa): shallow bicipital groove between greater and lesser tubercles for head of m. biceps brachii, char 209[1], olecranon fossa small, narrower in width than trochlea, char 222[1], and greater and lesser tubercles equal in proximal extent, char 223[1].

These features clearly identify the specimen as belonging to a pangolin, and moreover, it is closer in morphology to the extant taxa than any of the pre-Pliocene fossil genera.

The specimen greatly resembles the humerus of the ground pangolin genus *Smutsia* (Fig. 4). This impression is affirmed by a comparison with Gaudin et al.'s (2009) list of humeral synapomorphies for the three extant genera. Like the two extant species of *Smutsia*, the new specimen has a supinator crest that extends straight distally, and is bordered medially by an elongated, shallow concavity, char 217[1], and it loses the connection between the bicipital groove and a fossa anteromedial to the greater tubercle, char 225[1] (Table 1). The specimen also lacks five of the six humeral synapomorphies of the genus *Phataginus* (the African tree pangolins: chars 207[2], 208[1], 210[1], 216[3], and 219[1]), and two of the three humeral synapomorphies for the genus *Manis* (the Asian pangolins: chars 220[0] and 224[1]) (Table 1).

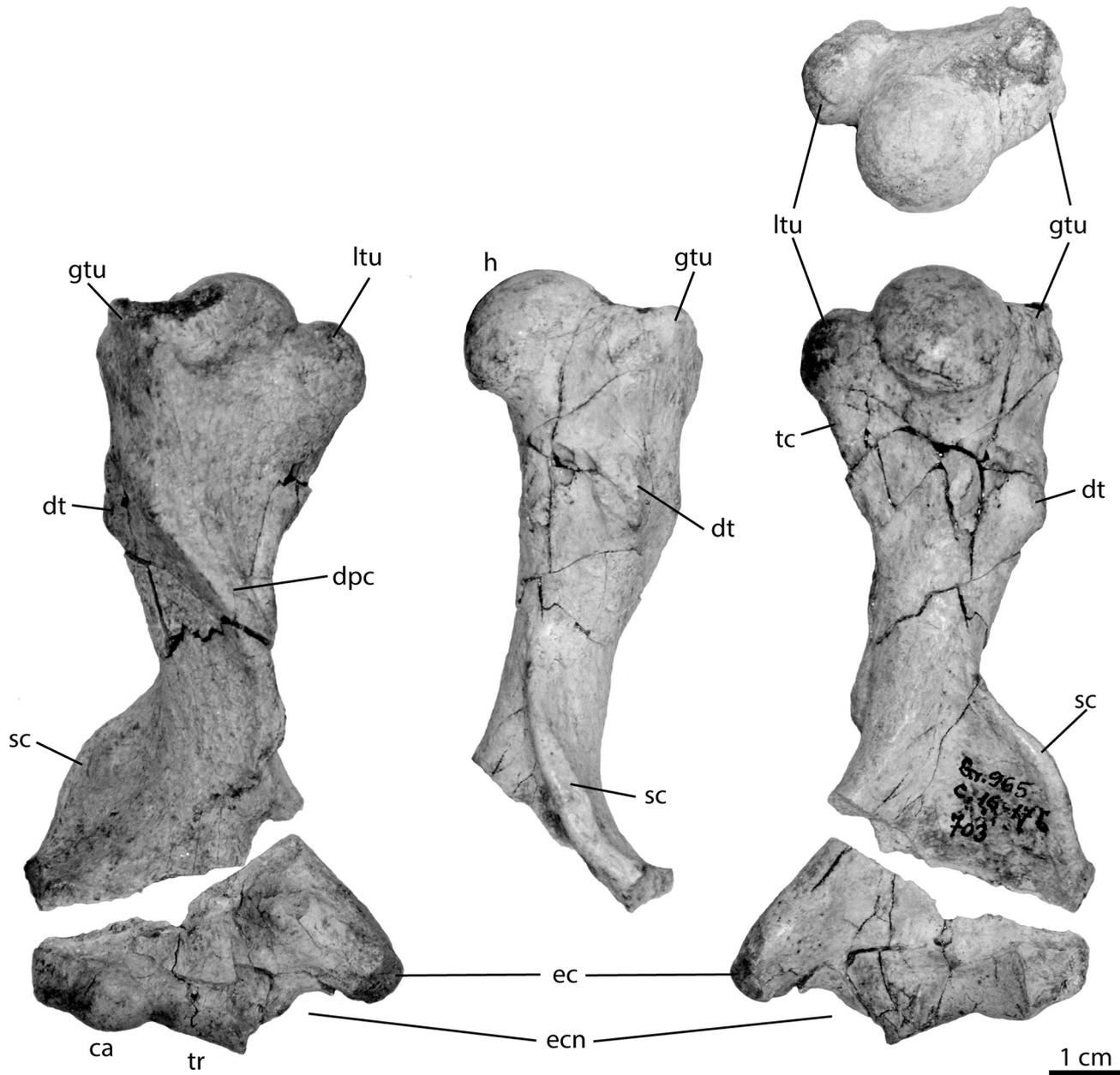


FIGURE 2. Right humerus of *Smutsia olteniensis*, sp. nov. Holotype specimen VGr.2362 in anterior (bottom left), lateral (middle), posterior (bottom right), and superior (top right) views. Abbreviations can be found in the main text.

The head of VGr.2362 is globose, somewhat taller than that of *S. temminckii* but also somewhat broader than that of *S. gigantea*. It is flanked by large greater and lesser tubercles, the former more robust than that found in either extant species of *Smutsia*. The elongate lesser tubercle is another point of resemblance with *Smutsia* not found in the other extant genera. In posterior view, the tubercles are separated by a broad, shallow bicipital groove. Extending distally from the lesser tubercle is a strong teres crest, as is found in the extant ground pangolins. The deltopectoral region strongly resembles that of *S. gigantea*. The deltoid tubercle is largely separate from the pectoral crest, offset posteriorly. The pectoral crest itself is formed by two separate crests which extend straight distally from the anterior and posterior edges of the greater tubercle, and then merge

anteriorly, the common crest slanting medially in an elongated diagonal to terminate in a groove for the m. biceps brachii. In *S. temminckii*, the deltopectoral crest is a single ridge that extends straight distally from the posterior edge of the greater tubercle until it reaches the deltoid tubercle, then extends in a much shorter, medially canted diagonal to its terminus. Both and Gaudin (2007) note the unique presence in both the Pliocene and extant *S. gigantea* of a broad muscular groove lateral to the deltopectoral crest, extending onto the anterior surface of the humerus medial to the supinator crest and ectepicondyle. This groove is absent in *S. olteniensis* sp. nov.

The distal end of VGr.2362 clearly possessed an entepicondylar foramen, though this area of the specimen is badly damaged. An entepicondylar foramen is also present in *S. gigantea* but is



FIGURE 3. Three-dimensional model of specimen VGr.2368, holotype of *Smutsia olteniensis*, sp. nov. For this model, the proximal and distal segments have been digitally reconstructed to form a single model, though these two parts do not perfectly refit. Click to activate in the PDF version. 3D image available online and 3D model available for download at Morphosource.org.

absent in *S. temminckii*. We have reconstructed the entepicondylar bridge covering the canal anteriorly based on the broken surfaces at either of its ends (Fig. 5). The bridge appears to be much narrower than that of extant *S. gigantea* but is similar in breadth to that of the Pliocene *S. gigantea* (Botha and Gaudin, 2007:fig. 3A). In both *S. olteniensis* sp. nov. and the Pliocene *S. gigantea*, the proximal opening of the entepicondylar canal is visible in anterior view (Gaudin et al., 2009, char 214[0]), as it is in *Manis* and *Necromanis*. In contrast, in extant *S. gigantea* and *Phataginus* it is only visible in posterior view (214[1]; though coded as 214[1] in Gaudin et al. [2009] *Patriomanis* actually shows an intermediate condition [TJG unpublished data]). The former condition (i.e., 214[0]) is likely the primitive one. The entepicondyle itself is quite elongated, comprising more than 40% of the distal width of the humerus, and has a relatively narrow tip. In this respect, the fossil is more like the living tree pangolins (*Phataginus* sp.) than the ground pangolins, where the process is shorter and broader (e.g., Fig. 4). The proximal/medial edge of the entepicondylar process is straight, as it is in *S. gigantea*, unlike the more concave contour in *S. temminckii* and extant *Manis*. The entepicondylar notch that forms the distal edge of the entepicondyle is shallow and concave, like that of *S. temminckii*, not as deeply incised as in *S. gigantea*. The trochlea has a relatively straight distal profile in anterior view, as in all pangolins except the two extant *Phataginus*

TABLE 2. Humeral measurements for VGr.2368 (in gray) compared with other fossil and extant pangolin taxa. All values in millimeters (mm). Data are taken from (1) Gaudin et al. (2016), (2) Crochet et al. (2015), (3) Botha and Gaudin (2007), and (4) Gaudin unpublished data. For *S. gigantea* (adults) specimens included are AMNH 53848, AMNH 53851, AMNH53858, and USNM 269706, for *S. temminckii* specimens are AMNH 168954, AMNH 168955, FMNH 35682, M 308, and NMB 3961, and for *P. tricuspis* specimens are USNM 537785, USNM 481808, and CM 16026.

	<i>Smutsia hungarica</i> (VGr.2368)	<i>Patriomanis americana</i> ¹ (USNM-P 299960)	<i>Necromanis francoconica</i> ¹ (SMF Me 94/1)	<i>Necromanis cf. francoconica</i> ² (PFY 4051)	<i>Necromanis quercyl</i> ² (MNHN QU 11181)	<i>Smutsia gigantea</i> ³ (SAM-POL-21793)	<i>Smutsia gigantea</i> (adult) ³		<i>Smutsia gigantea</i> (juvenile) ⁴ (USNM 268914)	<i>Smutsia temminckii</i> ³	<i>Phataginus tricuspis</i> ^{1,3,4}		<i>Phataginus tetradactyla</i> ³ (USNM 481806)	<i>Manis pentadactyla</i> ¹ (USNM 308733)
							mean (n = 4)	range			mean (n = 5)	range		
Total length	104.2	76.9	84.2	85 (est)	62.2	88.4	112.5–119.7	105.5	70.8	68.1–73.5	52.9–57.4	48.2–52.5	62.3	
Length of deltopectoral crest	71.8	8.8	66.9					60.8			30.3	26.5–33.3	41	
Proximal width	35.3					29.1	35–40.2	37.1	22	21–22.7	16.5	–	13.2	
Midshaft width	17.4			35 (est)		18.2	17.1–19.1		10.4	9.4–11.4	10.3	–	7.8	
Distal width	51.9	28.8	44		27.1	46.3	52.8–60.7	54.9	33.5	31.4–35.6	23.7	22–26.8	28.8	
Width of entepicondylar process	25.1	61.6	13.6					16.9		10.3	9.2–12.4		10.9	

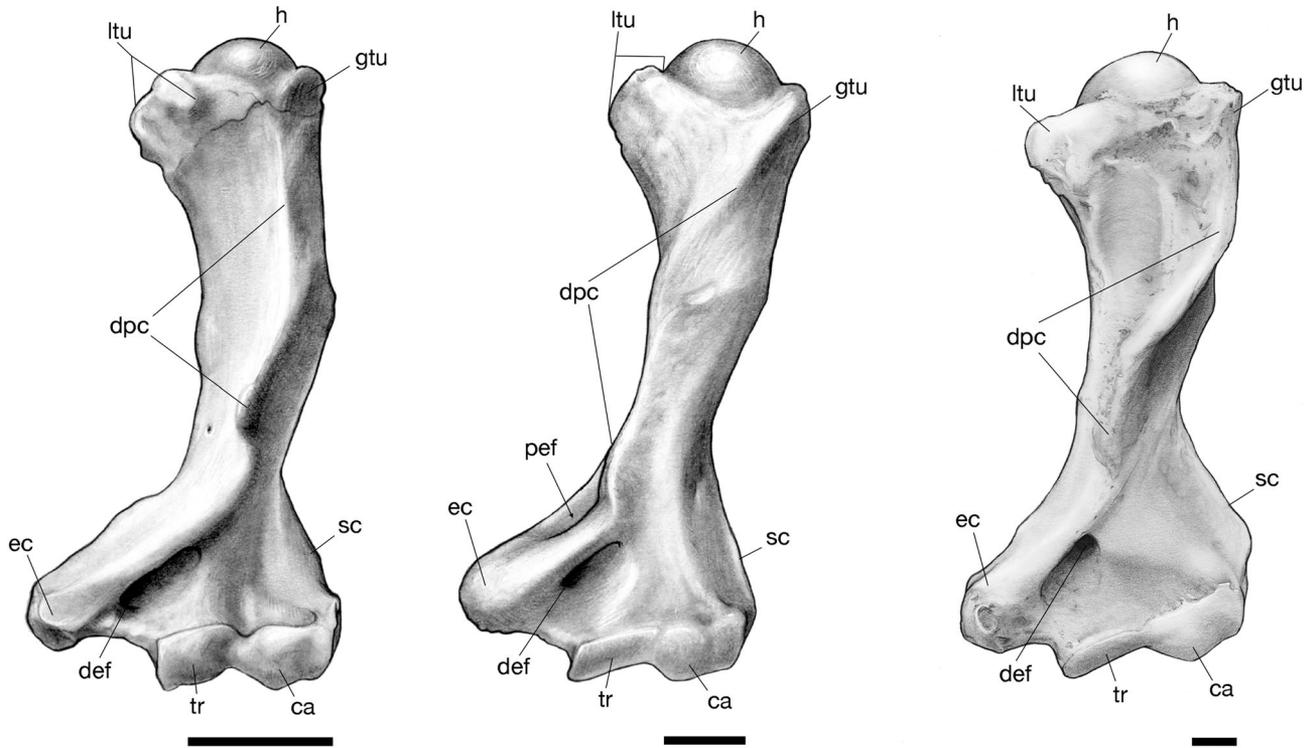


FIGURE 4. Left humeri of extant pangolins in anterior view: *Phataginus tricuspis* CM 16206 (left), *Manis javanica* USNM 198852 (middle), *Smutsia gigantea* AMNH 53858 (right). Drawings of *P. tricuspis* and *M. javanica* from Gaudin et al. (2009).

species and the Pliocene specimen of *S. gigantea*, where it may be pathological (Botha and Gaudin 2007). The capitulum is spherical, with a distinct lateral extension. In *S. gigantea*, this lateral extension reaches further proximally than the capitulum itself, whereas the reverse is true for the more bulbous capitulum of *S. temminckii*. In the fossil, the two are roughly equal in proximal extent. The supinator crest is quite well developed in the new fossil humerus, extending proximally past the distal end of the deltopectoral crest. It is much larger than the supinator crest in either extant species of *Smutsia*.

It is clear, based on our observations, that the new fossil humerus recovered from Grăunceanu not only derives from a pangolin, but very likely from the ground pangolin genus *Smutsia*. Although it is more similar to the giant pangolin (*S. gigantea*) than the ground pangolin *S. temminckii* in most respects, including size, it does share some points of resemblance with *S. temminckii* (e.g., globose capitulum and shallow entepicondylar notch, lack of groove lateral to deltopectoral crest), and it also has noteworthy differences from both the extant species, including a larger supinator crest (likely a primitive feature that characterizes other fossil pangolins – see Gaudin et al., 2006, 2009, 2016), an enlarged greater tubercle, and a more elongated and narrower entepicondyle. Given the balance of evidence, we believe that this specimen merits designation as a separate species.

DISCUSSION

The pangolin fossil we report here, which we assign to the species *Smutsia olteniensis* sp. nov., from Grăunceanu, Romania substantially updates the fossil record of pangolins in Europe. Because of the uncertainty surrounding the fossil of *Manis hungarica* previously described by Kormos (1934) from the site of Villány 3, Hungary, VGr.2362 now represents the

youngest (and presently only) fossil pangolin from the European Pleistocene and one of only a handful of fossil pangolins from the Pleistocene worldwide.

The presence of pangolins in Pleistocene Europe has substantial biogeographic implications for understanding pangolin evolution. Prior work (e.g., Gaudin et al., 2009; Gaubert et al., 2018) suggests pangolins may have been broadly distributed across Eurasia and into North America in the Eocene and may have maintained a broad Eurasian distribution into the Miocene. In the middle Miocene, a shift to cooler and more arid climates occurred due to Antarctic ice sheet expansion and the Himalayan orogeny, resulting in tropical and subtropical forests largely being replaced by more seasonal deciduous forests and woodlands (Agusti, 2007; Begun et al., 2012; Patnaik, 2016; Gilbert et al., 2020). This climatic shift could easily have fragmented the biogeographic range of Miocene pangolins and restricted this clade to the more tropical environments of Africa and Southeast Asia, as likely occurred for other taxa such as hominoids (Begun et al., 2012) and tragulids (Guzman-Sandoval, 2018). However, while the previous lack of more recent (i.e., Plio-Pleistocene) pangolin remains from Europe supported this interpretation, in light of the now well-documented presence of *Smutsia olteniensis* sp. nov. from eastern Europe c. 2 Ma this biogeographic scenario must be reassessed. In fact, if the original record of *M. hungarica* from Villány 3, Hungary is valid, then pangolins may have been relatively broadly distributed (but likely at low population densities) across eastern/central Europe in the early Pleistocene (specifically MN17).

It is particularly important that the specimen from Grăunceanu is clearly attributed to the genus *Smutsia*, which is found today only in Africa. The fossil record for *Smutsia* currently begins with specimens from Langebaanweg, South Africa, which is dated to the early Pliocene (~5 Ma; Botha and

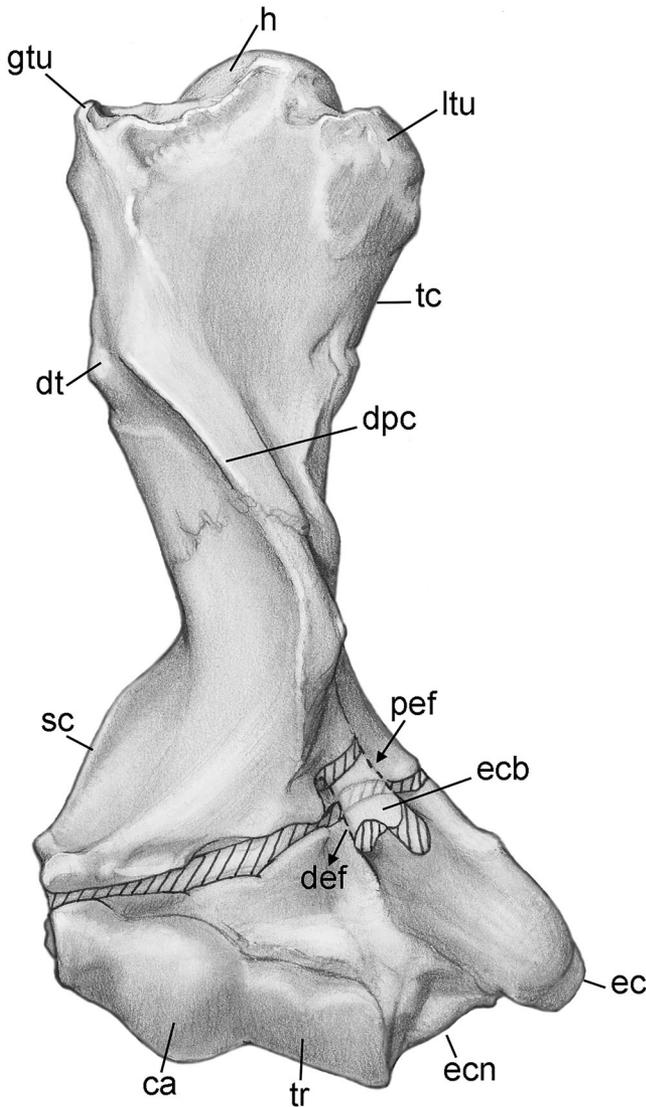


FIGURE 5. Reconstruction of VGr.2362, holotype of *Smutsia olteniensis*, sp. nov., in anterior view, with entepicondylar bridge reconstructed based on broken surfaces of the bone. Abbreviations can be found in the main text.

Gaudin, 2007). Originally identified as *Manis gigantea*, this partial skeleton is now placed in *Smutsia gigantea* (Gaudin, 2010). As noted above, the new fossil closely resembles *S. gigantea*, with some particular similarities to the Pliocene material from Langebaanweg (e.g., in the morphology of the entepicondylar bridge), but it also shares some traits with extant *S. temminckii*, and exhibits some unique features, justifying its allocation to a separate species. Without a phylogenetic analysis (which is not feasible for a single humerus), we cannot say whether this new species is more closely related to one of the other two species in the genus or represents a sister-taxon to both. That said, its allocation to this genus represents important new data for any attempts to reconstruct the biogeographic history of modern pangolins.

There are two possible scenarios to explain the presence of *Smutsia olteniensis* sp. nov. in Pleistocene Europe and to explain the present-day biogeography of members of the genus *Smutsia*. One possibility is that pangolins were present in Europe throughout the Miocene, Pliocene, and into the

Pleistocene. Pangolins are known from the early Miocene of western and central Europe in the form of the species *Necromanis franconica* (Koenigswald, 1999; Crochet et al., 2015), but their presence between ~13.5 Ma and ~2 Ma has yet to be documented. If this is indeed the case then this could suggest that the genus *Smutsia*, and perhaps all African pangolins, originally had a European origin, as has been suggested for the order Pholidota as a whole (Gaudin et al., 2009). If this scenario is valid then additional exploration of Neogene localities in Europe has the potential to shed further light on the origin of modern pangolins.

Alternatively, it may be that the absence of pangolin fossils from Europe during this more than 10-million-year gap represents a genuine absence of these animals from the continent. The presence of several *Smutsia* fossils in Africa from ~5 Ma (S. Africa; Botha and Gaudin, 2007) and ~3 Ma (Uganda; Pickford and Senut, 1991) could indicate that this genus does indeed have an African origin somewhere in the middle to late Miocene or very early Pliocene, and that some representatives of this genus then dispersed back into Europe. The timing of this potential dispersal back into Europe is unclear, however. One possibility is that members of *Smutsia*, after originally evolving in Africa, redispersed back into Europe during the late Miocene, perhaps around the time of the Messinian Salinity Crisis ~5.59 Ma (Krijgsman et al., 1999). This is consistent with other evidence for a broader faunal exchange between Africa and Eurasia at this time (e.g., Gibert et al., 2013), including the first appearance of macaques in Europe (Alba et al., 2018b). Alternatively, *Smutsia* could have dispersed back into Europe during the late Pliocene or early Pleistocene, perhaps coinciding with similar dispersals of *Hippopotamus*, *Megantereon*, and even *Homo* sp. (e.g., O'Regan et al., 2011). Unfortunately, current evidence does not allow us to differentiate among these scenarios for pangolins (i.e., cryptic presence in Europe vs. disappearance and redispersal back into Europe), though hopefully future fossil finds will shed light on this issue.

As evidenced here, at the very least pangolins were present in Europe by ~2.2–1.8 Ma, which has interesting paleoenvironmental implications. Myriad lines of evidence clearly demonstrate that Africa and Eurasia were experiencing very arid conditions and open habitats were expanding in the early Pleistocene (Denton, 1999; deMenocal, 2004; Lisiecki and Raymo, 2007; Leroy et al., 2011; Alçiçek et al., 2017; Palombo, 2018). Though this is seemingly difficult to reconcile with the tropical habitat preferences of most pangolins, *Smutsia temminckii* (the bipedal ground pangolin of southern, eastern, and central Africa) inhabits relatively open savannah woodlands (Pietersen et al., 2014). Though we do not have enough information from the fossil specimen reported here to assess its preferred habitat type, Gräunceanu has been reconstructed as relatively open with some nearby woodlands and water resources (Curran et al., 2021). Thus, the youngest pangolin in Europe may have been relatively open-adapted, similar to extant *S. temminckii*.

While VGr.2362 is currently the only pangolin specimen identified from the ORV, there is the potential that continued analyses of the ORV collection, and especially materials from Gräunceanu, may reveal additional pangolin remains. Ongoing research by our team aims to clarify the taphonomy of Gräunceanu and the ORV sites, more precisely date the ORV sites using radiometric techniques, and provide detailed analyses of multiple important taxonomic groupings.

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