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Original article

Suidae (Mammalia, Artiodactyla) from the late Miocene hominoid locality of Alsótelekes (Hungary) ☆

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ABSTRACT

The Suidae from the late Miocene of Alsótelekes (northeastern Hungary, Borsod-Abaúj-Zemplén county) are described and assigned to *Propotamochoerus palaeochoerus* (Suinae) and cf. *Parachleuastochoerus* (Tetraconodontinae). The co-occurrence of these two taxa agrees with a reference to the early Vallesian (MN 9), as previously indicated from biochronological correlation of the small mammal fauna, and suggests the presence of woodland environments, with abundance of below-ground resources and direct access to water. This fits well with the diverse wetlands and riparian forests that characterized Lake Pannon ~10 Ma, as documented in the geographically close site of Rudabánya. The convoluted taxonomy of European Tetraconodontinae is discussed.

Introduction

Suidae are a successful group of even-toed ungulates (Artiodactyla) native to and widespread in Africa and Eurasia (Melletti and Meijaard, 2017). Their past diversity was even greater than today (Harris and White, 1979; Pickford, 1988; Van der Made and Moyà-Solà, 1989; Orliac et al., 2010a). Fossils of the group are known since the Oligocene of Pakistan (Orliac et al., 2010b), with several putative earlier occurrences from East Asia (Ducrocq et al., 1998; Liu, 2001). During the Miocene, suids dispersed and diversified throughout the Old World, providing a valuable source of information for biochronological correlations and paleoecological inference (White and Harris, 1977; Cooke and Wilkinson, 1978; Fortelius et al., 1996a; Souron, 2017). Hungary has yielded an abundant record of Miocene to Pleistocene species (Kormos, 1913; Mottl, 1939; Kretzoi, 1952a, 1952b; Bernor and Fessaha, 2000; Fortelius et al., 2005; Iannucci et al., 2020a).

The early late Miocene (early Vallesian, MN 9, ~11.2–9.7 Ma) represented an optimum of diversity for suids and more generally for mammalian paleocommunities of Europe, with a high number of species adapted to forest environments (Begun et al., 2012; Agustí et al., 2013). This richness notably stands out when compared with the severe impoverishment that occurred soon after, i.e., the demise of woodland-adapted faunas often referred to as the (mid-)Vallesian Crisis (Agustí and Moyà-Solà, 1990; Fortelius et al., 1996a, 1996b; Agustí et al., 2013), even though the scope, magnitude, and pace of this event remain debated (e.g., Koufos, 2006; Casanovas-Vilar et al., 2014; Daxner-Höck et al., 2016). One of the key MN 9 localities is Rudabánya (~10 Ma), in northeastern Hungary, which provides an important window on the diverse early Vallesian ecosystems of central Europe. Alsótelekes is geographically and chronologically close to Rudabánya, and has yielded an abundant and diversified fauna not yet described, including crustaceans, fishes, turtles, snakes, amphibians, rhinos, equids (*Hippotherium*), bovids, cervids, moschids, sciurids, beavers and other rodents, eulipotyphlans, hominoids (*Rudapithecus*) and pliopithecoids (*Anapithecus*). Rudabánya and Alsótelekes are the only sites where the dryopithecin great ape *Rudapithecus hungaricus* is documented (Kretzoi et al., 1974; Kordos and Begun, 2002; Bernor et al., 2004b; Eastham et al., 2016, 2017; de Bonis et al., 2017). Rudabánya and Alsótelekes are also among the rare co-occurrences of a great ape and a pliopithecoid (Kordos and Begun, 2001; Sukselainen et al., 2015; Gilbert et al., 2020). The description of new sites and fossils from this timespan is of crucial relevance for gaining further insights on faunal and paleoenvironmental dynamics, including those related to the evolution and extinction of *Rudapithecus* and other dryopithecins, pliopithecoids, and their replacement with cercopithecoids (Begun, 2015).

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Here, as a first contribution to the study of the large mammal fauna recovered from Alsótelekes, we present the suid remains recovered from the site, discussing their systematic placement as well as the biochronological and paleoecological significance of the species identified.

The locality of Alsótelekes

Alsótelekes is a village in Borsod-Abauj-Zemplen county, at the southwestern edge of the Rudabánya mountains, an elongated chain of SW-NE striking bluffs in northeastern Hungary (Fig. 1). Quarrying at the nearby still active Triassic gypsum quarry (Zelenka et al., 2005), has led to the exposure of the overlying late Miocene fluvio-lacustrine sediments. In the early 1990s, a small "*Hipparion*" fauna was recovered from surface collecting and screen washing (Kordos, 1997). Some still undescribed large mammals were recovered at that time along with a small sample of eulipotyphlans and an unspecified number of *Anapithecus* specimens (Kordos, 1997). The insectivores were briefly described and attributed to MN 9, leading to the conclusion that Alsótelekes is close in age to, but possibly slightly older than the nearby rich late Miocene site of Rudabánya (Mészáros, 1999). Mészáros (1999) also concluded that the damage to the insectivore teeth suggests transport to some distance prior to deposition. Other fossils, including the suid described here as well as the *Rudapithecus* fossils, suggest minimal transport. Work is underway to analyze the geology and taphonomy of the Alsótelekes locality.

In 2015, 2016, and 2018, systematic excavations were undertaken following renewed surface collections by DRB at the edge of the quarry. Three localities have been identified at Alsótelekes. The main locality, Alsótelekes 2 (GPS coordinates: 48°25′23″ N, 20°39′30″ E), has yielded the vast majority of the fossils, including all the hominids and the suids described here. It occurs on a narrow ledge onto which a 4 × 21 meters grid was mapped. All specimens recovered from these excavations are documented within a centimeter horizontally and vertically, within their 1 × 1 meter map square. The sediments are similar to the hominoid bearing R. II locality at Rudabánya, with alternating lignite and clay. The clay sediments are richer in terrestrial and freshwater gastropods than R. II and the clay is less calcareous. The presence of fish and crustacean fossils also distinguishes Alsótelekes from Rudabánya. To date we have only recovered fauna from a single clay layer in the sequence, suggesting a relatively short time of accumulation.

Material and methods

The Suidae remains recovered from Alsótelekes are housed in the Geological Museum of the Mining and Geological Survey of Hungary in Budapest. The studied sample was compared with other remains stored in the same museum and in other institutions (see abbreviations below).

Measurements were taken using a digital caliper to the nearest 0.1 mm and are provided in Table 1. Dental terminology and measurements mainly follow Van der Made (1996). Upper and lower teeth are in upper and lower case, respectively, and a "d" precedes deciduous teeth (e.g., P3 = upper third premolar; di2 = lower second deciduous incisor). Dental rows are measured along the alveoli on the buccal side. Measurements of dental rows are inclusive of the indicated teeth (e.g., m1-m3 is the length of the lower molar row).

Synonymy between Suinae genera follows Iannucci et al. (2021), while the convoluted taxonomy of the European Tetraconodontinae is discussed more extensively where appropriate throughout the text. *Parachleuastochoerus* is abbreviated to *Pa.* and *Propotamochoerus* to *Pr.*, to avoid confusion when referring to different species.

Institutional abbreviations: **AFS**: Museum of Natural History, Accademia dei Fisiocritici, Siena; **HNHM**: Hungarian Natural History Museum, Budapest; **IGF**: Natural History Museum of the University of Florence, section of Geology and Paleontology; **MBFSZ**: Geological Museum of the Mining and Geological Survey of Hungary, Budapest; **MNCN**: National Museum of Natural Sciences, Madrid; **NMB**: Natural History Museum, Basel; **NHMMZ**: Mainz Natural History Museum/State Collection of Natural History of Rhineland-Palatinate.

Measurements abbreviations: **BLD**: buccolingual diameter in incisors; **MDD**: mesiodistal diameter in incisors; **ID-MP**: Infradentale-mental prominence (length of the mandibular symphysis); **HMm1**: height of the mandible in front of m1; **WMm1**: width of the mandible in front of m1; **L**: length; **W**: width (-m: mesial; -d: distal/second lobe in a molar; -t: third lobe in a molar);

Fig. 1. Outline of Hungary and geographic location of the late Miocene vertebrate locality of Alsótelekes.

Table 1
Tooth measurements (in mm) of *Propotamochoerus palaeochoerus* from Alsótelekes, Hungary (see material and methods for abbreviations).

Upper teeth	MBFSZ V 2019.15.1.	Lower teeth	MBFSZ V 2017.21.1.
P3 L	15.2	i1 MDD	6.9
P3 Wm	11.0	i1 BLD	9.6
P3 Wd	14.1	i2 MDD	8.6
P4 L	13.9	i2 BLD	10.5
P4 W	16.3	c L	9.2
M1 L	16.5	c W	7.3
M1 Wm	15.7	cLi	8.9
M1 Wd	14.8	cLa	8.8
M2 L	21.7	cD	5.1
M2 Wm	18.7	p1 L	10.4
M2 Wd	17.9	p1 W	5.3
P3-M2	63.4	p2 L	12.4
P3-P4	29.2	p2 Wm	5.2
		p2 Wd	5.5
	MBFSZ V 2017.127.1.	p3 L	13.9
dP4 Wm	11.8	p3 Wm	7.3
		p3 Wd	7.5
		p4 L	15.8
		p4 Wm	10.6
		p4 Wd	12.2
		m1 L	18.1
		m1 Wm	12.1
		m1 Wd	12.8
		m2 L	21.4
		m2 Wm	14.7
		m2 Wd	15.1
		m3 L	28.4
		m3 Wm	14.7
		m3 Wd	14.0
		m3 Wt	11.3
		ID-m3	167.1
		c-m3	139.7
		ID-MP	53.1
		p1-p4	65.7
		p2-p4	43.4
		p1-m3	135.8
		p2-m3	114.8
		m1-m3	68.3
		HMm1	38.8
		WMm1	28.9

cLa: length of the labial side in c; **cLi**: length of the lingual side in c; **cD**: length of the distal side in c.

Systematic paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Suidae Gray, 1821
Subfamily Suinae Gray, 1821
Tribe Dicoryphochoerini Schmidt-Kittler, 1971
Genus ***Propotamochoerus*** Pilgrim, 1925

Type species: *Propotamochoerus hysudricus* (Falconer and Cautley, 1847).

Propotamochoerus palaeochoerus (Kaup, 1833)

Type specimen: Din 3, right mandible with p3-m3, housed in Darmstadt (Hessisches Landesmuseum). First described by Kaup (1833), selected as the lectotype of the species by Hünermann (1968).

Type locality: Eppelsheim, Dinotheriensande (Germany).

Age of the type locality: Late Miocene, early Vallesian, MN 9 (but see Böhme et al., 2012).

Referred material from Alsótelekes: MBFSZ V 2019.15.1., left fragmentary maxilla with P3-M2 (Fig. 2(A)); MBFSZ V 2017.127.1., fragment of left dP4 (Fig. 2(B)); MBFSZ V 2017.103.1., fragment of right P2 (Fig. 2(C)); MBFSZ V 2017.21.1., almost complete female mandible (Fig. 2(D)); MBFSZ V 2019.78.1., fragment of m3 (Fig. 2(E)); MBFSZ V 2017.78.1., fragment of left di2 (Fig. 2(F)).

Measurements: See Table 1.

Diagnosis (mainly based on personal observations and on Mottl, 1966; Van der Made, 1999): *Propotamochoerus* species smaller than *Pr. provincialis* and *Pr. hyotherioides*, larger than *Pr. wui*; parietal lines meet to form a sagittal crest; P2 smaller than P3; M3/m3 relatively poorly elongated; lower male canines with all three sides convex; p3 usually relatively slender (low Wd); mesial cingulum in m3 usually well-developed.

Description *Maxilla and upper dentition: MBFSZ V 2019.15.1.* (Fig. 2(A)). The specimen is a fragmentary left maxilla that preserves P3-M2 and a small portion of the palatal area. The P3 has a pointed main cusp (paracone), a smaller one located distally along the same mesiodistal axis (metacone), and a well-developed distolingual protocone, separated from the rest of the tooth by a valley (protofossa). In the P4, the two buccal cusps are closer in dimension, though the paracone is the largest cusp in this tooth as well. The protocone is placed more forward than in P3, and the protofossa is filled by accessory developments of the main cusps, giving a more molariform appearance to this tooth. M1 and M2 share the same general structure: they are bilobed teeth with two main cusps in each lobe, and accessory cusplets placed medially along the mesiodistal axis of the tooth. The central accessory cusplet (tetrapreconule), situated in the valley between the two lobes, is relatively isolated, while the mesial and distal ones are part of the mesial and distal cingula, respectively.

MBFSZ V 2017.103.1. (Fig. 2(C)). The specimen is a fragment of a right P2. Only part of the distal portion of the tooth is preserved, including part of the lingually developed protocone. The specimen is not very informative, but it fits with an attribution to *Pr. palaeochoerus*.

MBFSZ V 2017.127.1. (Fig. 2(B)). The specimen is a tooth germ of a left dP4, damaged distally. The tooth is molariform and resembles a permanent M1, but the mesial cingulum is oblique to the medial axis of the tooth. Its mesial width is 11.8 mm, which is in the lower part of the dimensional range of dP4 from Rudabánya ($N = 14$, min = 11.2 mm, mean = 13.1 mm, max = 14.4 mm; Fortelius et al., 2005).

Mandible and lower dentition: MBFSZ V 2017.21.1. (Fig. 2(D)). This is an almost complete female mandible, lacking the ascending rami but preserving all teeth on both sides, apart from i3. It belonged to a young adult, considering the limited wear on the teeth. Preserved incisors, i1 and i2, have a similar morphology, with two mesiodistal ridges and valleys between each of them; they do differ in the orientation of these structures, which are more asymmetric in i2, the buccodistal side being longer. All incisors together form a protruding, shovel-like structure that is employed in suids in their most distinctive feeding activity, rooting. Canines are different from those of male representatives of the species in that they are smaller, they have a groove on their enamel-covered distal facet, and they are oriented more vertically (those of male point outwards). Sexual differences are also evident in the symphysis, which is markedly shorter and less wide than in males (e.g., ID-MP in MBFSZ V 2017.21.1. is 53.1 mm, while in the male mandible MBFSZ V 2021.1.1. from Rudabánya it is 75.3 mm). The p1 has two roots. In p1 there is a main cuspid (protoconid) that is placed forward, which is connected by a ridge to the small precristid. Other premolars have the protoconid placed more centrally, the mesial precristid more developed, and a distinct second cuspid (metaconid) distally to the protoconid. In p2 and p3 the two principal cuspids are almost located along the same mesiodistal axis, while in p4 they are shifted, with the metaconid projecting lingually. Premolars also have a talonid that hosts the hypoconid,

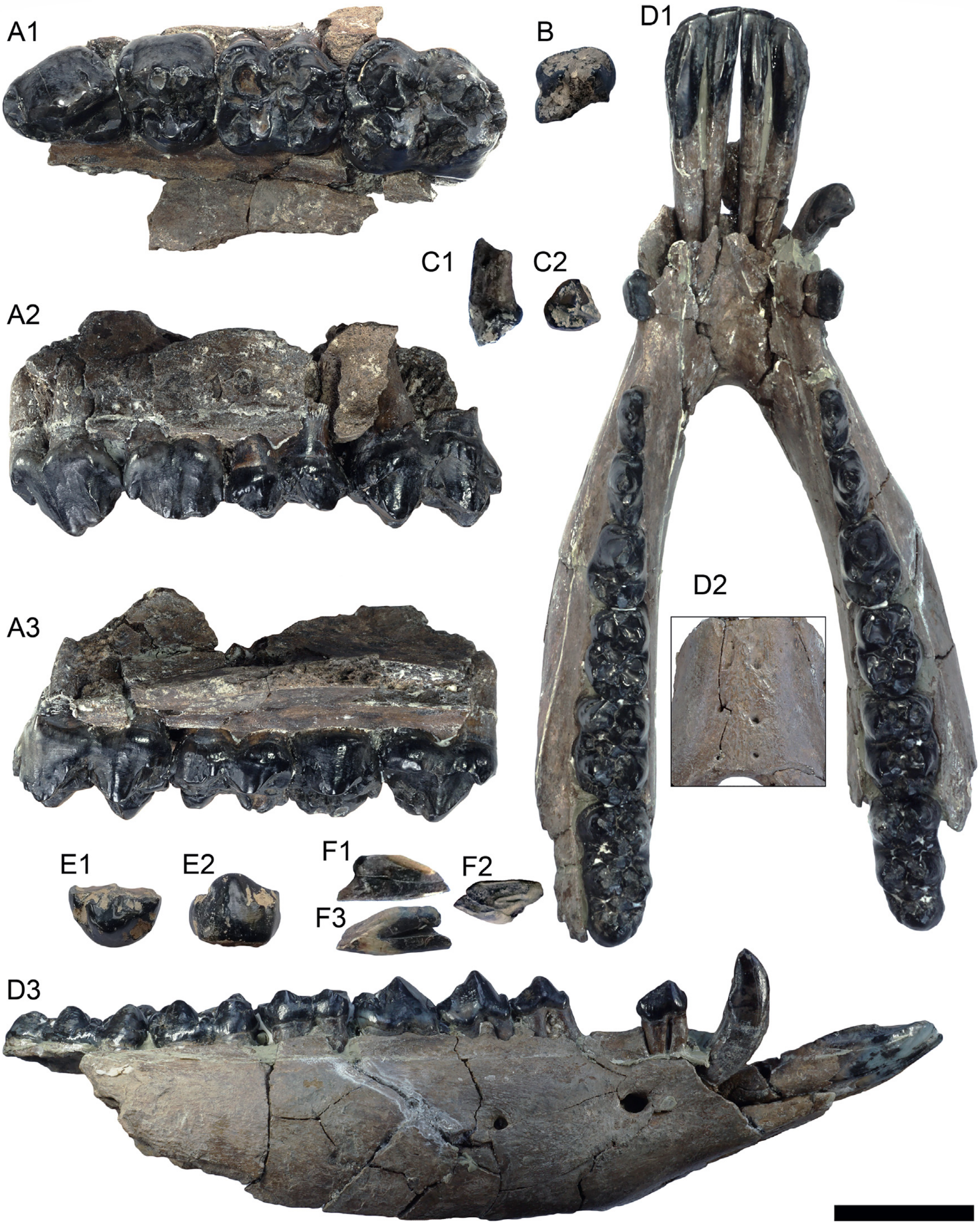

Fig. 2. *Propotamochoerus palaeochoerus* from Alsótelekes (Hungary). A. Left maxilla with P3-M2 (MBFSZ V 2019.15.1.) in occlusal (1), buccal (2), and lingual (3) views. B. Left dP4 fragment in occlusal view (MBFSZ V 2017.127.1.). C. Right P2 fragment (MBFSZ V 2017.103.1.) in lingual (1) and occlusal (2) views. D. Almost complete female mandible (MBFSZ V 2017.21.1.) in occlusal view (1), detail of the symphysis in ventral view (2), and right buccal view (3). E. m3 fragment (MBFSZ V 2019.78.1.) in occlusal (1) and distal (2) views. F. Left di2 fragment (MBFSZ V 2017.78.1.) in mesial (1), occlusal (2), and distal (3) views. Scale bar: 20 mm.

which becomes more developed and separated in p4. All premolars but p4 have a slight concavity on their lingual side. Lower molars have the same general morphology of their upper counterparts, but in comparison they are more symmetric and elongated. The m3 has three lobes, the distal one possessing only one main additional cuspid placed mediodistally, and smaller accessory developments at its sides. Its mesial cingulum is well-developed. The p1 is separated by a small diastema (~5 mm) from the canine, and by a larger one (~15 mm) from the p2. Two mental foramina are present on the mandibular corpi below the p1-p2 diastema and p3, respectively, the former being substantially larger. Three pairs of small openings also occur on the ventral portion of the symphysis. The mesial extremity of the mandible is fragmented but its ventral side is partly preserved.

MBFSZ V 2017.78.1. (Fig. 2(F)). It is a fragment of a left di2, lacking most of the root and the occlusal surface in an advanced wear stage, precluding a description of finer morphological details. The mesial side is almost devoid of enamel, and at its tip there is a marked interstitial facet evidencing the contact surface with di1.

MBFSZ V 2019.78.1. (Fig. 2(E)). A distal fragment of m3, only part of the third lobe of the tooth is preserved, possessing a mediodistal cuspid. The specimen is not very informative, but in its morphology and size is very close to m3 preserved on *MBFSZ V 2017.21.1.*

Remarks

MBFSZ V 2017.21.1. from Alsótelekes is compared with other European mandibles of *Propotamochoerus* and *Sus arvernensis* that preserve the p2-m3 series using a log-ratio diagram (Fig. 3). The standard is the mean value of specimens 22–1067 and 22–1068 of *Pr. palaeochoerus* from Grytsiv (Van der Made et al., 1999), whose teeth are in a stage of wear intermediate between other specimens of *Pr. palaeochoerus* considered herein (MBFSZ V 2017.21.1. from Alsótelekes and MBFSZ V 2021.1.1. from Rudabánya, locality II). It would be desirable to focus the comparison only on remains of similar wear (Zeder and Lemoine, 2020), but the fossil record of these species is too limited to allow it. The diagram shows that *Pr. palaeochoerus* is smaller than *Pr. provincialis* and larger than *S. arvernensis*, but there is overlap or little difference in several measurements. Within *Pr. palaeochoerus*, the female mandible from Alsótelekes is smaller than the male mandible from Rudabánya, although differences are not marked, aligning with the low sexual size dimorphism observed in tooth measurements of extant suid species (Iannucci et al., 2020b). On the other hand, as previously noted sexual differences in the symphysis are pronounced, as in other suid species (Souron, 2012; Boisserie et al., 2014). Distal widths of p2 and p3 are quite variable, but larger in *Pr. provincialis*, while p4 proportions are more similar between the different species compared. Differences in measurements of m1, especially m1 L, vary more in relation to wear stage than to taxonomy. Wear influences m2 variation as well, but the tooth is a more consistent indicator of the size differences between taxa. In m3, proportions of the different species seem generally similar, even if with fluctuations in the relative development of widths, especially m3 Wt. Considering differences in proportions along the dental row, it can be stressed that *S. arvernensis* has a relatively large m3, while *Pr. palaeochoerus* has proportionally larger premolars. Comparing the p4 L/m3 L ratio this characteristic becomes evident (Fig. 4). Moreover, it is worth noting that despite differences in size, this ratio aligns *Pr. provincialis* with *S. arvernensis*, allowing a separation from *Pr. palaeochoerus* that has p4 at least as long as half of m3 (i.e., p4 L/m3 L > 0.5). The individual from Alsótelekes falls close to the mean values of other samples of *Pr. palaeochoerus*.

The attribution of the Alsótelekes suine to *Pr. palaeochoerus* is strongly supported by the diagnostic morphology and dental proportions of the recovered specimens, showing e.g., large p4 with protoconid and metaconid not aligned along the same mesiodistal axis; slender p3; m3 relatively poorly elongated, with a pronounced mesial cingulum.

Propotamochoerus is a Eurasian genus with at least five recognized species: *Pr. hyotherioides*, *Pr. hysudricus*, *Pr. palaeochoerus*, *Pr. provincialis*, and *Pr. wui* (Hünermann, 1968; Schmidt-Kittler, 1971; Pickford, 1988, 2013; Van der Made and Moyà-Solà, 1989; Van der Made and Han, 1994; Fortelius et al., 1996a; Van der Made et al., 1999; Geraads et al., 2008; Sein et al., 2009; Hou et al., 2019; Iannucci et al., 2021). Isolated teeth of these species are of similar morphology and partly overlap in size, and hence they are often difficult to identify. For completeness it is worth mentioning that, in some cases, the same applies to remains of the Pliocene *S. arvernensis* (Azzaroli, 1952; Iannucci et al., 2022). For instance, Suidae from the early Pliocene of Alcoy (Spain) have been reported either as *Pr. palaeochoerus* (Gervais, 1853; Van der Made and Belinchón, 1991) or *S. arvernensis* (Crusafont and de Villalta, 1955; Hünermann, 1971) – in the former case substantially extending the chronological range of the species (Van der Made and Moyà-Solà, 1989). Eventually this material was assigned to *S. arvernensis* after the description of more diagnostic elements (Montoya et al., 2006). A specimen of *S. arvernensis* from Collepardo (Italy) displays a weak sagittal crest, but this trait is not as pronounced as the condition observed in *Pr. palaeochoerus*, and the morphology of the neurocranium differs in many respects

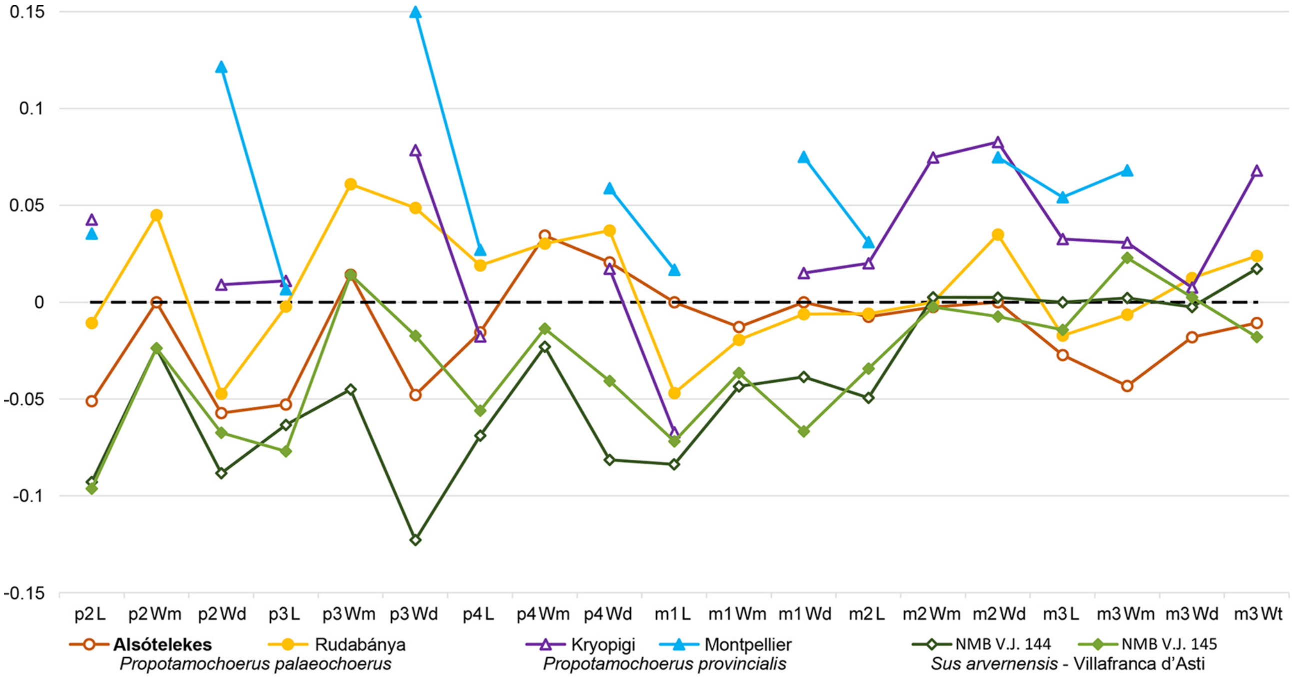

Fig. 3. Log-ratio diagram of *Propotamochoerus palaeochoerus* from Alsótelekes (MBFSZ V 2017.21.1.) and Rudabánya, locality II (MBFSZ V 2021.1.1.); *Pr. provincialis* from Kryopigi (KRY1094; Lazaridis, 2015) and Montpellier (FSL 40 072; Pickford, 2013); *Sus arvernensis* from Villafranca d'Asti (NMB V.J. 144, NMB V.J. 145). The standard is the mean value of specimens 22–1067 and 22–1068 of *Pr. palaeochoerus* from Grytsiv (Van der Made et al., 1999).

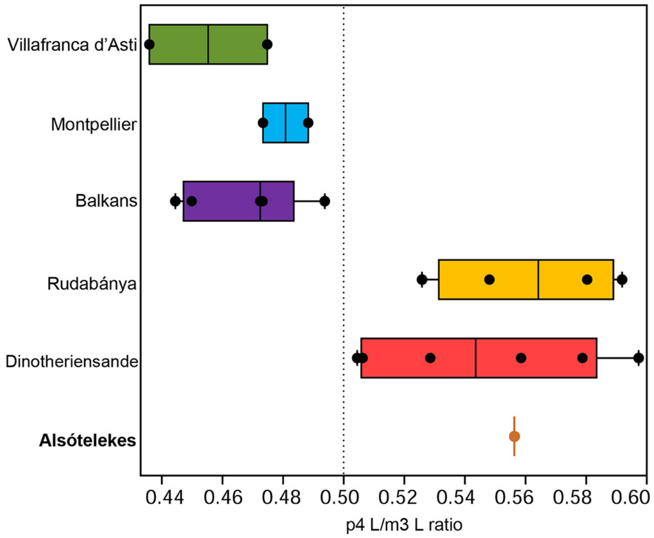

Fig. 4. Boxplot (whiskers from minimum to maximum values) of the p4 L/m3 L ratio of *Propotamochoerus palaeochoerus* from Alsótelekes (MBFSZ V 2017.21.1.), Rudabánya, locality II (MBFSZ; Fortelius et al., 2005), Dinotheriensande (NHMMZ; Hünermann, 1968), *Pr. provincialis* from the Balkans (Geraads et al., 2008; Lazaridis, 2015) and Montpellier (Pickford, 2013), and *Sus arvernensis* from Villafranca d'Asti (NMB).

(Iannucci et al., 2022). Another presumed late occurrence of *Pr. palaeochoerus*, from the latest Miocene of Maramena (Greece, Hellmund, 1995), was based on material first reassigned to *Propotamochoerus* sp. (Van der Made, 1999; Geraads et al., 2008) and then to *Pr. provincialis* (Iannucci et al., 2021). Once excluded the putative late records, the chronological distribution of *Pr. palaeochoerus* appears mainly limited to MN 9, with a few earlier (MN 7 + 8, Sant Quirze, Saint Gaudens) and a tentative later (MN 10, Can Jofresa) reports (Ginsburg, 1974; Van der Made and Moyà-Solà, 1989; Van der Made, 1990). *Propotamochoerus palaeochoerus* is the only of the aforementioned species of Suinae present in the Vallesian of Europe (Hünermann, 1968).

Subfamily Tetraconodontinae Lydekker, 1876
Tribe Parachleuastochoerini Van der Made, 1999
Genus ***Parachleuastochoerus*** Golpe-Posse, 1972
Type species: *Parachleuastochoerus crusafonti* Golpe-Posse, 1972.
Type locality: Can Llobateres (Spain).

Fig. 5. A. cf. *Parachleuastochoerus* from Alsótelekes (Hungary), left I2 fragment (MBFSZ V 2017.13.1.). B. *Propotamochoerus palaeochoerus* from Rudabánya, locality II (Hungary), left I2 (MBFSZ V.21162). Both specimens in buccal (1), lingual (2), and occlusal (3) views. Scale bar: 10 mm.

Age of the type locality: Late Miocene, early Vallesian, MN 9.
cf. *Parachleuastochoerus*
Fig. 5

Referred material from Alsótelekes: MBFSZ V 2017.13.1., fragment of left I2 (Fig. 5(A)).

Description: The only specimen attributed to cf. *Parachleuastochoerus* is a fragment of a left I2. The crown is preserved but it lacks almost all the root. The tooth is moderately worn but details of crown morphology are still observable. In occlusal view, it has an oval outline, with a small concavity on the lingual side. This concavity divides the tooth into two, while in *Pr. palaeochoerus* the mesial part is about one third of the whole occlusal surface. In fact, in comparison with I2 of *Pr. palaeochoerus*, this specimen is less elongated, especially distally (postcrista). Moreover, the buccomesial wear facet is orientated more outwards in MBFSZ V 2017.13.1., suggesting a slightly different occlusion with i2.

Remarks: The I2 recovered from Alsótelekes differs biometrically from those of the other suid present at the site, *Pr. palaeochoerus*: MBFSZ V 2017.13.1. MDD × BLD = 12.8 × 7.2 mm; *Pr. palaeochoerus* from Rudabánya (*N* = 7) MDD × BLD: min = 15.1 × 7.2 mm, mean = 15.7 × 7.5 mm, max = 16.8 × 7.8 mm (Fortelius et al., 2005); *Pr. palaeochoerus* from Gau-Weinheim (Dinotheriensande, NHMMZ; *N* = 5) MDD × BLD: min = 15.4 × 6.2 mm, mean = 16.7 × 7.5 mm, max = 18 × 8.7 mm. Considering other European Miocene species, Suinae have larger and/or more elongated I2, and Listriodontinae are markedly divergent (Van der Made et al., 2014). Compared with Tetraconodontinae, a subfamily whose taxonomy remains controversial (see below), the specimen is larger than I2 of *Pa. crusafonti* (Pickford, 1981) and smaller than I2 assigned to *C. simorrensis* and *Pa. steinheimensis* (Van der Made et al., 2014).

Measurements and morphology of the I2 MBFSZ V 2017.13.1. are compatible with those of a relatively small tetraconodont suid, smaller than *C. simorrensis* and *Pa. steinheimensis* and larger than *Pa. crusafonti* (Pickford, 1981; Van der Made et al., 2014). An attribution to *Parachleuastochoerus* seems the most reasonable, but considering the paucity of available comparative material we favor an open nomenclature, assigning MBFSZ V 2017.13.1. to cf. *Parachleuastochoerus*.

The name *Parachleuastochoerus* was coined by Golpe-Posse (1972) for the small-sized *Pa. crusafonti* from Can Llobateres, envisioning affinities with the Asian *Chleuastochoerus* Pearson, 1928 (hence the name). Pickford (1981) recognized that the species instead belongs to Tetraconodontinae.

The taxonomy of European Tetraconodontinae has been the subject of intense debate over the last couple of decades, with radically different classifications proposed (Bernor et al., 2004a; Fortelius et al., 2005; Daxner-Höck and Bernor, 2009; Pickford, 2014, 2016; Pickford and Laurent, 2014; Van der Made et al., 2014; Van der Made, 2020). Historically, most samples have been included within *Conohyus simorrensis* (Lartet, 1851), occasionally evidencing differences from *C. steinheimensis* (Fraas, 1870) (Stehlin, 1899; Thenius, 1952); it is only after Chen (1984) that the separation of the two forms has been widely accepted. The main divergent feature supporting the identification of two species is the presence of relatively smaller P3/p3 and P4/p4 in *C. steinheimensis* (Chen, 1984; Stehlin, 1899; Thenius, 1952).

Heissig (1989) named *C. huenermanni* based on a fragmentary mandible from Breitenbrunn, seeing it as evolving through size reduction from the line of *C. steinheimensis.* He also considered the species present within the material from the Dinotheriensande described by Hünermann (1968), although doubting a Vallesian age for Breitenbrunn. Several authors accordingly referred Breitenbrunn to the late MN 7 + 8 (e.g., Van der Made, 1999; Eronen and

Rössner, 2007; Seehuber, 2008), although references to MN 6 (Pickford, 2014, 2016) or to MN 9 (Bernor et al., 2004a) have also been suggested.

Van der Made (1990) transferred *C. huenermanni* into *Parachleuastochoerus*, assigned to the species all the material previously attributed to *Pa. crusafonti* (Golpe-Posse, 1972; Pickford, 1981) apart from that from Can Llobateres and La Tarumba (MN 10), and stressed the biochronological importance of the size reduction in the *Pa. huenermanni*–*Pa. crusafonti* lineage. Pickford (1993) agreed on the identification of two species within *Parachleuastochoerus*, emphasizing their full specific status and underlining again their potential value for correlations. Van der Made (1990) still placed *Pa. steinheimensis* within *Conohyus* but suggested an inclusion of the species in *Parachleuastochoerus*, eventually formalized by Fortelius et al. (1996a). Van der Made (1999) provided a biometric review of Tetraconodontinae, detailing dimensional trends within *Conohyus* and *Parachleuastochoerus* and using them for diagnosing different species.

Bernor et al. (2004a) named *Conohyus olujici* from the early Miocene of Lučane and reassigned the species *C. huenermanni* and *C. steinheimensis* to *Conohyus*, while retaining in *Parachleuastochoerus* only *Pa. crusafonti* and the sample from Rudabánya, soon after named *Pa. kretzoii* by Fortelius et al. (2005). Daxner-Höck and Bernor (2009) followed the same scheme and assigned the material from Atzelsdorf to *Pa. kretzoii*, expanding the chronological range of the species to the early MN 9 (~11.2 Ma).

Van der Made et al. (2014) retained three species within *Parachleuastochoerus*, namely *Pa. steinheimensis*, *Pa. huenermanni*, and *Pa. crusafonti*, further developing the interpretation of the lineage *Pa. huenermanni*–*Pa. crusafonti* as an offshoot that progressively acquired smaller dimensions, while *Pa. steinheimensis* evolved towards a larger size (Van der Made, 1990, 1999; Fortelius et al., 1996a). Van der Made et al. (2014) also rejected the validity of *C. olujici* and *Pa. kretzoii*, synonymizing them with *Pa. steinheimensis* and *Pa. huenermanni*, respectively.

Pickford (2014, 2016) and Pickford and Laurent (2014) adopted a splitter approach, partly separating *Parachleuastochoerus* into the newly named *Versoporcus* and recognizing a total of six species: *V. grivensis* (Gaillard, 1899), *V. steinheimensis*, *Pa. crusafonti*, *Pa. huenermanni*, and *Pa. valentini* (Filhol, 1882). Contrary to what this plethora of names would suggest, separations are still mainly based on biometry. The only cranial features highlighted as distinctive between *Parachleuastochoerus* and *Versoporcus* are the position of the root of the zygomatic arch, departing from the maxilla above M2 in *Parachleuastochoerus*, while above P4 in *Versoporcus*; and the position of the posterior choanae on the palate, far behind M3 in *Parachleuastochoerus*, while in line with the distal end of M3 in *Versoporcus* (Pickford, 2014, 2016). However, these characters are based on MNHN HGP17 from Le Fousseret or St. Gaudens (see Van der Made, 2020, for discussion) for *Pa. valentini* and SMNS M 20223 from Steinheim (Chen, 1984; Pickford, 2014) for *V. steinheimensis*. Considering that *Pa. valentini* is included in *C. simorrensis* by Van der Made (2020), the morphology underlined as diagnostic for *Versoporcus* by Pickford (2014, 2016) would apply to *Parachleuastochoerus* according to Van der Made (2020), while that of *Parachleuastochoerus* (*sensu* Pickford, 2014, 2016) would apply to *Conohyus* (*sensu* Van der Made, 2020). No adequately preserved remains of the species named *C. huenermanni*, *Pa. kretzoii*, and *Pa. crusafonti* are known that allow to observe these features.

It is predictable that with the recovery and description of new material our comprehension of the evolution and systematics of European Tetraconodontinae will improve, but up to now most of the samples are represented by isolated teeth, with few localities yielding abundant remains and having robust independent age constraints (Van der Made et al., 2014; Pickford, 2016). From a biometric perspective the long recognized relative enlargement of third and fourth premolars is still the best distinction criterion for separating species of the subfamily (Chen, 1984; Stehlin, 1899; Thenius, 1952). This led to the identification of two groups, one including the "classical" samples of *C. simorrensis* (e.g., Göriach; Thenius, 1956), the other *Pa. steinheimensis* and the type species of *Parachleuastochoerus*, *Pa. crusafonti* (Pickford, 2014; Van der Made et al., 2014). Accordingly, these two clusters can be referred to as *Conohyus* (relatively larger third and fourth premolars) and *Parachleuastochoerus* (same teeth relatively smaller). Within both genera, different species are recognized, mainly separated due to their size (Pickford, 2014, 2016; Van der Made, 2020). Envisioning gradually evolving lineages, the delimitation of chrono(sub)species is a rather subjective exercise, but for a subdivision to be valid and useful, it is at least necessary that named taxa allow an effective allocation. As for *Parachleuastochoerus*, the samples from Steinheim (early MN 7 + 8) and Can Llobateres (late MN 9) include abundant remains from two reference localities for the European biochronological framework (Mein, 1990; de Bruijn et al., 1992), providing convincing evidence of the biometric and chronological separation between *Pa. steinheimensis* and *Pa. crusafonti*. The attribution of the samples of intermediate dimension and age remains open to controversy. The material from Breitenbrunn is limited to the holotype mandible of *Pa. huenermanni*, whose presence has been stressed for correlating the deposit to the late MN 7 + 8 (Seehuber, 2008). There is a clear risk of circularity in this reasoning, and the other few species reported from Breitenbrunn do not provide further chronological constraints (Seehuber, 2008). Even assuming that the chronology of the site is correct, it is worth noting that measurements of *Pa. huenermanni* from Breitenbrunn fall in the lower part of the dimensional range of *Pa. steinheimensis* (Van der Made et al., 2014). The most important morphological feature underlined by Heissig (1989) in separating *Pa. huenermanni* from *Pa. steinheimensis* was the presence of three roots in p3 instead of two as in *C. simorrensis*. However, as pointed out by Fortelius et al. (1996a), there is variability in the degree of fusion of the roots when large samples are considered. Therefore, it cannot be ruled out that the material from Breitenbrunn belongs to a small individual of *Pa. steinheimensis* and it seems necessary to consider *Pa. huenermanni* a *nomen dubium* (*nomen vanum*, *sensu* Mones, 1989) that should be restricted to the holotype.

Discussion

Biochronology

The suid remains recovered from Alsótelekes are ascribed to cf. *Parachleuastochoerus* and *Pr. palaeochoerus*. These suids co-occur in several early Vallesian (MN 9) localities (e.g., Can Llobateres, Castell de Barberà, and Rudabánya), thus supporting previous biochronological correlations for Alsótelekes (Mészáros, 1999). Although scanty, the material of cf. *Parachleuastochoerus* from Alsótelekes is substantially larger than that of *Pa. crusafonti* from Can Llobateres (Golpe-Posse, 1972; Pickford, 1981). It is often assumed that *Pa. crusafonti* is the endmember of a lineage that reduced its size through time (Van der Made, 1990, 1999; Pickford, 1993; Van der Made et al., 2014). This suggests that Alsótelekes – and Rudabánya – predate the latest occurrences of *Parachleuastochoerus*. However, Can Llobateres and Rudabánya are both correlated with the upper part of MN 9 (~10 Ma; Kordos and Begun, 2002; Bernor et al., 2004b; Casanovas-Vilar et al., 2011). The observed biometric differences may therefore partly reflect geographical differences (e.g., due to differences in climate, trophic resources, competition with other sympatric species). For instance, dryopithecins from the same localities are represented by the two related and yet different genera, *Hispanopithecus laietanus* and *Rudapithecus hungaricus* (Begun, 2015; Urciuoli et al., 2021). *Rudapithecus* is also somewhat larger than *Hispanopithecus*, judging from craniodental fossils (Begun, 2002). Van der Made et al. (2014) and Van der Made (2020) assigned the Suidae material from Can Llobateres to four species, namely *Listriodon splendens*, *Pr. palaeochoerus*, *Pa. steinheimensis*, and *Pa. crusafonti*, while only two suids are present in Alsótelekes and Rudabánya. During the late Miocene, regional differences in climate are documented (Jiménez-Moreno et al., 2010), which were conceivably responsible for promoting differential responses of mammalian faunas even at a short geographical scale, as recorded between inland and coastland areas of the Iberian Peninsula (Madern et al., 2018). A study focused on a well-constrained geographical region in southern Italy during the Late Pleistocene revealed pronounced fluctuations in size in the extant wild boar, *Sus scrofa*, between glacial and interglacial stages, accounting for more than 20% variation in m3 L (Iannucci et al., 2020b). It cannot be assumed that extinct species were similarly prone to ecomorphological adaptations to cope with environmental changes, but this possibility should not be ruled out. Differences in m3 L between *Pa. steinheimensis* and *Pa. crusafonti* from their type localities are 27.3%, but both differ less than 20% from *Pa. kretzoii* from Rudabánya (data from Pickford, 1981, 2016; Fortelius et al., 2005). We refrain from attributing the Alsótelekes cf. *Parachleuastochoerus* material to a precise species and we remark that European Tetraconodontinae need an in-depth revision. Given that the assignments are mainly based on quantitative criteria, samples from localities with inadequate sample sizes are difficult to incorporate into current analyses. More effort needs to be done to compare these suid taxa using qualitative morphological criteria.

Paleoecology

The co-occurrence of cf. *Parachleuastochoerus* and *Propotamochoerus* also provides some paleoecological insights on Alsótelekes environment. Stable carbon and oxygen isotope compositions of tooth enamel of *Pr. palaeochoerus* and *Pa. kretzoii* from Rudabánya were analyzed by Eastham et al. (2016), revealing relatively high δ^{13}C and relatively low δ^{18}O values for both species. The recorded values of δ^{13}C were interpreted as suggestive of a consumption of C_3 plants in relatively open canopy environments (Eastham et al., 2016), although the variable feeding behavior of suids precludes easy interpretations (Souron, 2017). In any case, Alsótelekes and Rudabánya deposits accumulated during a period of high precipitation and humidity along the shoreline of Lake Pannon (Magyar et al., 1999; Harzhauser et al., 2007). The low oxygen isotope values observed for suids have been considered indicative of a frequent engagement in rooting (Eastham et al., 2016), as below-ground resources such as tubers and rhizomes are lower in ^{18}O compared to leaf or fruit water (Dunbar and Wilson, 1983; Yakir, 1992), but the obligate drinking behavior of suids likely played an important role in influencing these observations (Kohn et al., 1996; Levin et al., 2006). For instance, low oxygen isotope values are also recorded in *Hylochoerus* (the extant African giant forest hog), a suid whose rooting activity is relatively limited (Lazagabaster et al., 2021). In any case, the consumption of underground resources by suids at Rudabánya is supported by the analysis of enamel strontium/calcium ratios (Eastham et al., 2017). *Propotamochoerus palaeochoerus* displayed the highest δ^{13}C values among the ungulate species compared by Eastham et al. (2016), higher than those of *Parachleuastochoerus* from the same locality and other sites (Aiglstorfer et al., 2014). This suggests that *Parachleuastochoerus* relied more heavily on below-ground resources, while *Pr. palaeochoerus* exhibited a more flexible feeding behavior, consuming a larger proportion of leaves and fruits (Aiglstorfer et al., 2014; Eastham et al., 2016). This is seemingly in contrast with the development of morphological traits, especially the elongation of the incisors, which indicate a better developed rooting behavior in *Pr. palaeochoerus* (Van der Made et al., 2014). It is possible that *Pr. palaeochoerus* accessed below-ground resources proportionally less but more effectively than *Parachleuastochoerus*. Being better adapted to rooting could have been helpful in coping with fluctuations in the availability of different trophic resources, or in allowing feeding in suboptimal conditions or areas. Rooting should not have been too demanding in the soft substrates surrounding Lake Pannon, and it is conceivable that *Parachleuastochoerus* moved over significant distances when feeding, as ^{87}Sr/^{86}Sr isotope composition of *Pa. steinheimensis* from Gratkorn indicates that the species was not a permanent resident but inhabited a wide area (Aiglstorfer et al., 2014). Data on δ^{13}C and δ^{18}O as well as on trace element analysis for *C. simorrensis* from the middle Miocene of Somosaguas revealed heterogeneous values which were considered indicative of a certain degree of omnivory (Domingo et al., 2009, 2012). Reconstructing the environmental preferences of adaptable omnivores such as suids from isotope proxies is complicated by several confounding factors whose impact is difficult to properly evaluate, for instance the obligate drinking behavior of the group (Kohn et al., 1996; Levin et al., 2006), or the consumption of animal matter and aquatic plants (both of which may vary substantially in δ^{13}C values; Souron, 2017), but the coexistence of cf. *Parachleuastochoerus* and *Propotamochoerus* at Alsótelekes is in any case suggestive of woodland environments with abundance of below-ground resources and direct access to water. This fits well with the diverse wetlands and riparian forests that characterized Lake Pannon ~10 Ma (Magyar et al., 1999; Harzhauser et al., 2007; Eastham et al., 2016).

At a coarse scale, during the early late Miocene, the climate was particularly humid and warm, supporting subtropical evergreen forests and generally high levels of biodiversity (Van Dam, 2006; Harzhauser et al., 2007; Böhme et al., 2008, 2011; Pound et al., 2011; Begun et al., 2012; Agustí et al., 2013; Utescher et al., 2017). Alsótelekes and Rudabánya offer one of the few windows on the diverse ecosystems of central Europe before the Vallesian Crisis. This event, around 9.7 Ma, was associated with increased seasonality and lower precipitations and humidity which led to the spread of deciduous woodlands and faunas adapted to more open environments (Fortelius et al., 1996b; Van Dam, 2006; Domingo et al., 2013), although the Vallesian Crisis likely did not occur so abruptly as often portrayed and affected different regions heterogeneously (Agustí and Moyà-Solà, 1990; Fortelius et al., 1996b; Casanovas-Vilar et al., 2014; Daxner-Höck et al., 2016; Madern et al., 2018; Butiseacă et al., 2021). The sharpness of the turnover event may have been exacerbated by the uneven quality of the fossil record between different areas of Europe, by the over-identification of fragmentary remains based on contextual data, and/or by the biochronological attributions of localities that lack independent age constraints (Casanovas-Vilar et al., 2014; Madern et al., 2018), caveats especially relevant considering the case of the Dinotheriensande, one of the most important early Vallesian (MN 9) localities that also contains reworked sediments and fauna (Böhme et al., 2012). Abrupt or gradual, there was nonetheless an evident turnover of mammalian faunas during the late Miocene, which preferentially affected forest-adapted taxa, including suids and hominoids (Agustí and Moyà-Solà, 1990; Fortelius et al., 1996a, 1996b; Begun et al., 2012). A few remains of *Pa. crusafonti* were reported from the late Vallesian (MN 10) of La Tarumba (Van der Made, 1990; Van der Made et al., 2014), but both *Parachleuastochoerus* and *Pr. palaeochoerus* as well as the folivore listriodonts went extinct during the second half of the Vallesian (MN 10). After that, probably taking advantage of the concurrent environmental changes, Suinae became dominant and new species of *Propotamochoerus* and *Hippopotamodon* characterized Turolian (MN 11–MN 13; ~8.9–5.3 Ma) assemblages of Europe (Fortelius et al., 1996a; Iannucci et al., 2021).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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