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ARTICLE

Reassessment of '*Chilotherium wegneri*' (Mammalia, Rhinocerotidae) from the late Miocene of Samos (Greece) and the European record of *Chilotherium*

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ABSTRACT

Chilotherium represents one of the most characteristic rhinocerotid genera during the late Miocene of Eurasia. In Europe, it is restricted to the eastern parts of the continent (Balkan Peninsula and Peri-Pontic region). In total, eight *Chilotherium* species have been described from European material, with Samos (Greece) representing the type locality of four of them. Herein, the type material of '*Chilotherium wegneri*' is revisited. The type cranium is considered lost for the past half-century, but the associated mandible is still housed in the collections of the Geomuseum Münster (Germany). The '*C. wegneri*' type mandible is redescribed and, taking into account the original illustration of the type cranium, compared to other chilotheres from Europe and Asia. Accordingly, the previously proposed synonymy of '*C. wegneri*' and *Chilotherium schlosseri*, which was also initially described from the late Miocene of Samos, is further supported. Lastly, an overview of the late Miocene record of *Chilotherium* in Europe is provided.

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Taxonomy; rhinoceros; chilotheres; Neogene; Eastern Mediterranean; Greece

Introduction

The late Miocene of the Eastern Mediterranean is characterised by a very rich and diverse mammalian faunal assemblage, which is known from numerous localities from Greece (e.g. Halmyropotamos, Axios Valley, Nikiti, Kerassia), Bulgaria (e.g. Hadjidimovo, Kalimantsi, Gorna Sushitsa, Staniantsi), North Macedonia (e.g. Karaslari, Prevalets) and Turkey (e.g. Akkaşdağı, Kemiklitepe, Mahmutgazi) (Bakalov and Nikolov 1962; Koufos 1987, 2006; de Bonis et al. 1992; Sen 1994; Theodorou et al. 2003; Antoine & Saraç 2005; Spassov et al. 2006, 2018, 2019; Kostopoulos 2009; Hristova 2012; Koufos et al. 2016; Geraads 2017; Böhme et al. 2018; Lechner and Böhme 2020; Kampouridis et al. 2020). The most renowned fossil localities of this region are certainly Pikermi (Gaudry 1862–1867; Theodorou et al. 2010; Böhme et al. 2017; Roussiakis et al. 2019) and Samos (Kostopoulos et al. 2003; Koufos 2009; Koufos et al. 2011) in Greece. The existence of vertebrate fossils on the island of Samos (Figure 1) has been known since the 19th century. The first systematic excavations took place in the 1880s and were led by C. I. Forsyth Major (Koufos 2009). In the following years Samos attracted the attention of many more researchers, such as the German palaeontologist E. Fraas (Koufos 2009), the Greek palaeontologist T. Skoufos (Svorligkou et al. 2019) and even the famed American fossil hunter B. Brown (Solounias 1981). The most recent systematic excavations on Samos were carried out by G. Koufos from the Laboratory of Geology and Palaeontology of the University of Thessaloniki (LGPUT, Greece) (Koufos 2009). The excavated material led to a detailed study of the faunal assemblage (e.g. Giaourtsakis 2009; Konidaris and Koufos 2009; Vlachou and Koufos 2009; Koufos et al. 2009a, 2009b, 2011) and the stratigraphical context, including a refined dating for the different fossiliferous horizons (Kostopoulos et al. 2003, 2009). The material of the recent LGPUT excavations is housed in the Natural History Museum of the Aegean (NHMA, Greece), while the material from the numerous older excavations is scattered in several collections throughout the world, some of the largest include the historical collections of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG, Germany), which unfortunately lost many specimens during the Second World War, the Naturhistorisches Museum in Wien (NHMW, Austria) and the American Museum of Natural History (AMNH, USA).

Another large collection of Samos fossils, which has received only little attention in the past (Andree 1921, 1926; Wehrli 1941), exists in the Geomuseum of the University of Münster (GMM, Germany). This material was uncovered by T. Wegner during 3 months of excavations in 1909 (Andree 1926). Andree (1926) also mentioned that 'the material comes from volcanic tuffs north of Mytilinii' (Andree 1926, p. 135). Wehrli (1941) noted that four different types of sediments can be identified associated with the Samos material in the GMM, which could be correlated to the sediment types mentioned by Schlosser (1904). However, he did not specify this any further and thus it is impossible to attribute the material of the GMM to any specific horizon(s) of Samos now and the exact age of the material cannot be assessed.

The Samos collection, housed in the GMM, comprises the type material of two hornless rhinos, described by Andree (1921), *Aceratherium wegneri* Andree (1921) and *Aceratherium angustifrons* Andree (1921). Later, they were referred to the genus *Chilotherium* by Ringström (1924). Heissig (1975) proposed that *Chilotherium wegneri* and *Chilotherium angustifrons* are junior synonyms of *Chilotherium schlosseri* (Weber 1905) and *Chilotherium kowalevskii* (Pavlow 1913), respectively. The type material of '*C. wegneri*' and *C. angustifrons* has been lost,

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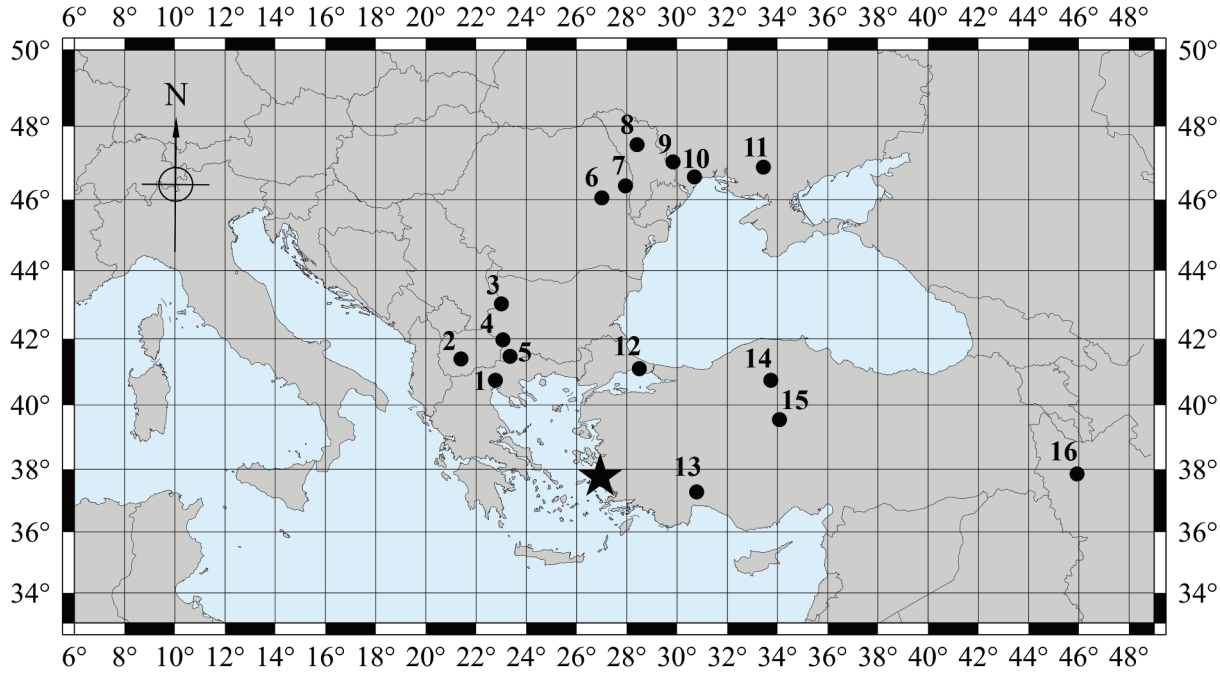

Figure 1. Distribution of *Chilotherium* spp. in the Balkan-Iranian province. Black star represents Samos (Greece) (Weber 1905; Andree 1921). 1, Pentalophos (Greece) (Geraads and Koufos 1990); 2, Morievo region (North Macedonia) (Spassov et al. 2018); 3, Staniantsi; 4, Oranovo; 5, Kromidovo (Bulgaria) (Geraads and Spassov 2009); 6, Reghiu (Codrea 1996); 7, Pogana (Romania) (Codrea 2011); 8, Raspopeni (Moldova) (Geraads et al. 2020); 9, Grebeniki (Pavlow 1913); 10, Odessa (unknown locality) (Niezabitowski 1913); 11, Berislav (Ukraine) (Korotkevich 1958); 12, Küçükçekmece (Antoine and Sen 2016); 13, Kayadibi (Geraads et al. 2020); 14, Sinap (several horizons) (Fortelius et al. 2003); 15, Akkaşdağı (Turkey) (Antoine and Saraç 2005); and 16, Maragha (Iran) (Pandolfi 2016).

with the type mandible of '*C. wegneri*' being the only exception (Meiburg and Siegfried 1970; Bertling pers. comm.), which is still housed in the GMM and, along with the associated skull described by Andree (1921), comprises the holotype of this species.

The aim of the present study is the redescription of the type mandible of '*C. wegneri*' and, based also on the original descriptions and illustrations of Andree (1921), the re-examination of the validity of this species. Additionally, a brief overview of all European *Chilotherium* species is provided (Table 1).

Institutional Abbreviations: AMNH, American Museum of Natural History, New York (USA); AMPG, Palaeontological and Geological Museum of the University of Athens (Greece); GMM, Geomuseum of the University of Münster (Germany); GPIT, Geologisch-Paläontologisches Institut der Universität Tübingen (Germany); LMU, Ludwig-Maximilians-University Munich (Germany); LGPUT, Laboratory for Geology and Palaeontology of the University of Thessaloniki (Greece); MNHN: Muséum national d'Histoire naturelle, Paris (France); NHMA, Natural History Museum of the Aegean, Samos (Greece); NHMW, Naturhistorisches Museum in Wien (Austria); NNPM, National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev (Ukraine).

Systematic palaeontology

Class Mammalia Linnaeus, 1758
Family Rhinocerotidae Gray, 1821

Tribe Chilotheriini Qiu et al., 1987

Genus *Chilotherium* Ringström, 1924

Chilotherium schlosseri (Weber, 1905)
Synonym: Aceratherium wegneri Andree 1921

Material: an almost complete mandible (GMM 567) (Figures 2–3)

Locality: Samos (unknown horizon; T. Wegner excavations in 1909)

Remarks: Andree (1921) erected the two hornless rhino species *Aceratherium wegneri* and *Aceratherium angustifrons* based on material from the late Miocene of Samos (Greece) housed in the GMM (Germany). He mentioned that the material of '*C. wegneri*' and *C. angustifrons* comes from the same sediment type and that the skull and the mandible, which represent the type material of '*C. wegneri*', were not found articulated, but right next to each

Table 1. Summary of the taxonomy of *Chilotherium* spp. from Europe.

Species	Authority	Type Locality	Current Status
Aceratherium schlosseri	Weber 1905	Samos (Greece)	*C. schlosseri*
Aceratherium wegneri	Andree 1921	Samos (Greece)	*C. schlosseri*
Aceratherium angustifrons	Andree 1921	Samos (Greece)	*C. schlosseri*
Teleoceras ponticus	Niezabitovski 1912	Odessa (Ukraine)	*C. schlosseri*?
Aceratherium samium	Weber 1905	Samos (Greece)	*C. samium*
Aceratherium kowalevskii	Pavlow 1913	Grebeniki (Ukraine)	*C. kowalevskii*
Chilotherium sarmaticum	Korotkevich 1958	Berislav (Ukraine)	*C. sarmaticum*?
Aceratherium kiliasi	Geraads and Koufos 1990	Pentalophos (Greece)	*C. kiliasi*

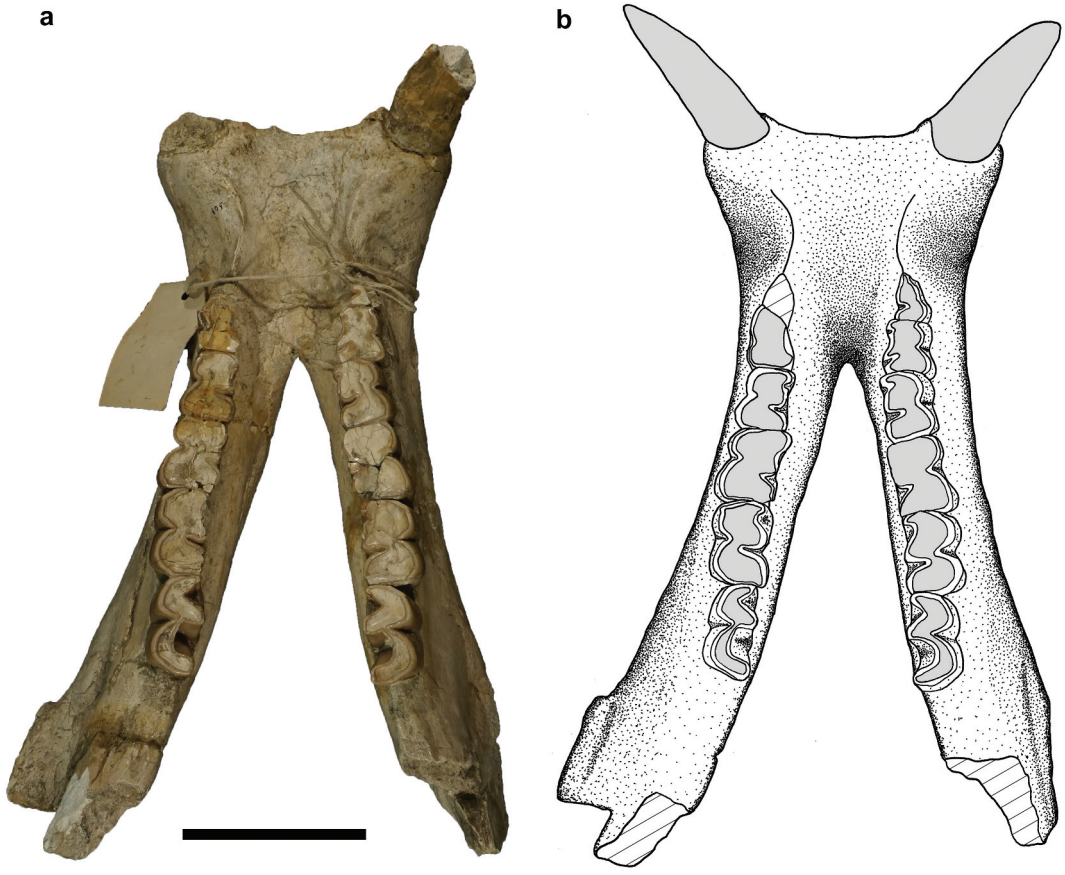

Figure 2. Type mandible of '*Chilotherium wegneri*' (GMM 567; herein assigned to *Chilotherium schlosseri*). (a), photograph; and (b), drawing in dorsal view, missing parts are reconstructed after Andree (1921, taf. I, Fig. 3). Scale bar is 10 cm.

other. However, their proximity and the similar wear stage should suffice to assign them to the same individual. The incisors, which were perfectly preserved during the time of their initial publication (Andree 1921), have been damaged since then and the left i2 is completely missing now (Figures 2, 3(b)). Therefore, the description of the incisors and the p2, which is also damaged, will take into account the description and illustrations provided by Andree (1921).

Description

Mandible: Specimen GMM 567 (Figures 2–3) represents an almost complete mandible. The well-preserved symphysis is very wide and massive. In ventral view, it is transversally concave, and several foramina are visible on the ventral side of the symphysis: three on the left side and two on the right side (Figure 3(a)). In anterior view, between the incisors three other very large foramina are visible, one pair is situated on the right side and the third is larger and situated on the left side; the anterior end of the symphysis forms a thin edge (Figure 3(b)). In dorsal view, the symphysis terminates posteriorly at the distal end of the p3 (Figure 2). A long diastema exists between the p2 and the i2, which is marked by a well-developed dorsal ridge between these two teeth, on both sides. The dorsal surface of the symphysis, between these ridges is concave. The transversally narrowest part of the symphysis is at the middle of the p2. The ventral side of the symphysis is almost horizontal, showing a slight dorsal curve at its anterior end, right before the incisors. In lateral view, two mental foramina are present on each side, the anterior one is placed at the level of the anterior portion of the p2, somewhat more ventrally than the posterior one, which is situated below the border of p2-p3 (Figure 3(c–d)). A slight indentation on the ventral side of the mandibular body can be observed on both hemimandibles at the level of the p3, approximately at the beginning of the symphysis. The height of the mandibular body gradually increases posteriorly, as far as the level of the m3. Posteriorly, on both sides, the rami are broken off; however, enough of the left ramus is preserved to observe that the front edge of the ascending ramus is probably inclined slightly backwards. In lateral view, at the ventral portion of the mandible, posterior to the m3, both hemimandibles exhibit a well-developed anteroposteriorly oriented rugose attachment area for the M. masseter (Figure 3(c–d)).

Lower dentition: The dentition is relatively well preserved (Figure 2). The left incisor is completely broken off, leaving only the outline of the root visible within the alveolus (Figure 3(b)), whereas the right incisor is only missing its tip. The left toothrow is represented by the p3-m3, while the right toothrow also preserves part of the p2. The dentition is heavily worn, indicating an old age for the individual.

The i2s are large, tusk-like and dorsolaterally curved. The crown, when complete, was 103 mm long and 46 mm wide (Andree 1921, p. 212) and the two i2s are about 84 mm apart. The cross-section of the incisors is medially pointed and laterally rounded, as well as subelliptical at the base and subtriangular at the tip. Some remnants of enamel are exposed on the labial side of the preserved anterior edge of the right i2 (Figure 3(b)). The diastema separating the i2 from the p2 has a length of about 60 mm.

Some of the cheek teeth preserve remnants of their cement. The premolar/molar length ratio (sensu Athanassiou et al. 2014) is

67.5%. Most cheek teeth are heavily worn, and their morphology cannot be accurately assessed accordingly, only the m3 is moderately worn, allowing a more detailed description of its morphology. Anterior and posterior cingula are present in most teeth, in some cases reaching the lingual or buccal side of the tooth. Lingual and buccal cingula are very weakly developed, if present at all. All cheek teeth exhibit a well-developed ectolophid groove, except the p2 in which only a very shallow groove is visible. In the p2, the paralophid is very small, straight, and anteriorly pointing; the posterior valley remains open, albeit very small; there is no anterior valley; and the morphology of the protoconid cannot be assessed due to the wear stage.

All other cheek teeth exhibit a lingually projecting paralophid, although badly preserved in some, such as the damaged left m2 and both worn-down m1s. All cheek teeth preserve anterior and posterior valleys that remain open down to the cervix. Only in the p3, it seems possible that an even more advanced stage of wear would potentially close the posterior valley, thus forming a small 'fossettid'. In the p4 specifically, the anterior valley is extremely small and almost completely worn, without closing. In the same tooth, the posterior valley is deeper and narrow, reaching the centre of the tooth, despite its advanced wear stage. This can even be observed in the extremely worn m1. Similarly, in the m2, the anterior valley is almost completely worn, and the posterior one remains long and narrow.

The only exception is the less worn m3, which exhibits an anterolingually projecting paralophid, and a moderately deep anterior valley, in the trigonid. The metaconid is more developed than the paralophid and does not show any constriction. The trigonid is barely connected to the talonid, through a narrow (pre-)hypolophid. The hypolophid is similarly developed as the metaconid.

Comparison

The mandible (GMM 567) bears two large, diverging incisors (Figures 2, 3(b)). This feature precludes the attribution of the mandible to any of the horned rhinos from the late Miocene of Europe, such as *Ceratotherium neumayri* (Osborn 1900) and *Dihoplus pikermiensis* (Toula 1906), which exhibit only small to moderate incisors if present at all, and never such tusk-like ones as seen in GMM 567 (Giaourtsakis et al. 2006; Giaourtsakis 2009; Pandolfi and Rook 2017). Furthermore, the premolar/molar length ratio (sensu Athanassiou et al. 2014) is relatively small (67.5%) and prevents its referral to the only other hornless rhino from the late Miocene of the Balkan Peninsula, *Acerorhinus neleus* Athanassiou et al. (2014) (compare Athanassiou et al. 2014, fig. 5).

Specimen GMM 567 exhibits the following features, characteristic for *Chilotherium*: a wide symphysis, with a strongly concave ventral surface; very strong i2s, separated from each other, and from the p2 by long diastemata (Ringström 1924; Deng 2001, 2006). Thus, the mandible (GMM 567) can be unambiguously attributed to the genus *Chilotherium*.

Within the genus *Chilotherium*, the identification of the species based solely on an isolated mandible is not possible. The morphology of both the mandibular body and the teeth is very uniform within the genus and shows only little variation which may be associated with intraspecific variability (Ringström 1924). In fact, Ringström (1924) does not provide any description of the lower teeth as a consequence. Furthermore, the anterior portion of the mandible is damaged in the, now lost, type material of *C. schlosseri* and no detailed description of the symphysis is available (Weber 1905, p. 346). Similarly, the type material of *C. samium* includes two mandibles, both of which lack the incisors. Only one of them, which Weber (1905, p. 356) considered belonging to a male individual, preserves the roots of the i2s and assumed that the teeth must have been large and tusk-like. The type material of *C. angustifrons*, which herein is considered a junior synonym of *C. schlosseri* (Table 1), does not include a mandible. Although no detailed comparison between the chilotheres from Samos is possible, some features such as the ramus that is slightly inclined backwards and the similarly developed attachment area for the M. masseter in the mandibles of both '*C. wegneri*' and *C. schlosseri* (Weber 1905, taf. VIII, fig. 1) indicate the great resemblance between the two species.

Taxonomic status of '*C. wegneri*'

Andree (1921) initially described '*C. wegneri*' as a relatively large hornless rhino, most similar to *C. schlosseri*. This identification, however, has subsequently been questioned by several authors.

Figure 3. Type mandible of '*Chilotherium wegneri*' (GMM 567; herein assigned to *Chilotherium schlosseri*) in: (a), ventral; (b), anterior; (c), right lateral; and (d), left lateral view. Scale bar is 10 cm for (a), (c–d) and 7 cm for (b).

Killgus (1922, 1923) studied the late Miocene material of Kutschwan (China) housed in the GPIT, which includes a rich collection of *Chilotherium habereri* (Schlosser 1903) specimens. He provided a detailed description of the material and compared it to most of the known chilotheres. In his comprehensive comparison to '*C. wegneri*', Killgus (1922) noted many similarities between the two species and proposed their synonymy, a view also supported by Schlosser (1924). However, many of these suggested similarities are features that are relatively widespread within the genus *Chilotherium*, including the flat dorsal profile of the skull, the depression of the frontals and longitudinal groove between the two nasals (Ringström 1924).

One specific feature of both '*C. wegneri*' and *C. habereri*, noted by Killgus (1922), is the ventral profile of the mandible, which in both species seems to exhibit an indentation on the ventral side, below the premolars. However, this feature is also observed in some mandibles of the primitive *Chilotherium wimani* Ringström 1924 (Ringström 1924, p. 44) and in the more derived *Chilotherium persiae* (Pohlig 1886) (MNHN – MAR 3860) and *C. kowalevskii* (Pavlow 1913, pl. IV, fig. 11, 13 and 14). Another feature, discussed by Killgus (1922), is the minimal distance between the parietal crests. However, as can be seen in Table 2, in '*C. wegneri*' and *C. schlosseri* the minimal distance between the parietal crests is significantly higher than in the other *Chilotherium* species and, in fact, illustrates the resemblance of '*C. wegneri*' to *C. schlosseri*.

Ringström (1924) included '*C. wegneri*' in his new genus, *Chilotherium*. He noted that the premaxillae of '*C. wegneri*' are most similar to *Chilotherium anderssoni* Ringström 1924 because they are straight without a medial process, in contrast to *C. habereri* and *C. persiae* in which a cone-like process is present on the medial side of the premaxillae. However, a closer look into the illustrations provided by Andree (1921, taf. I, fig. 2) reveals that indeed a cone-like structure is present on the medial side of the premaxillae. Furthermore, Ringström (1924) discussed three morphological similarities to his new species *Chilotherium planifrons* Ringström 1924), most likely a junior synonym of *C. anderssoni* (Deng 2006). The first one concerns the form of the occipital. However, its morphology can vary as already indicated by the differences between '*C. planifrons*' and *C. anderssoni* (Ringström 1924, fig. 34–35). Furthermore, the type cranium of '*C. wegneri*' is somewhat deformed. The second feature, discussed by Ringström (1924) concerns the similar morphology of their paroccipital processes. However, in *C. kowalevskii* from Grebeniki (Pavlow 1913) the paroccipital processes seem to be very similar to '*C. wegneri*'. In addition, a skull (NHMW-1911/0005/0128) from Samos, housed in the NHMW, which can be assigned to *C. schlosseri*, exhibits a short paroccipital process, which, in posterior view, does not cover the postglenoid process, just like in '*C. wegneri*'. Similarly, in some *C. habereri* skulls from Kutschwan (China), housed in the GPIT, the paroccipital process is relatively short, compared to the one illustrated by Ringström (1924, fig. 22). Thus, the morphology and relative size of the paroccipital process cannot be used to associate '*C. wegneri*' with '*C. planifrons*' and might in fact indicate its affinity to the European species. The last feature used by Ringström (1924) to stress the similarity between '*C. wegneri*' and '*C. planifrons*' is the flat dorsal profile of the skull. This represents a common feature in derived species of *Chilotherium*. Additionally, the degree of flatness or concavity of the dorsal profile of the skull may vary within the same population as seen in Pavlow (1913, pl. IV, fig. 6–7).

As already pointed out by Heissig (1975), Deng (2006) and Giaourtsakis (2009), '*C. wegneri*' probably represents a junior synonym of *C. schlosseri*. However, none of them provided any arguments in favour of this hypothesis. Herein, we follow the abovementioned authors regarding the synonymy of '*C. wegneri*' and *C. schlosseri* because both are morphologically nearly indistinguishable, exhibiting the following features in the skull: a well-formed ('muldenförmige') depression in the frontals; weakly, anteriorly ascending nasals, which are separated from each other by a median, longitudinal groove; a flat dorsal profile in the skull; an orbita that ends anteriorly above the anterior portion of the M3; and widely separated parietal crests (see Table 2). Regarding the dental morphology, the two preserved teeth (right M2 and M3) in the type cranium of '*C. wegneri*' are almost identical to the respective teeth in *C. schlosseri* featuring: in both M2 and M3, a closed medifossette, an extremely strong protocone constriction and a very strong antecrochet; in the M2, a closed postfossette, a small, closed medifossette, a closed median valley, a strongly constricted hypocone and no visible paracone rib; and in the M3, an unconstricted hypocone, an open median valley and a weak paracone fold. In general, *C. schlosseri* (including '*C. wegneri*') seems to be distinct from all other chilotheres by featuring a minimal distance separating the parietal crests of at least 70 mm (see Table 2), a feature already mentioned by Ringström (1924, p. 85), which might, in fact, represent an autapomorphy of the species.

Table 2. Minimal distance (in mm) between the parietal crests in *Chilotherium* spp. Data sources: 1, Andree (1921); 2, own data; 3, Krokos (1917); 4, Killgus (1922); 5, Ringström (1924); 6, Deng (2006).

Taxon	min	max	n
'*C. wegneri*'[1]	87	-	1
C. schlosseri[1,2]	70	90	4
C. samium[1]	~40	-	1
C. kowalevskii[3]	40	66	10
C. persiae[2]	32	50	4
C. habereri[4,5]	42	60	9
C. anderssoni[5]	50	63	5
C. wimani[6]	28	64	10
C. primigenius[6]	18	-	1

The European record of *Chilotherium*

The genus *Chilotherium* has a very limited stratigraphical and geographical distribution as it has only been reported from the late Miocene of Eurasia. *Chilotherium* was established by Ringström (1924), based on material from the late Miocene of China, for short-limbed, hornless rhinos, which are characterised by a depression in the frontals and a wide mandibular symphysis with enlarged tusks. In the late Miocene of Asia, especially in the '*Hipparion* Red Clay' localities (Flynn et al. 2011) of China, this group is extremely common, and, in some cases, it even appears as the dominant vertebrate taxon (Killgus 1922, 1923; Ringström 1924). The earliest representative of the genus is *Chilotherium primigenius* Deng 2006 from the early Late Miocene (early to middle MN9) of the Linxia Basin (China) (Deng 2006). Deng (2006) suggested that this species might have evolved into *C. wimani*, which in turn may be ancestral to several other species of the genus, such as *C. habereri* (Deng 2006). Heissig (1975) proposed the migration of the Chinese *C. habereri* into Anatolia during the Turolian, which then might have given rise to the European chilotheres.

Despite its rarity in Europe, at least eight chilotheres have been described from the Eastern and Southeastern parts of the continent. A short overview of the fossil record of the European *Chilotherium* representatives is given below, ordered by the date of their initial description:

Chilotherium schlosseri

Weber (1905) described the first European chilotheres while studying the rhinocerotid remains from the late Miocene of Samos housed in the BSPG – the slightly larger, more derived *C. schlosseri* and the smaller, primitive *C. samium*, (Weber 1904, 1905). Andree (1921) described a badly damaged skull of *C. schlosseri* from the Samos material of the GMM, which is considered lost (Meiburg and Siegfried 1970; Bertling pers. comm.). Later, Killgus (1922) confirmed the validity of *C. schlosseri*, pointing out numerous differences separating it from the Chinese *C. habereri*, as also supported by Schlosser (1924). Ringström (1924) discussed similarities between *C. schlosseri* and the Chinese *C. anderssoni*, such as the morphology of the paroccipital process, while also pointing out important differences which separate the two species. Many authors (Kiernik 1913; Krokos 1917; Korotkevich 1970; Heissig 1975; Giaourtsakis 2003, 2009; Deng 2006; Antoine & Sen 2016) considered most of the later described European chilothere species to be potential junior synonyms of *C. schlosseri*. Furthermore, the potential presence of *C. schlosseri* has been recognised in some other late Miocene fossil sites in the Eastern Mediterranean (Heissig 1975, 1996; Vangengeim and Tesakov 2013; Antoine and Sen 2016). Unfortunately, the type material of this species was lost during the Second World War (Giaourtsakis 2003, 2009).

Chilotherium samium

The second species described by Weber (1905), *C. samium*, represents a primitive chilothere. This species is based on two skulls and mandibles of very old individuals and Weber (1905) originally suggested a close affinity to *Aceratherium incisivum*, instead of *C. schlosseri*. Ringström (1924) included *C. samium* into *Chilotherium*, based on the high placement of the orbits, the straight nasals and the separated parietal crests, also pointing out the similarities to the other chilotheres instead of *Aceratherium incisivum*. Heissig (1975) also supported the attribution of *C. samium* to *Chilotherium* and described it as a primitive representative of the genus (or subgenus), distinct from *Acerorhinus* spp. and *Subchilotherium intermedium*. Geraads and Koufos (1990) followed the original assignment of *C. samium* to the genus *Aceratherium*, based on the description of Weber (1905). They also proposed a close relationship of *C. samium* and their new species *Aceratherium kiliasi* Geraads and Koufos 1990). Heissig (1996) mentioned *C. samium* as 'the most primitive form dentally', with its first occurrence in Anatolia potentially from the MN10. Fortelius et al. (2003) described *C. samium* as being at a comparable evolutionary stage as *C. wimani*, but because of the problematic taxonomy of *C. samium*, they proposed to restrict this name to its type material. Geraads and Spassov (2009) included this species in their new subgenus as *C.* (*Eochilotherium*) *samium* and pointed out important differences from the more derived *C. wimani*. The problems concerning *C. samium*, including the loss of the type material, have been discussed by several authors in the past (e.g. Geraads and Koufos 1990; Fortelius et al. 2003; Giaourtsakis 2003, 2009; Athanassiou et al. 2014).

Chilotherium ponticum

Niezabitowski (1912) erected the species *Teleoceras ponticus* Niezabitowski 1912), probably from the late Miocene (Turolian) of Odessa. One year later he published a description of the type cranium, with a comparison to *C. schlosseri* and some teleoceratines, suggesting that despite its close affinity to the former, it should be included in the genus *Teleoceras* (Niezabitowski 1913). Kiernik (1913) published a detailed description and comparison of the type cranium of *C. ponticum*, in which he rejects the results of Niezabitowski (1912, 1913), synonymising *C. ponticum* from Odessa and *C. schlosseri* from Samos. Killgus (1922, 1923) argued that the type cranium of *C. ponticum* in fact belongs to *C. habereri*, based on the similarities of the tooth morphology. Ringström (1924) assigned it to the genus *Chilotherium*, based on the depression in the frontals and the very strong antecrochet and kept the name *C. ponticum* for the fragmentary skull from Odessa. More recently, Heissig (1975) and Deng (2006) referred *C. ponticum* to *C. schlosseri*, as previously proposed by Kiernik (1913).

Chilotherium kowalevskii

Pavlow (1913) studied the rich fauna from the late Miocene of Grebeniki, including a large collection of rhino material, based on which she described the species *C. kowalevskii*. Krokos (1917) revised the Grebeniki material and attributed it to *C. schlosseri*. Ringström (1924, p. 93) mentioned it as 'a typical *Chilotherium* species' and pointed out that it resembles *C. habereri*, without synonymising them. Heissig (1975) attributed material from the late Miocene of Anatolia to *C. kowalevskii*, which he regarded as a valid *Chilotherium* species, noting its potential relationship to the younger '*Chilotherium*' *brancoi*. However, the latter in fact belongs to the distinct chilothere genus *Shansirhinus* (Kretzoi 1942; Deng 2005). Heissig (1996, 1999) supported the validity of *C. kowalevskii* and noted that it has sometimes been mentioned from Anatolia, but its presence there is rather doubtful. Geraads (2013) regarded the hornless rhino from Çorakyerler (Turkey), which had previously been identified as *C. kowalevskii* (Heissig 1975), as a potential new species, belonging to the genus *Acerorhinus*. In addition, Fortelius et al. (2003) assigned part of the hornless rhino material from the late Miocene (MN11-12) of Kavakdere (Turkey) to *C. kowalevskii*. Geraads and Spassov (2009) provided a short diagnosis for *C. kowalevskii* and referred material from the late Miocene of Yambol (Bulgaria) to *C.* cf. *kowalevskii*. Deng (2006) included *C. kowalevskii* in his revision of *Chilotherium* spp. and regarded it as a valid species. Vangengeim and Tesakov (2013, tab. 23.3) reported *C. kowalevskii* also from the late Miocene (MN10) of Raspopeni (Moldova). Antoine and Sen (2016) assigned the small hornless rhino material from the late Miocene of Küçükçekmece, which had previously been referred to *Aceratherium* cf. *kowalevskii* (Nicolas 1978), to *C. schlosseri*. Furthermore, they considered *C. kowalevskii* to be a junior synonym of *C. schlosseri*, based on their strong craniodental similarities and their overlapping spatio-temporal distribution. This hypothesis is further supported, although not explicitly stated, by the phylogenetic analysis of Pandolfi (2016), which considers the two species either as sister taxa or as synonyms (Antoine and Sen 2016). Herein, *C. kowalevskii* is kept as a separate species (Table 1) until its taxonomic issues are resolved.

Chilotherium angustifrons

Andree (1921) described two new hornless rhino species, '*C. wegneri*' and *C. angustifrons*, based on cranial material from the late Miocene of Samos, housed in the GMM. The first has been discussed above and represents a junior synonym of *C. schlosseri* (Table 1). The second was described as a relatively small hornless rhino, which may be more closely related to *C. samium* and *Aceratherium incisivum* (Andree 1921). Killgus (1922, 1923) compared his *C. habereri* material from Kutschwan (China) to

C. angustifrons and concluded that they should be attributed to the same species. Accordingly, Ringström (1924) ascribed *C. angustifrons* to *Chilotherium*, with its teeth morphology being a typical example of a chilothere and differing significantly from *Aceratherium incisivum*. He also noted the similarities of *C. angustifrons* to *Chilotherium gracile* Ringström 1924, a junior synonym of *C. habereri* (Deng 2006), without synonymising them. Heissig (1975) suggested that *C. angustifrons* represents a synonym of *C. kowalevskii* from Grebeniki. Whereas Giaourtsakis (2009) mentioned that *C. angustifrons* represents a junior synonym of either *C. kowalevskii* or *C. schlosseri*. The taxonomic status of *C. angustifrons* is quite problematic due to the fact that the type skull is heavily damaged, lacking a significant portion of its right side (Andree 1921, taf. III, figs. 1–2), and is currently considered lost (Meiburg and Siegfried 1970). The deep groove separating the nasals, the depression of the frontals, the marked protocone constriction and the strong antecrochet in the M1 confirm its attribution to the genus *Chilotherium* and preclude its attribution to *C. samium*. Due to the absence of any morphological traits that would distinguish it from *C. schlosseri, C. angustifrons* is herein considered a junior synonym of the latter (Table 1) as previously indicated by Giaourtsakis (2009).

Chilotherium sarmaticum

Korotkevich (1958) described the new species *Chilotherium sarmaticum* Korotkevich 1958) from the late Miocene of Berislav (Ukraine). This species is mainly discussed in Russian literature (Geraads and Spassov 2009) and is often neglected in most recent reviews of chilotheres (Heissig 1975, 1996, 1999; Fortelius et al. 2003; Deng 2006). A complete skull from Reghiu (Romania; MN10-11), which Codrea (1996) referred to as *Chilotherium* sp., was later associated with *C. sarmaticum* (Ştiucă 2003). However, Codrea (2011) noted that the skull from Reghiu (Romania) is regarded as 'lost or at least, mislaid'. Spassov et al. (2006) referred a single i2 from the late Miocene of Oranovo (Bulgaria) to *C.* cf. *sarmaticum*. Geraads and Spassov (2009) reviewed the Bulgarian fossil record of Neogene rhinos, ascribing additional material to this species. They provide a simplified diagnosis for *C. sarmaticum*, based on the ones given by Korotkevich (1958, 1970). However, neither the Romanian nor the Bulgarian material was definitively assigned to this species (referred to as *C.* cf. *sarmaticum*). Geraads and Spassov (2009) suggested that, despite the absence of *C. sarmaticum* in recent literature, it should be regarded as a valid species.

Chilotherium kiliasi

Geraads and Koufos (1990) described the species *Aceratherium kiliasi* from the early late Miocene (Vallesian) of Pentalophos 1 (Greece). The holotype of the species is a moderately well-preserved skull of an old individual, which was later assigned to the genus *Chilotherium* (Heissig 1996; Fortelius et al. 2003; Athanassiou et al. 2014). Geraads and Koufos (1990) also attributed to this species material, which actually belongs to the genus *Acerorhinus* (Heissig 1996; Fortelius et al. 2003; Athanassiou et al. 2014). Heissig (1996, 1999) interpreted *C. kiliasi* as a primitive *Chilotherium*, which could be closely related to *C. samium* or potentially even conspecific. Giaourtsakis (2003) preferred to keep this species under its original name '*Aceratherium*' *kiliasi*, as a detailed re-evaluation of the material was needed. Fortelius et al. (2003) also pointed out the problems concerning this species, attributing it to a primitive *Chilotherium*, and noting its similarities to *C. samium*. They also referred to this species a number of specimens from the late Miocene of Loc. 49 of the Sinap Formation (Turkey). Geraads and Spassov (2009) erected the new subgenus *Eochilotherium* with *C.* (*Eochilotherium*) *kiliasi* as its type species and also included *C. samium*. They studied numerous rhinocerotid remains from several late Miocene localities of Bulgaria, attributing a skull from the late Miocene of Kromidovo to *C.* (*Eochilotherium*) cf. *kiliasi*. Athanassiou et al. (2014) revised the record of the genus *Acerorhinus* from the late Miocene of the Eastern Mediterranean, erecting the new species *Acerorhinus neleus*. They attributed to this species much of the material from Pentalophos 1, which was initially included in *Aceratherium kiliasi*. Athanassiou et al. (2014) also noted that the type cranium of *C. kiliasi* represents a relatively primitive *Chilotherium*, but concerning the specific identification, the loss of the type material of *C. samium* does not allow a definitive association and thus preferred to refer to it as *C.* cf. *samium* (Athanassiou et al. 2014, tab. 5). Herein, it is considered as a valid species, pending further investigations (Table 1).

Chilotherium habereri

Lastly, the species *Aceratherium habereri* was initially described by Schlosser (1903) based on material from the late Miocene of China, but was later recorded in some European localities, many of these reports are however questionable and its presence outside Asia is doubtful. Killgus (1922, 1923) assigned a rich collection of cranial and postcranial elements from the late Miocene of Kutschwan (China), housed in the GPIT, to *Aceratherium habereri*. Later, Ringström (1924) incorporated it in *Chilotherium*, attributing new material from other late Miocene localities of China to *C. habereri*. In addition, the occurrence of the Chinese chilothere *C. habereri* has been suggested even in Europe, but the taxonomic status of this material is not clear (Antoine and Saraç 2005). As already discussed, Killgus (1922, 1923) proposed the synonymy of some European species with *C. habereri*, implying the presence of *C. habereri* in the late Miocene of Samos (Greece), but this hypothesis cannot be sustained. Heissig (1975) mentioned its presence in Anatolia, but without any detailed description (Heissig 1996). Saraç (1994) also identified the species based on material from the late Miocene of Turkey. Fortelius et al. (2003) attributed some material from the late Miocene fossil site Loc. 49 of the Sinap Formation (Turkey) to *C.* cf. *habereri* and noted that some material previously assigned to *C. habereri* belongs to an 'indeterminate *Chilotherium*'. Antoine & Saraç (2005) briefly discussed the issues concerning the taxonomy of this material and preferred to refer their specimen from the late Miocene of Akkaşdağı preliminarily to *Chilotherium* sp. until the issues concerning the presence of *C. habereri* in Turkey are resolved.

Conclusion

The re-examination of the type material of '*C. wegneri*', from the late Miocene of Samos (Greece), led to its attribution to the derived *C. schlosseri*, also known from Samos material. The type crania of the two chilothere species share many similarities in the cranial anatomy and an identical dental morphology in the preserved teeth, but most importantly they exhibit widely separated (>70 mm)

parietal crests, in contrast to most other *Chilotherium* species. Furthermore, we provide an overview of the fossil record of *Chilotherium* in Europe. In total, eight species have been described, many of which evidently represent synonyms. Despite the fact that *Chilotherium* spp. was very common in the late Miocene of Asia (especially China), it is a rare faunal component in Europe, with its distribution being limited to the Balkan Peninsula and the Peri-Pontic region.

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