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RESEARCH

Craniodental anatomy of the hornless rhinocerotid *Chilotherium schlosseri* (Mammalia, Perissodactyla) from the Late Miocene of Samos Island, Greece

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Abstract

The fossiliferous sites of Samos Island are of major importance amidst the numerous Turolian localities of Greece, partly because it is the type locality of two hornless rhinocerotids, *Chilotherium schlosseri* and *Eochilotherium samium* . For more than a century, the island has been excavated by Greek and international teams, leading to a dispersal of fossils in a plethora of museums around the World. In the present work, the entirety of the craniodental material of *Chilotherium schlosseri* available in different European and American collections is examined for the first time. Additionally, we compared the material to various *Chilotherium* species from the Late Miocene of Eurasia. A number of diagnostic characters are herein established for *C. schlosseri*: the markedly depressed frontal and nasal region, the widely separated parietal crests, the complicated enamel folds and the presence of enamel plications on the permanent upper dentition. In terms of morphology, the species that is phenotypically closest to *C. schlosseri* appears to be *C. orlovi* from the Late Miocene of Kazakhstan. Both species seem to be more distantly related to the other Samian chilothere, *E. samium*.

Keywords Biostratigraphy · Chilotheres · Eurasia · Taxonomy · Palaeoenvironment

Introduction

Nomenclatural and systematic review of the genus *Chilotherium*

Rhinoceroses are amongst the most iconic mammals that exist today. They are represented by five species that live in Africa and Asia, most of which are considered endangered. However, contrary to their limited taxonomic and phylogenetic diversity nowadays, rhinoceroses were much more diverse in the past, including multiple clades (Antoine et al. 2025). The most diverse clade was represented by the aceratheriines. They were very abundant during the Miocene in Eurasia, but they also spread to North America and Africa. The most frequent and characteristic genus of this group in Eurasia is probably *Chilotherium* Ringström, 1924. *Chilotherium* was extremely common during the Late Miocene, with its geographical distribution reaching from China all the way to Eastern Europe and, in many localities, it was among the most common large mammals (Deng et al. 2023). Representatives of this genus were characterised by the absence of horn-bosses (suggesting the absence of

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keratin horns), depressed skull, wide mandibular symphysis, well-developed lower incisors, and shortened limbs (e.g., Ringström 1924).

The genus *Chilotherium* was erected by Ringström (1924), based on abundant material from Upper Miocene strata in China that was collected in the beginning of the 20th century. Ringström erected the genus *Chilotherium* upon *Chilotherium anderssoni* Ringström, 1924, which he assigned as the type species for the genus; furthermore, he erected several new species for this genus: *Chilotherium planifrons* Ringström, 1924, and *C. wimani* Ringström, 1924. Ringström (1924) additionally referred 10 previously described species from Eurasia to this new genus. Some of these species are now considered junior synonyms (Table 1), while many of them have not be re-evaluated since then and their status remains somewhat unclear (e.g., Kampouridis et al. 2022; 2023). The situation is especially dire concerning the European chilotheres. Eight distinct chilothere species have been erected within the very restricted geographical region of southeastern Europe (Kampouridis et al. 2023, table 1): *Aceratherium schlosseri* Weber, 1905, *Aceratherium samium* Weber, 1905, *Teleoceras ponticus* Niezabitowski, 1912, *Aceratherium kowalevskii* Pavlow, 1913, *Aceratherium wegneri* Andrée, 1921, *Aceratherium angustifrons* Andrée, 1921, *Chilotherium sarmaticum* Korotkevich, 1958, *Aceratherium kiliasi* Geraads and Koufos, 1990. The generic attributions and relationships among these forms is discussed in detail below (Tables 2 and 3).

Many authors have suggested the synonymy of some of these species in the past (e.g., Kiernik 1913; Korotkevitch 1970; Heissig 1975; Antoine and Sen 2016; Ţibuleac et al. 2023). Nonetheless, the status of most of them remains unclear. One reason for this ambiguity is the fact that the type specimens of *C. schlosseri* and *E. samium*, stored in Munich, were destroyed during WWII bombings (Geraads and Spassov 2009; Kampouridis et al. 2022; Giaourtsakis 2022 and references therein). From the types of *C. wegneri* and *C. angustifrons*, originally housed in Münster, only a mandible of *C. wegneri* has been relocated and described (Kampouridis et al. 2022). Closely related to *Chilotherium* is the genus *Shansirhinus* Kretzoi, 1942, that shares the complicated enamel folds, including a medifossette often closed by the crochet, markedly constricted protocone, connection between protocone and hypocone in the premolars, and enamel plications in the upper teeth (Kampouridis et al. 2023). This similarity increases the complexity of the genus's taxonomy and the diversity of the chilotheres group overall. Kampouridis et al. (2023) suggested that some species that were considered as belonging to *Chilotherium* lack certain apomorphies seen in all other *Chilotherium* species, such as the depression of the frontal region, and should probably be placed in different genera. Kampouridis et al. (2023) revised the species from Samos by fixing neotypes for the two valid species and separated them on the generic level, based on their differing skull morphology: *Chilotherium schlosseri* (Weber, 1905) and *Eochilotherium samium* (Weber, 1905). Additionally, they suggested that two species from Upper Miocene deposits of China, regarded as primitive members of the genus, "*Chilotherium*" *wimani* Ringström, 1924, and

Table 1 Summary of the taxonomy of the Chilotheriina (modified after Heissig 1975; Deng 2006b; Kampouridis et al. 2022, 2023)

Species	Authority	Revised species	Type locality
Aceratherium schlosseri	Weber, 1905	*Chilotherium schlosseri*	Samos, Greece
Teleoceras ponticus	Niezabitovski, 1912	*Chilotherium schlosseri*	Odessa, Ukraine
Aceratherium angustifrons	Andree, 1921	*Chilotherium schlosseri*	Samos, Greece
Aceratherium wegneri	Andree, 1921	*Chilotherium schlosseri*	Samos, Greece
Aceratherium kowalevskii	Pavlow, 1913	*Chilotherium kowalevskii*	Grebeniki, Ukraine
Chilotherium sarmaticum	Korotkevich, 1958	*Chilotherium sarmaticum*	Berislav, Ukraine
Chilotherium orlovi	Bayshashov, 1993	*Chilotherium orlovi*	Pavlodar, Kazakhstan
Rhinoceros persiae	Pohlig, 1886	*Chilotherium persiae*	Maragheh, Iran
Chilotherium anderssoni	Ringström, 1924	*Chilotherium anderssoni*	Anlecun, China
Chilotherium planifrons	Ringström, 1924	*Chilotherium anderssoni*	Anlecun, China
Chilotherium fenhoensis	Tung et al., 1975	*Chilotherium anderssoni*	Anlecun, China
Chilotherium habereri	Schlosser, 1903	*Chilotherium habereri*	Lantian, China
Chilotherium gracile	Ringström, 1924	*Chilotherium habereri*	Lantian, China
Chilotherium wimani	Ringström, 1924	"*Chilotherium*" *wimani*	Wangdaifuliang, China
Chilotherium xijangensis	Ji et al., 1980	*Chilotherium xijangensis*	Xijang, China
Chilotherium primigenium	Deng, 2006a	"*Chilotherium*" *primigenium*	Zhongmajia, China
Chilotherium licenti	Sun et al., 2018	*Chilotherium licenti*	Gansu, China
Aceratherium samium	Weber, 1905	*Eochilotherium samium*	Samos, Greece
Aceratherium kiliasi	Geraads and Koufos, 1990	*Eochilotherium samium*	Pentalophos, Greece
Rhinoceros brancoi	Schlosser, 1903	*Shansirhinus brancoi*	Shanxi, China
Shansirhinus ringstromi	Kretzoi, 1942	*Shansirhinus ringstromi*	Shanxi, China
Chilotherium yunnanensis	Tang et al., 1974	*Shansirhinus brancoi*	Yunan, China
Chilotherium cornutum	Qiu and Yan, 1982	*Shansirhinus ringstromi*	Shanxi, China

Table 2 The main differences observed on the craniodental material of *Chilotherium schlosseri* (Weber, 1905) and *Eochilotherium samium* (Weber, 1905) from the Late Miocene of Samos Island in Greece (modified after Kampouridis et al. 2023: table S1)

Feature	*Chilotherium schlosseri*	*Eochilotherium samium*
Size	Somewhat larger	Smaller
Skull shape	More brachycephalic, wider, dorsoventrally compressed, not raised posteriorly	More dolichocephalic, narrower, dorsoventrally higher, raised posteriorly
Nasal bones	Longitudinal groove present	Longitudinal groove very weak or absent
Frontal bones	Prominent depression in frontal bones	Convex frontal bones
Parietal crests	Widely separated	Moderately separated
Zygomatic arches	Posteriorly widening	Constant width
Orbit position	Upper border at similar level to nasal bones	Lower than nasal bones
Occipital condyles	Wide	Narrow and high
Foramen magnum	Dorsal incision	Dorsally rounded border
Occipital fossa	Deeper	Shallow
Lateral occipital crests	Broad and not marked	Narrow and more pronounced
Outer lateral crests	Subtle and rounded	More prominent and longer
Median valley	Closing at early wear stage in premolars	Closing late or not at all
Protocone constriction	Very strong in premolars, molars	Weak or absent in premolars, strong in molars
Enamel plications on upper dentition	Sometimes present	Absent

Table 3 Distance between the parietal crests of all available *Chilotherium schlosseri* (Weber, 1905) skulls from the Late Miocene of Samos Island (Greece) and the Chilotheriina species discussed in text

Specimen or taxon	Distance (mm)	*N*	Source
Lectotype of *Chilotherium schlosseri*	90	-	Weber (1905)
Holotype of *Chilotherium angustifrons*	70	-	Andree (1921)
Holotype of *Chilotherium wegneri*	87	-	Andree (1921)
GPIH 3015 (neotype of *Chilotherium schlosseri*)	89	-	Present study
NHMW-GEO-1911/0005/0128	71	-	Present study
HLMD-Sam192	72	-	Present study
NMB-Sam.25	75	-	Present study
AMNH-20794	100	-	Present study
MGP-PD 25302	71.3	-	Present study
AMPG-SAM513	75.5	-	Present study
AMPG-SAM508	80	-	Present study
AMPG-SAM510	72	-	Present study
Chilotherium schlosseri (Weber, 1905)	71–100	12	Andree (1921); own data
Eochilotherium samium (Weber, 1905)	~40	2	Andree (1921); Kampouridis et al. (2023)
Chilotherium persiae (Pohlig, 1886)	36.5–53.7	11	Kampouridis et al. (2023)
Chilotherium habereri (Schlosser, 1903)	42–60	9	Killgus (1922); Ringström (1924)
Chilotherium kowalevskii (Pavlow, 1913)	40.1–66	10	Krokos (1917)
Chilotherium anderssoni Ringström, 1924	50–63	5	Ringström (1924)
"Chilotherium" wimani Ringström, 1924	15.3–66.7	57	Chen et al. (2010)
Chilotherium sarmaticum Korotkevich, 1958	51-76.2	4	Korotkevich (1970)
Chilotherium orlovi Bayshashov, 1982	45–75	3	Bayshashov (1982)
"Chilotherium" primigenium Deng, 2006b	18	1	Deng (2006b)

"*Chilotherium*" *primigenium* Deng, 2006a, also seem to be more similar to *E. samium* than to other *Chilotherium* species and should be excluded from this genus, either belonging to *Eochilotherium* Geraads and Spassov, 2009, or to a different genus. The study of Kampouridis et al. (2023) conducted such a revision of the Samian chilotheres by offering detailed descriptions and comparisons of the neotypes of the two chilothere species from Samos, along with diagnoses that clearly separate them from each other and from any other rhino species. However, it focused only on the two neotype skulls and their associated mandibles. There are several other skulls, mandibles and more fragmentary elements that would elucidate the relationship between these two hornless rhino species and assess their intraspecific variability.

Accordingly, the goal of the present work is to describe and compare all available skulls that can be assigned to *Chilotherium schlosseri* from the Upper Miocene horizons of Samos Island that are scattered throughout different institutions and provide a detailed overview of morphological variation of this species. Both skulls and mandibles are examined and compared to relevant chilothere species, evaluating the variability of *C. schlosseri*. This way, we aim to confirm the number of hornless rhinos co-occurring in Samos during the Late Miocene, as well as their interspecific abundance.

History of the Samos excavations

The palaeontological wealth of the Island of Samos has sparked the interest of researchers from Europe from the early 1850s until the first decade of the 21st century. The first systematic excavations on the island were conducted in 1885–1887 and 1889 by C. Forsyth Major, in the sites Adrianos ravine, Potamies ravine, and Stefana. German scientists T. Stutzel and A. Hentschel also contributed to the excavations on the island between 1897 and 1902 (Schlosser 1903; Andrée 1926). In 1901, the renowned German paleontologist E. Fraas carried out new excavations on the island (Koufos 2009). Later on, the famed American "fossil hunter" B. Brown excavated a notable number of specimens (Brown 1927). Additionally, during the same time, several lesser-known excavation campaigns, often not organized by palaeontologists, took place (e.g., Gürich 1911; Andrée 1921; Drevermann 1930). The material of these excavations was transferred to different institutions around the world, where it is housed today.

As far as Greek researchers are concerned, the Samian doctor A. Stefanidis from Mytilinii village was among the pioneers of excavating and collecting fossils. In 1879, Stefanidis delivered a number of his collected specimens to Professor I. Mitzopoulos (University of Athens), though he never received any response from the professor. The whereabouts of this collection are currently unknown. Eventually, Stefanidis, who kept collecting fossils, gave his collection to C. Forsyth Major the second time the British expatriate came to Samos, in 1887; this collection, along with the rest of the material Forsyth-Major collected in Samos, is now housed in the museums of Geneva, Basel and Lausanne (Koufos 2009).

The curator of the Athens Museum of Palaeontology and Geology and later University of Athens Professor, T. Skoufos, was the first Greek academic to lead an organized excavation in the sites Adrianos, Katikoumena, Bartzikos and Bailntaki in 1903 (Koufos 2009). Postdating Skoufos, Aristotle University of Thessaloniki Professor I. Melentis conducted two new excavations at the fossiliferous site Mytilinii-1 A (MTLA) of Adrianos ravine, in 1963 and 1985 (Melentis 1968; Koufos 2009). In 1976, N. Solounias led new excavations on the island under the auspices of University of Colorado (Black et al. 1980; Solounias and Ring 2007). Solounias was the first to also excavate for small mammals, which were found in locality S3 (Solounias and Ring 2007). The latest systematic excavations in Samos were led by Aristotle University of Thessaloniki Professors G. Koufos and D. Kostopoulos between 1990 and 2006, shedding light on an immense number of specimens and resolving important issues on the stratigraphy and palaeoecology of the island's fossiliferous localities (Koufos 2009).

Geological and stratigraphical context

The illustrious fossiliferous strata of Samos are part of the Mytilinii Formation, situated in the northwestern part of Mytilinii Basin, one of the three Neogene depressions present on the island (Mountrakis et al. 2003). The latter is characterized by a complicated stratigraphy, which has been an issue of study since the 19th century (Kostopoulos et al. 2009 and references therein). According to the most recent work of Kostopoulos et al. (2009), the vast majority of the fossils are found in the Main Bone Beds Member of the Mytilinii Formation, which consists mainly of brownish to reddish silty sands, along with yellow to brownish conglomerates, tuffaceous sandstones and white tuffites. The formation is overlain by tuffaceous red sandy silts with insertions of massive tuffs (Kostopoulos et al. 2009).

One major problem concerning the study of the Samos fauna is the striking lack of adequate stratigraphic data. The various excavations were led by different scientists, each one using their own methods for documenting their findings. Consequently, the same locality can be found in the literature under different names. Additionally, many specimens originate from unknown fossiliferous horizons. Thus, stratigraphic correlations between the different collections of fossil material from Samos, including the material studied herein, are not possible (Kostopoulos et al. 2009).

Institutional abbreviations: AMNH, American Museum of Natural History, USA; **AMPG**, Athens Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens, Greece; **GMM**, Geomuseum der Universität Münster, Germany; **GPIH**, Geologisch-Paläontologisches Institut der Universität Hamburg, Germany; **GPIT**, Geologisch-Palaeontologisches Institut Tübingen, Germany; **HLMD**, Hessisches Landesmuseum Darmstadt, Germany; **MGP-PD**, Museo di Geologia e Paleontologia, Padua, Italy; **MNHN**, Muséum national d' Histoire naturelle, Paris, France; **NHMW**, Naturhistorisches Museum Wien, Austria; and **NMB**, Naturhistorisches Museum Basel, Switzerland.

Systematic palaeontology

Mammalia Linnaeus, 1758
Perissodactyla Owen, 1848
Rhinocerotidae Gray, 1821
Aceratheriinae Dollo, 1885 (sensu Lu et al. 2023)
Aceratheriini Dollo, 1885 (sensu Lu et al. 2023)
Chilotheriina Qiu et al., 1987 (sensu Kampouridis et al. 2023)

Included genera: *Chilotherium* Ringström, 1924; *Shansirhinus* Kretzoi, 1942; and *Eochilotherium* Geraads and Spassov, 2009.

Remarks: The name Chilotheriini was originally proposed by Qiu et al. (1987) for a tribe that would encompass the genera *Acerorhinus* and *Chilotherium*, and to specifically exclude the more plesiomorphic genus *Aceratherium*. However, it has not yet been possible to prove that this comprises a monophyletic group. In fact, *Acerorhinus* shows many plesiomorphic characters separating it from representatives of the genus *Chilotherium*. It is therefore considered best to remove *Acerorhinus* from this group. Following the recommendation of Kampouridis et al. (2023), we herein use the name Chilotheriina at a subtribe rank that includes the genera *Chilotherium*, *Shansirhinus*, and *Eochilotherium*.

Genus *Chilotherium* Ringström, 1924

Type species: *Chilotherium anderssoni* Ringström, 1924

Other included species: *Chilotherium persiae* (Pohlig, 1886); *Chilotherium habereri* (Schlosser, 1903); *Chilotherium schlosseri* (Weber, 1905); *Chilotherium kowalevskii* (Pavlow, 1913); *Chilotherium sarmaticum* Korotkevich, 1958; *Chilotherium orlovi* Bayshashov, 1982; *Chilotherium licenti* Sun et al. 2018, and possibly *"Chilotherium" wimani* Ringström, 1924 and *"Chilotherium" primigenium* Deng 2006b.

Diagnosis: Aceratheriine rhinocerotids that bear the following features: flat and wide skull; flattened and depressed frontal region; absence of horn-bosses, suggesting the absence of keratin horns; well-developed postorbital processes; moderately to widely separated parietal crests; highly placed orbits; very wide mandibular symphysis that features a concave ventral side; very large, flattened, tusk-like second lower incisors, with a scalene triangle cross section and upturned, dorsomedially oriented wear facets; reduced premaxillary bones that lack upper incisors; and very strong secondary enamel folds, including a lingually flattened and strongly constricted protocone in the upper molars. The genus is also characterised by a relatively short length of the premolars compared with the molars, mainly due to the reduced size of the P2 and p2; and notably shortened metapodials and relative robust appendicular skeleton (modified after Ringström 1924; Geraads and Spassov 2009; Giaourtsakis 2022; Kampouridis et al. 2023).

Remarks: The validity of the different *Chilotherium* species and their potential synonymies have been debated for many years (see Kiernik 1913; Krokos 1917; Ringström 1924; Deng 2001; Kampouridis et al. 2022). We herein follow Geraads and Koufos (1990) and Kampouridis et al. (2023) and exclude *E. samium* from the genus *Chilotherium* and consider the species *"C." wimani* and *"C." primigenium* most likely not belonging to *Chilotherium*. Additionally, we consider *C. schlosseri* from Samos, *C. kowalevskii* from Grebeniki and *C. sarmaticum* from Berislav as distinct species, pending a comprehensive revision of the type material of these species. Many studies have argued in favour of *C. schlosseri* representing the senior synonym of *C. kowalevskii* (e.g., Krokos 1917; Korotkevich 1970; Antoine and Sen 2016; Ţibuleac et al. 2023). Nevertheless, in *C. schlosseri* the parietal crests are much more widely separated, with the measured values not exhibiting any overlap. Moreover, the upper premolars of *C. kowalevskii* lack the complex enamel plications and the closed medifossette present in *C. schlosseri*. Korotkevich (1970) showed that *C. sarmaticum* from Berislav can be differentiated from *C. kowalevskii* from Grebeniki based on the postcranial material.

Chilotherium schlosseri (Weber, 1905)

Neotype: a well-preserved skull (GPIH 3015) with an associated mandible (GPIH 3015a), designated by Kampouridis et al. (2023).

Type locality: Upper Miocene deposits of Samos Island; precise locality unknown.

Junior synonyms: *Teleoceras ponticus* Niezabitowski, 1912; *Aceratherium wegneri* Andrée, 1921; *Aceratherium angustifrons* Andrée, 1921.

Diagnosis: A large *Chilotherium* species characterised by widely separated parietal crests (minimal distance between parietal crests always over 70 mm in adult individuals), frontal region notably depressed in the middle, constriction of the protocone very strong;constriction of the protocone very strong;nasal bones that bear a central longitudinal groove on the dorsal side, and a unique combination of dental characters: crochet very long; mesial and distal constriction of the protocone very strong; protoloph lingually flattened; antecrochet very long; median valley usually closed off the at an early wear stage in all teeth; mesial constriction of the hypocone prominent; crista frequently present on the premolars; medifossette normally closed; lingual cingulum discontinuous and occasionally moderately developed in the upper premolars; prefossette often closed on P2; enamel plications sporadically present in the upper teeth; lingual and buccal cingulids discontinuous in the lower teeth (after Kampouridis et al. 2023).

Referred material: AMNH 20794, complete skull with associated mandible; AMPG-SAM513, complete skull missing nasal and premaxillary bones; AMPG-SAM503, partial skull; AMPG-SAM506, partial skull; AMPG-SAM508, partial skull; AMPG-SAM509, partial skull; AMPG-SAM510, partial skull; GPIH 3015, complete skull with associated mandible; HLMD-Sam192, complete skull, with reconstructed posterior portion of dorsal surface; MGP-PD 25302, complete skull; NHMW-GEO-1911/0005/0128, complete skull; NHMW-GEO-2009z0088/0001, complete skull with deciduous teeth, missing premaxillary bones; NMB-Sam.25, complete skull with associated mandible; AMNH 22815, mandible; AMPG-SAM500, mandible; NHMW-GEO-1911/0005/0032, mandible; NHMW-GEO-1911/0005/0033; mandible (Fig. 1).

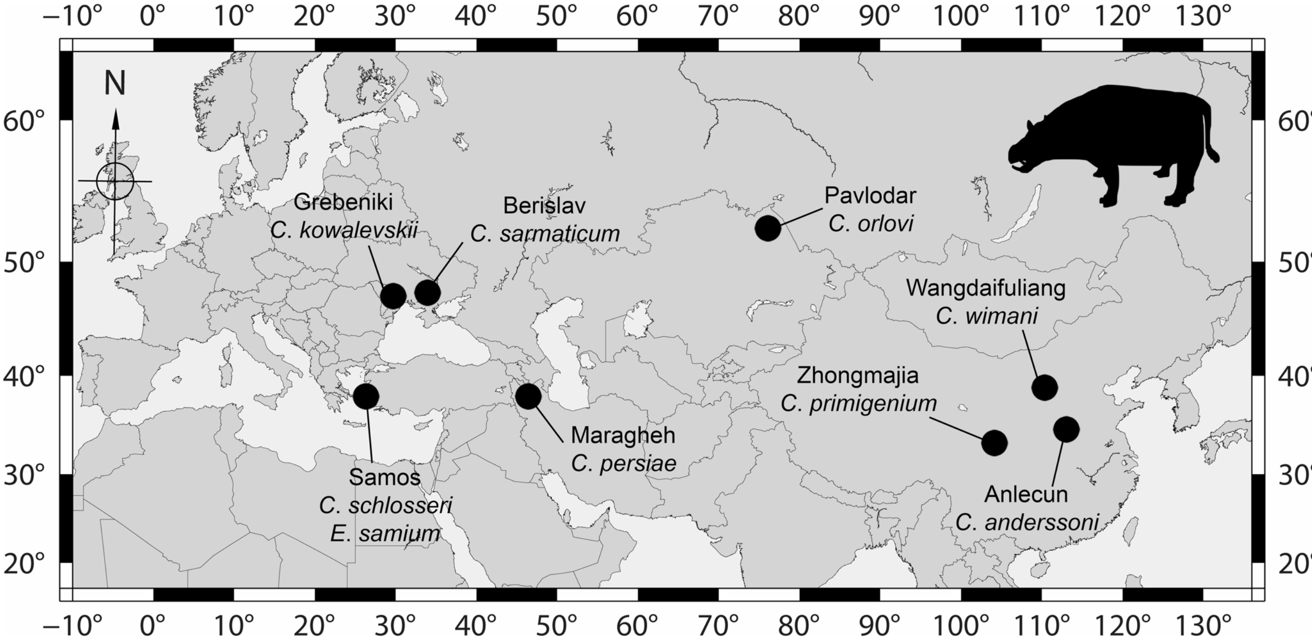

Fig. 1 Map of the type localities of the species of *Chilotherium* and *Eochilotherium* discussed in the text. The map was created using Generic Mapping Tool (GMT) 6 Source of the silhouette of *C. anderssoni*: phylopic.org (by Zimices; CC BY-SA 3.0)

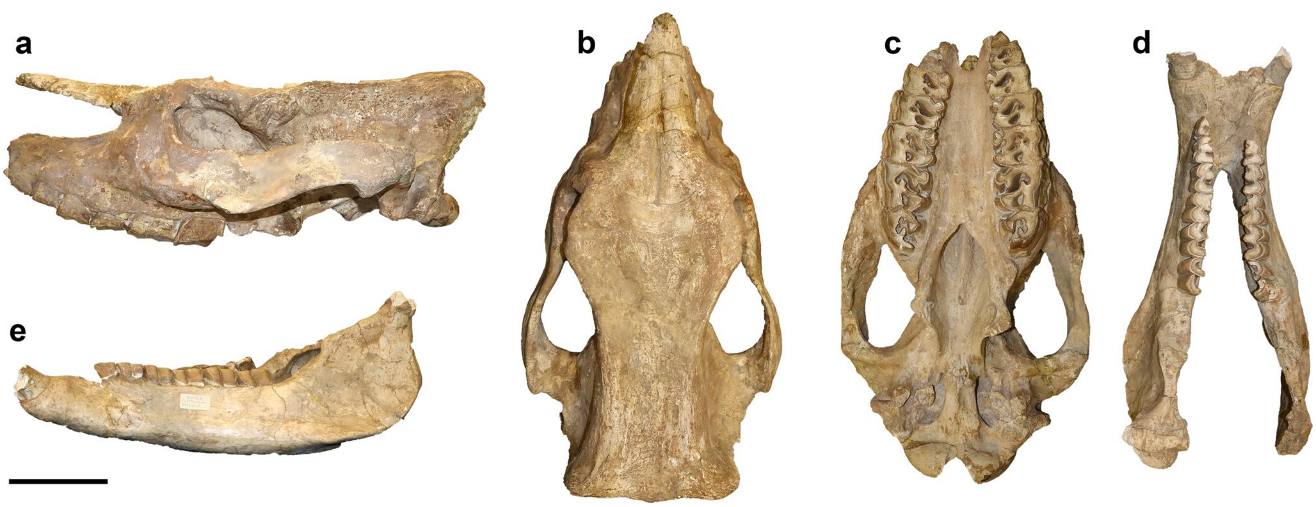

Fig. 2 Neotype of the hornless rhinoceros *Chilotherium schlosseri* (Weber, 1905) (GPIH 3015) from the Upper Miocene of Samos Island, Greece. **a-c.** skull in lateral (**a**), dorsal (**b**) and ventral (**c**) views; **d-e.** mandible in dorsal (**d**) and lateral (**e**) view. Scale bar equals 10 cm

Remarks: Numerous *C. schlosseri* skulls and mandibles from Samos Island are housed in various European and American collections. Most are in an adequate preservation stage, though missing certain parts. Consequently, the descriptions will be based on observations from the whole of the available material. *Chilotherium schlosseri* is the first described species of the genus from Europe (Weber 1905). It was described based on material from Samos and was recently revised (Kampouridis et al. 2023). The neotype shares all diagnostic traits with the referred material (Fig. 2). More specifically, the neotype has a deep depression in its frontal bones, which also leads to more ventrally placed nasal bones, in lateral view. This is also visible in several studied specimens, like GPIH 3015, NMB-Sam.25, and MGP-PD 25302 (Fig. 3). *Chilotherium schlosseri* exhibits the most widely separated parietal crests (always over 70 mm in adult specimens) among the representatives of the genus. This is also also the case in all studied specimens, where the parietal crests are observed. Furthermore, the upper dentition of our studied material is identical with the *C. schlosseri* material available in the literature (Weber 1905; Andrée 1921; Giaourtsakis 2022; Kampouridis et

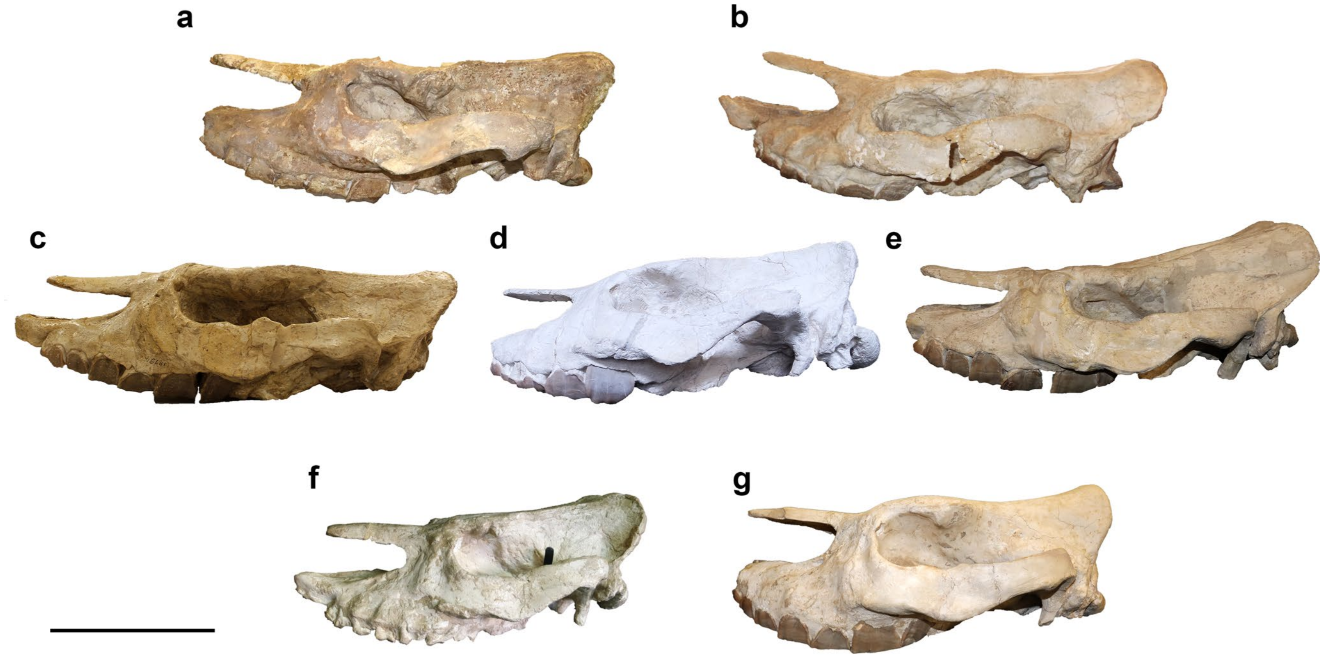

Fig. 3 Skulls of the hornless rhinocerotid *Chilotherium schlosseri* (Weber, 1905) from the Upper Miocene of Samos Island, Greece, in lateral view **a.** GPIH 3015; **b.** MGP-PD 25302; **c.** AMNH 20794; **d.** NHMW-GEO-2009z0088/0001; **e.** NMB-Sam.25; **f.** NHMW-GEO-1911/0005/0128; **g.** HLMD-Sam192. Scale bar equals 10 cm

al. 2023), featuring extremely strong protocone constrictions and marked hypocone constriction, especially in the molars. The antecrochet is long, bending mesiolingually bending and closing off the median valley at an early wear stage in the premolars and at a moderate to advanced wear stage in the molars. A strong crochet is present in all teeth, a crista is frequently present and the medifossette usually closes at a moderate to advanced wear stage on P4 and M1. A characteristic trait for *C. schlosseri* is the variable presence of enamel plication in the upper dentition, which are also observable in many of the studied specimens. Thereby, the attribution of the studied material from Samos to this species is justified.

Morphological description

Skull

There are several almost complete and well-preserved skulls in the historical Samos collections, such as AMPG-SAM513, NHMW-GEO-1911/0005/0128 and NHMW-GEO-2009z0088/0001, HLMD-Sam192, and NMB-Sam.25. However, certain specimens are slightly deformed, such as the taphonomically transversally compressed skull NHMW-GEO-1911/0005/0128. Other are partially reconstructed with plaster, like NMB-Sam.25, in which the anterior part of the skull was broken off and then put back together incorrectly using plaster, leading to a distortion of the skull, and HLMD-Sam192, in which case most of the dorsal surface of the skull is covered in plaster, not allowing the detailed description of this region (Fig. 4).

The skull form ranges from slightly dolichocephalic (width/length ratio of ~42 in the transversally somewhat taphonomically compressed skull NHMW-GEO-1911/0005/0128 and ~43 in the juvenile skull NHMW-GEO-2009z0088/0001) to brachycephalic (width/length ratio of ~53 in HLMD-Sam192 and ~55 in NMB-Sam.25). It is worth noting that the oldest and youngest skulls amidst the referred material (NHMW-GEO-1911/0005/0128 and NHMW-GEO-2009z0088/0001 respectively) bear an almost identical skull width/length ratio, indicating that ontogeny has no impact on this feature. The skull is relatively short dorsoventrally. Although there are no horn bosses, the anterior tip of the nasal bones is somewhat rugose, a character most visible in the specimens GPIH 3015, NHMW-GEO-2009z0088/0001 and NMB-Sam.25 (Fig. 4). The frontal region is depressed in the middle, appearing transversally concave, affecting the position of the nasal bones. The latter remain separated, with a visible internasal suture until in most adult specimens, including the oldest available specimen NHMW-GEO-1911/0005/0128, in which even the M3 is heavily worn (Fig. 5). The region from the nasals to the parietal bones is notably depressed, with the parietal crests being very prominent, and widely separated (70–100 mm). The transversal development of the zygomatic arches seems to vary a little, but in all skulls, they tend to widen

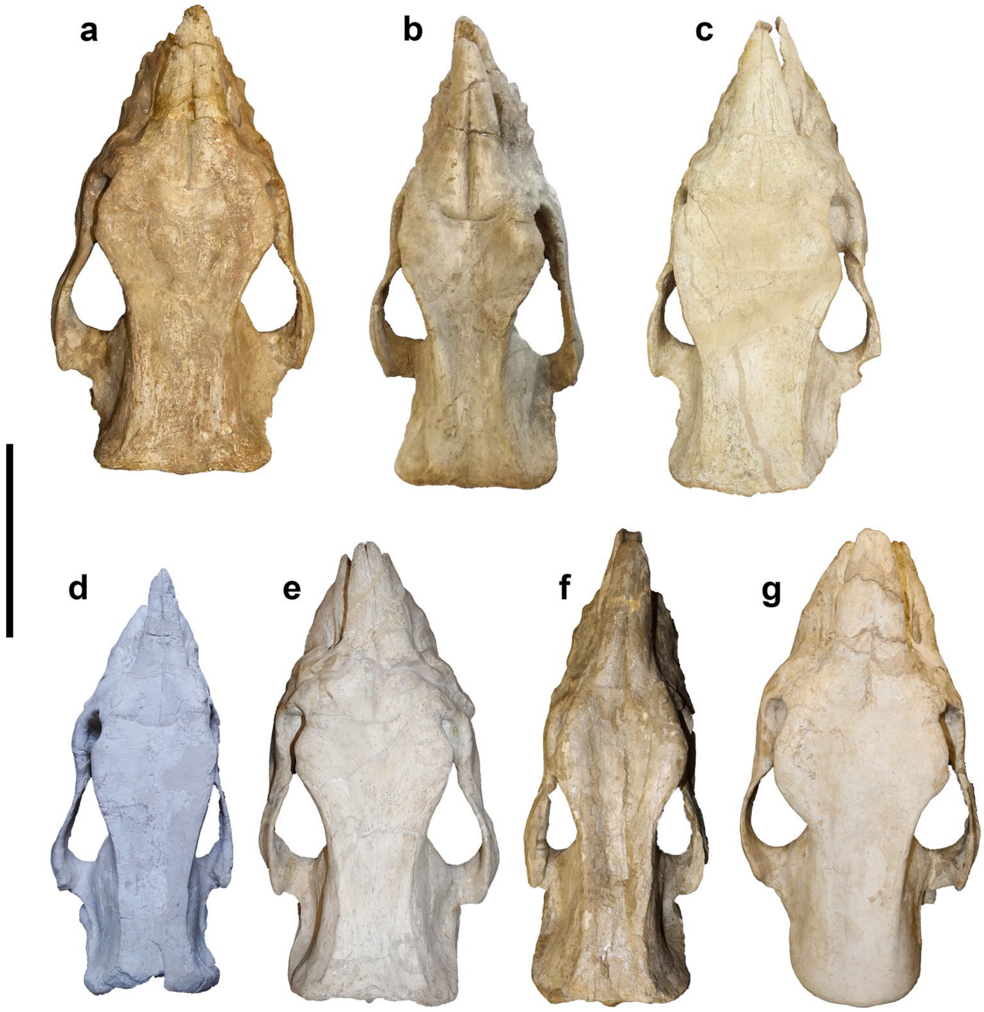

Fig. 4 Skulls of the hornless rhinocerotid *Chilotherium schlosseri* (Weber, 1905) from the Upper Miocene of Samos Island, Greece, in dorsal view. **a.** GPIH 3015; **b.** MGP-PD 25302; **c.** AMNH 20794; **d.** NHMW-GEO-2009z0088/0001; **e.** NMB-Sam.25; **f.** NHMW-GEO-1911/0005/0128; **g.** HLMD-Sam192. Scale bar equals 10 cm

posteriorly. In lateral view, the nasal notch is deep, the exact position of its posterior border varying between the skulls from the level above the anterior part of the M2 to the level of the contact between the P4 and the M1. This feature also appears to be independent of the ontogeny of the specimens, as it is similarly positioned in both juvenile NHMW-GEO-2009z0088/0001 (a specimen of young ontogenetic age with deciduous dentition) and old NHMW-GEO-1911/0005/0128 (a specimen of old ontogenetic age, with deeply worn teeth).

Correlatively, the anterior margin of the orbit varies between the level of the middle of the M3 and the level of the middle of the M2. The distance between the orbit and the nasal notch is relatively short. The post-glenoid process extends further ventrally than the post-tympanic process, and the two remain well-separated. In posterior view, the occipital region is wide. Its dorsal part is fan-shaped. The occipital condyles are strong, very wide, and saddle shaped. In ventral view, the posterior border of the incisive foramen is located between P2 and P3 and the mesial border of the choanae is located anterior to M3 or mid of M3 in old individuals (M3 in wear), while in younger individuals, the incisive foramen is at the level of P2 and the mesial border of the choanae is located between M1 and M2. The shape of the postglenoidal apophysis varies from subtrapezoidal to elliptical, the hypoglossal foramen is located anteriorly on the condylar fossa and the sagittal crest is barely visible in all the specimens, with the exception of NHMW-GEO-2009z0088/0001, which belongs to a young individual with deciduous dentition).

Upper dentition

Traces of cement are preserved in some of the specimens. The premolars have a quadrangular outline. Depending on the degree of the wearing of the enamel, the protocone and hypocone are either connected by a wide bridge or separated. The P2s bear an adamantine style and a lingual cingulum. They preserve a postfossette. A small, pointed crista is also present. The crochet is weak. The crista and crochet

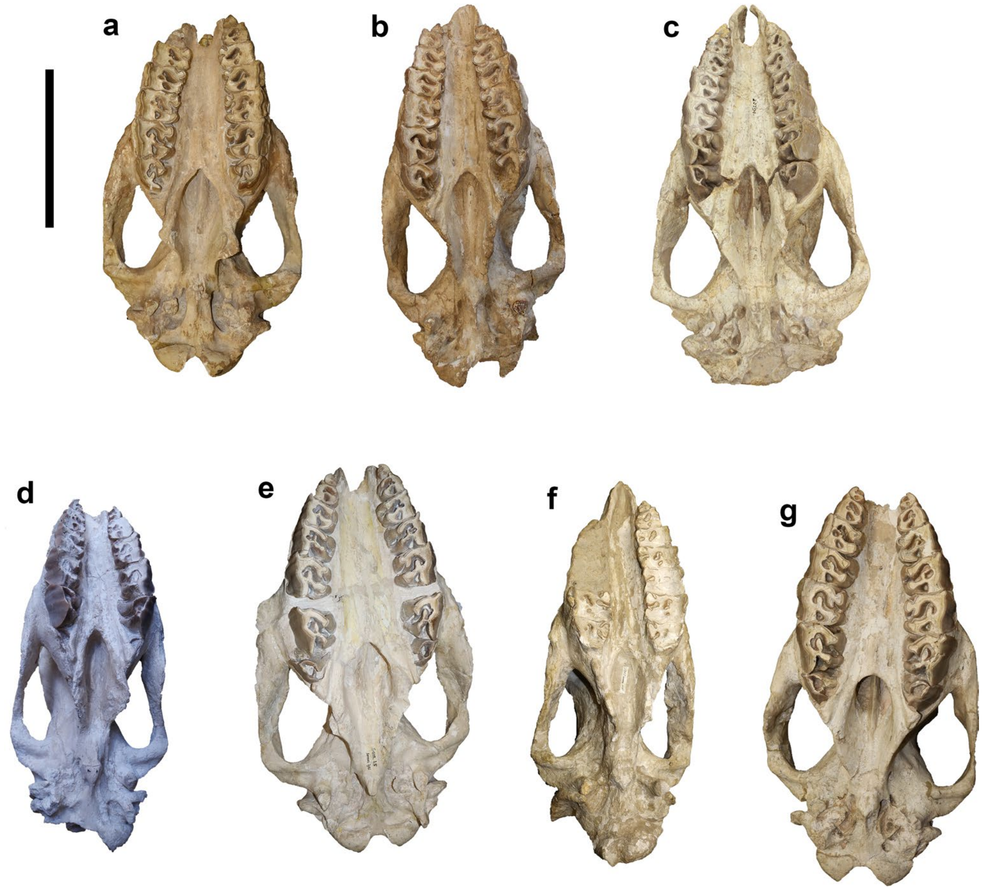

Fig. 5 Skulls of the hornless rhinocerotid *Chilotherium schlosseri* (Weber, 1905) from the Upper Miocene of Samos Island, Greece, in ventral view. **a.** GPIH 3015; **b.** MGP-PD 25302; **c.** AMNH 20794; **d.** NHMW-GEO-2009z0088/0001; **e.** NMB-Sam.25; **f.** NHMW-GEO-1911/0005/0128; **g.** HLMD-Sam192. Scale bar equals 10 cm

are not joined. The antecrochet is smooth and rounded. The median valley is open. The parastyle extends mesially. The mesial part of the ectoloph is curved.

The P3s preserve cement traces both labially and, to a lesser degree, lingually. The protocone has a curved lingual margin. The hypocone constriction is weaker than that of the protocone. The antecrochet is smooth and rounded. The crista, when present, is very weak. The crochet is markedly curved. The postfossette is wide. The paracone and metacone folds are weak. A lingual cingulum is present. The parastyle is short, the metastyle is slightly longer and sharper. The median valley is narrow.

On the P4s, the protocone and hypocone, both well constricted, are roughly of the same size. The lingual margin of the protocone is almost straight. The antecrochet is thin. The paracone fold is weak. The crochet is well developed and markedly curved. On the contrary, the crista is miniscule. The postfossette is large and roughly triangular. The posterior wall is strong. The median valley is open lingually. The parastyle is stronger than the metastyle.

The M1s bear a very marked protocone constriction. The hypocone is also constricted, though to a lesser degree. The antecrochet is very strong and curved lingually. There is no crista. The crochet is strong and curved labially. The postfossette is triangular. The paracone fold is very weak, almost absent. A weak, discontinuous lingual cingulum is present.

The M2s bears a very sharp, mesially extended parastyle. The metastyle is long. The protocone is notably more constricted than the hypocone and has a roughly straight lingual margin. The crochet is very large and markedly curved labially, almost tear shaped. There is no crista. The antecrochet is present, though weak and rounded. There is no posterior wall. The posterior valley has a triangular outline. A lingual cingulum is also present.

The M3 preserves faint cement traces labially. It has a sharp parastyle. The ectoloph and metaloph are fused together, thus explaining the triangular outline of the tooth. The paracone fold is very weak. The crochet, though thin, is long and curved. A weak lingual cingulum is present. The posterior valley is wide.

As far as the deciduous upper dentition is concerned, some of the characters previously discussed are also present, as observed in the specimen NHMW-GEO-2009z0088/0001 (Fig. 6). The specimen bears a constricted protocone and hypocone as well as lingual cingula on the preserved teeth.

The DP3 bears a marked protocone constriction. A medifossette is present, as well as a lingual cingulum. The

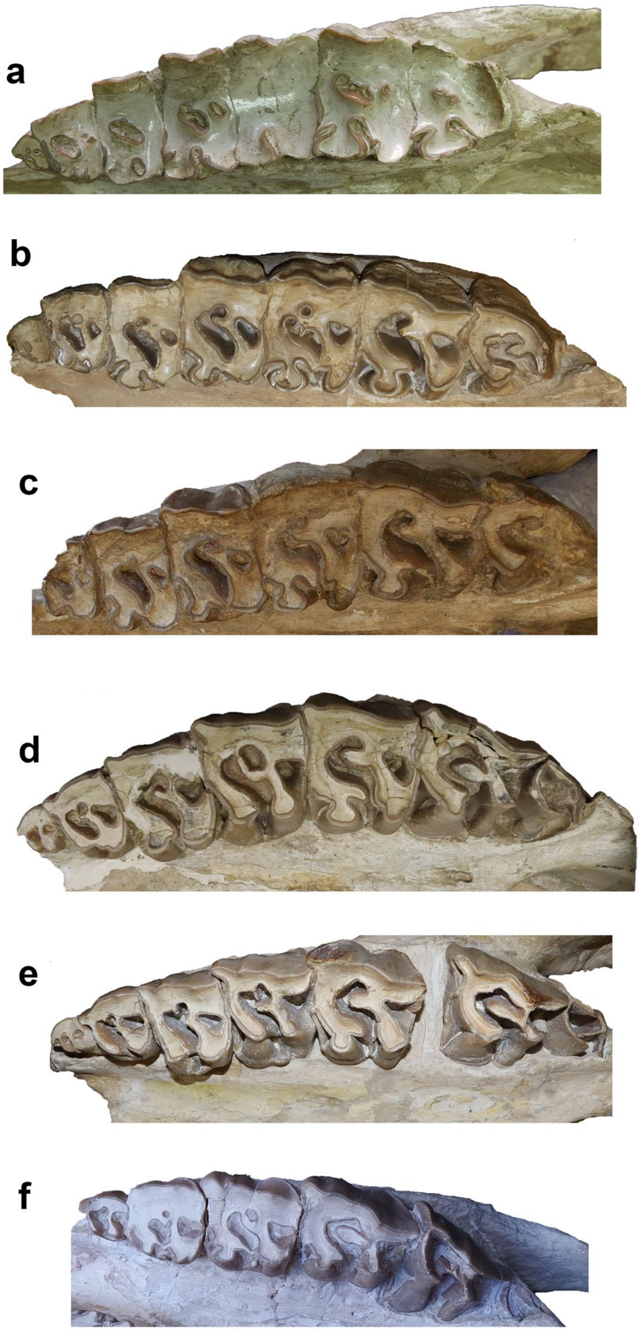

Fig. 6 Ontogenetic series of upper dentition of the hornless rhinocerotid *Chilotherium schlosseri* (Weber, 1905) from the Upper Miocene of Samos Island, Greece, in occlusal view, from oldest (**a**) to youngest (**f**) - featuring a complete deciduous dentition - specimen. **a.** NHMW-GEO-1911/0005/0128; **b.** GPIH 3015; **c.** MGP-PD 25302; **d.** HLMD-Sam192; **e.** NMB-Sam.25; **f.** NHMW-GEO-2009z0088/0001. Scale bar equals 10 cm

antecrochet is elongated and lingually curved. The median valley is closed.

The DP4 bears a strong, elongated crochet and a short, pointed antecrochet. The postfossette, though in a mediocre preservation stage, is deep. The median valley remains open. A lingual cingulum is present.

Mandible

The most notable characteristic of the mandible is the very wide symphysis, terminating posteriorly at the level of p3. The ascending ramus is preserved only on specimens AMNH 20794 and NMB-Sam.25 (Fig. 7). On AMNH 20794, which belongs to a male individual based on the large, dagger-like incisors (Chen et al. 2010), the ramus is markedly concave in lateral view. On the other hand, the ascending ramus of NMB-Sam.25, which based on the much shorter incisors belongs to a female individual, has a more concave shape in lateral view. The mandibular body is not very robust. Its base is nearly straight beneath the level of m3 to p2, gradually bending towards the symphysis. The angle between the body and the symphysis is somewhat more obtuse in NMB-Sam.25 compared to AMNH 20794. In lateral view, the foramen mentalis opens in front of p3. In the rostral part of the symphysis, a light sagittal linear groove is formed. In dorsal view, the referred material demonstrates a long diastema with a marked crista along the interalveolar margin.

Lower dentition

Traces of cement are preserved in some of the specimens. The morphology of the lower dentition is simple and relatively uniform within the genus *Chilotherium*, bearing metalophids relatively longer than the paralophids, weakly constricted metaconids, relatively sharp trigonids and a deep ectolophid groove. The lower incisors are tusk-like, more or less straight in dorsal view and distinctly curved in lateral view, wide close to the basis, getting progressively narrower. They grow divergently. When partly preserved, the roots of the i1s are small and somewhat meniscus shaped (Fig. 8). The size of the lower incisors is indicative of strong sexual dimorphism in chilotheres, as they are larger in alleged male individuals compared to females (Chen et al. 2010).

Comparison with non-chilothere aceratheriines

During the Turolian, three hornless rhinocerotid genera are present in Greece: derived *Chilotherium* and more "primitive" *Eochilotherium* and *Acerorhinus*. The type species of the latter genus is *Acerorhinus zernowi* (Borissiak, 1914). This species is well known from a rich collection of fossils from the Middle Miocene of Tung Gur in Mongolia (Cerdeño 1996). *Chilotherium schlosseri* presents significant differences with this species as well. *Acerorhinus zernowi* has narrowly separated parietal crests (Cerdeño 1996: fig. 2c), and a deeply concave dorsal skull profile, due to the

Fig. 7 Mandibles of the hornless rhinocerotid *Chilotherium schlosseri* (Weber, 1905) from the Upper Miocene of Samos Island, Greece, in lateral view. **a.** AMNH 20794; **b.** NMB-Sam.25; **c.** AMNH 22815. Scale bar equals 10 cm

Fig. 8 Mandibles of the hornless rhinocerotid *Chilotherium schlosseri* (Weber, 1905) from the Upper Miocene of Samos Island, Greece, in dorsal view. **a.** AMNH 20794; **b.** AMNH 22815; **c.** GPIH 3015; **d.** GMM SIII/1; **e.** NHMW-GEO-1911/0005/0032; **f.** NHMW-GEO-1911/0005/0033; **g.** AMPG-SAM500; **h.** GMM SIII/2. Scale bar equals 10 cm

prominent elevation of the occipital region (Cerdeño 1996: fig. 3a) compared to the well separated parietal crests and the flat dorsal skull profile of the studied skulls from Samos. The mandible of *A. zernowi* has a much narrower symphysis (Cerdeño 1996: fig. 3a) compared to the studied material. Furthermore, the upper dentition of *A. zernowi* lacks the strongly constricted protocone and the long, lingually bent antecrochet on the molars (Cerdeño 1996: fig. 4a) observed on the studied specimens.

The genus is represented in Greece by *Acerorhinus neleus* Athanassiou et al., 2014, first reported from the Turolian locality of Kerassia, Evia Island, but also present in the locality of Pikermi in Attica (Theodorou et al. 2003; Athanassiou et al. 2014; Kampouridis et al. 2019). There are several differences between the material under study and *A. neleus*: the dorsal profile of the Samos material is flat, with a notable depression in the frontal bones, whereas in *A. neleus* the skull is transversally convex and the dorsal profile is slightly concave (Athanassiou et al. 2014: pl. 1, fig. 3a–b); the parietal crests are less widely separated in *A. neleus* than in the Samos specimens (Athanassiou et al. 2014: table 1); the distance between the nasal incision and the rostral margin of the orbital fossa is longer in *A. neleus* (77 mm left and 88 mm right in *A. neleus*; Athanassiou et al. 2014: table 1), compared to 63.5–72.8 mm in the studied Samos material. The occipital region of *A. neleus* appeared to be bell-shaped and is dorsoventrally higher, compared with the wider and trapezium-like occipital region of the studied specimens (Athanassiou et al. 2014: pl. 1, fig. 3c). The mandibles from Samos bear one of the most notable apomorphies of the genus *Chilotherium*: the markedly wide symphysis (Ringström 1924), whereas in *A. neleus* the mandibular symphysis is much narrower. The diastema between i2 and p2 is longer and more curved in the Samos specimen than in *A. neleus*, and in lateral view, the anterior, incisors-bearing, part of the symphysis is straighter in the Samos specimens than in *A. neleus* (Athanassiou et al. 2014, pl. 2, fig. 2a–c).The upper teeth of the Samos specimens are generally more hypsodont compared to *A. neleus*, with a stronger protocone constriction, more pronounced and longer antecrochets and complicated enamel plications compared to *A. neleus* (Athanassiou et al. 2014: pl. 1, fig. 4a–b; pl. 2, fig. 1b). Finally, the Samos specimens bear shorter premolars mesio-distally, compared to *A. neleus* (Athanassiou et al. 2014). Thereby, the Samos material can easily be separated from that of *Acerorhinus*.

Persiatherium rodleri is an acerathere rhinocerotid from the early Upper Miocene of Maragheh, Iran, co-occurring with *C. persiae* (Pandolfi 2016) and coeval to the Samos fossil assemblage. As one badly preserved skull, preserving only a part of the basicranium and preserving M1-M2, D4, P3-P1 on the left hemimaxilla and M1-M2, D4, P3-P2 on the right hemimaxilla (Pandolfi 2016: fig. 2a), is the sole specimen available, the only possible comparison was with the available permanent dentition. Both the premolars and the molars of *P. rodleri* lack the marked protocone and hypocone constriction and the elongated, strong antecrochet that characterizes the referred material from Samos; additionally, the premolars of *P. rodleri* bear a notably strong, continuous lingual cingulum that is not present in the Samos material (Pandolfi 2016: fig. 2a, b).

Comparison with *Eochilotherium samium*

Two valid species of hornless rhinocerotids are reported in the Upper Miocene deposits from Samos Island: *E. samium* and *C. schlosseri* (Kampouridis et al. 2023). *Eochilotherium samium* has had a strongly debated taxonomy (Fortelius et al. 2003; Geraads and Spassov 2009; Athanassiou et al. 2014; Kampouridis et al. 2023). *Chilotherium schlosseri* can be distinguished from *E. samium* based on the following morphological variations: the frontal region of *E. samium* is convex in the anterior part and flattens posteriorly, whereas *C. schlosseri* has a markedly concave frontal region. Furthermore, the parietal crests of *C. schlosseri* are more widely separated (at least 70 mm apart in all adult specimens) than in *E. samium*, in which they are roughly 40 mm apart (Kampouridis et al. 2023).

The upper dentition of *C. schlosseri* is characterized by a very strong protocone constriction, which results in a marked antecrochet closing off the median valley. On the other hand, in *E. samium* this constriction is weaker, with the median valley remaining open until very advanced wear stage. *Chilotherium schlosseri* also features a strong crochet and, consequently, a closed medifossette at an early to moderate wear stage, whereas in *E. samium* the crochet is weaker and the medifossette remains open until an advanced wear stage.

In terms of the mandible, the foramen mentalis of the studied material is located in front of p3, and the symphysis terminates posteriorly before p3. On the other hand, in the *E. samium* neotype the only visible foramen mentalis is located below p3, and the symphysis terminates posteriorly at the middle of the p3 (Kampouridis et al. 2023). Thereby, the attribution of the Samos specimens to *E. samium* can be excluded.

Comparison with Chinese *Chilotherium* species

Chilotherium schlosseri from Samos was compared to the three chilotheres of the classical Chinese Linxia Basin: *"C." primigenium*, *"C." wimani*, and *C. anderssoni*. Small aceratheriine *"C." primigenium* is the most primitive species of *Chilotherium* yet described, constituting the ancestral morphotype of the genus (Deng 2005). *"Chilotherium" wimani* also represents a primitive form of the genus. Both species were first described in the early Late Miocene of China (Deng 2001, 2005). *"Chilotherium" primigenium* presents numerous differences with most *Chilotherium* species, to the point that its belonging to the genus was recently questioned, as well as that of *"C." wimani* (Kampouridis et al. 2023). Some of those differences excluding *"C." primigenium* from other chilotheres are the very poorly separated parietal crests, which form a sagittal crest rearwards, the convex frontal bones with a posterior flattening, the narrowing of the parietal region, the short distance between the bases of i2 and p2, the dentition lacking the complex enamel folding of most chilotheres, the narrow nasal notch and the somewhat flat ventral surface of the symphysis, and the weak post-tympanic process.

Medium-sized *"C." wimani* is the dominant species in Linxia Basin (Deng 2006a). The main characters of this middle-sized aceratheriine are the transversal expansion of the mandibular symphysis and the upturned medial flange of the huge i2s (Chen et al. 2010). Compared to the cranial specimens under study, the parietal crests are only slightly separated, the zygomatic arch is narrow, and the orbita is in low position (Deng 2001, 2006a). Moreover, the upper dentition of *"C." wimani* features less strong crochets and small antecrochets (Deng 2001), the connection between the protocone and hypocone is quite narrow and no protocone constriction is visible (Ringström 1924; Deng 2001), markedly different from *C. schlosseri*. The mandible, as is a common trait of the genus, has a markedly wide symphysis. However, the mandibular symphysis terminates at the level of the middle of p3, where the foramen mentalis opens, while in *C. schlosseri* the same border is situated in front of the same tooth and the foramen mentalis opens in front of p3.

Chilotherium anderssoni comes from the Late Miocene of Loc. 30, Daijiagou, China; compared to the previous more primitive forms, it bears some of the more advanced features of the *Chilotherium* genus, such as the widely separated parietal crests, the long distance between i2 and p2, the thick posttympanic process, the wide nasal notch, and the concave ventral surface of the mandibular symphysis (Deng 2006a). However, the parietal crests of *C. anderssoni* are more narrowly separated and its upper dentition, complex as it is, is lacking the enamel plications that can be observed in *C. schlosseri*. Moreover, *C. Schlosseri* preserves a crista and a lingual cingulum on the upper molars, which are missing from *C. anderssoni* (Ringström 1924).

Comparison with other Eurasian *Chilotherium* species

The specimens under study were also compared with a number of *Chilotherium* genera from the Late Miocene of Eurasia: *C. persiae*, *C. kowalevskii*, *C. sarmaticum* and *C. orlovi*.

Chilotherium persiae has been described from Maragheh, Iran, along with the tandem-horned *Diceros neumayri* Osborn, 1900, the huge elasmothere *Iranotherium morgani* (Mecquenem, 1908), and the acerathere *Persiatherium rodleri* (Pandolfi, 2016) (Pohlig 1886; Mecquenem 1908; Pandolfi 2016; Giaourtsakis 2022). Compared to *C. schlosseri*, *C. persiae* has less depressed frontals and a wider region before the orbit, the nasal incision is more rounded and smoother and the zygomatics are almost straight backwards. The dentition of *C. persiae* is also complex, similar to that of *C. schlosseri*. However, *C. persiae* is the only chilothere to bear a somewhat quadrangularly outlined M3 (Ringström 1924). Compared to *C. schlosseri*, the premolars of *C. persiae* bear a stronger and longer crochet, a more pointed crista and more pronounced paracone fold, while on the molars of the same species the antecrochet is less elongated. The mandibular symphysis is shorter in *C. persiae*, terminating at the mesial half of p2, instead of p3 as in *C. schlosseri*. The anterior part of the mandible is more markedly curved in *C. persiae*. This trait is easier to observe in juvenile mandibles compared to adult ones, indicating a potential correlation with the individual's ontogenetic stage, as this curve of the mandible probably facilitates the development of the tusks.

Chilotherium kowalevskii was originally described from the Upper Miocene of Grebeniki, Ukraine (Pavlow 1913). There are not many differences between *C. kowalevskii* and *C. schlosseri*. However, in *C. kowalevskii*, the frontal depression is less pronounced and the parietal parietal crests are less widely separated thank in *C. schlosseri*. Moreover, in lateral view, the zygomatics get posteriorly narrower more smoothly than in *C. schlosseri.* Unlike *C. schlosseri*, *Chilotherium kowalevskii* does not bear a closed medifossette on the upper premolars, the protocone and hypocone constriction is weaker, there is no crista present and the premolars do not have complex enamel plications. Additional differential characters can be detected looking at the morphology of the otic region, with the posttympanic process more narrow and straighter in *C. schlosseri* than in *C. kowalevskii*, and at the shape of the zygomatic arch, anteriorly higher in *C. kowalevskii*, in lateral view (Pavlow 1913).

Chilotherium sarmaticum comes from the Late Miocene locality of Berislav, Ukraine (Korotkevich 1958), and has also been reported from Romania and Bulgaria (Geraads & Spassov 2009; Kampouridis et al. 2022; Ţibuleac et al.

2023). The main difference with *C. schlosseri* is, similarly to *C. kowalevskii*, the lack of enamel plications on the upper permanent dentition. Furthermore, in *C. sarmaticum* the distance between the parietal crests (51–76.2 mm; *N*=4) (Korotkevitch 1970) is generally shorter than *C. schlosseri* and overlaps only little, not reaching the extreme range of up to 100 mm seen in *C. schlosseri*. While in *C. sarmaticum* this distance can be greater than in *C. kowalevskii*, where it is between 40.1 and 66 mm (Krokos 1917), in *C. schlosseri* the mean value for this measurement is about 78 mm, thereby greater than the greatest value provided for *C. sarmaticum*.

Chilotherium orlovi has been reported from the Upper Miocene deposits of Pavlodar, Kazakhstan (Bayshashov 1982, 1993). In similar manner to *C. sarmaticum*, it has not been thoroughly studied after its first description and is rarely included in morphological and phylogenetical revisions of the genus. It is a fairly large chilothere, which shares many similarities with *C. schlosseri*. The dorsal profile of the skull is relatively flat in *C. orlovi*, similar to *C. schlosseri* and unlike some other species like *"C." primigenium*, *"C." wimani*, *C. kowalevskii* and *C. persiae*. The parietal crests can be up to 75 mm apart from each other, making it, along with *C. sarmaticum*, the only species that reaches the value range seen in *C. schlosseri*. As far as the upper dentition is concerned, the molars exhibit a marked protocone constriction and a very large antecrochet that may close off the median valley. The teeth also exhibit a strong crochet and in some molars a crista is visible. The medifossete is closed in the P2 and P3 and a prominent postfossette is visible. Additionally, there also seem to be few enamel plications visible in some teeth, which is fairly rare even within chilotheres (Bayshashov 1982, 1993). In conclusion, despite a few similarities present on the craniodental material of the two species, the most important feature in the comparison between *C. orlovi* and *C. schlosseri* is that the maximum distance between the parietal crests in *C. orlovi* (75 mm) remains smaller than the mean value of 78 mm at *C. schlosseri* (Bayshashov 1993).

Discussion

Diagnostic features of *C. schlosseri*

Under the scope of the present paper, we described all the skulls and mandibles of *C. schlosseri* available in numerous collections around Europe and the USA. We managed to conclude that *C. schlosseri* has certain craniodental features that allow for a comprehensive diagnosis of the species: depressed frontal bones; low position of the nasal bones with respect to the skull roof; presence of longitudinal groove on the nasal bones; widely separated parietal crests (>70 mm in adult specimens of various ontogenetic stages); complicated enamel folds and prevalent enamel plications on the upper dentition. As examined in the different specimens, the main aspects of the morphological characters where some intraspecific variability can be observed are the following: the skull-form, ranging from somewhat dolichocephalic to brachycephalic; the transversal development of the zygomatic arches; the exact position of the posterior border of the nasal notch, varying from the level above the anterior part of the M2 to the level of the contact between the P4 and the M1, and, respectively, the exact position of the anterior margin of the orbit, varying between the level above the middle of the M3 and the level above the middle of the M2; the shape of the postglenoidal apophysis ranging from subtrapezoidal to elliptical; the crochet and the crista usually lead to the closure of the medifossette. Furthermore, the most important morphological diagnostic character of the species, the width of the parietal crests, presents some morphometric variability: it is 64 mm in the youngest specimen examined in this work (NHMW-GEO-2009z0088/0001, juvenile individual that was not fully grown, with deciduous dentition), 89 mm and 100 mm in two similarly old adult individuals (neotype GPIH 3015 and AMNH 20794), 70 mm and 87 mm in two oldest individuals (NHMW-GEO-1911/0005/0128 and holotype of the species). Demonstrating that in all adult individuals the minimal distance between the parietal crests is always over 70 mm.

Interspecific variability of craniodental features within *Chilotherium*

As previously discussed in the comparison chapters, many of these features are characterized by a marked variability among the different *Chilotherium* species. Chinese *C. anderssoni* features a prominent depression of the frontal region that does not affect the nasal bones. It also has widely separated parietal crests, yet to a lesser degree than *C. schlosseri*, while lacking the latter species' enamel plications on the upper dentition (Deng 2006a). *Chilotherium persiae* presents certain minor differences in the upper dentition along with flattened frontal bones, a wider preorbital region, a rounded nasal incision, straight zygomatics and a shorter mandibular symphysis, terminating at the mesial half of p2, instead of p3 as in the studied specimens. *Chilotherium kowalevskii* seems to lack a distinct frontal depression in contrast to *C. schlosseri*, as well as featuring narrower parietal crests and missing both a crista and any additional enamel plications on the upper dentition. The absence of enamel plication is also a main difference between *C. schlosseri* and *C. sarmaticum*, which also shares widely separated parietal crests, although this feature is much more prominent in *C.*

schlosseri. In general *C. schlosseri*, *C. sarmaticum*, and *C. orlovi* seem to be the only chilotheres where the parietal crests can have a minimal distance over 70 mm from each other, indicating, together with other characters such as the presence of a closed medifossette in the M1 and the premolars of *C. orlovi* (Bayshashov 1982) either a potential close relationship between these three species, or similar paleoecological adaptations. The more plesiomorphic species *E. samium*, *"C." primigenium* and *"C." wimani* feature an overall higher skull, thick nasal bones, convex frontal bones, narrowly separated parietal crests, and somewhat less complicated upper dentitions. *"C." primigenium* also has a narrow nasal notch, a shorter diastema between the i2 and p2, a ventrally flattened symphysis and a weak posttympanic process. *"Chilotherium" wimani* bears a narrow zygomatic arch, a lowly positioned orbit and no protocone of the orbit.

Biogeographical context and potential phylogenetic relations

Some chilotheres share specific morphological features, thus demonstrating a peculiar distribution of characters that may be affected by their biogeographical history. The widely separated parietal crests, a character that *C. schlosseri* shares with *C. sarmaticum* from Ukraine and *C. orlovi* from Kazakhstan, may indicate either a closer relationship between *C. schlosseri* and these two species than with other chilotheres, or similar palaeodietary habits, since the distance between the parietal crests is a character related to herbivory, as the parietal crests themselves represent attachment areas for the temporalis muscle, one of the main muscles associated with mastication. On the other hand, *C. persiae* from Iran and *C. kowalevskii* from Ukraine seem to be more distantly related to *C. schlosseri*, since they both lack the widely separated parietal crests, the strongly depressed frontal and nasal region, the flat dorsal profile of the skull, and usually the absence of a closed medifossette in the upper premolars. Additionally, in both *C. persiae* and *C. kowalevskii* the sutures between the nasal bones and between the nasal and the frontal bones seem to completely close in adult individuals *(C. persiae*: MNHN.F.MAR.3072 and *C. kowalevskii*: Pavlow 1914: pl. 5, fig. 31). Therefore, the morphological similarities observed between *C. schlosseri*, *C. sarmaticum*, and *C. orlovi* could either represent a close phylogenetic relationship or possibly similar palaeodietary habits. Based on the current data, it is not clear how they are related.

According to Kampouridis et al. (2023), C. *schlosseri*, *C. sarmaticum*, *C. kowalevskii*, *C. persiae*, *C. orlovi*, and *C. anderssoni* belong to *Chilotherium* sensu stricto, showcasing all apomorphies of the genus, such as complex upper dentition, wide mandibular symphysis and well separated parietal crests. Within *Chilotherium* sensu stricto, certain morphological features seem to separate the genus into distinct morpho-groups. If they are considered to be of phylogenetic value, it would mean *C. schlosseri*, *C. sarmaticum*, and *C. orlovi* are more closely related to each other than to *C. kowalevskii* and *C. persiae*. Additionally, *E. samium* is only distantly related to all of these species, as it does not exhibit any of the apomorphies of *Chilotherium*. This would mean that there must have been at least three different dispersal events from Eastern Asia, where the most primitive chilotheres originated (Deng 2006b), to the West, that led to the establishment of the European and western Asian chilotheres. The exact timing of these dispersal events cannot currently be assessed. The chilotheres vanished by the end of the Miocene from Europe, marking the end for the once abundant and diverse aceratheriines, or hornless rhinos, that inhabited the subcontinent for several millions of years.

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Declarations

Competing interests The authors declare no competing interests.

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