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Chilotherium schlosseri (Weber, 1905) (Rhinocerotidae, Mammalia) from the late Miocene of the foreland of the Eastern Carpathians in Romania

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ABSTRACT
The paper provides an overview of the *Chilotherium* Ringström, 1924 fossils from Romania, which are recorded so far in three different Upper Miocene localities of the Eastern Carpathians Foreland: mammal localities of Reghiu, Bacău and Pogana. The fossils include a partial skull, several maxillary and mandible fragments and isolated teeth. They have been partially illustrated, but never described excepting the isolated teeth of Pogana. The previous assignments were confusing, ranging from *Chilotherium schlosseri* (Weber, 1905) and *C.* cf. *sarmaticum* for Reghiu specimens to an indeterminate species close to *C. sarmaticum* Korotkevich, 1958, *C. kiliasi* (Geraads & Koufos, 1990), and *C. kowalevskii* (Pavlow, 1913) for Pogana teeth. Based on descriptions and comparisons with other *Chilotherium* remains, all specimens from Romania can be referred to *C. schlosseri*. *Chilotherium schlosseri* is the most widespread species of the genus, ranging from Eastern Europe to Central Asia. The presence of this genus in Romania, and more globally in Eastern Europe, attests to a transition area between the more closed and wooded environments of Western Europe (where *Chilotherium* is absent) to the more open ones in Asia.

KEY WORDS
Late Miocene,
Chilotherium,
Rhinocerotidae,
Romania.

RÉSUMÉ
Chilotherium schlosseri *(Weber, 1905) (Rhinocerotidae, Mammalia) du Miocène supérieur de l'avant-pays des Carpates orientales en Roumanie.*
Cet article présente une vue d'ensemble des fossiles de *Chilotherium* Ringström, 1924 de Roumanie, signalés jusqu'à présent dans trois localités différentes du Miocène supérieur de l'avant-pays des Carpates orientales : les localités à mammifères de Reghiu, Bacău et Pogana. Les fossiles comprennent un crâne partiel, plusieurs fragments de maxillaires et de mandibules et des dents isolées. Ils ont été partiellement illustrés, mais jamais décrits, à l'exception des dents isolées de Pogana. Les attributions précédentes étaient douteuses, allant de *Chilotherium schlosseri* (Weber, 1905) et *C.* cf. *sarmaticum* pour les spécimens de Reghiu à une espèce indéterminée proche de *C. sarmaticum* Korotkevich, 1958, *C. kiliasi* (Geraads & Koufos, 1990) et *C. kowalevskii* (Pavlow, 1913) pour les dents de Pogana. Sur la base des descriptions et des comparaisons avec d'autres restes de *Chilotherium*, tous les spécimens de Roumanie peuvent être rattachés à *C. schlosseri*. *Chilotherium schlosseri* est l'espèce la plus répandue du genre, allant de l'Europe de l'Est à l'Asie centrale. La présence de ce genre en Roumanie, et plus globalement en Europe de l'Est, atteste d'une zone de transition entre les milieux plus fermés et arborés de l'Europe de l'Ouest (où *Chilotherium* est absent) et les environnements plus ouverts de l'Asie.

MOTS CLÉS
Miocène supérieur,
Chilotherium,
Rhinocerotidae,
Roumanie.

INTRODUCTION

In Romania, the hornless rhinoceros *Chilotherium* Ringström, 1924 has only been recorded so far throughout three localities in the eastern areas. Two fossil-bearing outcrops (Bacău and Pogana) are confined to the Eastern Carpathians Foreland (Moldavian and Scythian platforms, respectively), and the third one (Reghiu) within the foredeep zone (Fig. 1). In the Republic of Moldova, in the same foreland framework, the *Chilotherium* fossils are more common among the terrestrial vertebrates than on Romanian territory (e.g. Lungu & Rzebik-Kowalska 2011). The first report of the genus within the Romanian scientific literature is actually related to this area, Macarovici (1936) describing several isolated teeth of "*Aceratherium*" *schlosseri* Weber, 1905 from the upper Miocene sandy clay of Gura Galbenei (Cimșlia District, Republic of Moldova).

Later, Ioniță (1963) noticed a significant assemblage of fossil vertebrates originated from a Miocene succession, which is cropping out on the Reghiu River slopes, upstream of its confluence with the Milcov River (Reghiu locality, Vrancea District). "*Aceratherium*" *schlosseri* and *Aceratherium incisivum* Kaup, 1832 are listed among other fossil mammals (Ioniță 1963). Into an overview of mammal fauna from Reghiu, Știucă (2003) re-assigned the *Chilotherium* remains to *C.* cf. *sarmaticum* due to the higher level of hypsodonty than in *C. schlosseri* (Weber, 1905). He also highlighted a skull and postcranial bones of medium size whereas the length of upper and lower tooth rows are larger than those of "*Aceratherium*" *kowalevskii* Pavlow, 1913 (junior synonym of *C. schlosseri* after Antoine & Sen 2016) from Grebeniki 1 in Ukraine. Știucă (2003: fig. 2) partially illustrated the Reghiu specimens (only the occlusal view of the right upper tooth row of the skull and the lingual view of the left unrestored hemimandible. However, in the text there is no reference to Ioniță's original paper (Ioniță 1963).

Rădulescu & Șova (1987) acknowledged the mammal fossils collected during the excavations for the thermal power station of Bacău city as "the most important Late Miocene bone accumulation in the Extracarpathian area of Romania" (Fig. 1). Among the numerous mammal remains, *Aceratherium incisivum* and *Chilotherium* sp. have been mentioned and summarily discussed and illustrated in this preliminary report. At least two specimens of *Chilotherium* (fragments of a maxillary and a mandible) were illustrated by Rădulescu & Șova (1987: pl. 2, figs 1-4). They were thought to represent an intermediate hypsodont stage between *Chilotherium schlosseri* (Weber, 1905) of lower Maeotian and *Chilotherium sarmaticum* Korotkevich, 1958 of upper Sarmatian s.l. (synonym of Khersonian). Most mammal remains from Bacău were housed in the collections of the Museum of Natural Sciences "Ion Borcea" Bacău, but for a long time this fossil fauna was thought to be lost (e.g. Codrea *et al.* 2011). Recently, after repeated research in the collections, these remains as well as other important fossils have been retrieved (Ţibuleac 2018, 2019). Thanks to these rediscoveries, the previous Maeotian age of the faunal assemblage (Rădulescu & Șova 1987) has been re-assigned to the late Bessarabian (MN10) instead (Ţibuleac 2019).

The last *Chilotherium* fossils so far in Romania have been collected from the Pogana Quarry (Scythian Platform, Vaslui District, Fig. 1). Codrea *et al.* (2011: fig. 3) described two isolated teeth of *Chilotherium* sp. from fluvial deposits of upper Miocene. The specimens were compared to *C. sarmaticum*, *C.* (*Eochilotherium*) *kiliasi* Geraads & Koufos, 1990, and *C. kowalevskii* Pavlow, 1913 of late Sarmatian s.l. (synonym of Khersonian) – Maeotian age (late Vallesian – late early Turolian).

The primary purpose of this paper is the taxonomical reassessment of the *Chilotherium* fossils found up to now in Romania involving the morphological description of the fossils and their critical comparison. Secondly, the biostratigraphical and paleogeographical significance of their occurrences is highlighted.

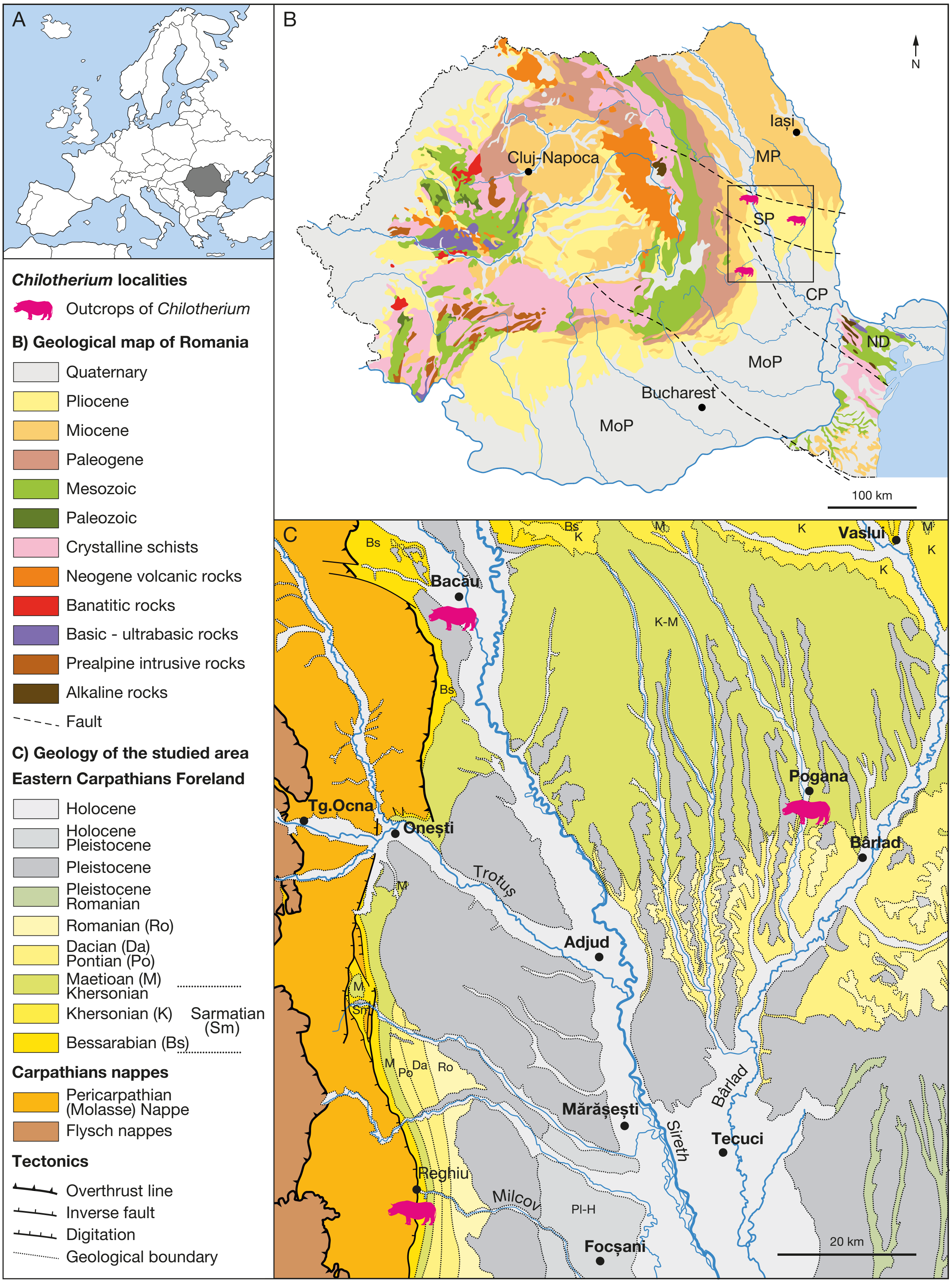

FIG. 1. — General setting of the late Miocene *Chilotherium* Ringström, 1924 (Rhinocerotidae, Perissodactyla) localities from Romania: **A**, geographical location of Romania (**black area**) in Europe; **B**, geological map of Romania (simplified after Săndulescu *et al.* 1978); **C**, detailed geological setting of the late Miocene *Chilotherium* (Rhinocerotidae, Perissodactyla) localities of Romania in Eastern Carpathians Foreland. Abbreviations: **CP**, Covurlui Platform; **MoP**, Moesian Platform; **MP**, Moldavian Platform; **ND**, North Dobrogea; **SP**, Scyhtian Platform.

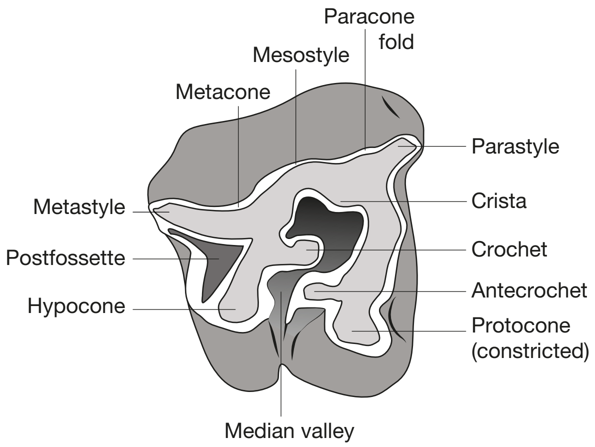

Fig. 2. — Terminology of upper cheek teeth used for *Chilotherium schlosseri* (Weber, 1905), based on the M2 (MNS-IBB 112) from Bacău, Bacău District, Romania, Late Miocene (MN10).

GEOLOGICAL FRAMEWORK

The Romanian occurrences of the genus *Chilotherium* are confined to the Eastern Carpathians Foreland (Bacău and Pogana) and its foredeep (Reghiu). The Eastern Carpathians Foreland (ECF) includes the major pre-alpine platforms of north-eastern Romania (Fig. 1). The most widespread is the Moldavian Platform, which represents the south-westernmost part of the East-European/Russian Platform prolonged under the Carpathian Orogenic Belt. The Scythian and Covurlui platforms are developing towards the south and are separated by the major crustal faults Bistrița and Trotuș, respectively. The latter is an Alpine basin, having as a basement the prolongation of North Dobrudja Orogen also known as North Dobrudja promontory west of the Danube (Ionesi 1994). The ECF also covers a Moesian Platform sector located north-east of the Intramoesian Fault (Dobrogean sector or Eastern Moesia) with heterogeneous pre-alpine basements of Central and Southern Dobrogea (e.g. Săndulescu & Visarion 1988; Visarion *et al.* 1988; and references therein).

Starting from the Neogene, the Eastern Carpathians Foreland evolved roughly similarly to the large framework of the Galiczian Gulf (Popov *et al.* 2004). The different depositional systems are related to the main tectonic events and resets of the land-sea report. Generally, after the middle Bessarabian, when the Eastern Carpathians uplifted, the Paratethys Sea retreated southeastward favouring the development of a river network on the emerged land. Consequently, a large prograding fluvial-deltaic depositional system developed in the widespread areas of Romania, the Republic of Moldova, and Ukraine (Matoshko *et al.* 2016; and references therein) coeval with the brackish sea retreat.

The Miocene successions have not been wholly and accurately formalized due to various reasons. From the literature, there are two main attempts. Ionesi *et al.* (2005) proposed several lithostratigraphic units, but only for the middle and upper Sarmatian, using geochronological boundaries to delineate each one. Following the "Balta Stage" *sensu* Barbot de Marny (1869), Matoshko *et al.* (2016) basically argued the Balta Formation (upper Bessarabian – Pontian = upper Tortonian – Messinian stages of the geological time scale after Raffi *et al.* 2020) on a unique depositional system, and not on the lithology, which largely changes within its framework.

Reghiu

According to Ioniță (1963) and Rădulescu *et al.* (1995), the most important fossils of *Chilotherium* have been sampled from the surroundings of the Reghiu locality (Vrancea District). The outcrop (Reghiu Stream slopes) is confined to the Focşani Sub-basin/Depression of the ECF foredeep. During the Bessarabian, the last orogenic nappe (Pericarpathian/Molasse Nappe) emerged and thrust over the Miocene successions of the foreland marking the major shortening event of Eastern Carpathians. Along with the orogen-foreland tectonic contact, a syn- and post-orogenic foredeep develops striking variations of width and thickness. Among its framework, Bacău, Adjud, and Focșani areas started to evolve as Badenian – Sarmatian s.l. depocenters along to the basement faults of the ECF (Tărăpoancă *et al.* 2003; Krézsek & Olariu 2021; and references therein).

In the Focșani sub-basin, the sedimentation starts on the top of the northeastern Moesian Platform. There is a pre-tectonic succession including predominant Badenian evaporites and tuffs, and Sarmatian s.l. siliciclastic rocks. Coeval with the molasse thrusting over ECF, turbidites and shallow lacustrine rocks of upper Sarmatian s.l. – Pliocene are accumulated. Finally, massive gravels deposited in a shallow lacustrine to alluvial environments (?latest Pliocene – Pleistocene) and loess and alluvial deposits of middle Pleistocene-Holocene fill the basin (Leever *et al.* 2006; and references therein).

Ioniță (1963) sampled the vertebrate remains from the last meter of a 4 m thick sedimentary succession corresponding roughly to the Khersonian (Rădulescu *et al.* 1995). The outcrop emerges at approximately 200 m upstream from the confluence of the Milcov and Reghiu brooks (La Scruntar place). The lithology consists of greenish tuffaceous sandstone changing to marly sandstone towards the top. "*Aceratherium*" *schlosseri* (re-assigned as *Chilotherium* cf. *sarmaticum* in Știucă (2003: 114) and *Aceratherium incisivum* are listed among other mammal fossils (Ioniță 1963: 201), as well as "*Mastodon*" (*trilophodont*) *pentelici* = *Choerolophodon pentelici* (Gaudry & Lartet, 1856), *Hipparion gracile* Kaup, 1833 = *Hippotherium primigenium* (von Meyer, 1829), *Sus major* Gervais, 1848, *Camelopardalis parva* Weithofer, 1888, and *Gazzela deperdita* (Gervais, 1848). It also contains frequent fresh and brackish-water mollusks and ostracods. There are no formal lithostratigraphic units proposed yet.

Bacău

The second outcrop is located in the southern part of Bacău city (Fig. 1). The age of the *Chilotherium* host-beds is not certainly assessed, because the succession was open only during the excavation for a thermal power plant and cannot be seen nowadays. All remains of various large vertebrates (Rădulescu & Șova 1987) have been recovered from a succession of grey silty clay and fine sand laying at 8-12 m depth on the left bank of Bistrița River (Fig. 1). It is not conspicuously stated that the fossils have been sampled or not from one single bed. However, taking into account the geological context (Simionescu 1977) the vertebrate remains have been sampled from a succession of predominant sand/sandstone and conglomerate which could be assigned to the upper Bessarabian (Țibuleac 2019) or roughly Bessarabian – Khersonian. The area evolved during the upper Sarmatian s.l. in a near-shore environment, from fluvial to open basin facies (Simionescu 1977). The succession would belong to the Șcheia Formation from where several vertebrate remains have also been sampled (Ionesi *et al.* 2005; and references therein).

Pogana

The *Chilotherium* teeth from the Pogana craft stone quarry (Vaslui District) represent the third occurrence. They have been sampled from coarse sand and sub-angular mud clasts, which are filling one fluvial channel dug into the oblique laminated sands. The age of the host beds is roughly of late Sarmatian s.l., close to the Khersonian/Maeotian boundary (Codrea *et al.* 2011), because the cineritic tuff, which marks the boundary in the field, proves an inconsistent development. Consequently, these stages cannot be always obviously separated in the area (Saulea *et al.* 1967; Codrea *et al.* 2011). According to Ionesi *et al.* (2005), the succession would belong to the Huși Formation.

MATERIAL AND METHODS

The referred *Chilotherium* specimens from Reghiu (Vrancea District), Bacău (Bacău District), and Pogana (Vaslui District) are currently stored in the collections of "Emil Racoviță" Institute of Speleology Bucharest, "Ion Borcea" Natural Sciences Museum of Bacău, and "Vasile Pârvan" Museum – Natural Science Branch Bârlad, respectively. The material represents an incomplete skull with partial upper and lower tooth rows (Reghiu), fragments of maxillary with teeth and a mandible (Bacău) or isolated teeth (Bacău and Pogana). Other partial bones (e.g. a tibia with the distal epiphysis) and scrap bones are housed in the repositories of Bucharest and Bacău museums but cannot be certainly assigned to the genus *Chilotherium*, and so will not be discussed here.

The description and identification of the fossils are made by means of anatomical descriptions, comparative anatomy, and biometrical measurements. The dental characters used mainly correspond to the cladistic characters defined by Antoine (2002) and completed by Pandolfi (2015). The dental nomenclature follows Heissig (1969) and Antoine (2002). The terminology used for upper cheek teeth is illustrated on Figure 2. The measurements are taken according to Guérin (1980) and all dimensions are in millimetres.

The stratigraphical framework is based on geological timescales and European Land Mammal Ages (ELMA) for the Neogene (Hilgen *et al.* 2012; Raffi *et al.* 2020). Successions of European Mammal Neogene units (MN) were correlated based on biostratigraphic and magnetostratigraphic data (BiochroM'97 1997) and Steininger (1999). The Regional stages of Eastern Parathethys are after Vangengeim & Tesakov (2013) and the Mammal stages of China after Deng (2006b).

Abbreviations

APD	anteroposterior diameter;
D/d	decidual tooth;
ECF	Eastern Carpathians Foreland;
ELMA	European Land Mammal Ages;
ERIS	"Emil Racoviță" Institute of Speleology in Bucharest;
H	height;
HI	hypsodonty index;
$I_{P/M}$	upper premolars/molars index;
$I_{p/m}$	lower premolars/molars index
L	length;
M/m	upper/lower molar;
MN	Mammal Neogene units;
MNS-IBB	Museum of Natural Sciences "Ion Borcea", Bacău;
P/p	upper/lower premolar;
TD	transverse diameter;
VPM	"Vasile Pârvan" Museum, Natural Science Branch, Bârlad;
W	width.

SYSTEMATIC PALEONTOLOGY

Remark

According to numerous phylogenetic analyses, *Chilotherium* is usually considered as belonging to the tribe Aceratheriini (e.g. Antoine *et al.* 2010; Pandolfi 2015; Sun *et al.* 2018; Lu *et al.* 2023). However, the suprageneric systematics of Rhinocerotidae remains broadly discussed. Antoine (2002), Antoine *et al.* (2003, 2010), Becker *et al.* (2013) and Pandolfi (2015) and Sun *et al.* (2018) classically recognized two subfamilies within the family, the Elasmotheriinae and the Rhinocerotinae, the latter including Aceratheriini and Rhinocerotini as sister-groups. Recently, Lu *et al.* (2023) united Aceratheriini and Teleoceratini within the subfamily Aceratheriinae as a clade, a result consistent with those of Heissig (1989, 1999) and Cerdeño (1995). Moreover, Lu *et al.* (2023) considered Elasmotheriinae and Rhinocerotinae as more closely related than Aceratheriinae. Resolving the suprageneric phylogeny within the Rhinocerotidae is not the aim of this study, and given the lack of consensus of the subfamily assignment of the tribe Aceratheriini, it is not specified hereafter.

Order PERISSODACTYLA Owen, 1848
Suborder TAPIROMORPHA Haeckel, 1866
Family Rhinocerotidae Gray, 1821
Tribe Aceratheriini Dollo, 1885

Genus *Chilotherium* Ringström, 1924

Chilotherium anderssoni Ringström, 1924: 26.

Type species. — *Chilotherium anderssoni* Ringström, 1924, by original designation.

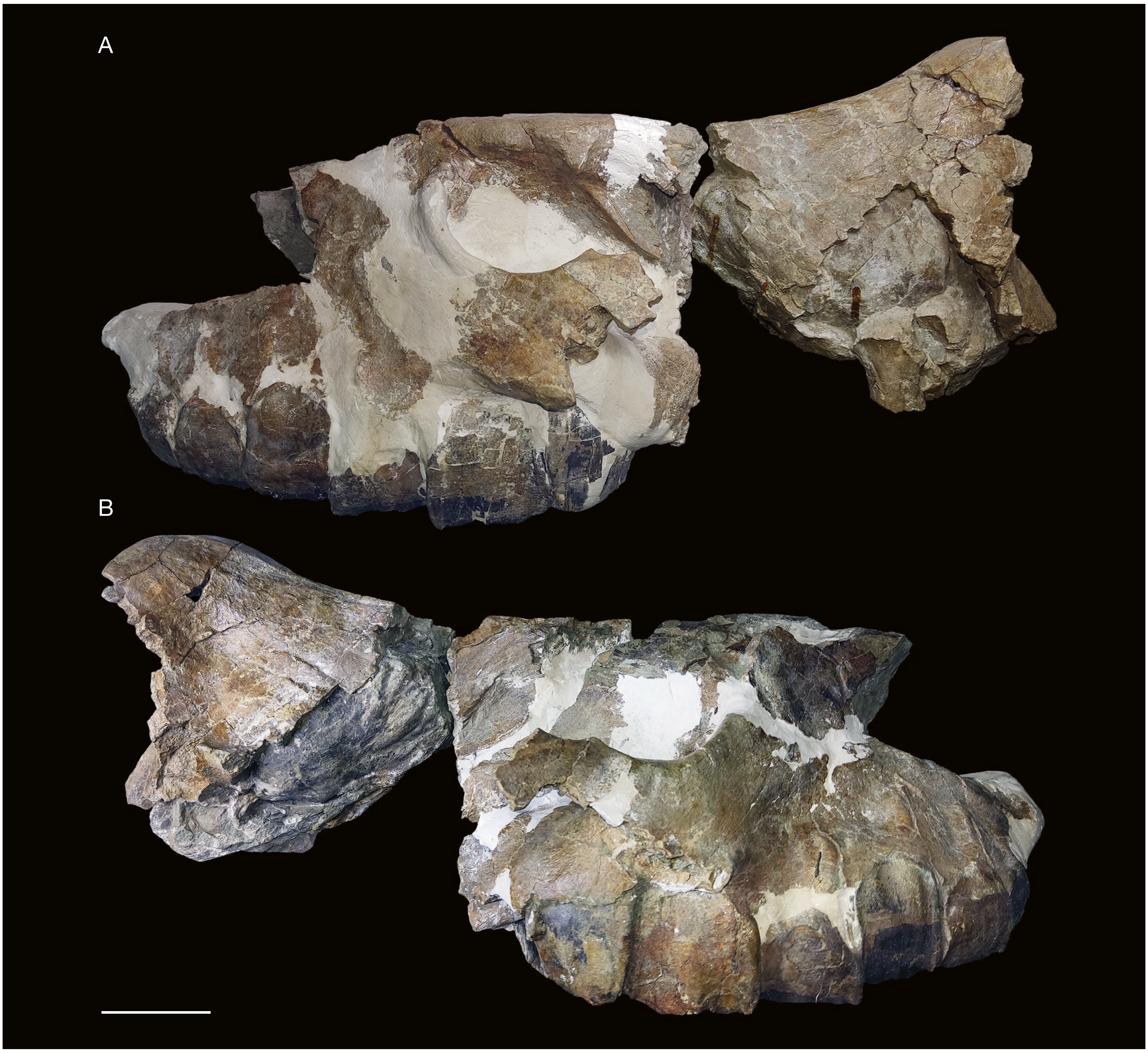

Fig. 3. — Skull of *Chilotherium schlosseri* (Weber, 1905), ERIS-Rg/1987 001/6, Reghiu, Vrancea District, Romania, Late Miocene (MN10/11): **A**, left lateral view; **B**, right lateral view. Scale bar: 5 cm.

Included species. — *Chilotherium samium* (Weber, 1905), *Chilotherium schlosseri* (Weber, 1905), *Chilotherium kiliasi* (Geraads & Koufos, 1990), *Chilotherium anderssoni* Ringström, 1924, *Chilotherium habereri* (Schlosser, 1903), *Chilotherium wimani* Ringström, 1924, *Chilotherium sarmaticum* Korotkevich, 1958, *Chilotherium xizangensis* Ji, Xu & Huang, 1980, *Chilotherium primigenius* Deng, 2006a, *Chilotherium licenti* Sun, Li & Deng, 2018, and *Chilotherium persiae* (Pohlig, 1886).

Chilotherium schlosseri (Weber, 1905)
(Figs 3-8; Tables 1-3)

Aceratherium schlosseri Weber, 1905: 344, pl. VIII, figs 1-4, pl. IX, figs 1-3.

Teleoceras ponticus Lubicz-Niezabitowski, 1912: 1, 1913: 223, pl. XXIV, figs 1-2, pl. XXV, figs 3-5.

Aceratherium kowalevskii Pavlow, 1913: 48, pl. 4-5.

Aceratherium wegneri Andrée, 1921: 189, pl. I-II.

Aceratherium angustifrons Andrée, 1921: 202, pl. III.

Chilotherium schlosseri – Ringström 1924: 85.

Aceratherium sp. – Malik & Nafiz 1933: 44, pl. VII figs 4, 5.

Aceratherium cf. *kowalevskii* [partim] – Nicolas 1978: 456.

Chilotherium cf. *sarmaticum* – Ştiucă 2003: 114, fig. 2.

Type material. — Lectotype, a relatively well-preserved adult cranium with associated mandible described and figured as *Aceratherium schlosseri* by Weber (1905: taf. VIII, figs 1-4; taf. IX, fig. 1 pars). The specimen is believed to have been destroyed during the Second World War (Giaourtsakis 2022).

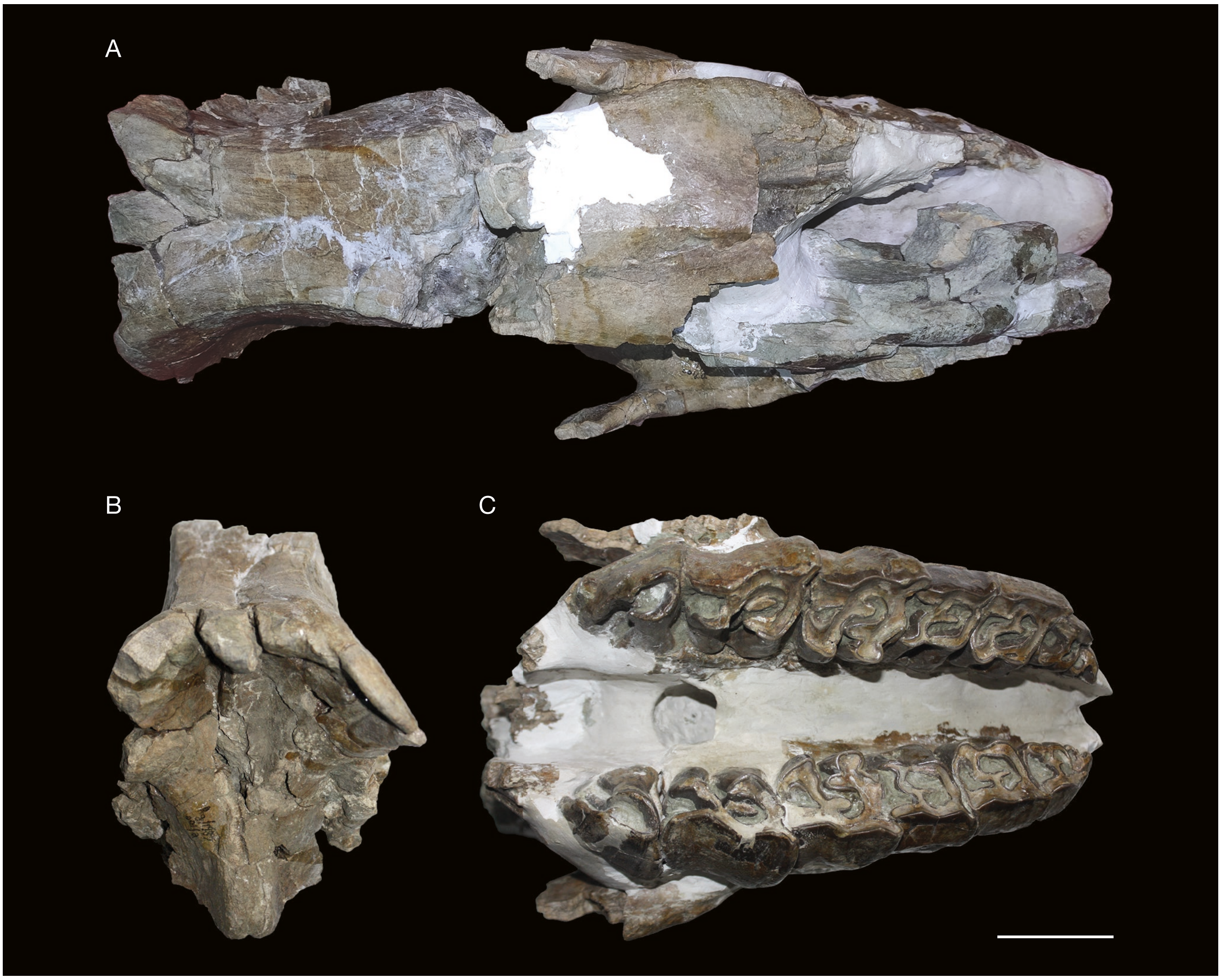

Fig. 4. — Skull of *Chilotherium schlosseri* (Weber, 1905), ERIS-Rg/1987 001/6, Reghiu, Vrancea District, Romania, Late Miocene (MN10/11): **A**, dorsal view; **B**, occipital view; **C**, ventral view. Scale bar: 5 cm.

Refered material. — From Reghiu (Late Miocene, Khersonian, MN 10/11, Rădulescu *et al.* 1995; Codrea 1996; Ştiucă 2003; Geraads & Spassov 2009; Codrea *et al.* 2011): partial skull with maxillary tooth rows (P1-M3) and associated mandible with left p3-m3 and right p2-m3 (ERIS-Rg/1987 001/6) (Figs 3-5).
From Bacău (Late Miocene, latest Bessarabian, MN10, Ţibuleac 2019): right P4-M3 (MNS-IBB 112); rightM1-2 (MNS-IBB 113); fragmented left M3 (MNS-IBB 114); fragmented mandible with left p4-m3 and right p3-m1 and m3 (MNS-IBB 115) (Figs 6; 7).
From Pogana (Late Miocene, latest Khersonian-earliest Maeotian, MN11/12, Codrea *et al.* 2011): left M2 (VPM – P/355); right dp3 (VPM – P/354); both illustrated by Codrea *et al.* (2011: figs 3.1-3.2) (Fig. 8).

Type locality and age. — Samos Island, Greece; Late Miocene fluvio-lacustrine volcanoclastic deposits of the Mytilinii formation; MN11-13 (Weber 1905; Vlachou & Koufos 2009; Giaourtsakis 2022).

Description

Cranial features

The skull of *Chilotherium schlosseri* from Reghiu includes a partial dolichocephalic cranium associated with a better-preserved mandible. It belongs to a young adult, with unworn M3, and very slightly worn m3. The skull has been broken into two fragments during the extraction from the host beds, and several cranial bones are lost. Moreover, the specimen is largely restored with gypsum. The rough restoration preserves together the bones but also partially covers several ones as well as the sutures between them precluding accurate observations. Consequently, only the maxillae with DP1-M3 tooth rows and incomplete nasals, frontals, parietals and jugals can be clearly identified (Figs 3; 4). The lacrymal bones are largely covered by the gypsum during the skull restoration, and they can only be inferred. The best-preserved jugal bone is on the right side of the skull. The occipital bone does not preserve the condyles, but it keeps the external occipital crest (Fig. 4B). No foramina have been depicted within the skull.

In dorsal view (Fig. 4A), the skull is rather narrow, having subparallel zygomatic arches and an apparently roughly straight occipital crest. Both nasal and frontal bones are flattened, without an obvious suture between them. The posterior end of the nasal notch can be inferred above the posterior border of P4 in the lateral view. The frontoparietal crests are distant

TABLE 1. — Upper and lower premolars/molars indices (IP/M = 100xLP3-4/LM1-3), Ip/m = 100xLp3-4/Lm1-3) of *Chilotherium schlosseri* (Weber, 1905) from Reghiu (ERIS-Rg/1987 001/6) and Bacău (MNS-IBB 115).

	LP3-4	LM1-2	IP/M	Lp3-4	Lm1-3	Ip/m
ERIS-Rg/1987 001/6 (left)	66.3	146.4	45.29	57.9	124.8	46.39
ERIS-Rg/1987 001/6 (right)	67.8	136.5	49.7	61.8	129.0	47.91
MNS-IBB 115 (right)	–	–	–	64.5	129.9	49.66

(*sensu* Antoine 2002), the minimum distance between them being of 64.2 mm. In lateral view (Fig. 3A), the postorbital processes are present on the frontal, and on the zygomatic arch, located on the jugal. The orbits are located high near the cranial roof, their anterior borders reaching the anterior border of M2. The dorsal profile of the skull is slightly concave.

In ventral view, the maxillae are fragmented but the upper tooth rows are complete and well preserved. The zygomatic process of the maxilla starts at the level of M1. The anterior base of the *processus zygomaticus* is high in lateral view (Fig. 3) and its transition from the maxilla follows a brutal inflection in the ventral view (Fig. 4C).

Mandibular features

In lateral view, the *corpus mandibulae* is lower in the specimen from Reghiu (ERIS-Rg/1987 001/6; Fig. 5) than that from Bacau (MNS-IBB 115; Fig. 7), with a rather constant height (H at the front of p3: 76.0 mm, of m1: 79.0 mm, of m3: 76.5 mm in Reghiu; H at the front of m1: 92.0 mm, of m3: 94.0 mm in Bacău). The ventral border is straight in Reghiu, but more ventrally convex in Bacău. These differences may reflect sexual dimorphism, which is known in another *Chilotherium* species (*C. wimani* Ringström, 1924) and significant in the mandible (Chen *et al.* 2010). The symphyseal angle is approximately of 15° in the mandible from Reghiu. The *foramen mentale* is below the posterior border of p2 on the specimen of Bacău. The mandibular angle can only be partly observed because of the incompleteness of the specimens. The fragmentation of the mandibles precludes the observations on the masseteric fossa, but a very low ridge marks its basal extension (Figs 5; 7). The condylar process, preserved on the left part of the mandible from Reghiu is very wide transversally. Underneath, the neck is wide and the mandibular notch is obtuse. The ramus is roughly vertical on the mandible from Reghiu, although its anterior border follows a very slightly anteriorly curved line (Fig. 5A). In dorsal view, the symphysis is massive (observable on the mandible from Bacau, Fig. 7C), with a posterior margin located at the level of the p3 on both specimens. The *spatium retromolare* is short. The orientation of the tooth rows is not parallel to the long axis of the mandible (*sensu* Pandolfi 2015, character 81).

General dental features

The maxillary cheek teeth are high-crowned (*sensu* Antoine 2002, character 69) and without enamel foldings (*sensu* Antoine 2002, character 64). The enamel is wrinkled and covered with patches of cement. From the skull and the mandible of Reghiu, the premolar series are short with respect to the molar series (*sensu* Antoine 2002, 42 < $I_{P/M}$ and $I_{p/m}$ > 50, character 63; Table 1), but p2 remains elongated (Fig. 5B). No d1/p1 are present, as attested by the sharp ridges running anterior to p2s, whereas a DP1 is present in the upper tooth series of the skull of Reghiu (Fig. 4C).

The symphysis of the mandible is mostly encased in gypsum or broken on the two mandibles and the presence of the central incisors (i1s) or alveoli cannot be assessed. The lower tusks (i2) are broken on ERIS-Rg/1987 001/6 and not preserved on MNS-IBB 115 (Figs 5; 7). They are triangular-shaped in cross section with an acute posterior edge, divergent and quite strong.

Upper dentition

The occlusal morphology of the upper cheek teeth of all the specimens mainly differ according to the stage of wear, almost unworn in Reghiu to a very advanced wear in Bacău. Several teeth are incompletely preserved (Figs 4C; 6; 8). The dental pattern of the upper cheek teeth is rather complicated due to the presence of secondary enamel folding (= crochet, antecrochet and crista *sensu* Antoine 2002; see Fig. 2). In occlusal view, the lingual rims of the upper tooth rows are straight.

The skull from Reghiu (ERIS-Rg/1987 001/6) preserves both P1-P4 premolar rows, whereas only P4 is known in Bacău (MNSB – 112). The P1 is triangular-shaped and the anterolingual cingulum is absent. The anterior groove of the ectoloph and a simple parastyle can be observed. The paracone fold is noticeable on both teeth. The protoloph is absent and the metaloph is transverse, with an incipient crochet. The lingual border of the paracone forms an incipient crista. The hypocone is posteriorly elongated. The metaloph is transverse on P2 and the protocone is as developed as the hypocone. The protoloph is present and weakly connected to the ectoloph. All P2-4 have a closed median valley (lingual bridge to lingual wall; semimolariform to submolariform *sensu* Heissig 1969) and a lingual groove between the protocone and hypocone. In occlusal view, the P2-P4 are almost quadrangular if we pass over the very long and acute parastyle (not preserved on MNS-IBB 112). The crochet is strong and anteroposteriorly elongated (Figs 4C; 6A) and the crista is absent. The P3-P4s of ERIS-Rg/1987 001/6 develop a large metastyle and an S-shaped metaloph. The hypocone is more posterior than the metacone. The postfossette is closed by a high and narrow posterior cingulum. The protocone is constricted on P4 from Bacău (Fig. 6A) and this constriction should appear with wear on the specimen from Reghiu. Only the parastyle is noticeable on the ectoloph of the premolars from Reghiu (the labial border of the P4 from Bacău is broken). The lingual cingulum is limited to an isolated bulge on the lingual border. There is a very thin labial cingulum on premolars.

Fig. 5. — Mandible of *Chilotherium schlosseri* (Weber, 1905), ERIS-Rg/1987 001/6, Reghiu, Vrancea District, Romania, Late Miocene (MN10/11): **A**, right lateral view; **B**, occlusal view; **C**, left lateral view. Scale bar: 5 cm.

The upper molars from Reghiu are almost complete, whereas the other specimens are partially broken (e.g. the right M2 of MSN-IBB 113 from Bacău misses the mesiolingual and distolabial borders; Fig. 6B). The protoloph and the metaloph are fully continuous and connected to the ectoloph. All referred specimens lack lingual and labial cingulum and a medifossette. All M1-M2 are quadrangular with a long parastyle and metastyle except for the broken M1 MNS-IBB 112 (Fig. 6A). A moderate mesostyle is developing on all M1-M2s except on the M1 MSN-IBB 113 (Fig. 6B).

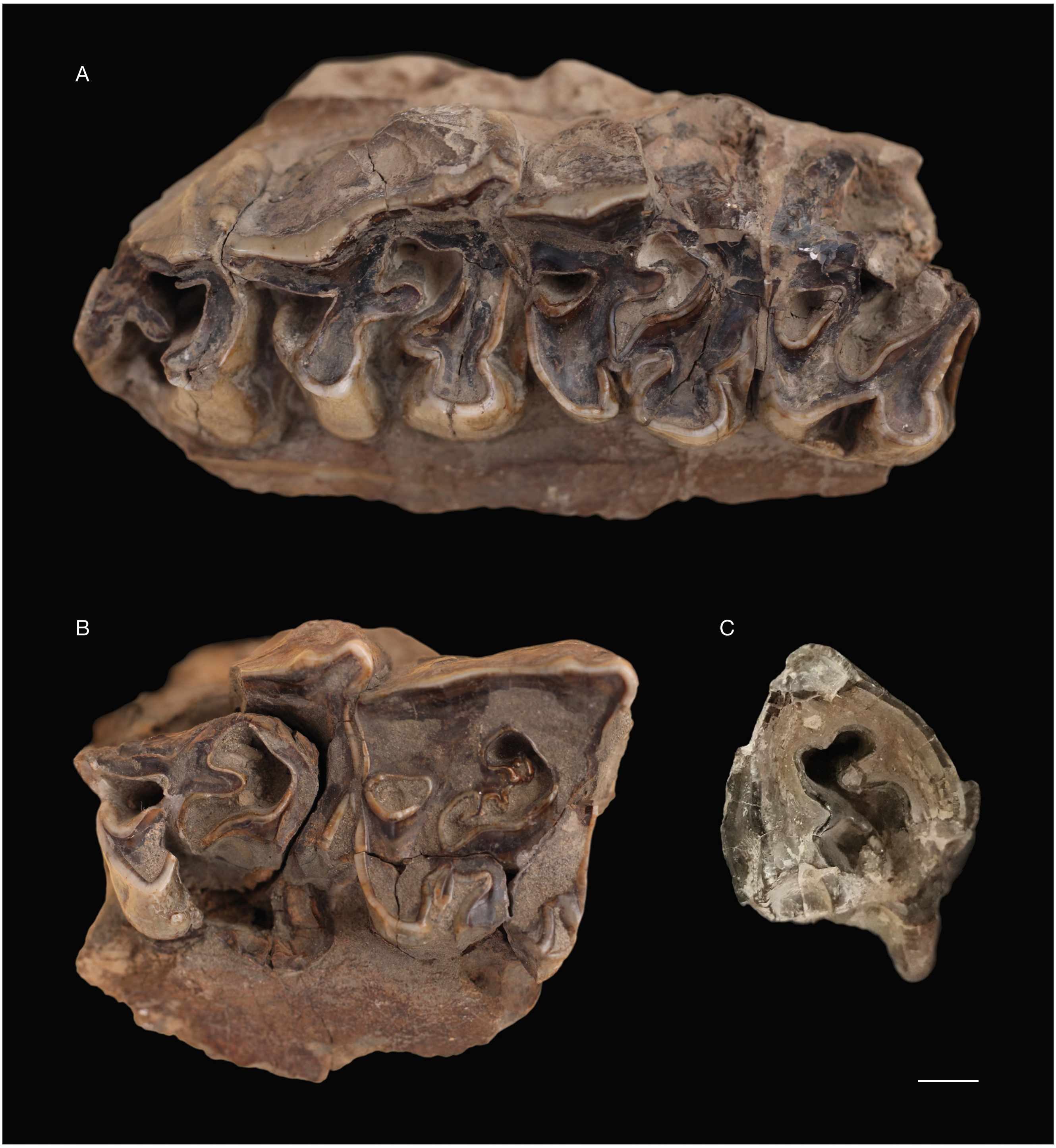

Fig. 6. — Dental remains of *Chilotherium schlosseri* (Weber, 1905), Bacău, Bacău District, Romania, Late Miocene (MN10): **A**, right P4-M3 (MNS-IBB 112), occlusal view; **B**, right M1-2 (MNS-IBB 113), occlusal view; **C**, left M3 (MNS-IBB 114), occlusal view. Scale bar: 1 cm.

The median valley is closed on M1 by the lingually projected antecrochet on worn teeth, but slightly open on unworn M1 from Reghiu. It is open on M2-3. The postfossette is triangular on unworn teeth and oval shaped on worn teeth. The protocone is strongly and simply constricted in all teeth of the specimen MNS-IBB 112 from Bacău (Fig. 6A) and those from Pogana, whereas on the Reghiu specimens the constriction is visible only on M1, but should appear with wear on M2-3. The crista is not generally present, except a very weak one on the M2 (MNS-IBB 112: Fig. 6A) and M3 (MNS-IBB 114: Fig. 6B) from Bacău. The crochet is anteroposteriorly oriented and simple, with the exception of the M1 MNS-IBB -113, where it has multiple projections. On the M2s from Reghiu, the crochet is isolated from the metaloph near the unworn occlusal surface, but is connected to it with an increased wear. The M3s are subtriangular in

Fig. 7. — Mandible of *Chilotherium schlosseri* (Weber, 1905), MNS-IBB 115, Bacău, Bacău District, Romania, Late Miocene (MN10): **A**, left lateral view; **B**, left medial view; **C**, occlusal view; **D**, right lateral view; **E**, right medial view. Scale bar: 5 cm.

occlusal view due to the fusion of the ectoloph and metaloph. The ectometaloph displays a smooth posterior groove. The protocone is very large and shows a trefoil-shaped constriction in worn teeth. The M3s also have well-developed antecrochet and crochet.

Lower dentition
The labial cingulum of the lower cheek teeth is missing, except a short and weak extension of the anterior one until the level of the paraconid in lower premolars. The ectolophid groove is deep, V-shaped and developed until the neck in occlusal view, and oblique in lateral view. The lingual cingulum is present in the openings of the posterior valleys of p3-4 and the anterior valleys of p2-4 (Fig. 5).

The dp1 is absent.

The dp3 is only preserved at Pogana (VPM – P/354) and was originally identified as a p4 (Codrea *et al.* 2011). However, based on the very thin enamel, we consider it as a decidual premolar. It is much worn, especially the trigonid, which might explain its very small dimension compared with those given by Pavlow (1913). The external groove of the ectolophid is deep. The enamel has rugosities on its labial side.

The p2 can be observed only on the right tooth row of Reghiu. The paralophid is short, anteriorly curved without constriction, and the paraconid is developed. The protolophid is oblique, forming an acute angle with the lingual border towards the anterior part. The metaconid is very large and not constricted. It is bigger than the protoconid and entoconid, but roughly same-sized as the hypoconid. The talonid is also larger than the trigonid. The posterior valley is much bigger than the anterior one, both are open.

Both p3s of the specimen from Reghiu are preserved, but only one is preserved on the specimen from Bacău, and very worn. The hypolophid is bigger than the protolophid, which is also bigger than the paralophid. The labial branch of the paralophid is similarly oriented as on p2. The metaconid is simple and large. Both valleys are open and V-shaped in lingual view, the posterior being very large. In occlusal view, the trigonid is narrow and almost V-shaped whereas the talonid is large and rounded.

The p4s are preserved on the mandibles from Reghiu and Bacău. The lingual branch of the paralophid is long, reaching the same level as the protolophid and hypolophid. The posterior valley is bigger that the anterior valley, and are U-shaped. The metaconid is rounded. The trigonid is narrow and almost V-shaped and the talonid is rounded on p4.

The m1s from Reghiu and Bacău are similar to p4s, but due to their different stage of wear the metaconid is larger and the anterior valley is smaller. The m2s also have the similar pattern as p4s except for the square-shaped trigonid in occlusal view. The m3s are all preserved. The metaconid and entoconid are round and simple. The protolophid and hypolophid are very oblique in occlusal view and become more transverse with wear, as noticeable on the mandible from Bacau (Fig. 7C). On the mandible from Bacau, the left m3 is much more worn than the right one, indicating a possible dental pathology of this individual.

Remarks
The studied material can be undoubtedly assigned to Aceratheriini by the following set of characters: presence of wrinkled enamel on the cheek teeth, the developed crochet and the usual absence of a crista on upper molars, the constricted protocone and of a weak paracone fold on M1-2, as well as by the lingual bridge between the hypocone and protocone on P4 (Antoine *et al.* 2010; Lu 2013; Becker *et al.* 2013; Pandolfi 2015).

According to Pandolfi (2015), the combination of additional morphological features, such as high-crowned cheek teeth with the presence of cement patches, a lingual cingulum usually present on lower premolars as well as short metaloph on M1-2, allow for assigning them to an informal cluster (Pandolfi 2015), including “chilothere” *sensu lato* (Antoine & Sen 2016; i.e., *Persiatherium* Pandolfi, 2016, *Acerorhinus* Kretzoi, 1942, *Shansirhinus* Kretzoi, 1942, *Chilotherium* Ringström, 1924) as well as *Subchilotherium intermedium* (Lydekker, 1884) and *Plesiaceratherium gracile* Young, 1937.

Subchilotherium intermedium differs by the general absence of antecrochet (only present on M1) and protocone constriction, by the separated protocone and a hypocone on P4, by a strong paracone fold, a weak constriction of the protocone and a short metaloph on upper molars, an antecrochet and a hypocone separated on M1, an hypocone isolated on M2, and the presence of lingual and labial cingulum on lower cheek teeth (Lydekker 1884; Colbert 1935; Pandolfi 2015).

Plesiaceratherium gracile differs by an arched lingual rim of the upper tooth row, the absence of cement on cheek teeth, the presence of a continuous lingual cingulum on upper premolars and of usual medifossette on P2-4, as well as a protocone constriction and an antecrochet missing on P4 (Young 1937; Yan & Heissig 1986; Pandolfi 2015; Becker & Tissier 2020).

The referred dental specimens share the following features with the “chilothere” *sensu lato* (following Antoine & Sen 2016): presence of a protocone constriction on P3-4, strong antecrochet on upper molars, deep ectolophid groove reaching the neck on lower cheek teeth and absence of labial cingulum on the lower cheek teeth.

However, they differ from *Persiatherium rodleri* Pandolfi, 2016 by the absence of lingual cingulum on M1-2, and a stronger antecrochet on M1 (Pandolfi 2015).

Shansirhinus ringstroemi Kretzoi, 1942 can be excluded by the presence of elaborate enamel plications on cheek teeth, a well-developed medifossette on P3-4, strong lingual cingulum on P2-4, antecrochet and hypocone separated on P4 and M1, and a trigonid angular and U-shaped on lower cheek teeth (Deng 2005; Pandolfi 2015).

The species assigned to *Acerorhinus* differ by the presence of lingual cingulum on P2-4, a weak constriction of the protocone on M1, a posterior groove on the ectometaloph of M3, and of an external groove vanishing before the neck on lower cheek teeth (Deng 2005; Pandolfi 2015).

Among the “chilotheres”, the Reghiu specimens can basically be identified as belonging to *Chilotherium* based on the well-marked *processus postorbitalis* of the frontal and squa-

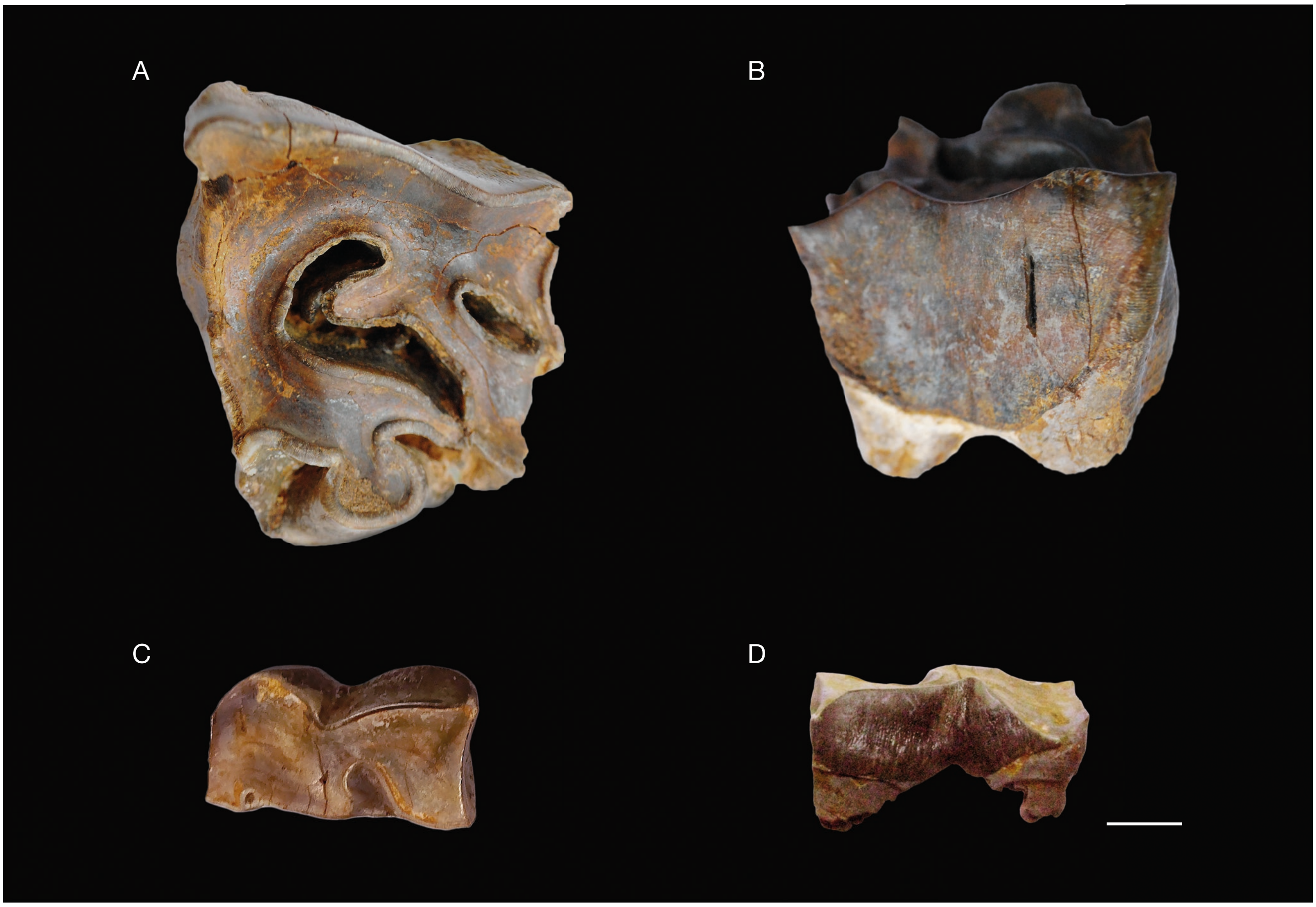

Fig. 8. — Dental remains of *Chilotherium schlosseri* (Weber, 1905), Pogana, Vaslui District, Romania, Late Miocene (MN11/12): **A**, **B**, left M2 (VPM – P/355), occlusal view (**A**), labial view (**B**); **C**, **D**, right dp3 (VPM – P/354), occlusal view (**C**), labial view (**D**). Scale bar: 1 cm.

mosal, and a massive mandibular symphysis bearing large tusk-like i2s (Geraads & Spassov 2009). More broadly, the referred dental remains can be assigned to *Chilotherium* by having a protocone constriction and a strong antecrochet on P4, usually a strong protocone constriction and an absence of lingual cingulum on upper molars, and an external groove developed until the neck on lower cheek teeth (Pandolfi 2015; Antoine & Sen 2016). From their dimensions (Tables 2; 3), the referred dental specimens roughly match most of those of *Chilotherium* species, except *C. primigenius* Deng, 2006a that are clearly smaller and *C. anderssoni* that are slightly larger (Weber 1905; Ringström 1924; Ji *et al.* 1980; Deng 2001, 2006a; Antoine & Sen 2016; Sun *et al.* 2018).

Following mainly Deng (2006a), Sun *et al.* (2018) and Kampouridis *et al.* (2022b), ten species of *Chilotherium* can be considered with confidence as valid: *Chilotherium samium* (Weber, 1905), *Chilotherium schlosseri*, and *Chilotherium kiliasi* (Geraads & Koufos, 1990) from Europe, *Chilotherium anderssoni, Chilotherium habereri*, *Chilotherium wimani*, *Chilotherium xizangensis*, *Chilotherium primigenius*, and *Chilotherium licenti* from China, and *Chilotherium persiae* from Iran.

Regarding *C. schlosseri*, many authors have suggested a series of European *Chilotherium* species more recently described as junior synonyms (e.g. Heissig 1975; Giaourtsakis 2003, 2009; Deng 2006b; Antoine & Sen 2016). Unfortunately, the type material of *C. schlosseri* was lost during the Second World War (e.g. Giaourtsakis 2003). Likewise, the holotype of *Chilotherium angustifrons* (Andrée, 1921) is also considered lost (Meiburg & Siegfried 1970; Giaourtsakis 2009). However, following the recent overview on European *Chilotherium* of Kampouridis *et al.* (2022b), *Chilotherium wegneri* (Andrée, 1921) and *Chilotherium angustifrons* (Andrée, 1921) are treated as junior synonyms of *C. schlosseri.* Likewise, *Chilotherium kowalevskii,* described in the Late Miocene locality of Grebeniki 1 in Ukraine, is also considered as a junior synonym of *C. schlosseri* as suggested by Antoine & Sen (2016) and this study (see below). Finally, we also consider *Teleoceras ponticus* Lubicz-Niezabitowski, 1912 from Odessa (Ukraine) as a junior synonym of *C. schlosseri* because of their very similar morphology and dimensions (Appendices 1; 2), as mentioned by Giaourtsakis (2022).

In contrast, according to Geraads & Spassov (2009) and despite the lack of well-known specimens and the absence of recent literature, the species *Chilotherium sarmaticum* from Berislav in Ukraine is also regarded as a valid species.

According to Deng (2006a: figs 1, 2), the very worn dental remains of the primitive species *C. primigenius* from Zhongmajia (Hezheng County, Gansu Province, China) differ by

Table 2. — *Chilotherium schlosseri* (Weber, 1905). Measurements (mm) of the upper cheek teeth from Romania and Samos (type locality, taken from Weber 1905). Measurements in brackets are indicative and are presented as left/right.

Anatomy	Inventory	Locality	Length	Width	Height
P1	ERIS-Rg/1987 001/6	Reghiu	17.0/17.5	22.0/–	16.5/–
		Samos	20.0	18.5	–
P2	ERIS-Rg/1987 001/6	Reghiu	30.5/28.0	34.5/29.5	30.0/29.5
		Samos	25.0	34.0	–
P3	ERIS-Rg/1987 001/6	Reghiu	38.5/36.5	42.0/43.5	37.0/38.0
		Samos	30.5	47.0	–
P4	MNS-IBB 112	Bacău	37.5	(36.9)	21.6
	ERIS-Rg/1987 001/6	Reghiu	37.0/34.0	44.5/46.0	–/48.0
		Samos	31.0-42.0	58.0-54.0	–
M1	MNS-IBB 112	Bacău	(44.8)	(42.0)	30.3
	MNS-IBB 113	Bacău	46.9	51.0	30.2
	ERIS-Rg/1987 001/6	Reghiu	46.0/45.5	48.0/48.0	–/44.0
		Samos	36.0–51.0	56.0-57.0	–
M2	MNS-IBB 112	Bacău	50.8	58.2	38.1
	MNS-IBB 113	Bacău	(52.9)	(59.8)	39.0
	VPM – P/355	Pogana	50.0	58.0	–
	ERIS-Rg/1987 001/6	Reghiu	47.5/50.0	50.0/48.5	49.0/45.0
		Samos	46.0-59.0	58.0-60.0	–
M3	MNS-IBB 112	Bacău	33.7	47.3	46.9
	MNS-IBB 114	Bacău	–	–	–
	ERIS-Rg/1987 001/6	Reghiu	32.5/32.0	34.0/36.0	–/38.0
		Samos	56.0-59.0	50.0-54.0	–

Table 3. — *Chilotherium schlosseri* (Weber, 1905). Measurements (mm) of the lower cheek teeth from Romania, Samos (type locality, taken from Weber 1905) and Grebeniki (decidual dp3, taken from Pavlow 1913). Measurements in brackets are indicative and are presented as left/right.

Anatomy	Inventory	Locality	Length	Width	Height
dp3	VPM – P/354	Pogana	35.4	21.0	–
		Grebeniki	35.0	–	20.0
p2	ERIS-Rg/1987 001/6	Reghiu	–/21.0	–/17.0	–/23.0
		Samos	20.0	15.0	–
p3	MNS-IBB 115	Bacău	27.6	24.3	12.6
	ERIS-Rg/1987 001/6	Reghiu	32.0/30.5	22.0/22.0	22.0/25.0
		Samos	30.5	25.0	–
p4	MNS-IBB 115	Bacău	36.4/33.1	27.6/25.8	19.0/13.5
	ERIS-Rg/1987 001/6	Reghiu	35.0/33.5	24.0/25.5	30.0/29.5
		Samos	32.0	30.0	–
m1	MNS-IBB 115	Bacău	37.0/38.2	26.5/27.3	18.0/10.5
	ERIS-Rg/1987 001/6	Reghiu	43.0/39.0	22.5/23.0	26.0/27.5
		Samos	36.5	32.0	–
m2	MNS-IBB 115	Bacău	40.5	27.6	13.5
	ERIS-Rg/1987 001/6	Reghiu	43.5/43.0	23.5/23.5	29.5/33.5
		Samos	41.0	30.0	–
m3	MNS-IBB 115	Bacău	42.5/42.2	26.2/23.5	13.5/20.0
	ERIS-Rg/1987 001/6	Reghiu	45.5/45.5	23.5/24.0	31.0/27.0
		Samos	48.0	29.0	–

a sagittally oriented antecrochet on upper molars and an almost transverse hypolophid on m3. The i2s are also much more upraised and nearly vertical (Deng 2006a: fig. 2.3).

Chilotherium wimani is also precluded by a strong and continuous lingual cingulum as well as usually the presence of a medifossette on upper premolars (Ringström 1924: pl. VII, figs 2, 3).

Chilotherium xizangensis and the more derived *C. licenti* points to specific differences by low crowned cheek teeth and a poorly developed parastyle on upper molars for the former (Ji *et al.* 1980; Deng 2001), as well as the presence of a crochet and a well-developed crista linked together to form a medifossette on P2–M2 for the latter (Sun *et al.* 2018).

Chilotherium xizangensis also displays a reduced lingual cingulum on upper molars, a pronounced crista on M3, a medifossette on P2-4, and a narrow mandibular symphysis (Ji *et al.* 1980: pl. IV).

The type species *Chilotherium anderssoni* and *C. habereri* differ by a protoloph and metaloph separated on P4 and an antecrochet not connected to the hypocone on M1(Ringström 1924: pl. III, figs 3, 4, pl. IV, fig. 3). The small-sized *Chilotherium samium* differs by the absence of antecrochet and a protocone and hypocone separated on P4 (Weber 1905: pl. IX, fig. 5). Finally, *Chilotherium kiliasi* differs by having pronounced crista on upper premolars, separated protocone and hypocone on P2, a poorly-developed antecrochet on upper

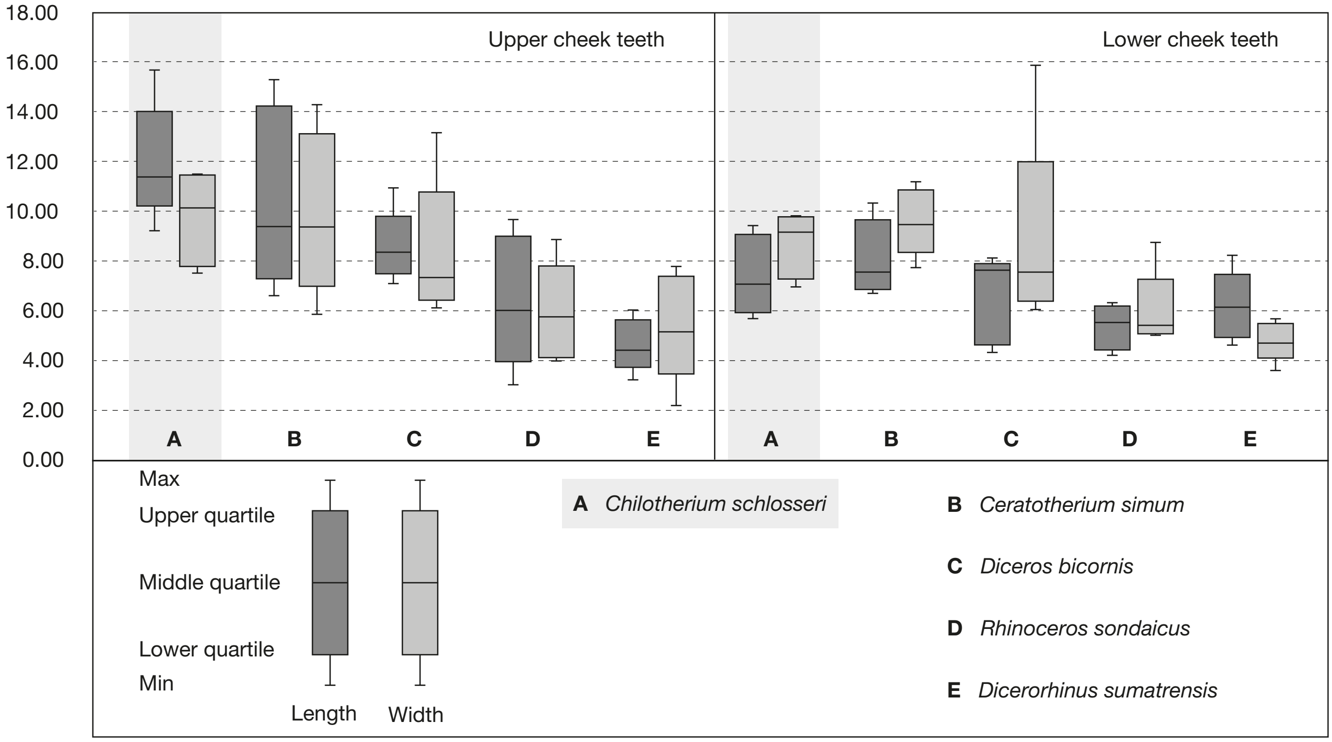

FIG. 9. — Box plots (min, lower quartile, middle quartile, upper quartile, max) of coefficients of variation of upper and lower cheek teeth measurements (length and width) of *Chilotherium schlosseri* (Weber, 1905) compared to those of current Rhinocerotidea, based on data from Table 4 and Appendix 3.

TABLE 4. — Coefficient of variation of cheek teeth measurements (length and width) of *Chilotherium schlosseri* (Weber, 1905) from Romania (after data from Appendix 1). Abbreviations: **CV**, coefficient of variation; **MAX**, maximum; **MIN**, minimum; **N**, number of teeth measured; **σ**, standard deviation.

	Length						Width					
Anatomy	**N**	**MIN**	**MAX**	**Mean**	**σ**	**CV**	**N**	**MIN**	**MAX**	**Mean**	**σ**	**CV**
P1	17	15.00	22.20	19.25	2.19	11.36	17	14.00	22.20	19.83	2.27	11.44
P2	21	20.00	32.00	26.00	2.91	11.19	21	18.00	34.50	30.98	3.55	11.46
P3	22	27.80	41.00	33.72	3.84	11.40	22	37.00	49.00	44.69	3.49	7.81
P4	26	31.00	43.50	38.20	3.52	9.22	26	36.90	59.00	49.82	5.72	11.48
M1	28	32.00	57.00	43.69	6.86	15.69	28	42.00	61.00	53.35	4.01	7.51
M2	34	34.80	63.00	50.86	6.40	12.59	34	40.00	62.00	55.22	4.87	8.81
M3	26	32.00	59.00	45.45	6.22	13.68	26	34.00	54.80	48.37	5.42	11.21
p2	13	19.90	26.40	22.81	2.06	9.02	13	14.90	20.10	17.20	1.66	9.63
p3	15	27.00	33.80	29.95	1.86	6.22	15	20.80	27.30	23.11	1.62	7.00
p4	16	23.00	36.40	33.23	3.14	9.46	16	24.20	30.00	27.24	1.99	7.30
m1	16	33.70	42.80	36.99	2.29	6.19	16	22.50	32.00	26.01	2.56	9.83
m2	15	37.80	50.20	41.90	3.36	8.03	15	23.50	30.60	26.65	2.62	9.82
m3	16	40.50	49.60	45.60	2.62	5.75	16	22.00	31.00	25.55	2.24	8.76

molars, and a labial cingulum on lower premolars (Geraads & Koufos 1990: pl. 3, figs 4, 5).

The Iranian *C. persiae* is distinguished by the presence of a thin anterior transverse branch (protoloph) on D1, separated protocone and metacone on P2, the unusual presence of crista and medifossette on upper cheek teeth, the quadrangular shape of the M3 in occlusal view, labial cingulum on lower premolars, an isolated and a constricted paralophid on p2 (Deng 2006a; see specimens MNHN-27802,-27803 and AMNH.F.MAR3053, 3859, 3073D, 38223827, 3860 and 3892). According to the descriptions and illustrations of Korotkevich (1958: figs 1, 2; 1970: figs 9-12), *C. sarmaticum* differs by having a more developed lingual cingulum and a crista on upper premolars, a labial cingulum on P2, a medifossette on P3-4, a weak antecrochet on upper molars, a labial cingulum on lower molars as well as a convex ventral border and an anteroposteriorly weakly increasing height of the *corpus mandibulae*.

Taking into account the evolution of the occlusal morphology regarding the state of tooth wear, the studied chilotheres remains of the Romanian Eastern Carpathians Foreland share the closest affinities with *Chilotherium schlosseri* from the type-locality of Samos in Greece and its junior synonym

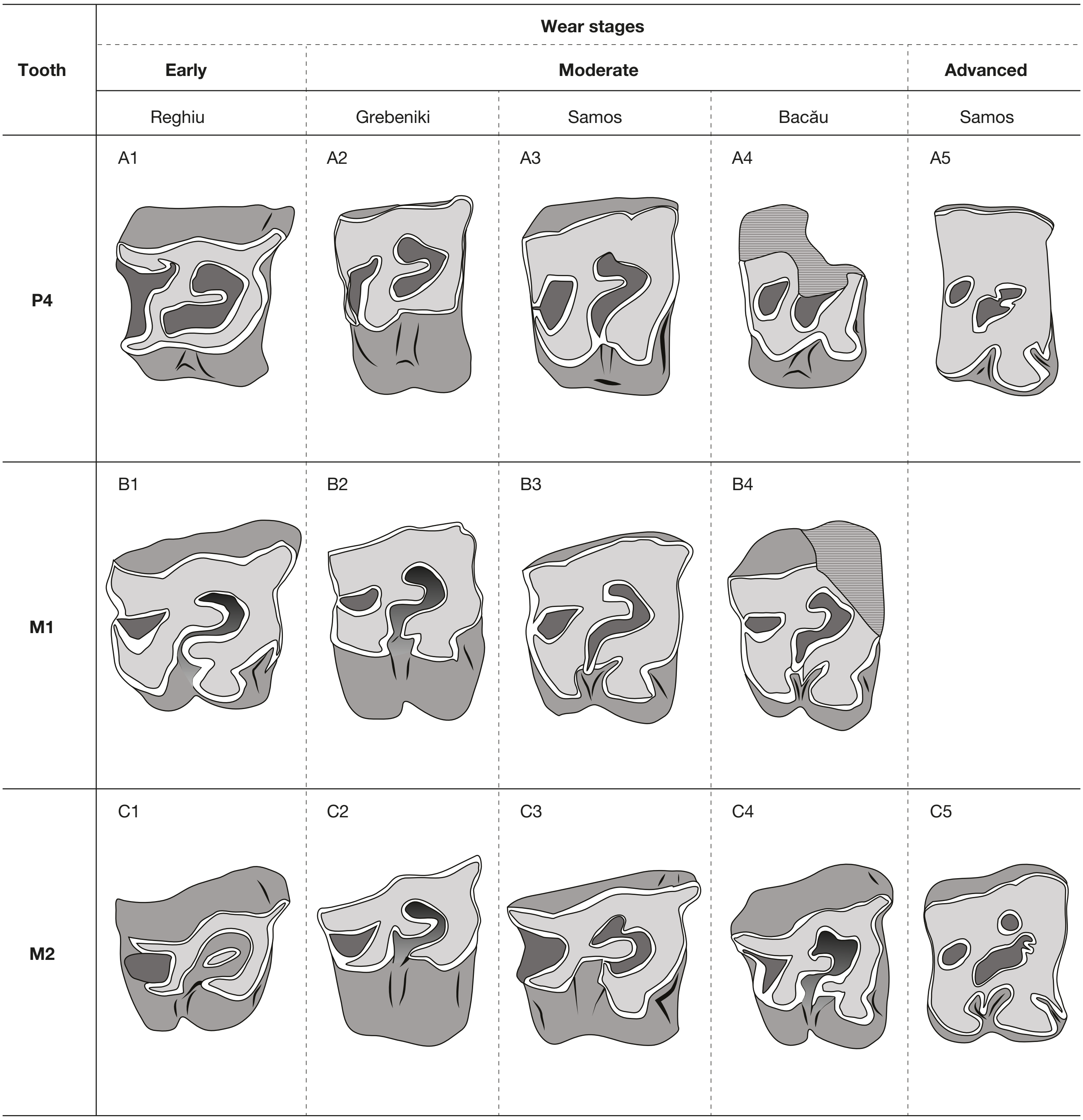

Fig. 10. — Schematic drawings of P4 (**A1-4**), M1 (**B1-4**) and M2 (**C1-4**) of *Chilotherium schlosseri* (Weber, 1905) at different stages of wear and in different localities: **A1**, **B1**, **C1**, Reghiu, Romania (ERIS-Rg/1987 001/6); **A2**, **B2**, **C2**, Grebeniki 1, Ukraine (after Pavlow 1913: pl. 4, fig. 6a, reversed); **A3**, **B3**, **C3**, Bacău, Romania (MNS-IBB 112); **A4**, **A5**, **B4**, **B5**, **C4**, Samos Island, Greece (**A4**, **B4**, **C4**, after Weber 1905: pl. VIII, figs 1-3, reversed; **A5**, **C5**, after Weber 1905: pl. VIII, fig. 1, holotype of *Chilotherium schlosseri*, reversed).

Chilotherium kowalevskii from the type-locality Grebeniki 1 in Ukraine (Weber 1905: pl. IX, figs 1-3; Pavlow 1913: pls IV-V; Krokos 1917: pls I-II; Pandolfi 2015; Antoine & Sen 2016). In particular, they share dental features such as the absence of labial cingulum, the presence of strong crochet and antecrochet on upper cheek teeth, a lingually-projected antecrochet joining the metaloph on worn upper cheek teeth, a weak mesostyle and a concave posterior profile of the ectoloph on unworn M1-2, a reduced lingual cingulum on lower premolars, missing on lower molars, semimolariform to submolariform upper premolars, a medifossette usually absent on upper premolars, and a curved paralophid without constriction on p2. Regarding the mandible's morphology, they additionally share a straight ventral border of the corpus mandibulae (Figs 5A, C; 7A, B).

Regarding the cheek teeth dimensions, the coefficients of variation are rather high for the specimens referred to *C. schlosseri*. However, *C. schlosseri* actually displays very close

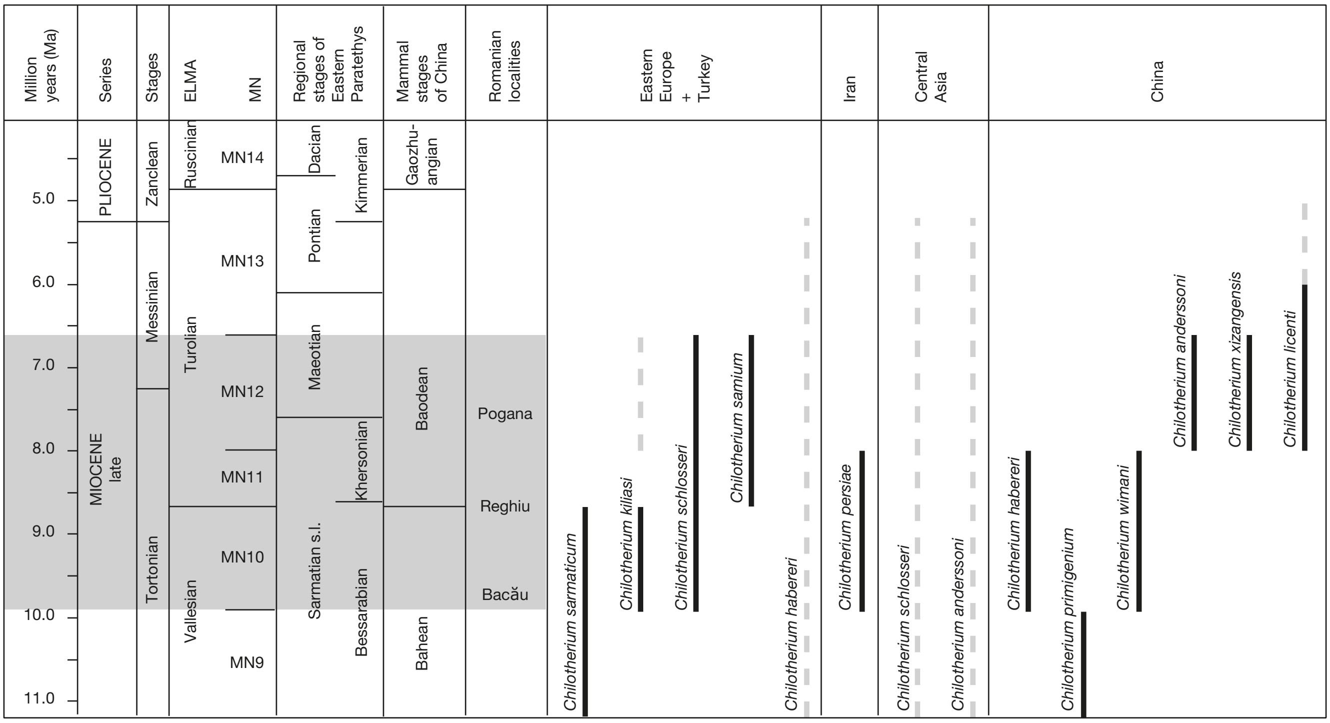

FIG. 11. — Occurences of species of *Chilotherium* Ringström, 1924. The **gray area** underlines the stratigraphical range of the Romanian localities. The geological time scale is based on Raffi *et al.* (2020). The European Land Mammal Ages (**ELMA**) and the Mammal Neogene units (**MN**) are from BiochroM'97 (1997) and Steininger (1999). The Regional stages of Eastern Parathethys are after Vangengeim & Tesakov (2013) and Lazarev *et al.* (2020) and Raffi *et al.* (2020), and the Mammal stages of China after Deng (2006b). The age of the Romanian localities are after Rădulescu *et al.* (1995); Codrea (1996); Ştiucă (2003); Geraads & Spassov (2009); Codrea *et al.* (2011) and Ţibuleac (2019). The biostratigraphical ranges of the *Chilotherium* species are after Sickenberg *et al.* (1975); Heissig (1975, 1996); Gabunia (1981); Heissig *et al.* (1996); Fortelius *et al.* (2003); Giaourtsakis (2003); Kostopoulos *et al.* (2003); Deng (2006a, b); Spassov *et al.* (2006); Geraads & Spassov (2009); Ataabadi *et al.* (2013); Koufos (2013); Vangeneim & Tesakov (2013); Wang *et al.* (2013); Sun *et al.* (2018) and Geraads *et al.* (2021).

coefficients of variation to extant Rhinocerotidae (Table 4; Fig. 9). The apparent high variation in cheek teeth measurements of *C. schlosseri* can be considered as normal for the family Rhinocerotidae and does not disqualify the assignation of the referred specimens from Romania to this species and the suggested synonymies.

DISCUSSION

The revision of the dental remains of Romanian *Chilotherium* highlights very close affinities of the dental specimens with advanced wear of Pogana (MN10, Codrea *et al.* 2011) and Bacău (MN10, Codrea 1996) with the type-material of *Chilotherium schlosseri* from Samos in Greece. As for the associated skull and mandible of a young adult of Reghiu, identified as *Chilotherium schlosseri* by Ioniță (1963) and *C.* cf. *sarmaticum* by Ştiucă (2003), they are similar to the unworn dental specimens assigned to *Chilotherium kowalevskii* from the type-locality Grebeniki 1 in Ukraine.

By observing the evolution of the dental patterns according to the stages of dental wear of the material–type of these two species and of the studied material, some characters, such as a concave profile of the posterior part of the ectoloph and a mesostyle on M1-2 or a very oblique orientation of the hypolophid on lower molars, can be modified, fade or even vanish with dental wear.

Comparing different dental morphologies at different stages of wear has always been problematic in mammals, including Rhinocerotidae. It is particularly difficult in those taxa that have very complex teeth, with numerous features, that sometimes totally disappear with wear, or radically change their morphology. A notable example is the connection between the protocone and hypocone that sometimes only appears with wear, but that are clearly separated when the tooth is unworn (see, e.g., Antoine 2002: fig. 103). High crowned teeth are even more problematic, as they can vary through more different stages of wear than low-crowned teeth. This is especially true in *Chilotherium*, which has both high-crowned cheek teeth and a complex dental morphology, with numerous features varying with wear such as the crochet or antecrochet. Although modern methods such as CT-scan can be used in such cases (as recently done by Kampouridis *et al.* 2022a), these methods are not always available.

Therefore, we illustrate here and describe the morphology of three different cheek teeth of *Chilotherium schlosseri* (P4, M1 and M2), through four different stages of wear (from early wear stage to advanced), including the specimens from Romania (Fig. 10). The main differences are reported in Tables 5-7.

These results led to assign the referred specimens from Romania to a single species, *Chilotherium schlosseri*, and to confirm *C. kowalevskii* as a junior synonym of *C. schlosseri*, as suggested by Antoine & Sen (2016) and apparently supported

TABLE 5. — Differences of the dental morphology at different stages of wear on the P4 of *Chilotherium schlosseri* (Weber, 1905) from Reghiu (ERIS-Rg/1987 001/6), Grebeniki (Pavlow 1913), Samos Island (Weber 1905) and Bacău (MNS-IBB 112), as illustrated on Figure 10. The crown height of the holotype of *C. schlosseri* from Samos Island is estimated based on Weber (1905: pl. VIII, fig. 1).

Dental feature	Early wear stage (Reghiu, Romania)	Moderate wear stage (Grebeniki, Ukraine)	Moderate wear stage (Samos Island, Greece)	Moderate wear stage (Bacău, Romania)	Advanced wear stage (Samos Island, Greece; holotype)
Crown height	48	25	–	22	(20)
Connection between the protocone and hypocone	Long and thin horizontal bridge	Short horizontal bridge	Short bridge	Short oblique bridge	Short and wide oblique bridge
Constriction of the protocone	Absent	Absent	Weak	Weak	Strong
Crochet	Long and thin, horizontal	Medium	Medium	Unknown	Very short, oblique
Hypocone	Weak and posteriorly elongated	Round	Round and almost connected to posterior cingulum	Round and connected to posterior cingulum	Round and large
Parastyle	Long and thin	Medium	Medium	Unknown	Absent
Postfossette	Wide and thin	Less wide, thinner	Round	Round	Round and small

TABLE 6. — Differences of the dental morphology at different stages of wear on the M1 of *Chilotherium schlosseri* (Weber, 1905) from Reghiu (ERIS-Rg/1987 001/6), Grebeniki (Pavlow 1913), Samos Island (Weber 1905) and Bacău (MNS-IBB 112), as illustrated on Figure 10.

Dental feature	Early wear stage (Reghiu, Romania)	Moderate wear stage (Grebeniki, Ukraine)	Moderate wear stage (Samos Island, Greece)	Moderate wear stage (Bacău, Romania)
Crown height	44	28	–	30
Antecrochet	Large, rounded and directed posteriorly	Smaller, rounded and directed posteriorly	Long, acute and directed lingually	Long, acute and directed lingually
Parastyle	Large	Short	Short	Unknown

TABLE 7. — Differences of the dental morphology at different stages of wear on the M2 of *Chilotherium schlosseri* (Weber, 1905) from Reghiu (ERIS-Rg/1987 001/6), Grebeniki (Pavlow 1913), Samos Island (Weber 1905) and Bacău (MNS-IBB 112), as illustrated on Figure 10. The crown height of the holotype of *C. schlosseri* from Samos Island is estimated based on Weber (1905: pl. VIII, fig. 1).

Dental feature	Early wear stage (Reghiu, Romania)	Moderate wear stage (Grebeniki, Ukraine)	Moderate wear stage (Samos Island, Greece)	Moderate wear stage (Bacău, Romania)	Advanced wear stage (Samos Island, Greece; holotype)
Crown height	45-49	40	–	38-39	(23)
Antecrochet	Indistinct from the protocone, positioned lingually	Indistinct from the protocone, positioned lingually	Indistinct from the protocone, positioned labially, short	Distinct from the protocone, positioned labially, short	Distinct from the protocone, positioned labially, directed lingually, very long and connected to the metaloph
Constriction of the protocone	Weak	Weak	Weak	Strong	Very strong
Crochet	Isolated from the protoloph	Connected to the protoloph, long	Connected to the protoloph, long	Connected to the protoloph, short	Connected to the protoloph and to the ectoloph (presence of a medifossette), long
Hypocone	Weak and posteriorly elongated	Posteriorly elongated and connected to posterior cingulum	Posteriorly elongated	Round and connected to posterior cingulum	Round and large, constricted anteriorly
Parastyle	Long and thin	Medium and wide	Medium and wide	Medium and wide	Absent

by the phylogenetic analysis of Pandolfi (2015). In contrast, the poorly known *C. sarmaticum*, although similar to the referred material, is kept as a valid species on the base of the description of Korotkevich (1958, 1970) and as suggested by Geraads & Spassov (2009). These results are proposed herein until a taxonomic revision of *Chilotherium* species and their definite need for phylogenetic analysis.

Biostratigraphically (Fig. 11), the Romanian occurrences of *C. schlosseri* correspond most probably to late Bessarabian – early Khersonian (late Vallesian – early Turolian, MN10-11 units in Europe), which is consistent with the overall record of the species (late Vallesian-early Tortonian, MN10-12) and, more broadly, of the genus (Late Miocene, MN9-13). Among the *Chilotherium* species, the stratigraphical range of *C. schlosseri* is the most important and its geographical distribution, from Eastern Europe (Greece, Ukraine, Republic of Moldova, Bulgaria) to Turkey and Central Asia (Kyrgyzstan, Tajikistan, Uzbekhistan), makes it one of the most common species of the genus.

Chilotherium schlosseri, as most of the genus representatives, is considered as a grazer (high-crowned cheek teeth and short limbs compared to other Aceratheriini, according to Deng 2002) inhabiting steppe environment in arid or subarid habitat (Liang & Deng 2005). In Eastern Europe, *C. schlosseri* is commonly associated with *Aceratherium incisivum*, a browser form from forested habitats (Becker 2003). The latter is not recorded in Central Asia and China, whereas *Chilotherium* species are absent in Western Europe (Heissig 1999). This is probably the result of climatic changes that divided the European continent in two really distinct environments from the Late Miocene onward. Indeed, Western Europe environments were still dominated by closed and semi-humid tropical forests whereas Eastern Europe had more open and drier forest landscapes due to a more continental climate (Vislobokova & Sotnikova 2001). Thus, Eastern Europe can be regarded as a transition area between the more closed and wooded environments of Western Europe to the more open ones in Asia.

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APPENDICES

APPENDIX 1. — Measurements (length × width in mm) of upper and lower cheek teeth of *Chilotherium schlosseri* (Weber, 1905) from Romania (Reghiu, Bacău and Pogana) and other localities, based on literature (Lubicz-Niezabitowski 1913; Krokos 1917; Andrée 1921; Leonardi 1947).

Upper cheek teeth of *Chilotherium schlosseri* (Weber, 1905)

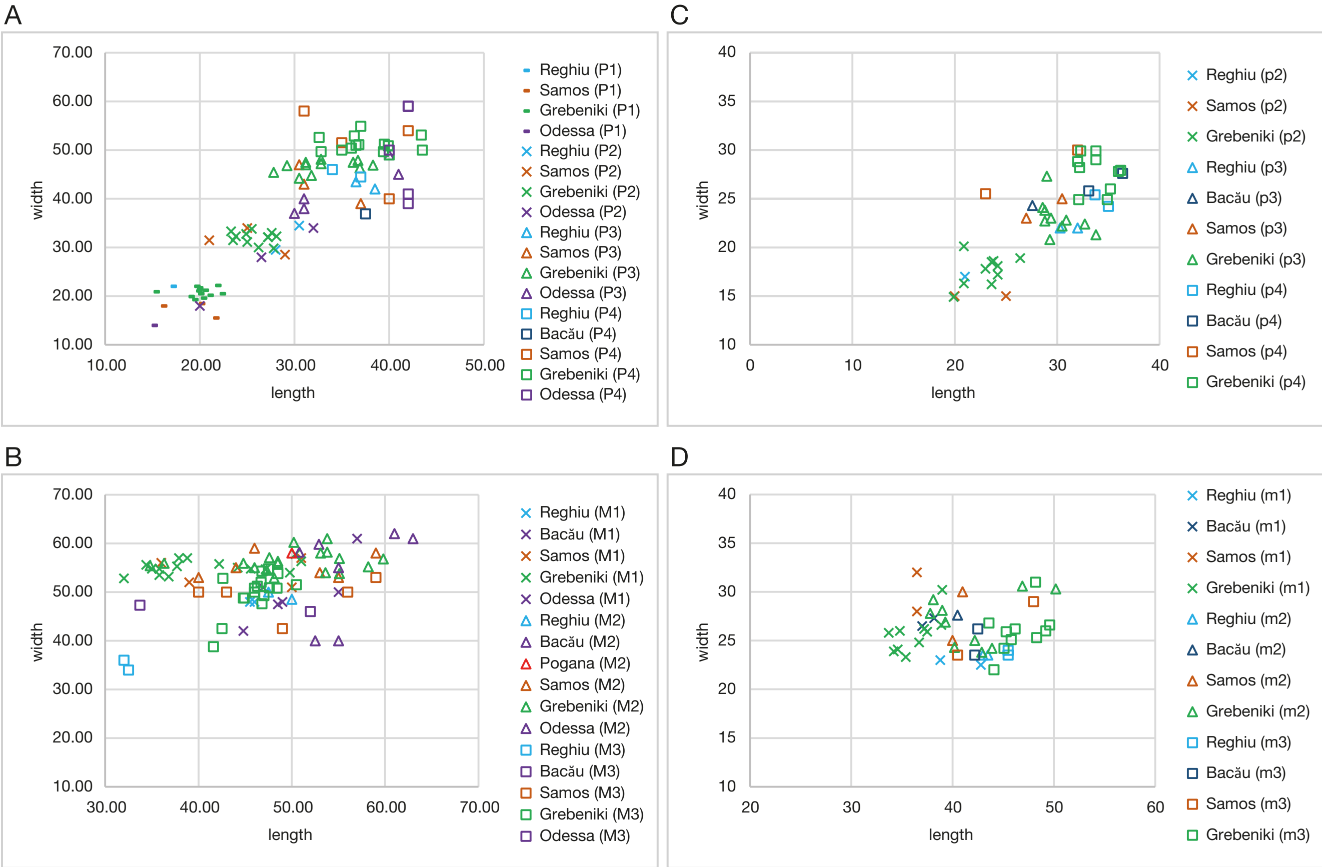
	C. schlosseri Reghiu eris-Rg/1987 001/6	*C. schlosseri* Bacău MNS-IBB 112	*C. schlosseri* Bacău MNS-IBB 113	*C. schlosseri* Pogana VPM – P/355	"*C. wegneri*" Samos Andrée 1921	"*C. angustifrons*" Samos Andrée 1921	"*Teleoceras ponticus*" Odessa Niezabitowski 1913	*C. schlosseri* Grebeniki no. 6 Krokos 1917	*C. schlosseri* Grebeniki no. 1 Krokos 1917	*C. schlosseri* Grebeniki no. 4 Krokos 1917	*C. schlosseri* Grebeniki no. 4 Krokos 1917
P1	17.0 × 22.0	–	–	–	–	21.5 × 15.5	15.0 × 14.0	21.7 × 22.2	15.2 × 20.9	–	19.9 × 20.5
	–	–	–	–	–	–	–	19.7 × 21.1	18.9 × 19.9	–	–
P2	30.5 × 34.5	–	–	–	–	29.0 × 28.5	20.0 × 18.0	25.0 × 31.1	24.9 × 32.8	–	–
	28.0 × 29.5	–	–	–	–	–	–	23.5 × 31.5	25.5 × 33.8	–	–
P3	38.5 × 42.0	–	–	–	–	37.0 × 39.0	31.0 × 40.0	31.8 × 44.8	32.8 × 47.2	31.2 × 47.5	–
	36.5 × 43.5	–	–	–	–	–	–	30.5 × 44.2	29.2 × 46.8	–	–
P4	37.0 × 44.5	37.5 × 36.9	–	–	–	40.0 × 40.0	40.0 × 50.0	36.0 × 50.4	36.8 × 51.1	36.3 × 52.9	–
	34.0 × 46.0	–	–	–	–	–	–	36.5 × 51.0	32.6 × 52.6	37.0 × 54.9	–
M1	46.0 × 48.0	44.8 × 42.0	46.9 × 51.0	–	–	50.0 × 51.0	55.0 × 50.0	36.8 × 53.2	35.0 × 54.8	37.7 × 55.3	32.0 × 52.8
	45.5 × 48.0	–	–	–	–	–	–	35.8 × 54.8	35.8 × 53.5	42.2 × 55.8	–
M2	47.5 × 50.0	50.8 × 58.2	52.9 × 59.8	50.0 × 58.0	40.0 × 53.0	53.0 × 54.0	55.0 × 55.0	46.0 × 55.0	47.6 × 57.1	53.8 × 61.0	34.8 × 55.4
	50.0 × 48.5	–	–	–	–	–	–	47.3 × 54.5	44.8 × 55.9	53.8 × 58.2	36.3 × 55.9
M3	32.5 × 34.0	33.7 × 47.3	–	–	43.0 × 50.0	49.0 × 42.5	52.0 × 46.0	44.8 × 48.8	46.7 × 52.0	48.5 × 53.8	46.0 × 50.8
	32.0 × 36.0	–	–	–	–	–	–	44.9 × 48.8	47.6 × 50.9	47.5 × 54.8	46.3 × 51.2

	C. schlosseri Grebeniki no. 3 Krokos 1917	*C. schlosseri* Grebeniki no. 5 Krokos 1917	*C. schlosseri* Grebeniki no. 7 Krokos 1917	*C. schlosseri* Grebeniki no. 8 Krokos 1917	*C. schlosseri* Grebeniki no. 21 Krokos 1917	*C. schlosseri* Samos Krokos 1917	*C. schlosseri* Samos 2 Krokos 1917	*C. schlosseri* Samos 3 Krokos 1917	"*C. wegneri*" Samos Leonardi 1947	*C. schlosseri* Odessa 1 Krokos 1917	*C. schlosseri* Odessa 2 Krokos 1917
P1	19.5 × 22.0	22.2 × 20.5	19.3 × 19.3	20.2 × 19.6	–	20.0 × 18.5	–	–	16.0 × 18.0	–	–
	19.8 × 21.7	20.4 × 21.2	20.9 × 20.2	–	–	–	–	–	–	–	–
P2	23.3 × 33.3	27.2 × 32.1	27.6 × 33.0	27.2 × 32.1	–	25.0 × 34.0	–	–	21.0 × 31.5	32.0 × 34.0	26.5 × 28.0
	23.8 × 32.3	26.2 × 30.0	28.1 × 32.3	27.8 × 29.8	–	–	–	–	–	–	24.0 × 28.5
P3	27.8 × 45.4	38.3 × 46.9	36.2 × 47.5	32.8 × 48.1	–	30.5 × 47.0	–	–	31.0 × 43.0	41.0 × 45.0	31.0 × 38.0
	–	36.9 × 46.3	36.7 × 47.9	31.2 × 47.0	–	–	–	–	–	40.0 × 49.0	30.0 × 37.0
P4	35.0 × 50.0	40.0 × 49.0	43.5 × 50.0	39.5 × 51.2	–	31.0 × 58.0	42.0 × 54.0	–	35.0 × 51.5	42.0 × 59.0	42.0 × 41.0
	32.8 × 49.7	39.4 × 49.7	43.4 × 53.1	39.9 × 50.9	–	–	–	–	–	42.0 × 59.0	42.0 × 39.0
M1	37.9 × 57.0	49.8 × 54.0	51.0 × 56.3	45.6 × 54.8	34.4 × 55.6	36.0 × 56.0	51.0 × 57.0	–	39.0 × 52.0	57.0 × 61.0	49.0 × 48.0
	38.8 × 57.0	47.2 × 54.7	50.4 × 57.8	44.2 × 55.0	–	–	–	–	–	–	48.5 × 47.5
M2	48.5 × 55.9	55.1 × 53.8	59.8 × 56.8	55.1 × 56.9	50.2 × 60.2	46.0 × 59.0	59.0 × 58.0	55.0 × 53.0	44.0 × 55.0	63.0 × 61.0	52.5 × 40.0
	48.5 × 56.3	53.6 × 54.0	58.2 × 55.2	53.1 × 58.0	48.1 × 52.9	–	–	–	–	61.0 × 62.0	55.0 × 40.0
M3	50.5 × 51.5	42.5 × 42.5	46.8 × 47.6	42.6 × 52.8	46.8 × 54.3	59.0 × 53.0	56.0 × 50.0	–	40.0 × 50.0	–	–
	48.4 × 50.8	41.6 × 38.8	47.0 × 49.3	46.0 × 50.0	–	–	–	–	–	–	–

Lower cheek teeth of *Chilotherium schlosseri* (Weber, 1905)

	C. schlosseri Reghiu eris-Rg/1987 001/6	*C. schlosseri* Bacău MNS-IBB 115	"*C. wegneri*" Samos Andrée 1921	*C. schlosseri* Grebeniki no. 13 Krokos 1917	*C. schlosseri* Grebeniki no. 14 Krokos 1917	*C. schlosseri* Grebeniki no. 15 Krokos 1917	*C. schlosseri* Grebeniki no. 1 Krokos 1917	*C. schlosseri* Grebeniki no. 22 Krokos 1917	*C. schlosseri* Samos Krokos 1917
p2	21.0 × 17.0	–	25.0 × 15.0	20.9 × 20.1	26.4 × 18.9	20.9 × 16.3	23.0 × 17.8	24.2 × 17.2	20.0 × 15.0
	–	–	–	19.9 × 14.9	24.2 × 18.1	23.6 × 16.2	23.8 × 18.6	23.6 × 18.5	–
p3	32.0 × 22.0	27.6 × 24.3	27.0 × 23.0	29.0 × 27.3	32.7 × 22.4	28.8 × 23.8	28.8 × 22.7	30.9 × 22.8	30.5 × 25.5
	30.3 × 22.0	–	–	30.5 × 22.2	33.8 × 21.3	29.4 × 23.0	28.6 × 24.1	29.3 × 20.8	–
p4	35.0 × 24.2	36.4 × 27.6	23.0 × 25.5	33.8 × 29.0	36.2 × 27.9	33.8 × 29.9	32.2 × 28.2	34.9 × 24.9	32.0 × 30.0
	33.7 × 25.4	33.1 × 25.8	–	32.1 × 24.9	36.0 × 27.8	32.0 × 28.8	32.3 × 29.9	35.2 × 26.0	–
m1	42.8 × 22.5	37.0 × 26.5	36.5 × 28.0	39.0 × 30.2	34.8 × 26.0	33.7 × 25.8	34.6 × 24.1	35.4 × 23.3	36.5 × 32.0
	38.8 × 23.0	38.2 × 27.3	–	38.9 × 26.6	37.5 × 25.9	37.2 × 26.2	34.2 × 23.9	36.7 × 24.8	–
m2	43.5 × 23.5	40.5 × 27.6	40.0 × 25.0	50.2 × 30.3	39.3 × 26.9	39.0 × 28.1	40.2 × 24.3	42.9 × 23.8	41.0 × 30.0
	43.0 × 23.5	–	–	46.9 × 30.6	42.2 × 25.0	38.1 × 29.2	37.8 × 27.8	43.9 × 24.2	–
m3	45.5 × 23.5	42.5 × 26.2	40.5 × 23.5	48.2 × 31.0	49.2 × 26.0	45.3 × 25.9	45.1 × 24.2	45.8 × 25.1	48.0 × 29.0
	45.5 × 24.0	42.2 × 23.5	–	49.6 × 26.6	48.3 × 25.3	43.6 × 26.8	44.1 × 22.0	46.2 × 26.2	–

Appendix 2. — Bivariate plots of the length and width of cheek teeth of *Chilotherium schlosseri* (Weber, 1905), based on the measurements (mm) from Appendix 1. **A**, upper premolars; **B**, upper molars; **C**, lower premolars; **D**, lower molars.



Appendix 3. — Coefficient of variation (**CV**) of cheek teeth measurements (length and width) of current Rhinocerotidae (after data from Guérin 1980).

	CV (length)				CV (width)			
	Ceratotherium simum	***Diceros bicornis***	***Rhinoceros sondaicus***	***Dicerorhinus sumatrensis***	***Ceratotherium simum***	***Diceros bicornis***	***Rhinoceros sondaicus***	***Dicerorhinus sumatrensis***
P1	–	10.93	8.04	–	–	13.15	8.85	–
P2	9.29	8.47	8.49	6.02	5.85	7.66	6.75	7.77
P3	9.46	7.09	8.40	4.36	7.66	8.67	6.63	7.53
P4	6.61	8.21	4.56	3.20	9.61	6.96	4.00	5.31
M1	15.30	8.72	2.99	4.15	9.55	6.61	3.97	4.95
M2	7.53	7.75	5.76	4.42	12.70	6.10	4.86	4.65
M3	14.40	9.77	9.66	5.48	14.30	7.60	6.62	2.17
p1	–	–	–	–	–	15.87	–	–
p2	10.37	6.73	5.78	5.13	7.78	7.66	8.79	5.72
p3	7.58	8.15	5.37	5.78	7.92	8.67	5.85	5.53
p4	6.89	7.44	4.46	6.79	10.59	6.96	5.19	4.81
m1	9.46	4.38	4.27	8.27	8.56	6.61	5.70	4.71
m2	7.64	4.42	6.37	6.60	10.43	6.10	5.07	4.64
m3	6.74	7.80	6.22	4.67	11.21	7.60	5.22	3.65