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RESEARCH PAPER

New remains of *Acerorhinus* (Perissodactyla, Rhinocerotidae) from the Late Miocene of Romania and implications for the taxonomic diversity of the genus

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Abstract

This study presents newly-discovered Rhinocerotidae material, including a cranium, a partial mandible, and a femur, from the Late Miocene (late Kersonian, MN 11, or possibly younger, Meotian, MN 12) of Crețești 1 in Romania. The specimens are analysed morphometrically and morphologically, and compared with various Aceratheriinae taxa. The combination of features observed in the Crețești 1 specimen aligns most closely with *Acerorhinus simplex*, a species previously described from the late Vallesian-middle Turolian of Eurasia. This discovery represents the first well-documented occurrence of *Acerorhinus* in Romania, contributing to the understanding of the diversity and paleobiogeographic distribution of acerathere rhinoceroses during the Late Miocene. Along with recent revisions, this work allows for refining the species content of *Acerorhinus*: *Acerorhinus simplex*, *Acerorhinus palaeosinensis, Acerorhinus tsaidamensis*, *Acerorhinus hezhengensis*, *Acerorhinus yuanmouensis, Acerorhinus fuguensis, Acerorhinus lufengensis* and *Acerorhinus neleus*. In addition, we consider that *Acerorhinus*' remains from Ciobruciu (late Vallesian-middle Turolian) do belong to *A. simplex*, which *Acerorhinus belaevi* is here regarded as a junior synonym.

Keywords *Acerorhinus* · Morphology · Biochronology · Paleobiogeography · Eurasia

Introduction

The fossil vertebrate locality of Crețești 1 is situated in the southern area of the “Moldavian Platform”, in Vaslui County, on the E 581 road that connects the villages of Crasna and Huși, on the right bank of the Lohan Valley (Fig. 1). The outcrop of interest is located near Satu Nou, a village which belongs to the municipality of Crețești. The fossil site was discovered by a team led by Mircea Mamalaucă from the “Vasile Pârvan” Bârlad Museum during road modernization works. The fossil vertebrates were collected through systematic excavations carried out over several years by a team of paleontologists led by one of us (VAC) and other enthusiasts who supported this work.

The outcrop is small, measuring between 0.5 and 1 m in vertical section (Pérez-García et al., 2022). The rocks consist of greenish mudstone and silty sand. While the basal silty sand is barren, the mudstone contains numerous vertebrate remains. To date, the following taxa have been reported for Crețești 1: amphibians (Salamandridae indet., *Pelobates* sp., Bufonidae indet., Anura indet.), lizards (*Chalcides* sp., *Lacerta* sp., *Ophisaurus* (s.l.) sp.), snakes (*Coronella* cf.

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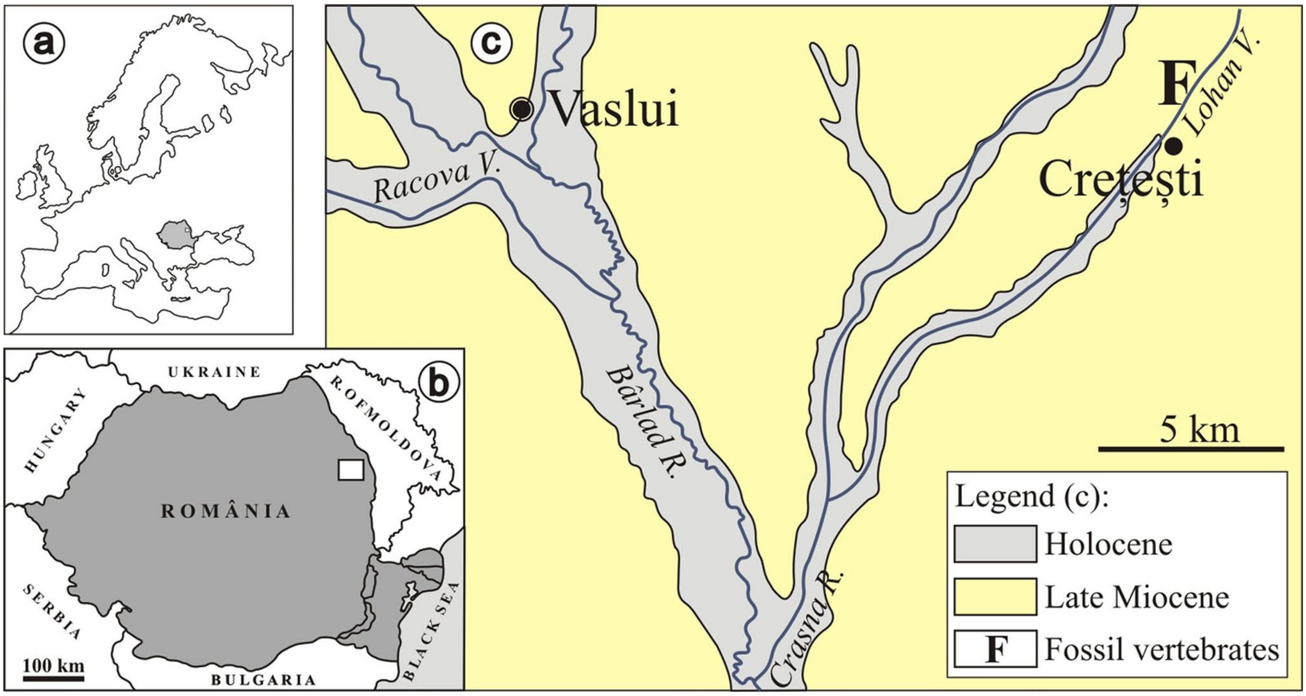


Fig. 1 Location map of the fossil−bearing locality Crețești 1 (Vaslui County, Romania; early Turolian, MN 11, late Miocene). **A** Location of Romania in Europe; **B** Location of the village of Crețești in the eastern part of Romania; **C** Location of the Crețești vertebrate locality on the geological map of the area

miocaenica, *Hierophis* sp., Colubrinae indet., *Macrovipera* sp.), and turtles (*Testudo lohanica*, ''*Protestudo*'' sp.), birds (Aves indet.), various small mammals (*Schizogaleryx* sp., *Spermophilinus bredai*, ?*Lophocricetus cimishliensis*, *Ochotona* (*Proochotona*) cf. *eximia*) and large mammals (*Pristifelis attica*, *Adcrocuta eximia*, *Protictitherium crissum*, ?*Metailurus* sp., *Yoshi* sp., *Choerolophodon pentelici*, "*Hipparion*" sp., *Hippotherium* sp., *Aceratherium incisivum*, *Acerorhinus* sp., *Chalicotherium* sp., *Hippopotamodon* sp., *Miotragoceros leskewitschi*, *Paleotragus* sp., *Samotherium major*, "*Paramachaerodus orientalis*") (Codrea et al., 2013, 2017a, 2017b; Ursachi et al., 2015, 2016, 2018; Bordeianu et al., 2019, 2022; Pérez-García et al., 2022; Codrea & Solomon, 2022; Kargopoulos et al., 2024; Țibuleac et al., 2025).

From an environmental point of view, based on sedimentology, these rocks illustrate an ancient floodplain. During these episodes, teeth and bones of various vertebrates were dispersed along intermittently active watercourses. The majority of the bones came from vertebrates already dead, with remains in various stages of weathering. On the other hand, some remains came from animals trapped and downed during floods, such as the numerous turtles assigned to *Testudo lohanica* (Pérez-García et al., 2022). Initially considered Vallesian in age (Codrea et al., 2017a, 2017b), the age of Crețești 1 has been recently revised and assigned to early Turolian (= late Sarmatian s.l., late Kersonian, MN 11; Kargopoulos et al., 2024) or to late Turolian (= Maeotian, MN 12; Pérez-García et al., 2022).

Here we describe and compare several Rhinocerotidae specimens from the Crețești 1 locality referable to the genus *Acerorhinus*.

Material and methods

The studied material includes a partially preserved cranium, an incomplete mandible and a left femur, housed at the "Vasile Pârvan" Bârlad Museum, Natural History Branch, under inventory number BMNH C5694. The cranium and the mandible were found at a relatively short distance from each other and display a comparable stage of wear of the dentition, suggesting they probably belong to the same individual. The femur was unearthed somewhat farther away but displays the same fossilization status as the other two specimens. The specimens were measured following Guérin (1980) and Mazza (1988). The comparison is based on a set of direct observations and data from published sources (see Comparison section).

Abbreviations. BMNH, "Vasile Pârvan" Bârlad Museum, Natural History Branch, Bârlad, Romania; Btl, breadth at the temporal ridges; L, maximal length; LM/Lm, length of the upper/lower molar row; Lm1, length of the first lower molar;

LP, length of the premolar row; M/m, upper/lower molar; P/p, upper/lower premolar; PoL, postorbital length.

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758
Order **Perissodactyla** Owen, 1848
Family **Rhinocerotidae** Gray, 1821
Subfamily **Aceratheriinae** Dollo, 1885 (sensu Lu et al., 2023)
Tribe **Aceratheriini** Dollo, 1885 (sensu Lu et al., 2023)

Genus ***Acerorhinus*** Kretzoi, 1942

Type species. Acerorhinus zernowi (Borissiak, 1914).

Emended diagnosis. According to Lu (2013), *Acerorhinus* (excluding *A. lufengensis*) is diagnosed by the following characters: presence of a depression at the external surface of the anterior part of the zygomatic arches, widest part of the dorsal surface of the cranium at the level of supraorbital process, protocone constricted just anteriorly on the upper teeth, presence of a constriction on the mandibular symphysis before the lower cheek tooth row, stout crest along the mandibular diastema, and absence of dp1/p1 in adults. Additional characters of the genus are: bell-shaped occipital face, concave ventral side of the mandibular symphysis, relatively narrow mandibular symphysis, and long premolar series (Athanassiou et al., 2014; Borissiak, 1914; Giaourtsakis, 2022; Lu, 2013; Lu et al., 2023; Pandolfi, 2016).

Included species. Acerorhinus simplex (Krokos, 1914); *Acerorhinus palaeosinensis* (Ringström, 1924); *Acerorhinus tsaidamensis* (Bohlin, 1937); *Acerorhinus hezhengensis* Qiu et al. (1987); *Acerorhinus yuanmouensis* Zong, 1998; *Acerorhinus fuguensis* Deng, 2000; *Acerorhinus lufengensis* Deng & Qi, 2009; *Acerorhinus neleus* Athanassiou et al. (2014).

Geographic distribution. The genus is well-documented in eastern Europe (Moldova, Greece, Romania), Ukraine, Caucasus, Turkey, central Asia, and China, and it is reported in Thailand (Antoine et al., 2025; Chaimanee et al., 2004; Geraads et al., 2021). The westernmost occurrence of the genus is a single specimen at Monte delle Piche (Italy) (Pandolfi et al., 2013). The oldest record is from the latest Middle Miocene (MN8) of Tung-gur Formation (Inner Mongolia; Cerdeño, 1996) but *Acerorhinus* is mainly recorded from MN9 to MN13.

Acerorhinus simplex (Krokos, 1914)
Figures 2, 3, 4

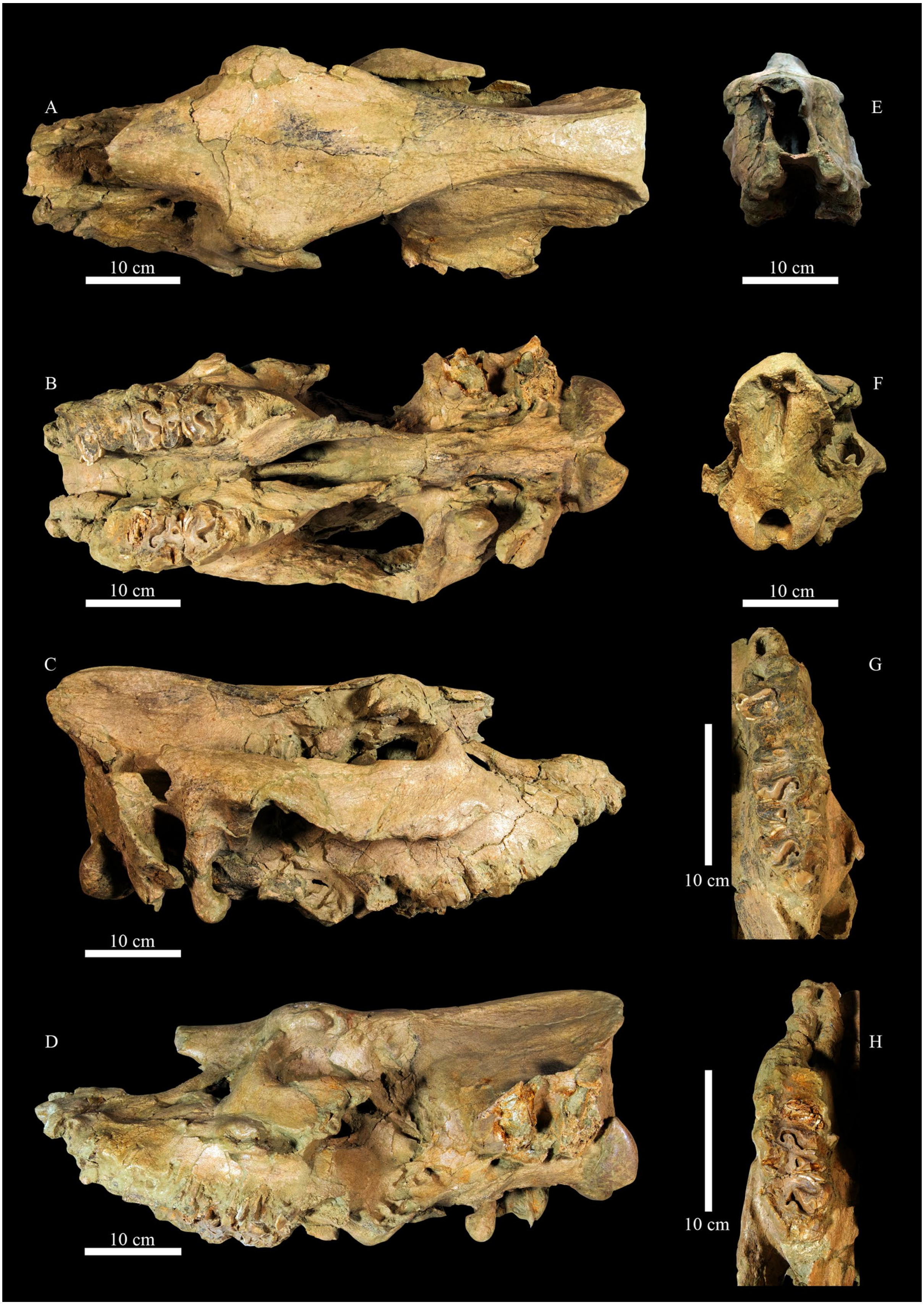
1914 *Aceratherium incisivum* Kaup−Pavlow: p. 5−15, pl. V, figs. 1−29.
1974 *Acerorhinus belaevi* n. sp.−Korotkevich: p. 38−44, fig. 1.

Emended diagnosis. Medium−sized hornless rhinocerotid, differing from other species of the genus by the following combination of features: (1) cranium moderately elongated, with relatively narrow hornless nasal bones; (2) infraorbital foramen located below the nasal notch; (3) developed posttympanic apophysis almost reaching the posterior border of the postglenoidal one; (4) widely separated frontal−parietal crests, and slightly concave posterior border of the nuchal crest; (5) anterior border of the choana located at the level of M3 hypocone; (6) upper molars with moderately developed protocone constriction and antecrochet; (7) mandibular symphysis short and upturned, terminating at distal side of p3; (8) lower cheek teeth with wide and shallow labial groove; (9) femur robust with a strongly asymmetric distal trochlea, with the medial lip of the trochlea abruptly stepped with the diaphysis and much more developed than the lateral lip and relatively small third trochanter.

Studied material. C5694, associated partial cranium (Fig. 2), incomplete mandible (Fig. 3) and left femur (Fig. 4), housed at the "Vasile Pârvan" Bârlad Museum, Natural History Branch.

Morphological description

Cranium. In dorsal view, the fronto−parietal crests are widely separated, and the posterior border of the nuchal crest is slightly concave (Fig. 2A). In ventral view (Fig. 2B), the anterior border of the choana is at the level of M3 hypocone. The posttympanic process is oblique and antero−laterally directed, the postglenoidal apophysis is curved, the vomer is rounded and the sagittal crest on the basilar process is sharp but barely visible. The hypoglossal foramina are placed anteriorly to the condylar fossa. In lateral view (Fig. 2C, D), there is a well−developed lacrimal process, a long postglenoidal apophysis, a developed posttympanic apophysis almost reaching the posterior border of the postglenoid one, a wide auditory pseudomeatus, and a flattened articular surface on the squamosal. The anterior border of the orbit lies above the mid of M2, the infraorbital foramen is located below the nasal notch. The supraorbital process is massive (Fig. 2E) and the orbital process above the jugal is evident. The posterior side of the zygomatic arch is low, and its posterior border is sinuous. The temporal crest, in lateral view, shows a strong concavity above the auditory pseudomeatus. The occipital face is bell−shaped (Fig. 2F) and, in lateral


A
E
10 cm
10 cm
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◂**Fig. 2** *Acerorhinus simplex* (Rhinocerotidae, Aceratheriini) from Crețești 1 (Romania, early Turolian, MN11). BMNH C5694, partial cranium: **A** dorsal; **B** ventral; **C** right lateral; **D** left lateral; **E** anterior; **F** occipital; **G** left M2–M3; **H** right P4–M3

view, is vertical. The nuchal tubercle is poorly developed, and the nuchal crest is slightly postero−ventrally directed.

Upper dentition. Right P4−M3 and left M2−M3 are preserved (Fig. 2G, H). P4 bears a remnant of a lingual cingulum at the entrance of the median valley and protocone and hypocone close to each other. M2 and M3 bear a strong crochet, a strong protocone constriction and a well−developed antecrochet that does not reach the metaloph. A mesial cingulum is present on these molars, while a labial cingulum is barely visible on the distal side of M2. The right M3 is subtriangular, with a convex ectometaloph, and bears a strong distal cingulum, while left M3 is badly preserved.

Mandible. The mental foramen is located below the p2/p3 transition (Fig. 3A). The posterior border of the mandibular symphysis approximately reaches the mid of p3 (Fig. 3B, C). The ventral border of the horizontal ramus is almost straight (Fig. 3A, D), raising at the p3/p2 transition. The posterior border of the ascending ramus is straight between the condyle and the ventral angle, displaying a convexity

Fig. 3 *Acerorhinus simplex* (Rhinocerotidae, Aceratheriini) from Crețești 1 (Romania, early Turolian, MN11). BMNH C5694, partial mandible: **A** right labial; **B** right lingual; **C** right dorsal; **D** left labial; **E** left lingual; **F** left dorsal


10 cm
C
B
A
10 cm
D
10 cm

◀**Fig. 4** *Acerorhinus simplex* (Rhinocerotidae, Aceratheriini) from Crețești 1 (Romania, early Turolian, MN11). BMNH C5694, left femur: **A** anterior; **B** posterior; **C** dorsal; **D** distal

at the level of the angular process. The articular condyle is well–developed (Fig. 3C). In lingual view, the mandibular foramen is located below the crown level (Fig. 3E).

Lower dentition. Left p3–m3 and right p2–m3 series are preserved, although left p2 and right p3 are missing. The enamel is rough. On p2 (Fig. 3F), the labial groove is faint, the paralophid is short, the ectolophid fold is barely visible, and the paraconid is developed. On the labial side (Fig. 3A, D), the p3 and p4 bear a crenulated and weak cingulum. A lingual cingulum is visible at the entrance of the anterior valley on p3. The labial groove is wide and shallow on p3–m3 and it reaches the base of the crown. The preserved lingual valleys are V–shaped but the posterior ones on m3 are wide V–shaped (Fig. 3B, E). There is a weak entoconid constriction on the left m2 (Fig. 3C), not observable on the right one.

Femur. The femur is relatively complete, though fractured (Fig. 4). The articular head is slightly higher than the greater trochanter in anterior view (Fig. 4A). The fovea capitis (Fig. 4B) is low and wide, and the articular head is regularly hemispheric (Fig. 4C). The third trochanter is poorly developed transversely, barely surpassing the level of the greater trochanter. In medial view, the medial lip of the trochlea is abruptly stepped with the diaphysis and much more developed than the lateral lip. The distal epiphysis (Fig. 4D) is wide and massive.

Comparison

General comparison. The cranial material from Crețești 1 differs from Elasmotheriini and Rhinocerotina by lacking rugosities on nasal and/or frontal bones and by having brachycephalic proportions. Furthermore, the studied teeth differ from Elasmotheriini (cfr. Antoine, 2002) in the absence of complex enamel folds on upper and lower teeth and by having labial cingula on lower teeth. They also differ from Rhinocerotina (cfr. Pandolfi, 2015; Pandolfi & Martino, 2024) in the presence of a short paralophid, a strongly constricted protocone and a well–developed antecrochet. Their attribution to Teleoceratina (cfr. Antoine, 2002; Lu et al., 2023) can be ruled out because of the separation between posttympanic and postglenoidal processes and the tooth morphology, particularly the absence of labial cingula on the upper teeth, the presence of a labial cingulum on the lower premolars, and the presence of V–shaped lingual valleys on the lower teeth. The general morphology of the cranium and mandible closely resembles Aceratheriini representatives. The specimens from Crețești 1 differ from *Alicornops* (from Bugti Hill, Sansan and several Spanish localities; Antoine et al., 2003; Cerdeño & Sánchez, 2000; Heissig, 2012; Santafé–Llopis et al., 1982) in their larger size, higher occipital face, and longer lower teeth, and from *Aceratherium* (from central and western Europe; Cerdeño & Sánchez, 1998; Guérin, 1980; Hünermann, 1989) in having connected protocone and hypocone on P4, stronger protocone constriction on upper molars, shorter cranium, wider frontal parietal crests, and a straight posterior border of the nuchal crest. In contrast to the studied specimen, *Chilotherium* shows a flat and wide cranium, flattened and depressed frontal region, long nasal bone, upper dentition characterized by a very strong protocone constriction, a marked antecrochet closing off the median valley, and normally a closed medifossette (Kampouridis et al., 2022; Ţibuleac et al., 2023; Ringström, 1924). The studied specimen also differs from *Eochilotherium samium* (from Samos, cfr. Kampouridis et al., 2023; Svorligkou et al., 2025) in having a straight posterior profile of the nuchal crest in dorsal view, wider frontal bones, wider auditory pseudomeatus, more developed paraoccipital process, temporal crests with a strong concavity above the auditory pseudomeatus, rounded vomere, shorter antecrochet on M2–M3, and weaker protocone constriction. After excluding all these aceratheriines, the remains from Crețești 1 are close to those of the genus *Acerorhinus* (e.g., in having a bell–shaped occipital face, a short cranium, a strong protocone constriction, an antecrochet that does not reach the metaloph on the upper molars).

The femur from Crețești 1 differs from that of *Chilotherium* sp. (Ringström, 1924: Pl. IX–Fig. 4) in having a higher medial lip of the distal trochlea in anterior view, and less transversally expanded medial and lateral tuberosities on the distal epiphysis. The third trochanter on the studied specimen is relatively small compared with those in other aceratheriines, such as *Chilotherium*.

Comparison with Eurasian Acerorhinus. The position of the anterior border of the choana and the rounded vomer in the cranium C5694 (Fig. 5A; Table 1) are similar to the condition observed in *A. zernowi* from Sebastopol (MN9, Crimea Peninsula) (Borissiak, 1914: Pl. VI; Fig. 5B), but differences do exist, such as: a less marked protocone constriction and a less prominent antecrochet, a narrower auditory pseudomeatus, a smaller and posteriorly oriented posttympanic process, a strongly concave dorsal profile of the cranium, and frontoparietal crests forming a sagittal crest (Borissiak, 1914: Pl. VI). Contrary to the studied specimen, the mandible of *A. zernowi* bears a mental foramen below p2 and a ventral border of the mandible upraising in front of p2 (Borissiak, 1914: Pl. VII). The preserved anterior border of the ascending ramus is almost vertical, in contrast with the slightly backward inclined border in C5694. The lower teeth of *A. zernowi* present more developed labial cingula.

Contrary to the studied cranium, in *A. neleus* from Kerassiá (MN11–MN12, Greece) (Athanassiou et al., 2014: Pl. I; Fig. 5C; Table 1), the cranium is dorsally

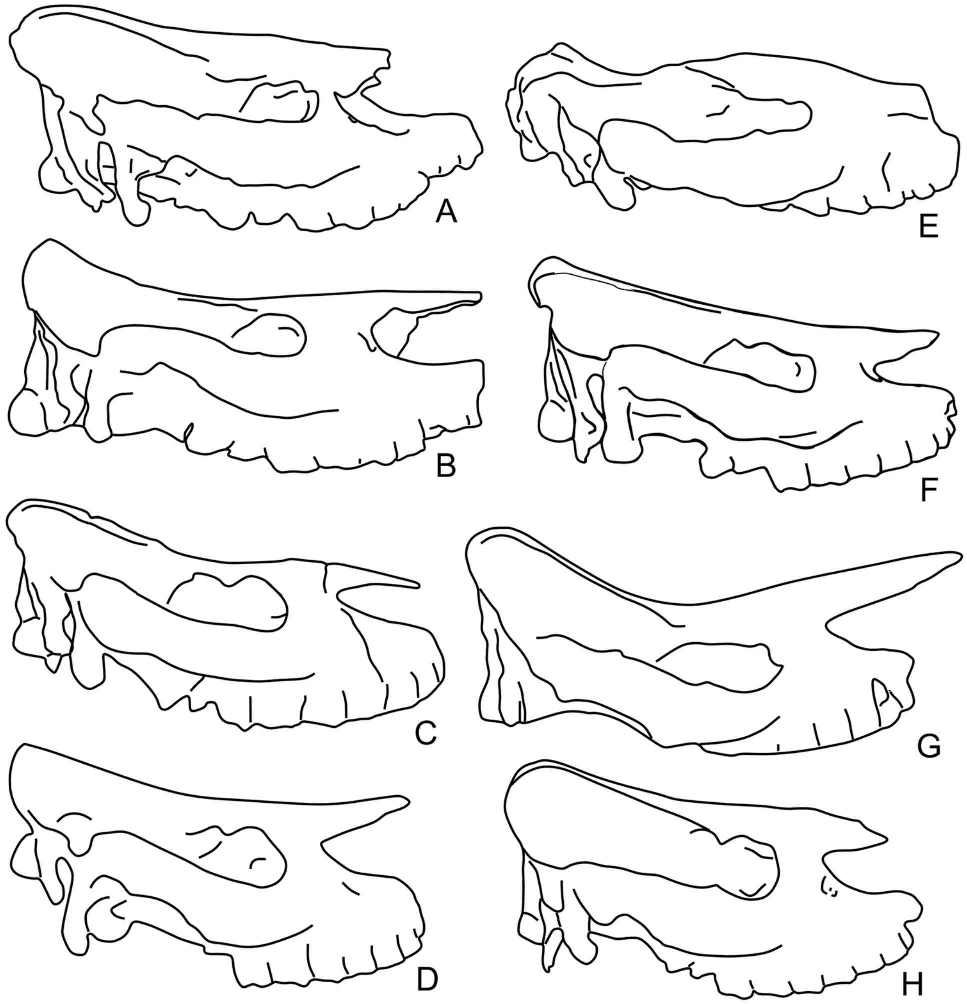

Fig. 5 Comparative right–lateral views of Late Miocene cranial specimens from Eurasia. **A** *Acerorhinus simplex*, BMNH C5694, Crețești 1; **B** *Acerorhinus zernowi*, Sebastopol (after Pavlow, 1913, pl. IV, fig. 2); **C** *Acerorhinus neleus*, Kerassiá (after Athanassiou et al., 2014, pl. I, fig. 3a); **D** *Acerorhinus* sp., Yulafli (after Kaya & Heissig, 2001, fig. 3–1); **E** *Acerorhinus simplex*, Tudora (after Krokos, 1914, pl. XLI, fig. 1); **F** *Acerorhinus simplex*, Ciobruciu (after Pavlow, 1914, pl. V, fig. 1); **G** *Acerorhinus zernowi*, Tung–gur (after Cerdeño, 1996, fig. 3A); **H** *Acerorhinus palaeosinensis*, Shansi (after Ringström, 1924, pl. X, fig. 1). Not to scale

slightly concave, the auditory pseudomeatus is narrow, the P4 bears a strong lingual cingulum, and the hypocone and protocone are close to each other, suggesting a possible fusion at an advanced stage of wear; the posttympanic process is more massive than on the studied cranium, the paraoccipital process is posteriorly directed, the articulation on the squamosal is more posterior–external oriented, and, in ventral view, the anterior border of the choana is at the M2–M3 transition. The cranium from Kerassiá is larger and has longer teeth (Supplementary File 1) than the new specimen from Crețești 1. The postorbital length (from the orbital cavity to the nuchal crest) of the studied specimen (PoL = 334-330 mm; respectively right and left side) is smaller than that of *A. neleus* from Kerassiá (PoL = 390 mm; Athanassiou et al., 2014), while the breadth at the temporal ridges (Btl = 43.2 mm) is greater (*A. neleus*: Btl = 24 mm). Further, *A. neleus* differs from Crețești 1 in having a straight ventral border of the mandibular corpus, a strong concavity below the articular condyle and a strong convexity at the level of the mandibular angle, and a longer mandible (L = 542–550 mm contra ca. 480 mm estimated in Crețești 1). The length of the lower molar series in the studied specimen (Lm = 128.6–132 mm) is similar to that of *A. neleus* from Chomaterí (Lm = 129.3–135.1 mm) and Pikermi (Lm = 131.2 mm), but smaller than the specimen from Kerassiá (Lm = 155.6–159.5 mm).

The cranium of *Acerorhinus* sp. from Çorlu–Yulafli (MN10, Turkey) (Kaya & Heissig, 2001: fig. 3; Fig. 5D, Table 1), shares several traits with the material from Crețești 1, such as the widely separated frontal–parietal crests, a slightly convex posterior profile of the nuchal crest in dorsal view and similar size, but it differs from the studied specimen in having a shorter occipital face, and a longer postglenoidal apophysis. The length of the molar and premolar series (LM = 124 mm; LP = ca 100 mm) and the breadth at the temporal ridges (Btl = 43.2 mm) of the specimen from Crețești 1 are close to those of *Acerorhinus* from Çorlu–Yulafli (LM = 124 mm; LP = 101 mm; Btl = 41 mm; Kaya & Heissig, 2001).

The type specimen of *Acerorhinus simplex* from Tudora (= Tudorowo; late Vallesian–middle Turolian), Moldova, represented by a poorly preserved cranium, differs from

Table 1 Summary table of morphological characters of eastern European *Acerorhinus* specimens considered in the comparative section: *A. simplex* from Crețești (Romania, early Turolian, MN11), *A. zernowi* from Sebastopol (Crimean Peninsula, Vallesian, MN9), *A. neleus* from Kerassiá (Greece, Turolian, MN11−MN12), *Acerorhinus* sp. from Çorlu−Yulafli (Turkey, Vallesian, MN10), *A. simplex* from Tudora (= Tudorowo, Moldova, late Vallesian−middle Turolian MN10−MN11), *A. simplex* from Ciobruciu (Moldova, late Vallesian−middle Turolian MN10−MN11)

Character/Species	Crețești C5694	*A. zernowi*	*A. neleus*	*Acerorhinus* sp. from Çorlu-Yulafli	*Acerorhinus simplex*	*Acerorhinus simplex* from Ciobruciu
Dorsal profile of the cranium	Almost flat	Concave	Concave	Almost flat		Almost flat
Orbit	Mid of M2	Between M1/M2	Above the mesial side of M2	Above the mesial side of M2	Mid of M2	Mid of M2
Auditory pseudomeatus	Wide	Narrow	Narrow	Wide		Wide
Frontal-parietal crests	Wide	Forming a sagittal crest	Wide	Wide	Wide	Wide
Anterior border of choana	At the level of M3 hypocone	At the level of M3 median valley	M2–M3 transition	At the level of M3 hypocone		At the level of M3 hypocone
Vomere	Rounded	Rounded				Rounded
M3	Convex ectometaloph and strong distal cingulum	Weak distal cingulum	Weak distal cingulum	Convex ectometaloph and strong distal cingulum	Convex ectometaloph and strong distal cingulum	Convex ectometaloph and strong distal cingulum
Mental foramina	Below p3	Below p2	Below p3			Below p3
Raising of the ventral border	At the p3/p2 transition	In front of p2	At the p3/p2 transition			At the p3/p2 transition
Lower premolars buccal cingulum	Absent or discontinuous	Present and continuous	Present and continuous			Absent or discontinuous

the studied material by a more massive and shorter postglenoidal apophysis, and a less developed lacrimal process (Krokos, 1914; Fig. 5E; Table 1). However, these characters can be evidently affected by the deformation of the cranium, whereas other features are shared by both specimens (shape of temporal−parietal crests, auditory pseudomeatus, postorbital process position of the anterior border of the orbit; Krokos, 1914). Contrary to the studied specimen, in *A. simplex* it is possible to observe a medifossette on M1−M3, separated hypocone and protocone on P4, and the presence of a lingual cingulum at the entrance of the median valley. These characters are hardly observable on the studied specimen because of the advanced wear, but it is still possible to detect the presence of a lingual cingulum at the entrance of the median valley of P4 and see protocone and hypocone close to each other (suggesting they were probably separated). The two considered specimens share similar size of the teeth (Supplementary File 1), and similar shape of M3.

The *Acerorhinus* material from Ciobruciu (late Vallesian−middle Turolian, Moldova; Pavlow, 1914: pl. V, Figs. 1a–c, 2) shares many features in common with the studied material (Table 1) such as the anterior border of the choana at the level of the M3 hypocone, the anterior border of the orbit above the mid of M2, the straight posterior profile of the nuchal crest, the widely separated frontal−parietal crests, and the robust M3 with a convex wall of the ectometaloph and a strong distal cingulum. The ventral border of the horizontal ramus in the mandible from Ciobruciu is almost straight, upraising at the p3/p2 transition, and the mental foramen lies below the anterior side of p3 similarly to Crețești 1. The length of the studied mandible, approximately 480 mm, is close to that of *Acerorhinus* from Ciobruciu (L = 440−450 mm).

The upper teeth of *Acerorhinus* from Ciobruciu published by Pavlow (1914) resemble those from Tudora. The two specimens share a constricted protocone with a moderately developed antecrochet, a flattened lingual side of the protocone on M2, a robust M3 with a strong and evident distal cingulum, a long parastyle on M1−M3. A prominent crochet is present in teeth of *A. simplex* but it is partially or completely fused with the ectoloph due to the advanced stage of wear according to Athanassiou et al. (2014). Accordingly, we regard *Acerorhinus* from Ciobruciu as *A. simplex*.

The mandible of *Acerorhinus belaevi* from Oselivka (late Vallesian, MN11, Ukraine) (Korotkevich, 1974: fig. 1) has a length of 470 mm, close to the specimens from Ciobruciu and Crețești. The length of the lower molar series in *Acerorhinus belaevi* (Lm = 131) is similar to that of the studied specimen (Lm = 128.6−132 mm). The material published by Korotkevich (1974) displays a straight posterior border of the ascending ramus, a low horizontal ramus and high ascending ramus. These characters are more similar to those observed on the studied material than on other *Acerorhinus* species.

The *Acerorhinus* crania from Tung−gur (MN8, Inner Mongolia; Cerdeño, 1996: fig. 2; Fig. 5G) show closer frontal−parietal crests compared to the studied cranium, but a straight posterior profile of the nuchal crest, as well as well−developed lacrimal and postorbital processes and a long and distinct paraoccipital process. In contrast to the specimen from Crețești 1, the Tung−gur crania show a strongly concave dorsal profile (Cerdeño, 1996: fig. 3a), higher occiput, anterior border of the orbit at the level of M1, longer nasals, and the anterior border of the choana at the level of M2 protocone (Cerdeño, 1996: fig. 4a). In addition, the postglenoidal apophysis can be separated from, in contact with, or fused to the posttympanic process, suggesting that this character is highly variable within the Tung−gur rhinocerotids.

The cranium of *A. tsaidamensis* (Tsaidam Basin, China, Vallesian−early Turolian, MN9−MN11) (Bohlin, 1937: figs. 90−91) differs from C5694 in bearing very close frontal−parietal crests and a concave posterior profile of the nuchal crest in dorsal view, having a more concave dorsal profile in lateral view, higher zygomatic arches, narrower auditory pseudomeatus, more anteriorly placed choana (anterior border at the level of the M2 hypocone) and larger hypoglossal foramina connected to the condylar fossa. In the mandible of *A. tsaidamensis* (Deng & Wang, 2004: fig. 2), the posterior border of the mandibular symphysis reaches the posterior side of p3.

Contrary to the studied cranium, *A. palaeosinensis* (late Turolian, China; Ringström, 1924. Pl. X−fig. 1; Fig. 5H) has the position of the orbit at the level of the mid of M1, it lacks the lacrimal process and the marked concavity along the temporal crest, and bears separated and more developed posttympanic and paraoccipital processes. Except for the shape of the occiput, none of these characters appear dimorphic, thus representing what we interpret as being valid specific differences. The mandible of *A. palaeosinensis* (Ringström, 1924. Pl. X−fig. 3) has a similar posterior profile of the ascending ramus and ventral profile of the horizontal ramus, the mandibular symphysis reaches the posterior side of p3.

The breadth at the temporal ridges on the studied cranium (Btl = 43.2 mm) is greater than that of *A. tsaidamensis* (Btl = 10 mm; Bohlin, 1937), and *A. palaeosinensis* (Btl = 23−31 mm; Bohlin, 1937).

The studied specimen differs from *Acerorhinus lufengensis* (MN12, China; Deng & Qi, 2009: fig. 1) in having a strong protocone constriction on M2 and M3, a shorter and more labial−lingually oriented metaloph on M2, a strong distal cingulum on M3 and a strong antecrochet on M2 and M3. Lower m1 and p4 of this Chinese taxon show a deep labial groove and a rounded trigonid, with the metalophid

Table 2 Revised taxonomy of *Acerorhinus* species discussed in the text

Species	Locality	Age	Original designation	Athanassiou et al. (2014)	Giaourtsakis (2022)	Lu (2013), Lu et al., (2014, 2023) and Pandolfi (2016)	This work
Aceratherium zernowi	Sebastopol (Crimean Peninsula)	MN9	Borissiak (1914)	*Acerorhinus zernowi*	*Acerorhinus zernowi*	*Acerorhinus zernowi*	*Acerorhinus zernowi*
Aceratherium simplex	Tudora (Moldova)	MN10–MN11	Krokos (1914)	*Acerorhinus simplex*	Potentially *Acerorhinus zernowi*	Not included	*Acerorhinus simplex*
Aceratherium zernowi var. *asiaticum*	Sebastopol (Crimean Peninsula)	MN9	Borissiak (1915)	Not included	Potentially *Acerorhinus zernowi*	Not included	*Acerorhinus zernowi*
Diceratherium palaeosinensis	Lok. 49 (Shansi, China)	MN12	Ringström (1924)	*Acerorhinus palaeosinensis*	*Acerorhinus palaeosinensis*	*Acerorhinus palaeosinensis*	*Acerorhinus palaeosinensis*
Diceratherium tsaidamensis	Qaidam Basin (Qinghai, China)	MN9–MN11	Bohlin (1937)	*Acerorhinus tsaidamensis*	*Acerorhinus tsaidamensis*	*Acerorhinus tsaidamensis*	*Acerorhinus tsaidamensis*
Aceratherium ggadzhievi	Eldari (Azerbaijan)	MN10-11	Dzhafarov (1958)	Not included	Potentially *Acerorhinus zernowi*	Not included	*Acerorhinus zernowi*
Aceratherium belaevi	Oselivka (Ukraine)	MN11	Korotkevich (1974)	Not included	Potentially *Acerorhinus zernowi*	Not included	*Acerorhinus simplex*
Chilotherium eldaricum	Eldari (Georgia)	MN10–11	Tsiskarishvili (1987)	Not included	*Acerorhinus eldaricus*	Not included	*Acerorhinus zernowi*
Acerorhinus hezhengensis	Dashuigou (Hezheng, China)	MN10	Qiu et al. (1987)	*Acerorhinus hezhengensis*	*Acerorhinus hezhengensis*	*Acerorhinus hezhengensis*	*Acerorhinus hezhengensis*
Acerorhinus yuanmouensis	Yuanmou Basin (Yunnan,China)	MN11–12	Zong (1998)	?*Acerorhinus* sp.	*Acerorhinus yuanmouensis*	*Acerorhinus yuanmouensis*	*Acerorhinus yuanmouensis*
Acerorhinus fuguensis	Wangdaifuliang (Fugu, China)	MN10	Deng (2000)	*Acerorhinus fuguensis*	*Acerorhinus fuguensis*	*Acerorhinus fuguensis*	*Acerorhinus fuguensis*
Acerorhinus lufengensis	Lufeng (Yunnan, China)	MN12	Deng and Qi (2009)	?*Acerorhinus* sp.	*Acerorhinus? lufengensis*	*Acerorhinus lufengensis*	*Acerorhinus lufengensis*
Acerorhinus neleus	Kerassiá (Greece)	MN11–12	Athanassiou et al. (2014)	*Acerorhinus neleus*	*Acerorhinus neleus*	Not included	*Acerorhinus neleus*
Aceratherium blanfordi var. *hipparionum*	Yunnan (China)	MN12?	Koken (1885)	Not included	*Acerorhinus? hipparionus*	Not included	Rhinocerotidae indet
Diceratherium palaeosinense var. *minus*	Lok. 12 (Honan, China)	MN12	Ringström (1924)	Not included	*Acerorhinus? minus*	Not included	*Acerorhinus palaeosinensis*
Chilotherium (Acerorhinus) cornutum	Hanchiawa (Yushe, China)	MN12	Qiu and Yan (1982)	*Shansirhinus* sp.	Not included	Not included	*Shansirhinus* sp.
Chilotherium (Acerorhinus) tianzhuense	Songshan (Tianzhu, China)	MN12	Zheng (1982)	*Shansirhinus* sp.	Not included	Not included	*Shansirhinus* sp.
Acerorhinus xiaoheensis	Yuanmou Basin (Yunnan, China)	MN11–12	Gao and Ma (1997)	?*Acerorhinus* sp.	*Acerorhinus? xiaoheensis*	*Subchilotherium intermedium*	*Subchilotherium intermedium*
Aceratherium kiliasi	Pentalophos-1 (Greece)	MN10	Geraads and Koufos (1990)	*Acerorhinus* sp. in partim; *Chilotherium* in partim	*Acerorhinus* sp. in partim; *Chilotherium kiliasi* in partim	*Chilotherium samium*	*Acerorhinus* sp. in partim; *Eochilotherium samium* in partim

Table 2 (continued)

Species	Locality	Age	Original designation	Athanassiou et al. (2014)	Giaourtsakis (2022)	Lu (2013), Lu et al., (2014, 2023) and Pandolfi (2016)	This work
Acerorhinus huadeensis	Huade (China)	MN12?	Qiu (1979)	Not included	*Acerorhinus huadeensis*	*Persiatherium huadeensis*	*Persiatherium huadeensis*
Persiatherium rodleri	Maragha (Iran)	MN10	Pandolfi (2016)	Not included	potentially *Acerorhinus eldaricus*	*Persiatherium rodleri*	*Persiatherium rodleri*
Aceratherium porpani	Tha Chang (Thailand)	MN12	Deng et al. (2013)	Not included	*Acerorhinus porpani*	*Aceratherium porpani*	*Acerorhinus? porpani*

more lingually directed. Furthermore, in dorsal view, *A. lufengensis* displays closer parietal crests and a strongly concave posterior border of the nuchal crest, while in ventral view, the anterior border of the choana is at the level of M2 hypocone.

Acerorhinus fuguensis from Fugu (MN10, China) displays larger teeth than the studied material. The cranium of *A. fuguensis* (Deng, 2000: Pl. I) differs from the studied cranium in having a smaller lacrimal process, a narrower postglenoidal apophysis, a more developed posttympanic process, a narrower auditory pseudomeatus, and a concave articular surface on the squamosal. The postorbital length of the studied specimen (PoL = 334-330 mm) is close to that measured for *A. fuguensis* (PoL = ranging 328−337 mm; Deng, 2000).

The cranial material of *A. yuanmouensis* from the Yuanmou Basin (MN11, China; Lu, 2013) differs from the studied specimens in having narrower frontal−parietal crests, V−shaped nuchal crest in dorsal view, longer crochet, and distal−lingually directed metaloph. A mandible of *A. yuanmouensis* from the Yuanmou Basin (Lu et al., 2014) has a posterior border of the symphysis at the level of p3, but a more regularly convex posterior border of the ascending ramus, lacking the concavity below the articular condyle. Despite the similar stage of dental wear, teeth of PDYV 0697 bear a deeper labial groove, deeper lingual valleys and lack both lingual and labial cingula.

Acerorhinus hezhengensis from Hezheng (MN10, Gansu Province, China) differs from the studied cranium in having shorter postglenoidal apophysis, longer posttympanic process, narrower auditory pseudomeatus, higher posterior side of the zygomatic arch, and upwardly turned nuchal crest (Deng et al., 2023; Qiu et al., 1987). The length of the upper molar and premolar series of the specimen from Crețești 1 (LM = 124 mm; LP = ca 100 mm) is close to those of *Acerorhinus hezhengensis* from Dashuigou (Hezheng; GSMV 8001, LM = 124 mm; Qiu et al., 1987).

Unfortunately the femur is known only in a few species of the genus *Acerorhinus*, limiting the comparison. The studied femur is long, with a wide diaphysis and a strongly asymmetric distal trochlea, resembling the femur from Tung−gur (Inner Mongolia) assigned to *A. zernowi* (Cerdeño, 1996: p. 10). The third trochanter on the femur of *A. tsaidamensis* (Tsaidam, China) is relatively low (Bohlin, 1937: Pl. IX−Fig. 4, p. 36), as in the studied specimen, contrary to *A. palaeosinensis*. The femur of *A. yuanmouensis* is slenderer than the studied material, and displays a lowermost positioned third trochanter, a less massive greater trochanter and a narrower distal epiphysis (Lu et al., 2021; fig. S43a−d). Finally, as stated for the cranium, the femur from Crețești 1 resembles that from Ciobruciu (Pavlow, 1914: Pl. V−fig. 13) in having a hemispherical articular head which is higher than the greater trochanter, a small third trochanter and a strongly asymmetrical distal trochlea with a concave proximal border.

The studied femur (L = 460 mm) is longer than that of *A. tsaidamensis* (L = 395−403 mm; Bohlin, 1937), *A. yuanmouensis* (L = 382 mm; Lu et al., 2021), and it is similar in size to that of *Acerorhinus* from Ciobruciu (L = 460 mm, estimated from Pavlow, 1914) and *A. zernowi* from Tung−gur (L = ca 493 mm; Cerdeño, 1996).

Discussion

The description and comparison of the partially preserved cranium with associated mandible and femur (C5694) allow us to assign this material to *Acerorhinus simplex*. The main characters shared between the type (and only material) of *A. simplex* figured by Krokos (1914) and that collected at Crețești 1 are: (1) convex ectometaloph in M3, bearing a strong distal cingulum; (2) anterior border of the orbit above the mid of M2; and (3) wide frontal−parietal crests. This species was first described from the late Vallesian−middle Turolian site of Tudora (= Tudorowo) and has not been revised or redescribed during the past century, nor included in a comprehensive comparative study. C5694 is also close to the material from Ciobruciu herein recognized as *A. simplex*. C5694 differs from other aceratheriines and coeval hornless rhinocerotids by the combination of a robust posttympanic process approaching the postglenoid process, choanae reaching the M3 hypocone, moderately constricted protocones on M1–M3, a short, upturned mandibular symphysis, together with a robust femur bearing an asymmetric distal trochlea. The inferred age of Crețești 1 (late Sarmatian, MN11—possibly Meotian, MN12) overlaps the previously–known late Vallesian–early Turolian range of *Acerorhinus* (Antoine et al., 2025; Geraads et al., 2021), and it is consistent with the taxonomic interpretation of the studied material.

Although the sample from Crețești 1 is limited, its assignment to *Acerorhinus simplex* further contributes to the debate on the subfamily Aceratheriinae. The systematics of the genus *Acerorhinus* is difficult to assess, and it is characterized by a conspicuous number of species within a short time span (Table 2); thus, a detailed revision of the genus is still required.

Athanassiou et al. (2014) revised several aceratheres reported in Eurasia and suggested seven valid species of *Acerorhinus* (Table 2), namely *A. neleus*, *A. zernowi*, *A. simplex*, *A. palaeosinensis*, *A. tsaidamensis*, *A. hezhengensis* and *A. fuguensis*. The authors considered *Chilotherium (Acerorhinus) cornutum* and *C. (A.) tianzhuense* as *Shansirhinus* sp., and *A. xiaoheensis*, *A. yuanmouensis* and *A. lufengensis* as ?*Acerorhinus* sp. According to Athanassiou et al. (2014), *Aceratherium kiliasi* is a composite taxon including partially *Chilotherium* cf. *samium* (*Eochilotherium samium* in Kampouridis et al., 2022) and partially *Acerorhinus* sp. Recently, Giaourtsakis (2022) suggested a possible synonymy between *A. zernowi* and *A. simplex*, and listed as other species of *Acerorhinus*: *A. asiaticus*, *A. ggadzhievi*, *A. belaevi*, *A. eldaricus*, *A. huadeensis*, and with doubts *A.? hipparionus*, *A.? minus* and *A.? xiaoheensis*. In this complex framework, a few considerations must be added concerning some doubtful taxa not discussed elsewhere.

Acerorhinus xiaoheensis from Yuanmou Basin (China) (Gao & Ma, 1997) has been regarded as a junior synonym of *Subchilotherium intermedium* (Deng & Gao, 2006; Lu et al., 2014), while *A. huadeensis* from Huade (Inner Mongolia) (Qiu, 1979) has been assigned to the genus *Persiatherium*, being the sister taxon of *P. rodleri* (Pandolfi, 2016). The latter species, contrary to Giaourtsakis's (2022) proposal, cannot be considered a junior synonym of *Acerorhinus eldaricus* (see below), the Georgian species similar to *A. zernowi*.

Acerorhinus belaevi from Oselivka (Ukraine) (Korotkevich, 1974) resembles *A. simplex* from Crețești 1 in the mandibular features and therefore both species are herein proposed as synonyms, the name *A. simplex* having priority.

Acerorhinus asiaticus from Sebastopol (Borissiak, 1915) is morphologically similar to *A. zernowi*, and considering the cranial material published by Borissiak (1915: fig. 3A, Pl. II, Fig. 2) it is possible to consider the two species as synonyms.

A. ggadzhievi from Eldari (Azerbaijan; Dzhafarov, 1958) is documented by partial mandibles with morphological characters comparable to *A. zernowi*, in particular the presence of a labial cingulum on the premolars and the upraised lower border of the mandible at the level of p2. Based on this similarity, we consider *A. ggadzhievi* a junior synonym of *A. zernowi*.

Aceratherium blanfordi var. *hipparionum* from Yunnan (China) is based on isolated M2 and lower molar (Koken, 1885: Pl. V, figs. 9–10) that do not warrant any discussion about this species, as isolated teeth are poorly suited for taxonomic attribution at specific level in certain aceratheres. Therefore, we consider *Aceratherium hipparionum* as nomen dubium and the holotype is considered as Rhinocerotidae indet. (Table 2).

Aceratherium porpani from Tha Chang (Thailand), has been recently proposed as belonging to *Acerorhinus* (Giaourtsakis, 2022). The material described by Deng et al. (2013) shares several characters with *Acerorhinus*, such as the concave ventral side of the symphysis and the short distance between the orbit and the nasal notch, and an attribution to the latter genus seems more plausible than to *Aceratherium*.

Acerorhinus? minus from Honan (China), described as *Diceratherium palaeosinensis* var. *minus* by Ringström (1924), differs from *A. palaeosinensis* in the smaller size of the occiput and shorter molar row. Both the shape of the occiput and the length of the molar row have been shown to be affected by sexual dimorphism in Rhinocerotidae, for instance in fossil teleoceratines and rhinocerotines (e.g., Mead, 2000; Pandolfi et al., 2025). In the extant *Rhinoceros unicornis*, the main differences between old males and females are at the circumference of the neck, the circumference of the cranium and the width behind the head, implying the presence of larger muscle attachments at the occiput and consequently a larger and higher occiput area (Dinerstein, 1991). Similarly, in the extinct *Chilotherium wimani*, males are characterized, among other characters, by a wider occipital area (indicating massive cranium and robust neck), higher occiput, wider mastoids, greater antero–posterior diameter of the ascending ramus and longer molar row than females (Chen et al., 2010).

The mandible of *A. eldaricus* from Eldari (Georgia) is morphologically similar to the mandible of *A. zernowi* from Sebastopol figured by Borissiak (1914: Pl. VII–figs. 2–3), both specimens sharing a relatively straight ventral profile of the horizontal ramus, upraising in front of p2, and having the posterior border of the symphysis at the level of the anterior side of p3. The morphology of the teeth is also similar in having a marked labial cingulum, a marked mesial–lingual cingulum on the premolars, narrow lingual valleys, wide labial grooves on the molars and a marked ectolophid fold on p2. Accordingly, *A. eldaricus* is here considered a junior synonym of *A. zernowi* (Table 2).

In summary, after the new nomenclatural acts herein proposed, the recognized species of *Acerorhinus* are: *Acerorhinus zernowi*, *Acerorhinus simplex*, *Acerorhinus palaeosinensis, Acerorhinus tsaidamensis*, *Acerorhinus hezhengensis*, *Acerorhinus yuanmouensis, Acerorhinus fuguensis, Acerorhinus lufengensis* and *Acerorhinus neleus*.

Acerorhinus is extremely rare in Romania, having been reported exclusively from the eastern region of the country, and in Moldova. The first report belongs to Trelea and Simionescu (1985), who described and illustrated a left upper cheek tooth referred to "*Aceratherium zernovi* Borissiak, 1915", originating from the Zupăita quarry in Șcheia (Iași Country), a vertebrate locality located in the East–European Platform. According to these authors, the tooth was unearthed from the basalmost portion of the succession in the quarry, from a level of carbonaceous clays of Middle Sarmatian age (Bessarabian). From the overlying layer, with oolitic limestones, a fragment of mandible was initially referred by the authors to "*Hipparion* aff. *platygenis* Gromova 1953", and later reconsidered as *Hipparion sarmaticum* (Lungu, 1984; Lungu et al., 1993), part of the *Hippotherium primigenium* complex (cfr. Vangengeim et al., 2006; Bernor et al., 1996, 2021, 2023). However, we agree with Ionesi et al. (2005) who considered uncertain the levels where these remains originated, as they were found by local people, not by professional geologists. Moreover, shortly after the discovery, Codrea (1996, 2000) reassigned the upper cheek tooth to *Aceratherium incisivum*. Subsequently, Ursachi et al. (2015) mentioned a vertebrate assemblage from Crețești 1 including *Acerorhinus* sp., a report that was reiterated shortly thereafter in some lists, without any detailed description (Ursachi et al., 2016). Accordingly, the described record represents the first well–documented record of *Acerorhinus* in Romania.

Conclusion

The study of a partial cranium with potentially associated mandible and femur from Crețești 1 leads to the first well–documented evidence of the genus *Acerorhinus* in Romania. Through detailed morphological and morphometric comparisons, this material is confidently assigned to *Acerorhinus simplex*. This identification is based on a suite of cranial and dental features that closely resemble the holotype of this species from the Late Miocene Tudora locality (Krokos, 1914), as well as the material from the Moldavian locality of Ciobruciu, previously determined as *Aceratherium incisivum* and then *Acerorhinus* sp. (Athanassiou et al., 2014; Pavlow, 1914) and herein recognized as *A. simplex*.

This new, relatively complete specimen from Romania represents a valuable contribution to the ongoing efforts to revise the taxonomy of this diverse group of hornless rhinoceroses. The performed comparative study allows some new taxonomic proposals concerning species previously assigned to *Acerorhinus*: *A. ggadzhievi*, *A. asiaticus* and *A. eldaricus* are considered synonyms of *A. zernowi*; *Aceratherium blanfordi* var. *hipparionum* is a *nomen dubium*; and *Diceratherium palaeosinense* var. *minus* is considered a female individual of *A. palaeosinensis*.

Despite our conclusions, a comprehensive understanding of the Eurasian *Acerorhinus* still requires a thorough reassessment of all material attributed to the genus and a corresponding phylogenetic analysis, for which further research, integrating the new Romanian material and other well–preserved specimens, is essential to achieve a comprehensive systematic revision. The application of geometric morphometric techniques and 3D scanning would allow a more quantitative assessment of intra– and interspecific variation and facilitate comparisons of fragmentary material. Furthermore, analyses of dental microwear and stable isotopes could shed light on paleoecological aspects such as diet and habitat, placing *Acerorhinus* within the broader environmental context of the Miocene Moldavian Platform. Such work will be instrumental in improving our understanding of the evolutionary patterns, adaptations, and paleobiogeographic distribution of these successful rhinoceroses during the Late Miocene, a period of significant mammalian faunal turnover across Eurasia.

Finally, the Crețești 1 finding highlights the paleontological significance of the "Moldavian Platform" and underscores the potential for future discoveries to further refine our understanding of the regional ancient biodiversity.

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Data availability All data generated during this study are included in this published article.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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