



# A new hornless rhinoceros of the genus *Acerorhinus* (Perissodactyla: Rhinocerotidae) from the Upper Miocene of Kerassiá (Euboea, Greece), with a revision of related forms

by

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With 3 plates, 6 text-figures and 5 tables

## Abstract

The Late Miocene locality of Kerassiá (North Euboea, Greece) has yielded a rich Turolian fauna, which forms part of the Eastern Mediterranean Pliocene biogeographic realm. A prominent specimen of the Kerassiá collection, a well-preserved rhinocerotid skull with associated mandible, is described herein. The specimen demonstrates the diagnostic cranial, mandibular, and dental characters of the genus *Acerorhinus*, but it is distinct enough in several anatomical aspects from the known samples of this genus to justify the establishment of a new species, *A. neleus*. It is characterised by the absence of horns, dolichocephaly, a moderately concave dorsal cranial profile, closely converging parietal crests, a relatively high-positioned orbit, a markedly robust zygomatic arch, a bell-shaped occipital outline, and a robust mandible. Its strong but relatively narrow mandibular symphysis has a short diastema, a concave ventral surface, and bears a pair of moderate-sized second lower incisors suggesting a female individual. The salient features of the upper dentition include a proportionally long premolar section and traces of a thin cement coating on the labial wall of the ectoloph. The upper premolars are characterised by the presence of a faint protocone constriction and a strong lingual cingulum, whereas the upper molars by the absence of lingual cinguli and the presence of a moderate protocone constriction. Clusters of numerous borings on the specimen's surface were attributed to bioerosion induced by dermestid beetle activity. The Kerassiá specimen is closely related to the few known acerotheriine specimens from Pliocene and Chomaterí, which are described and referred to *A. neleus* n. sp. The taxonomic relationships among certain Eurasian acerotheriine samples are discussed and an updated systematic list of the *Acerorhinus* species is provided.

**Keywords:** Rhinocerotidae, Acerotheriinae, *Acerorhinus*, Late Miocene, Turolian, cranial morphology, taxonomy, taphonomy, palaeoecology, Greece

## Zusammenfassung

Die obermiozäne Fundstelle Kerassiá (Nord-Euböa, Griechenland) hat eine reichhaltige turoliche Fauna geliefert, die zum Pliocene-Biom des östlichen Mittelmeerraumes gehört. Hier wird ein besonders wichtiger Fund aus der Kerassiá-Sammlung beschrieben, nämlich ein Nashornschädel mit dem dazugehörigen Unterkiefer. Das Exemplar zeigt die diagnostischen Schädel-, Unterkiefer-, und Zahnmerkmalen der Gattung *Acerorhinus*, unterscheidet sich aber so deutlich in mehreren anatomischen Aspekten von den bisherigen Arten dieser Gattung, dass die Aufstellung einer neuen Art, *A. neleus* n. sp., gerechtfertigt erscheint. Die neue Art ist durch die völlige Hornlosigkeit, Dolichocephalie, ein mäßig konkav dorsales Schädelprofil, die eng konvergierenden Parietalcristae, die relativ hochgestellten Orbitae, die besonders kräftigen Jochbögen, und das glockenförmige Occipitale charakterisiert sowie durch einen

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robusten Unterkiefer. Die kräftige aber relativ schmale Unterkiefersymphyse hat ein kurzes Diastema und eine konkave Ventralseite. Die unteren zweiten Inzisiven sind mittelgroß, was auf ein weibliches Individuum hindeutet. Die obere Zahnreihe besitzt einen verhältnismäßig langen Prämolarenanteil sowie deutliche Spuren einer dünnen Zementablagerung am Ectoloph der Zähne. Die oberen Prämolaren sind durch eine geringe Einschnürung des Protocons und durch die Entwicklung eines starken lingualen Cingulums charakterisiert, während die oberen Molaren durch eine mäßige Protoconeinschnürung und das Fehlen von lingualen Cinguli gekennzeichnet sind. Die zahlreichen Bohrungen auf der Oberfläche des Fundes werden als Bioerosion durch die Aktivität von Dermestid-Käfern erklärt. Der Schädel aus Kerassiá bezieht sich taxonomisch auf entsprechende Funde aus Pikermi und Chomaterí, die erneut beschrieben und *A. neleus* n. sp. zugeordnet werden. Die taxonomischen Beziehungen zwischen europäischen Exemplaren aceratheriiner Nashörner wurden überarbeitet und eine aktualisierte systematische Liste der *Acerorhinus* Arten wird vorgeschlagen.

**Schlüsselwörter:** Rhinocerotidae, Aceratheriinae, *Acerorhinus*, Obermiozän, Turolium, Schädelmorphologie, Taxonomie, Taphonomie, Paläoökologie, Griechenland

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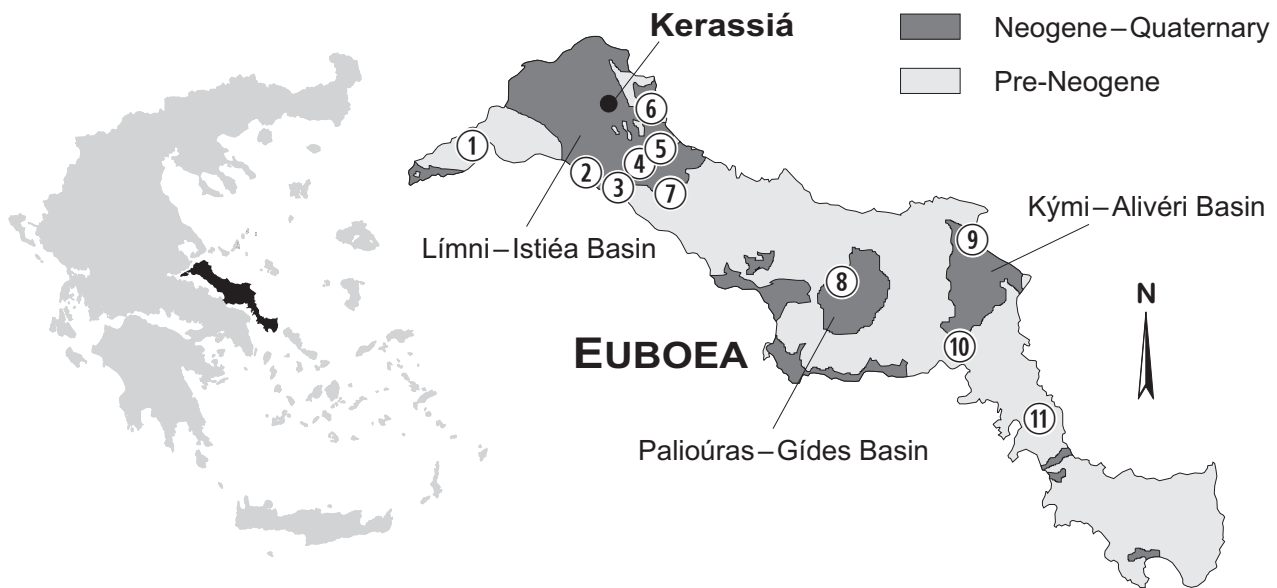
## 1. Introduction

The island of Euboea in Central Greece is prosperous in fossil mammal remains. Palaeontological research on the island during the late 19th – 20th centuries has produced several large mammal localities dated to the Early Miocene – Early Pleistocene, including the well-known locality of Halmyropótamos (Text-fig. 1, CORDELLA 1878, WOODWARD 1901, DEPRAT 1904, MITZOPOULOS 1947, PSARIANOS & THENIUS 1954, MELENTIS 1966, 1970a, 1970b, SCHMIDT-KITTLER 1983). Most of these localities are found on the northern part of the island, which is largely covered by continental Neogene deposits. The high relief contributes to the formation of several outcrops and sections, which facilitates the stratigraphic correlation of the fossiliferous layers, despite the generally thick vegetation cover.

The locality of Kerassiá was discovered in 1982 by a Dutch team led by HANS DE BRUIJN and ALBERT VAN DER MEULEN, during a palaeontological survey on the island. Kerassiá, situated on the Northern part of the island, turned out to be the richest mammal-

bearing locality of the area. The first fossil mammal specimens from the initial 1982 collection were briefly reported by KÖHLER (1983), who stated the presence of *Microstonyx* sp., bovids, giraffids, two species of *Hipparion*, two species of Proboscidea and a large carnivore. In a study on the European Suidae, VAN DER MADE & MOYÀ-SOLÀ (1989) mentioned the occurrence of *Microstonyx major erymanthius*, *Deinotherium* sp. and *Dorcatherium* sp. in Kerassiá, based also on specimens from the initial 1982 collection.

Systematic palaeontological field studies at Kerassiá began in 1992 by the National and Kapodistrian University of Athens (THEODOROU et al. 1995, THEODOROU et al. 2003), revealing a wealth of fossil material. Until now, seven fossil mammal sites have been discovered in the area, dubbed K1 – K7 (ILIOPOULOS 2003a, THEODOROU et al. 2003). The sites are grouped in two main fossiliferous levels, an upper one and a lower one, that have a stratigraphical level difference of about 7 m. The upper fossiliferous level



Text-fig. 1. Simplified geological map of Euboea Island (based on KATSIKATSOS et al. 1981). The Neogene deposits are located in three major sedimentary basins. The locality of Kerassiá is situated in the northern part of the island, in the Límni–Istiéa Basin. The position of other Neogene and Quaternary large mammal-bearing sites is indicated: 1: Aedipsós, 2: Rhoviés, 3: Límni, 4: Palaeóvrissi, 5: Haghía Anna, 6: Achládi, 7: Drázi (also known as Prokópi or Ahmét Agá), 8: Eria, 9: Kalimeriáni, 10: Alivéri, 11: Halmyropótamos.

comprises the sites K1 and K6, and the lower one the sites K2, K3 and K4. In September 2006 a fossiliferous horizon corresponding stratigraphically to the upper level was spotted above K4, but it has not been excavated yet. The relative position of K5 and K7 remains presently unknown. The initial site, where H. DE BRUIJN and A. VAN DER MEULEN excavated in 1982, is most likely the same as K1, but to avoid confusion the material from this collection is dubbed as KER. Additional information about the research history of the locality is provided by THEODOROU et al. (2003) and ILIOPOULOS (2003a).

The fossil fauna of Kerassiá's upper level (sites K1 and K6) comprises *Metailurus parvulus*, ?*Adcrocuta eximia*, *Choerolophodon* sp., *Microstonyx major*, *Palaeotragus rouenii*, *Helladotherium duvernoyi*, *Bohlinia attica*, *Samotherium major*, *Tragoportax* cf. *amalthaea*, *Gazella* sp., *Hipparion* sp., *Ancylotherium* sp., *Amphiorcyteropus* sp. (THEODOROU et al. 2001, THEODOROU et al. 2003, ILIOPOULOS 2003a, ROUSSIAKIS et al. 2006). VAN DER MADE & MOYÀ-SOLÀ (1989) and KOSTOPOULOS et al. (2001) also mention the presence of *Dorcatherium* sp. and *Microstonyx major* respectively from the KER site.

The lower level (sites K2 – K4) has yielded *Adcrocuta eximia*, cf. *Ictitherium pannonicum*, *Plioviver-*

*rops* sp., *Tetralophodon* cf. *longirostris*, *Palaeotragus rouenii*, *Palaeotragus* sp., *Helladotherium duvernoyi*, *Samotherium major*, *Gazella* sp., *Hipparion* sp., *Ceratottherium neumayri*, *Dihoplus pikermiensis*, *Ancylotherium* sp. and *Pavo archiaci* (THEODOROU et al. 2001, THEODOROU et al. 2003, ILIOPOULOS 2003a, GIAOURTSAKIS et al. 2006, ROUSSIAKIS et al. 2006, MICHAILEDIS et al. 2010). Based on the faunal content, the age of both levels is considered as middle Turolian (MN 12), though an early Turolian age cannot be literally rejected (THEODOROU et al. 2003).

## 2. Material and Methods

The material described herein comprises a nearly complete skull with articulated mandible of an adult hornless rhinoceros that was discovered at Kerassiá during the 1996 field season. In a preliminary faunal list of the locality provided by THEODOROU et al. (2003), it was referred to as *Rhinocerotidae* sp. nov. The specimen, labelled K4/119.37, originates from the site K4, which has also yielded remains of the tandem-horned rhinoceros *Dihoplus pikermiensis* (TOULA 1906), (GIAOURTSAKIS et al. 2006).

For the description of the specimen we used standard anatomical terminology (BARONE 1999,

I.C.V.G.A.N. 2005). Where an orientation was involved the alveolar plane was considered as the horizontal one. The dental nomenclature mainly follows PETER (2002, figs 8, 11). The capital letters P and M indicate the upper premolars and molars respectively, while the lowercase letters p and m were used for the corresponding lower cheek teeth. The tooth at the first upper premolar position is conventionally referred to as P1, although it is not literally known whether it is a real premolar (that is a second generation tooth) or a persisting deciduous tooth (D1). The lower incisors are referred to as i2. The premolar/molar series length ratios (abbreviated as L P1 – P4 / L M1 – M3 and L p2 – p4 / L m1 – m3) are expressed as percentages. All measurements are in mm and follow partially the methodology proposed by GUÉRIN (1980); additional measurements are described in the relevant tables. The metrical parameters measured on individual teeth are the mesiodistal (L) and the labio-lingual (W) diameters. The use of parentheses in the

tables denotes inaccurate measurements because of specimen distortion or incomplete preservation. To avoid ambiguities about the cited sources, citations to figures, plates, tables etc. of referenced publications are given in lowercase (e.g. pl. 1, fig.1), while citations to figures etc. of the present paper are given with a capital first letter (e.g. Text-fig. 1, Plate 1, Table 1).

Direct comparative studies with extensive *Ac-ratheriinae* material from several key Eurasian localities, as well as with additional fossil and extant rhinocerotid species, have been conducted at the collections of the following museums and institutes: **AMPG**: Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens; **BSPG**: Bayerische Staatssammlung für Paläontologie und Geologie, München; **HLMD**: Hessisches Landesmuseum, Darmstadt; **IPUW**: Institut für Paläontologie der Universität Wien; **LGPUT**: Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki; **MNHB**: Museum für Naturkunde Humboldt

Table 1. Measurements (in mm) of the Kerassía skull K4/119.37. The numbers in the first column correspond to the measurements used by GUÉRIN (1980, fig. 4).

Kerassía (K4/119.37)		sin.	dext.
–	Mesial end of P1 to occipital condyles	558	552
–	Mesial end of P2 to occipital condyles	535	528
2	Rostral end of nasals to occipital condyles	—	546
3	Rostral end of nasals to nuchal crest		549
14	Rostral end of nasals to the rostral margin of the orbital fossa	187	216
4	Length of the nasal notch	—	131
9	Distance from the distal end of the nasal notch to the rostral margin of the orbital fossa	77	88
–	Rostral end of the orbital fossa to the nuchal crest	390	—
6	Postorbital process to the nuchal crest	314	308
13	Distal end of M3 to occipital condyles	276	279
21	Maximal width at the zygomatic arches		> 272
19	Maximal supraorbital width		> 170
5	Minimal cranial width		90
17	Minimal distance between the parietal crests		25
16	Width at the posttympanic processes	> 188.5	
32	Width at the occipital condyles	> 107	
26	Skull height at P4/M1 level	188	—
27	Skull height at M3 level	201	—
–	Maximal depth of the zygomatic arch	81.6	84.0
23	Height from opisthion to the middle of the nuchal crest		158
31	Transverse diameter of the foramen magnum		(31.6)
–	Height of the foramen magnum		(56.5)

Universität zu Berlin; MNHN: Muséum National d'Histoire Naturelle, Paris; NHML: Natural History Museum, London; NHMW: Naturhistorisches Museum, Wien; RBINS: Royal Belgian Institute of Natural Sciences, Brussels; SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; SMNK: Staatliches Museum für Naturkunde, Karlsruhe; SMNS: Staatliches Museum für Naturkunde, Stuttgart; ZMUC: Zoological Museum of the University of Copenhagen.

### 3. Geological setting

Euboea is the second largest island of Greece, situated off the east coast of Central Greece (Text-fig. 1). It is elongated in a NW-SE direction and is separated from the mainland by a narrow sea channel. The geological basement of its northern part consists of upper Palaeozoic and Mesozoic rocks of the alpine orogen, belonging to the Pelagonian geotectonic zone. The succession includes metaplutonic rocks, Late Permian – Middle Triassic limestones, Middle – Late Triassic volcanoclastic sediments, Late Triassic – Late Jurassic limestones, Late Jurassic radiolarites and Early Cretaceous ophiolites. The series is covered by a marine transgression during the Late Cretaceous. Southern Euboea is mostly metamorphic (marbles and schists), and stratigraphically and geotectonically similar to east Attica and the Cyclades.

Euboea is covered by extensive Neogene deposits, primarily fluviolacustrine, occurring in three major sedimentary basins: the “Alivéri-Kými”, the “Palioúras-Gídes”, and the “Límni-Istiéa” ones (KATSIKATSOS et al. 1981, METTOS et al. 1991), but several minor basins do also exist. These Neogene basins are lithologically homogeneous, implying similar geological history (KATSIKATSOS et al. 1981); they overlay unconformably the Palaeozoic and Mesozoic sedimentary and igneous rocks. The Neogene is also characterised by sporadic volcanic activity, mainly in the central part of the island.

The Neogene sediments of the Kerassiá area are part of the Límni-Istiéa Basin. The deposits of this basin are divided in two sequences, a lower and an upper one (KATSIKATSOS et al. 1981, METTOS et al. 1991). The lower sequence, as well as the ophiolitic basement, are exposed NE of the village Kerassiá. The upper sequence covers a wide area north of Kerassiá and comprises the fossiliferous sites. The bone-bearing layers are reddish-brown fluvial deposits that include a succession of clays, conglomerates, sands and silt-

stones. They exhibit a dip of about 10–15° to the south. The fossils are found in the more fine-grained, clayey or clayey-silty deposits. Additional information about the geology and stratigraphy of the locality is provided by KATSIKATSOS et al. (1981), METTOS et al. (1991) and THEODOROU et al. (2003).

### 4. Taphonomy

The studied cranial specimen is part of the larger fossil assemblage of the site K4, consisting mainly of hipparion and antelope dental and postcranial material. No postcranial elements from the same individual were identified at close vicinity. The K4/119.37 parts, skull and mandible, were found articulated lying on their right side (Plate 1, Fig. 1). The specimen shows no sign of abrasion or breakage, preserving fragile parts, as the nasals, the tusks and the paroccipital processes. This implies either that the specimen has not suffered any substantial transport from the death site, or that it was transported soon after death, when the skin, muscles, and ligaments remained mostly still in place. The absence of any other skeletal parts of the same individual supports the latter option, as does the general taphonomical setting of the site, which suggests a low energy water current as the accumulating agent of the bones (ILIOPOULOS 2003a).

Previous taphonomic studies have documented microscopic bioerosional damage (microbial focal destruction) in many sampled bones from the Kerassiá sites, due to post-mortem bacterial activity (ILIOPOULOS 2003a, 2003b, 2004). The K4/119.37 offers additional data about the post-mortem biological activity at the locality, as it is extensively perforated by deep borings of circular or elliptical shape. The borings measure about 1–2 cm in diameter (Plate 1, Fig. 2); a more precise measurement is not possible, as their margins are poorly preserved and in many cases they have apparently collapsed. The borings do not occur exclusively to a particular area of the specimen, though they are more frequent at places where the bone is less dense (orbits, temporal and occipital areas), while they are absent from the mandible, the zygomatic arches and the right maxilla. In certain areas, as at the supraorbital processes, the orbital fossa and the occipital surface, the bioerosion is more extensive; the borings apparently join together and form wide pits. The detailed morphology of these structures cannot be appreciated due to the generally fragile condition of the specimen.

Several insect taxa are known to infest and create traces on cadaver bones in terrestrial environments: tineid moths, certain termites, polymitarcyid ephemeropters and beetles (dermestids, silphids and hispterids) (ROBERTS et al. 2007, WEST & HASIOTIS 2007, BRITT et al. 2008). These insects produce a variety of bone modification features, such as surface trails, grooves, tunnels, subcortical cavities, borings, pits etc. Large-sized circular or elliptical borings are associated with the activity of the dermestid beetles, necrophagus insects which bore into decaying carcasses to build pupation chambers for their larvae. The dermestid traces generally have diameters less than 10 mm, but borings as wide as 28 mm are also reported (BRITT et al. 2008, tab. 1). The morphology of the Kerassiá borings, though not observable in detail, is consistent with dermestid beetle activity. Dermestids usually infest cadavers in one or two weeks after death, when the tissues are already desiccated, and their life cycle lasts about 45 days (MARTIN & WEST 1995). Thus the presence of pupation chambers in the studied skull indicates open-air exposure of at least two months.

Another taphonomic indication is the presence of longitudinal cracks on the labial side of the left mandibular corpus (Plate 2, Fig. 2a), which are attributed to weathering. Such cracks are absent from the right corpus (Plate 2, Fig. 2b), which is consistent with the fact that the specimen was found lying on its right side. The heavily fragmented cranial surfaces exhibit instead a mosaic cracking pattern, which may be partly attributed to weathering, but most likely is the result of diagenetic processes. Apart from the mandible, weathering cracks have been also observed on other bone specimens from K4 (ILIOPOULOS 2003a). Their morphology is generally consistent with 'weathering stage 1' (according to actualistic studies of BEHRENSMEYER 1978), which indicates a fairly long-time open-air exposure of several months up to two years.

Both taphonomic observations, i.e. the presence of dermestid traces and weathering cracks, imply that K4/119.37 remained unburied for several months, but preserved enough connective tissue to keep the mandible articulated to the skull until the final burial. The burial itself happened without any appreciable transport of the specimen, as evidenced by the retained anatomical association of its parts and the preservation of fragile elements. Insect trace preservation is a rare encounter in the mammal fossil record, as the rapid burial of a carcass is a prerequisite for increased

fossilisation probability. Dermestid trace fossils were unknown until now in the fossil record of Greece and the fauna of Kerassiá presents the first taphonomic evidence of such an insect activity in the region.

## 5. Systematics

Order Perissodactyla OWEN, 1848

Family Rhinocerotidae GRAY, 1821

Subfamily Aceratheriinae DOLLO, 1885

Genus *Acerorhinus* KRETZOI, 1942

*Acerorhinus neleus* n. sp.

- 1862–1867 *Acerotherium?* – GAUDRY, p. 211, pl. XXXIII, fig. 6.  
 1973 *Aceratherium* sp. – MARINOS & SYMEONIDIS, p. 165.  
 1975 *Diceros* aff. *pachygnathus* – MARINOS & SYMEONIDIS, pl. VI, fig. 2.  
 1975 *Aceratherium* sp. – MARINOS & SYMEONIDIS, p. 8, pl. X.  
 2003 Rhinocerotidae sp. nov. – THEODOROU et al., p. 528.

**Holotype:** K4/119.37, skull with articulated mandible (Plates 1, 2). AMPG collection, currently on display at the local Fossil Mammal Museum of Kerassiá (Northern Euboea).

**Etymology:** Neleus is the name of the main stream that flows in the area of Kerassiá.

**Type locality:** Kerassiá, site K4.

**Stratigraphy:** Upper sequence of the Límni-Istiéa Basin (Upper Miocene, Turolian).

**Diagnosis:** A large-sized *Acerorhinus* with narrow dolichocephalic skull, short hornless nasals, moderately concave cranial profile, closely converging parietal crests, rostrally deep zygomatic arch, and bell-shaped occipital outline; mandibular symphysis narrow and ventrally concave, with very short diastema; mandibular corpus deep; low and robust mandibular ramus with short coronoid process; long premolar series, though proportionally shorter than in most other *Acerorhinus* species; cheek teeth with thin cement coating; upper premolars with continuous lingual cingulum, faint protocone constriction, no crista, and weak paracone fold; upper molars with moderate protocone constriction and antecrochet, no crista, and marked paracone fold; lower premolars with continuous crenulated labial cingulum.

## 5.1 Description

### 5.1.1 Skull

The skull is almost completely preserved; however, it is somewhat laterally compressed, skewed relatively to the sagittal plane, and bears numerous fractures. Moreover, it has undergone damage due to post-mortem biological activity (see Section 4). These resulted in the lack of its rostral part anteriorly of P2, of the left nasal rostral end, of a part of the nuchal crest, of the right paroccipital process, as well as of both supraorbital processes.

In lateral view (Plate 1, Fig. 3a, b), the dorsal profile of the skull is moderately concave. The free end of the nasals was, however, broken at its base and turned downwards during the burial, reducing the impression of the profile concavity. The nasals are short and bear no trace of rugosities that would indicate the presence of a horn during life; the internasal suture remains open. Their rostral end is narrow and does not extend beyond the P2. The nasal notch is angular; it terminates at a level above the distal half of P4. There is no conspicuous facial crest. The infraorbital foramen opens above the mesial root of P4, very close to the ventral margin of the nasal notch. The orbit is located high in the skull and slightly rostrally; its anterior margin is above the mesial root of M2. There is a lacrimal tubercle, preserved in the left orbital fossa, as well as two lacrimal foramina. The suprorbital processes of the frontal bone are incompletely preserved, but must have been well developed, as it can be deduced by the frontal morphology. A postorbital process of the frontal bone is present. A small process is present on the zygomatic arch. The latter is deep and strong, particularly at its rostral part; it is deepest above M3, becoming much thinner caudally. Its rostralmost part is moderately steep and fades out above the M1/M2 contact; its ventral margin is positioned 35 mm above the alveolar level. The postglenoid and posttympanic processes are in contact but not fused to each other. The latter extends up to the lower level of the occipital condyle, while the postglenoid and the paroccipital ones are much longer. The postglenoid and the posttympanic processes are perpendicular to the alveolar plane, whereas the paroccipital one is directed slightly caudally.

The parietal crests converge closely to one another, but remain separate without forming a sagittal crest (Plate 2, Fig. 1a). Caudally, they curve posterolaterally into the nuchal crest. In dorsal view, the nuchal crest is

straight, without a median notch. The occipital plane is inclined slightly rostrally (considering the alveolar plane as the horizontal one) (Plate 1, Fig. 3a, b). In caudal view the outline of the occipital face is bell shaped (Plate 1, Fig. 3c). The squamous occipital fossa is moderately concave. The area above the foramen magnum is damaged and incompletely preserved but markedly convex, suggesting the presence of a well-developed nuchal tubercle. The foramen magnum is ovate, higher than wide, but its shape is distorted because of lateral compression.

In ventral view (Plate 2, Fig. 1b), the rostral margin of the choanae is pointed and terminates at the level of the mesial part of M3. The pterygoid processes are bifid. The body of the basioccipital bone is smooth, without a sagittal crest. The intercondylar notch is V-shaped and the condyles are widely separated.

### 5.1.2 Mandible

The mandible is completely preserved, though slightly distorted and laterally compressed, as the skull (Plate 2, Fig. 2a–d). The mandibular corpus is deep; its depth remains fairly constant from p3 to m3. The corpus' ventral margin is nearly straight (with a weak inflation under m2, observed only on the right side) but bends abruptly below p2, forming with the symphysis an angle of about 140°. The symphysis is robust, without appreciable median constriction (its minimum and maximum widths differ by less than 6% – Table 2) and extends caudally to the level of the middle of p3. Its width is maximal at the i2 alveoli. Prominent bilateral ridges run along the interalveolar (i2 – p2) margins; the lingual (dorsal) surface of the symphysis in-between them is concave. The diastema is very short (Plate 2, Fig. 2d, Table 2). The labial (ventral) surface of the symphysis is transversely concave. The rostral margin between the second lower incisors is incompletely preserved; however, a small structure on the left side resembling a tooth socket possibly corresponds to a diminutive i1 alveolus.

In lateral view (Plate 2, Fig. 2a, b), the mental foramen is situated below the mesial root of p3. The mandibular angle is particularly strong and extends caudally beyond the articular condyle. On its lateral side, its ventral margin forms a prominent crest (masseteric tuberosity), which demarcates the ventrolateral border of the deep masseteric fossa. The latter extends rostrally to the level of m3. There is no marginal crest developed on the medial side of the mandibular angle; however, two small but prominent tubercles are

Table 2. Measurements (in mm) of the Kerassía mandible K4/119.37. The numbers in the first column correspond to the measurements used by GUÉRIN (1980, fig. 4).

Kerassía (K4/119.37)		sin.	dext.
1	Total length	542	550
16	Maximal height (at coronoid process)	–	271.4
15	Height at articular condyle	238.5	224
–	Minimal ramus height (at the lowest point between coronoid process and condyle)	213	207.5
–	Maximal length of the ramus (at condyle level)	156	153
–	Minimal length of the ramus (below the condyle)	135	133
–	Length of diastema (i2–p2) at alveole	(35.5)	43.2
–	Maximal width of symphysis (at i2 level)		89.2
–	Minimal width of symphysis		84.2
–	Width at the bilateral interalveolar ridges of diastema		45.8
–	Width at the base of i2 (lateral, at enamel base)		85.2
–	Width between i2 (at enamel base)		42.3
11	Symphyseal length (measured ventrally)		129
–	Symphyseal depth (perpendicular to the alveolar level)		99
14	Articular condyle width	104.7	102.8
3	Corpus height at p2/p3 level	81	83
5	Corpus height at p4/m1 level	(84.7)	91.8
8	Corpus height behind m3	103.5	104.0

formed: the first one is placed ventromedially, below the coronoid process, while the second one is located posteromedially, under the articular condyle and slightly above the alveolar level. These tuberosities may have served as attachments for the medial pterygoid muscle. The temporal fossa is deep and bears a single, triangular-shaped mandibular foramen located at the alveolar level.

The mandibular ramus is low, and forms a right angle with the corpus. The articular condyle is transversely elongated and slopes medially. Its dorsal surface is transversely weakly concave, without marked constriction. The coronoid process is short and rostrocaudally wide; its rostral margin is almost vertical; its apex is rounded and turns caudally, forming a concave caudal margin. The mandibular notch is U-shaped, wide and shallow.

### 5.1.3 Upper dentition

The studied specimen preserves all cheek teeth (P1 – M3) of both sides. The teeth of the left side are better preserved, apart from M3 which is better preserved on the right side. The premolar series (including P1) measures 150.5 mm (left side), while the molar series is longer, measuring 159.8 and 157.7 mm (left and right

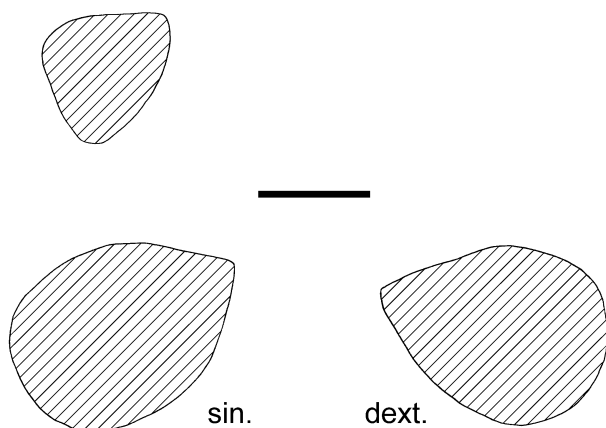
side respectively). The premolar series (Plate 1, Fig. 4a) is rather long relative to the molar one (L P1 – P4 / L M1 – M3 = 94%, L P2 – P4 / L M1 – M3 = 84%). Detailed measurements are given in Table 3. In all cheek teeth a thin layer of cement is observed on the labial side of the ectolophs, especially near the crown bases. The enamel surface is weakly wrinkled and the occlusal pattern is simple. The protolophs and metalophs of P2 – M2 are parallel to each other and slightly oblique in relation to the ectolophs. There are weak labial cingular traces in all upper teeth except for P1, mostly restricted at the base of the metacone. The labial wall of P2 – M3 bears a moderately developed paracone fold; otherwise it is smooth. The metaloph is directed almost perpendicularly to the sagittal plane.

The first cheek tooth, P1 (presumably a persisting D1), is subtriangular and mesiolingually open, due to the absence of the protoloph. The P2 – P4 are characterised by the presence of a strong continuous lingual cingulum which also extends to the mesial and distal sides of these teeth. The mesial and distal protocone grooves are faint and the antecrochet is weakly expressed. The lingual face of the faintly constricted protocone is flat or slightly concave, while the hypocone is rounded and not constricted. The medifossette is



closed in P2 and P3, whereas in the less worn P4 the crochet is in contact, but not yet fused, with the lingual wall of the ectoloph. A crista is not developed in any premolar. The medial valley is narrow and open lingually in P3 and P4; in P2 it is closed by the fusion of the protocone and the hypocone, due to the more advanced wear stage of this tooth in relation to the other premolars. The postfossette is deep and bordered distally by the cingulum; a hypostyle is not present. The parastyle is relatively wide and flat. The paracone fold is weak in P2, but strengthens gradually in P3 and P4. Distally to the paracone fold the labial wall is essentially flat, without a metacone fold.

Contrary to the P2 – P4, the molars (Plate 1, Fig. 4b) do not possess a lingual cingulum, but only a mesial and distal one. The medial valley is open almost till the base of the crown. The labial wall has the same morphology with that of the premolars; merely the paracone fold becomes increasingly prominent towards M3. The protocone is moderately constricted in all molars; its lingual wall is rounded, but flattens towards its base. The antecrochet is weak to moderate. The crochet is well developed; it is directed parallel to the sagittal plane in M1 – M2, whereas in M3 it is rather oblique and double. As in the case of the premolars a crista is absent and the postfossette morphology is quite similar. The hypocone is rounded and less robust than the protocone. The M3 is triangular, featuring a continuous ectometaloph.



Text-fig. 2. Cross sections of the Kerassiá mandibular tusks (left and right i2s): the large sections were taken at the enamel base, while the smaller section at 35 mm above the enamel base (10 mm below the crown apex). The labial side is at the top. Graphical scale: 10 mm.

#### 5.1.4 Lower dentition

The lower dentition (Plate 2, Fig. 2a–d) is characterised by the presence of two moderately developed incisors (i2). No other incisors are preserved in the specimen. However, the presence of i1s in the living individual is quite possible as indicated by a poorly preserved alveolus-like structure. The i2s are sub-triangular in cross section and divergent. They present a crest mesially, while their labial faces are rounded (Text-fig. 2). Their lengths along their labial side are 48.5 and 46.9 mm (left and right respectively). They are separated from the premolars by a short diastema. All lower cheek teeth have thin cement deposits on their labial side. The premolar/molar length ratio ( $L\ p2 - p4 / L\ m1 - m3$ ) is 77%. Detailed measurements are given in Table 4.

The premolars are characterised by the presence of a crenulated continuous labial cingulum; on the lingual side cingular traces are variably present at the entrances of the trigonid valleys. All premolars possess a well-defined labial groove, except in the reduced p2 where it is rather weak. The paralophid is less developed than the metalophid and the hypolophid. In occlusal view, the lophids are directed distolingually, especially the metalophids. The mesial valleys in p3 – p4 are narrower and less deep than the distal ones; in p2 the mesial valley is open, due to the underdevelopment of the paralophid. The p3 – p4 mesial valleys are V-shaped in lingual, as well as in occlusal view. The distal valleys are rounded in occlusal view and V-shaped in lingual view. The hypoconid exhibits a weak constriction.

The labial cingulum of the molars is less developed in comparison to that of the premolars, discontinuous and variably distributed; it is generally restricted to their mesial and distal parts. The molars bear a proportionally larger trigonid with respect to the premolars. In m2 there is a weak entoconid constriction. The mesial valley is narrower than the distal one.

## 6. Comparisons

The subfamily Aceratheriinae DOLLO, 1885, constitutes a diverse extinct clade of Rhinocerotidae which comprises mostly hornless rhinoceroses. The Late Miocene Eurasian representatives include the nominal genus *Aceratherium* KAUP, 1832, together with the related genera *Alicornops* GINSBURG & GUÉRIN, 1979, and *Hoploaceratherium* GINSBURG & HEISSIG, 1989,

as well as another distinct group, the mainly Asian chilotheres: *Chilotherium* RINGSTRÖM, 1924, *Shansirhinus* KRETZOI, 1942, and *Acerorhinus* KRETZOI, 1942. These two groups appear to have been biogeographically distinct during the Late Miocene: the aceratheriine assemblages of Central and Western Europe are characterised by the former group of genera, whereas those of the Eastern Mediterranean region, the peri-Pontic region, and the Asian faunas are dominated by the latter one (HEISSIG 1996, 1999).

### 6.1 Comparison with related aceratheriine genera

*Aceratherium* is well known from several European localities. Its type species *Aceratherium incisivum* KAUP, 1832 is based on two skulls from Eppelsheim, Germany (KAUP 1832, 1834) (however, there are still some complications regarding the formal definition of this species; GIAOURTSAKIS & HEISSIG 2004). Exceptionally complete skeletons of *A. incisivum* have been excavated at the Vallesian locality of Höwenegg (SW Germany) and described in detail by HÜNERMANN (1989), though the associated skulls are fragmentarily preserved and dorsoventrally compressed. In comparison to K4/119.37 the skulls of *A. incisivum* from Eppelsheim and Höwenegg are smaller and more slender rostrally. The mandible is slenderer, its corpus tapers rostrally and the ramus is proportionally higher. The symphysis is rostroventrally flattened or slightly convex, unlike the markedly concave ventral face in-between the incisors observed in K4/119.37. This feature also constitutes one of the main diagnostic differences between the rest of the aceratheriine genera on the one hand and *Acerorhinus* plus *Chilotherium* on the other. In spite of the marked cranial and mandibular differences, the dentition of *A. incisivum* does not differentiate essentially in morphology with respect to Kerassía; *A. incisivum* has also similar dental segment proportions, though it is dimensionally smaller.

*Chilotherium* is a common Asian genus described in detail by RINGSTRÖM (1924), who provides a list of diagnostic characters. Its essentially flat frontoparietal region with widely separated parietal crests and a trapezium-shaped occipital surface are quite unlike the morphology of K4/119.37. Other aspects of the skull, such as the relative positions of the orbit and the nasal notch are, though, very similar. The *Chilotherium* mandible exhibits a markedly broad symphysis with strongly diverging tusks (a notable autapomorphy of this genus), contrary to the much narrower

symphyseal region of the Kerassía specimen and all other samples referred to *Acerorhinus*. The moderate protocone constriction of the K4/119.37 molars contrasts with the strong constriction and well-developed antecrochet of *Chilotherium*.

The genus *Shansirhinus* is primarily characterised by the complex enamel plications in the upper teeth, resulting in multiple folds around the medifossette, the formation of a lingual bridge uniting the proto-loph and metaloph on the premolars and the strong protocone constriction. The genus has been recently revised by DENG (2005a), who described a skull and a mandible of *Sh. ringstroemi* KRETZOI, 1942. Apart from its peculiar dental morphology, the skull of *Shansirhinus* differs from the Kerassía specimen in several characters that include: smaller total length, stronger nasals that are constricted in their base and bear a roughened tuberosity at their tips, presence of a facial crest, rather stronger zygomatic arch, and longer paroccipital processes. The mandible was reportedly associated to the skull, but their upper and lower third molars present totally different eruptional and wear stages. Compared to K4/119.37, it is more slender, with longer and notably wider symphysis, which is only slightly upturned.

The main characters of the Kerassía specimen – short hornless nasals, concave dorsal cranial profile, bell-shaped occipital, closely convergent parietal crests, narrow mandibular symphysis with concave ventral face, weak antecrochet, faint protocone constriction on the premolars, moderate protocone constriction on the molars – are consistent with those of *Acerorhinus* (KRETZOI 1942, QIU et al. 1988, HEISSIG 1999), and K4/119.37 is attributed to this genus. *Acerorhinus*, as a genus name, was erected by KRETZOI (1942) for the species *Aceratherium zernowi* BORISSIAK, 1914. KRETZOI's genus remained unused for many years, till HEISSIG (1975) utilised this name at a different rank (as a subgenus of *Chilotherium*) while preliminary studying aceratheriine material from Turkey. The usage of the name at generic rank was re-established in more recent publications (e.g. QIU et al. 1988, CERDEÑO 1996, HEISSIG 1996, DENG 2000). *Acerorhinus* has been reported from several localities in Eastern Europe and Asia, as Hezheng, Wangdaifuliang, Tung-gur (China), Yulafli, Sinap Tepe (Turkey), Sebastopol (Ukraine), Ciobruciu (Moldova) and Kalimantsi (Bulgaria) (QIU et al. 1988, CERDEÑO 1996, DENG 2000, KAYA & HEISSIG 2001, FORTELIUS et al. 2003, GERAADS &

SPASSOV 2009). HEISSIG (1996, 1999) and GIAOURTSAKIS (2003, 2009) suggested its presence in Greece, at Pikermi and Pentálophos, but the available material was until now rather inadequate for detailed comparisons. The completeness of the Kerassiá specimen enables a more accurate taxonomic evaluation of *Acerorhinus* in Greece and adjacent regions.

## 6.2 Comparison with *Acerorhinus* species

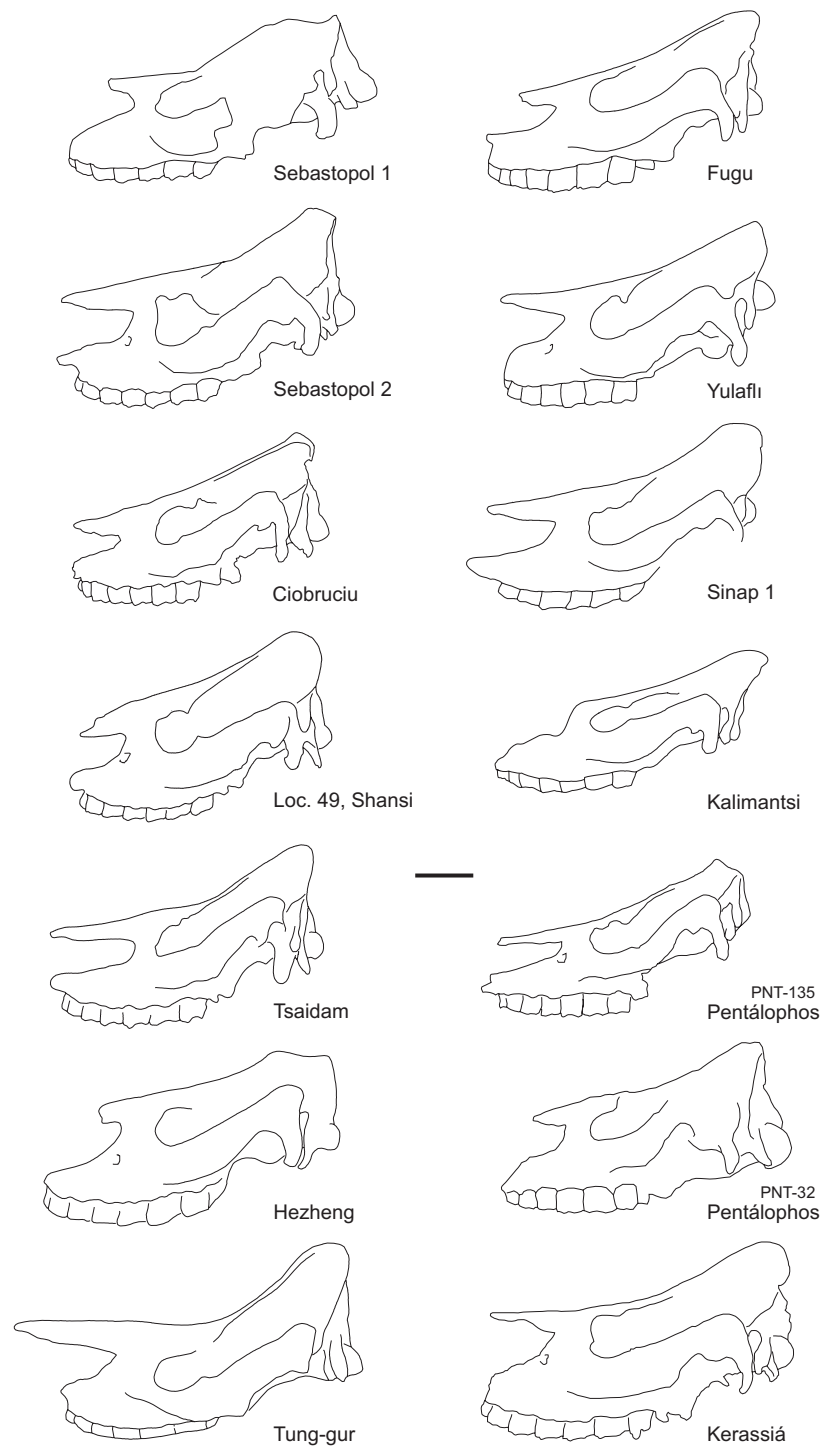
### 6.2.1 The type material and adjacent peri-Pontic samples

The genus *Acerorhinus* comprises several species throughout its palaeobiogeographic area. Its type species was erected as *Aceratherium zernowi* by BORISSIAK (1914), based on an almost complete skull with associated mandible and several other remains from the renowned Vallesian locality of Sebastopol in Ukraine. The type skull of *A. zernowi* (BORISSIAK 1914, pl. 6, fig. 1, pl. 7, figs 1, 2) exhibits a concave dorsal profile, a deep nasal notch (above the P4/M1 contact), a highly placed orbital fossa (in case the skull is not deformed), a deep temporal process at the zygomatic bone, an occiput with bell-shaped outline in caudal view, a slightly rostrally inclined occipital plane, and a rather short and caudally directed paroccipital process. In dorsal view, the parietal crests are almost in contact caudally, but they diverge strongly rostrally. The upper dentition is characterised by the development of strong cingulum on the premolars, and the presence of a well-developed antecrochet on P3 and P4, which closes the entrance of the mediusinus valley at a moderate stage of wear. The ratio  $L P2 - P4 / L M1 - M3$  is about 91% (based on BORISSIAK 1914, pl. VII, fig. 1a). The type mandible (BORISSIAK 1914, pl. VII, fig. 2) has an almost straight ventral margin and a relatively short and narrow symphysis, which bends moderately upwards. The depth of the mandibular corpus increases gradually towards m3. The ratio  $L p2 - p4 / L m1 - m3$  is about 81% (based on BORISSIAK 1914, pl. VII, fig. 2a).

In his second contribution on the Sebastopol fauna, BORISSIAK (1915) attributed several well-preserved cranial specimens to *A. zernowi*, which though were collected from a different site than the type material. Three additional skulls, figured by BORISSIAK (1915, figs 1–3), appear rostrocaudally shorter than the type specimen: judging from the single length measurement provided by BORISSIAK (1914, p. 137, 1915, p. 37) and the figures, the length between P1

and the occipital condyles of the holotype skull measures about 550 mm, while the three later skulls range from 470 to 500 mm. They are also deeper in the orbitofrontal region with respect to the type skull (unless the latter is distorted). Furthermore, their nasal notch is less deep and their orbital fossae appear less elevated with respect to the frontal level. Their upper dentitions (BORISSIAK 1915, pl. II) lack the more markedly expressed antecrochet observed on the P3 and P4 of the type specimen, a feature which might be though considered as idiosyncratic.

The skull from Kerassiá is similar to the type specimen of *A. zernowi* considering the deep temporal process on the zygomatic arc, the narrow praeorbital bar, the deep nasal notch, the slightly forward inclined occiput with bell-shaped outline, as well as the same configuration of the postglenoid, posttympanic, and paroccipital processes. These similarities are further shared with the three additional skulls figured subsequently by BORISSIAK (1915). However, K4/119.37 differs from the Sebastopol type skull by its absolutely and relatively longer tooththrow (ca. 22–27%, 304 mm vs. 240–250 mm), although the size of the skull is essentially the same, the less converging parietal crests, and the smoother lateral profile of the maxilla. Compared to the second Sebastopol sample (BORISSIAK 1915), K4/119.37 is larger and more dolichocephalic: as it can be judged by BORISSIAK's figures and measurements, the specimen from Kerassiá is proportionally longer in relation to its width and depth (Text-fig. 3). The upper dentition of K4/119.37 features an absolutely longer but proportionally shorter premolar series than all specimens described by BORISSIAK (1914, 1915). Morphologically, the main dental features are quite similar in all specimens, variably expressed at different ontogenetic stages. K4/119.37 resembles to some extent the dentitions figured by BORISSIAK (1915), since the antecrochet in P3 and P4 is less marked with respect to the type specimen of *A. zernowi*, indicating that the mediusinus valley would have remained longer open above the lingual cingulum. The mandible from Kerassiá differs from the type of *A. zernowi* by its markedly shorter diastema, the more abruptly upraised symphysis, and the deeper mandibular corpus that does not taper rostrally (Text-fig. 4). Further, the ventral margin of the Sebastopol specimen ascends shortly after the level of m3 towards the mandibular angle, implying a rostrocaudally shorter mandibular ramus, in marked contrast to K4/119.37. Overall, the type mandible of *A. zernowi*



Text-fig. 3. Comparative morphology of cranial specimens from several Late Miocene Eurasian localities, which are discussed in the text. The drawings are aligned according to the rostral margin of the orbit and are based on photographs and metrical data published by BORISSIAK (1914, 1915), PAVLOW (1914), RINGSTRÖM (1924), BOHLIN (1937), QIU et al. (1988), CERDEÑO (1996), DENG (2000), KAYA & HEISSIG (2001), FORTELIUS et al. (2003), GERAADS & SPASSOV (2009) and GERAADS & KOUFOS (1990). Sebastopol 1 and 2 refer to the two Sebastopol sites of BORISSIAK (1914) and BORISSIAK (1915) respectively. The broken and displaced nasals of the Kerassía skull are restored to their supposed original position. Note the considerable morphological and metrical variation among the figured specimens, particularly in the nasal and frontal areas, the development of the nuchal crest, the cranial depth and the overall size (despite any possible perspective differences, as well as distortions because of imperfect preservation). Graphical scale: 10 cm.

exhibits a more slender appearance, despite the fact that it belongs to a male individual, as deduced by its large-sized second lower incisors.

Almost concurrently with BORISSIAK (1914, 1915), two other studies have been published, comprising significant specimens from the northern peri-Pontic region with presumable *Acerorhinus* affinities. KROKOS (1914) erected *Aceratherium simplex* based on a partial skull from the locality of Tudora (also known as Tudorowo), whereas PAVLOW (1914) described as *Aceratherium incisivum* a rich sample from the nearby locality of Ciobruciu (also known as Tchobroutschi, Ciubărciu, or Cioburciu). Both localities were discovered on the right bank of the Dniester River, at the Ștefan Vodă district of the modern Republic of Moldova. The continental deposits with *Hipparion* faunas from Ciobruciu and Tudora are attributed to the local strata of Cahul and their geological age is firmly recognised as Maeotian (LUNGU & DELINSCHI 2006, DELINSCHI 2009, LUNGU & RZEBIK-KOWALSKA 2011), which ranges roughly from the late Vallesian to the middle Turolian (for relevant stratigraphic calibrations and discussions compare STEININGER et al. 1996, STEININGER 1999, VANGENGEM & TESAKOV 2008a, 2008b).

The holotype skull of *A. simplex* is severely compressed and deformed, obscuring the detailed observation of its morphological features. The illustration provided by KROKOS (1914, pl. XLI, fig. 1) shows a very robust zygomatic arch, at least at its rostral part, which seems to be deeper than the corresponding element of the Kerassiá specimen, as well as seemingly less converging parietal crests. The few assessable cranial measurements provided by KROKOS (1914) are comparable or somewhat smaller with respect to K4/119.37. On the contrary, the total length of the toothrow of the Moldavian specimen, reported as 240 mm, is significantly smaller, indicating a reduced dental series with respect to the skull's total length. Judging from KROKOS (1914, pl. XLI, fig. 3), the Tudora specimen has also a proportionally shorter premolar section. The dental features of the premolars are rather similar to that of K4/119.37, expressed at a later stage of wear. The main differences in the molars of the Moldavian specimen include the more pronounced protocone constriction and the more prominent crochet, which forms a closed medifossette. In the molars of K4/119.37, the medifossette is open and the crochet remains distinct till the very base of the crown. Originally, KROKOS (1914) differentiated *A.*

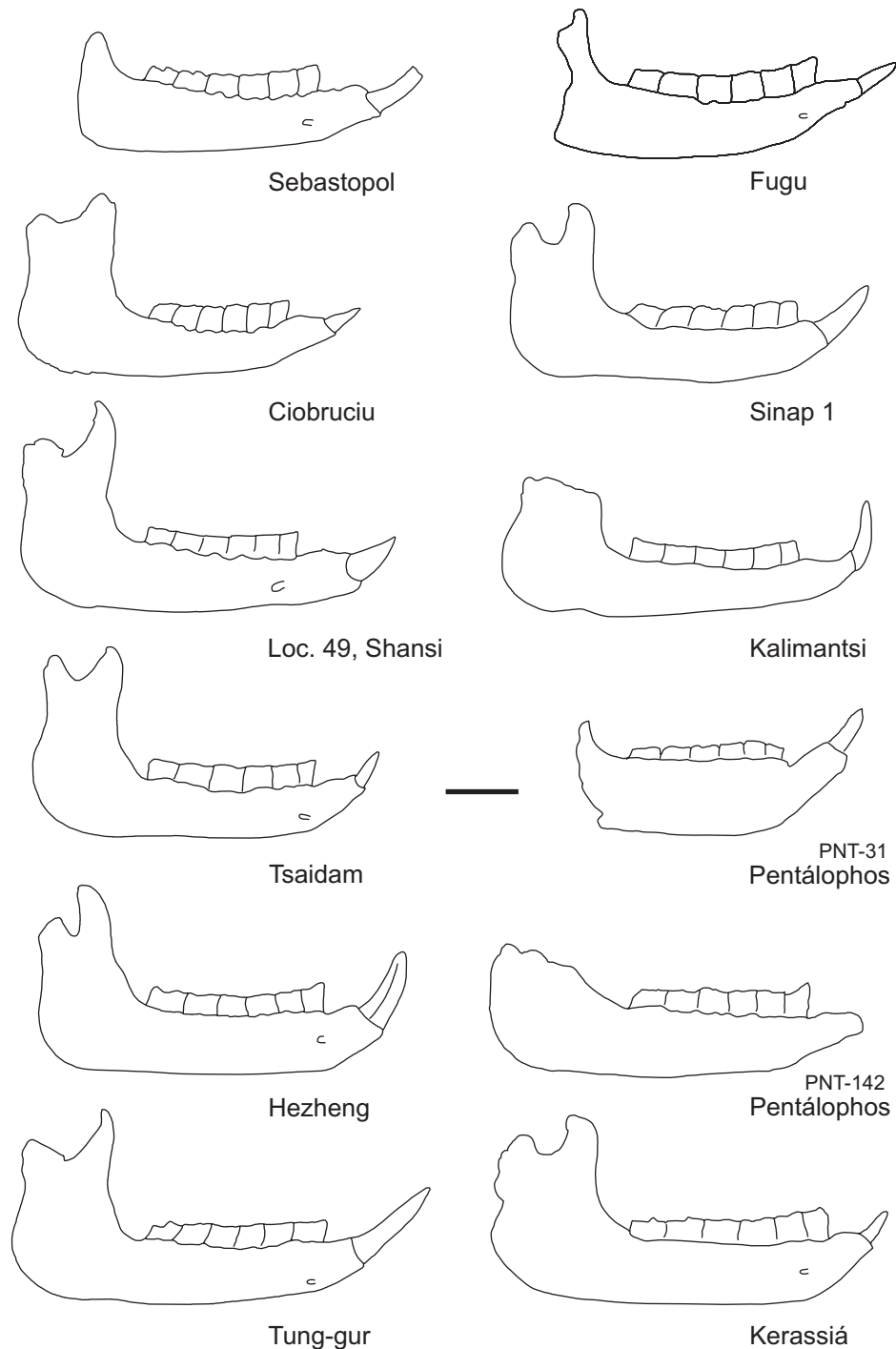
*simplex* from *A. zernowi* based on a few dental features, considering primarily that the former is lacking completely a crochet. However, a prominent crochet is present in the teeth of *A. simplex*, but was apparently misapprehended, due to its partial or complete fusion with the ectoloph caused by the quite advanced stage of occlusal wear. In the less worn P4, the crochet is well visible; its tip is fused mesially with the lingual wall of the metacone, forming a closed medifossette that is filled with sediment. In M1, both the crochet and the medifossette are obliterated, due to the more advanced stage of wear, while in the slightly less worn M2 only a remnant of the medifossette remains visible (KROKOS 1914, pl. XLI, fig. 2).

During the same year, PAVLOW (1914) referred to *Aceratherium incisivum* a rich aceratheriine sample from the nearby Moldavian locality of Ciobruciu, which included several well-preserved cranial, mandibular, and postcranial specimens. Five more or less complete skulls were reported, which belong to aged individuals. The best preserved specimen, a senile skull with associated mandible (PAVLOW 1914, pl. V, figs 1a–c, 2), is morphologically similar to the Sebastopol ones in several aspects (short nasal notch, narrow cranial roof, rostrally-inclined occipital plane), but it differs in its dorsal cranial profile, which is apparently almost straight, as well as in its shorter nasals. The specimen from Kerassiá differs from the Ciobruciu one in being significantly larger and featuring a concave dorsal cranial profile; in further morphological aspects the skull from Kerassiá exhibits the same differences with respect to the Ciobruciu sample, as when compared to the second sample from Sebastopol (BORISSIAK 1915). Concerning the mandible, the figured adult specimen from Ciobruciu, which belongs to a male individual (PAVLOW 1914, pl. V, fig. 1c), differs significantly from the Kerassiá one by its smaller size, the longer diastema, the less upturned symphysis, the less straight ventral margin, and the proportionally higher mandibular ramus (compare the relevant outlines in Text-fig. 4).

The initial attribution of the Ciobruciu material to *Aceratherium incisivum* by PAVLOW (1914) seems reasonable, since she only had the opportunity to compare it on the one hand with samples that are presently attributed to *Chilotherium* (primarily with *Ch. kowalevskii* from Grebeniki, but also with *Ch. schlosseri* from Samos, and *Ch. persiae* from Maragheh), and on the other hand with the figured specimens of *Aceratherium incisivum* (KAUP 1834, 1854) from the

renowned German Vallesian locality of Eppelsheim. Thus, not taking into account the almost simultaneously published contributions of BORISSIAK (1914,

1915) and KROKOS (1914), an attribution to *Aceratherium incisivum* was apparently the more rational choice at that time, due to the marked differences with



Text-fig. 4. Comparative morphology of mandibular specimens from several Late Miocene Eurasian localities, which are discussed in the text. The drawings are aligned according to the caudal margin of the dentition and are based on photographs and metrical data published by BORISSIAK (1914, 1915), PAVLOW (1914), RINGSTRÖM (1924), BOHLIN (1937), QIU et al. (1988), CERDEÑO (1996), DENG (2000), GERAADS & SPASSOV (2009) and GERAADS & KOUFOS (1990). The Sinap drawing is based on an unpublished photograph kindly provided by DENIS GERAADS. Note the variation in robustness, ramus shape and proportions, ventral margin shape and inclination of the symphysis. Graphical scale: 10 cm.

respect to the other chilothere (*sensu stricto*) species. However, the Ciobruciu skull is fairly stout rostrally, unlike *Aceratherium*, and less dolichocephalic than the latter (HÜNERMANN 1989, GIAOURTSAKIS & HEISSIG 2004). Recently published opinions on the Ciobruciu sample did not conclude about its generic attribution; it is referred to *Acerorhinus* by QIU et al. (1988) and FORTELIUS et al. (2003), but excluded from this genus by CERDEÑO (1996), while GERAADS & SPASSOV (2009) regarded its characters as being perhaps closer to *Aceratherium incisivum*. Based on the comparison above we agree with its assignment to *Acerorhinus*, though this should be corroborated by a detailed evaluation of key features undocumented by PAVLOW (1914), such as the ventral surface of the mandibular symphysis. The rather modest cranial and dental differences observed between the material from Tudora and Ciobruciu on one side, and the Sevastopol samples on the other, may justify a local specific or sub-specific evolutionary lineage in the northern peri-Pontic region from the Sarmatian *A. zernowi* to the Maeotian *A. simplex*, though direct comparisons would be further required to firmly support this hypothesis.

Partially studied or unpublished specimens referred to as *Aceratherium* in the faunal lists from other Maeotian sites of Moldova such as Taraclia, Gura Galbenă, and Cimişlia, as well as from stratigraphically older late Sarmatian sites such as Calfa, Varniţa and Căinari may also represent *Acerorhinus* or *Chilotherium* (SIMIONESCU 1940, LUNGU 2008, DELINSCHI 2009, LUNGU & RZEBIK-KOWALSKA 2011). The same seems to be true for some neighbouring Late Miocene localities from Romania (CODREA 1996, CODREA et al. 2011), as well as for other prominent *Hipparion* fauna localities discovered close to the Black Sea coast of Ukraine (ALEXEJEW 1916, KOROTKEVICH 1988, KRAKHMALNAYA 1996, 2001, 2008). In several localities of the northern peri-Pontic region, the aceratheriine specimens are readily referable to *Chilotherium*, especially those comprising ample material such as Grebeniki (PAVLOW 1913, KROKOS 1917) and Berislav (KOROTKEVICH 1958a, 1958b, 1970), where the hypodigms of *Ch. kowalevskii* and *Ch. sarmaticum* have been respectively described. A partial skull from an unknown locality in the region of Odessa, originally described as *Teleoceras ponticus* by NIEZABITOWSKI (1912, 1914) and later referred to as *Aceratherium schlosseri* by KIERNIK (1914), belongs also to *Chilotherium*, as already argued by RINGSTRÖM (1924).

### 6.2.2 Chinese samples

The Asiatic fossil record has yielded several hornless rhinocerotid specimens, which have been attributed to *Acerorhinus*. RINGSTRÖM (1924) described an aceratheriine skull and mandible from Loc. 49, Shansi, China, which he assigned to a new species, *Diceratherium palaeosinense*. The specimen belongs to a male individual, as deduced by its large mandibular tusks. It features many characters of *Acerorhinus* (bell-shaped occipital, onion-shaped foramen magnum, closely convergent parietal crests, constricted nasal base, unplicated upper premolars lacking significant protocone constrictions, upper molars with moderate ones, narrow mandibular symphysis with concave ventral face) and was evidently transferred to this genus following the subsequent amendments by HEISSIG (1975) and QIU et al. (1988) on the initial misconceptions regarding the “Chinese diceratheres”. The skull of *A. palaeosinensis* is smaller and less dolichocephalic than K4/119.37, with the nasal notch and the orbit placed more rostrally (Text-fig. 3). The upper border of the zygomatic arch is almost straight, featuring a more prominent postorbital process. The paroccipital process reaches the level of the postglenoid one, unlike K4/119.37. The nuchal crest is wider and thicker. The upper premolar series is longer than the molar one (QIU et al. 1988, Text-fig. 5), resulting in a higher L P1–P4 / L M1–M3 ratio of 102%. The mandible of *A. palaeosinensis* differs markedly from K4/119.37 by its nearly horizontal symphysis, the significantly longer diastema, the proportionally much higher ramus, and the long and pointed coronoid processes (RINGSTRÖM 1924, pl. X; see also Text-fig. 4).

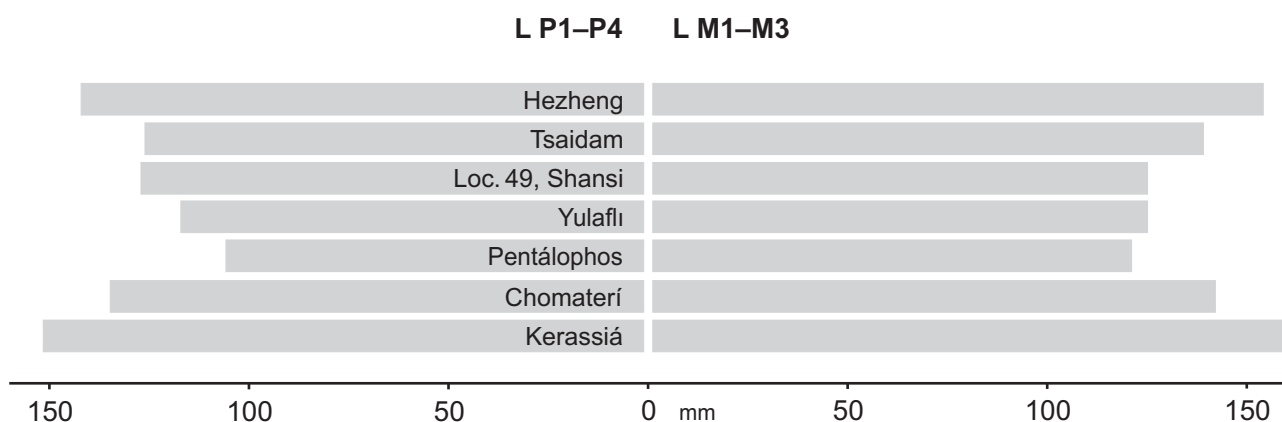
An aceratheriine sample from Tsaidam, China, studied by BOHLIN (1937), was also initially referred to as a new diceratheres species: *Diceratherium tsaidamense* BOHLIN, 1937. The available cranial material comprises a complete skull and mandible (No. 503, belonging to a partial skeleton) and a damaged skull (No. 504) with clear *Acerorhinus* affinities, such as the dorsally gently concave cranial profile with very closely convergent parietal crests, and the narrow mandibular symphysis with a ventrally concave surface. The best preserved specimen (No. 503, BOHLIN 1937, pl. VII–VIII) differs from the Kerassiá one by its smaller dimensions, the longer nasals, the much deeper nasal notch, the presence of a marked notch at the middle of the nuchal crest, the shorter posttympanic and longer paroccipital processes, the proportionally longer mandibular diastema, the higher and less robust mandibu-

lar ramus, and the more prominent coronoid process (Text-figs 3, 4). The dentitions though are very similar morphologically and proportionally (L P1 – P4 / L M1 – M3 ranges from 91% to 94% according to QIU et al. 1988; see also Text-fig. 5), but the Chinese specimens have shorter tooththrows, and more prominent protocone constriction in the molars. According to measurements provided by QIU et al. (1988), the damaged skull from Tsaidam No. 504 is larger than No. 503 and comparable to that of Kerassiá, though its dentition is smaller with respect to latter.

QIU & YAN (1982) described an incompletely preserved skull with complete dentition from the Late Miocene locality of Hanchiawa in Yushe (Shansi, China), which they referred to a new species, *Chilotherium (Acerorhinus) cornutum*. Apart from some distinctive cranial features, such as the short uplifted nasals that bear a small roughened tuberosity at their tips (QIU & YAN 1982, figs 1, 4, pl. II), its upper dentition exhibits several derived features, such as the markedly constricted protocone and hypocone in both molars and premolars, and the prominent antecrochet fusing with the hypocone in the premolars (QIU & YAN 1982, fig. 5, pl. I), which are characteristic of the recently revised genus *Shansirhinus* (DENG 2005a, p. 310–311). Concurrently with QIU & YAN (1982), ZHENG (1982) described another new species as *Chilotherium (Acerorhinus) tianzhuense*, based on a maxillary fragment with P2 – M2 and some isolated teeth from the Late Miocene locality of Songshan in Tianzhu (Gansu, China). The derived dental characters of the Tianzhu specimens (ZHENG 1982, pl. I, figs 5, 6) are similar to those of the Hanchiawa skull, a

fact also underlined by the author, who noted that they could be conspecific. We agree with DENG (2005a) that both *Chilotherium (Acerorhinus) cornutum* and *Chilotherium (Acerorhinus) tianzhuense* must be included within the genus *Shansirhinus*.

QIU et al. (1988) described a well-preserved skull with associated mandible from the Upper Miocene (MN 10 or MN 11) of Hezheng (Gansu, China), which they referred to a new species, *Acerorhinus hezhengensis*. The skull is of similar size to K4/119.37, but it has relatively longer praeorbital part (Text-fig. 3). Additionally, it differs from the Kerassiá specimen in the following characters: It has much more elongated posttympanic processes that extend till the ventral level of the postglenoid ones, while its paroccipital processes are situated more medially in relation to the posttympanic ones. The parietal crests are more widely separated and less curved. The dorsocaudal angle of the zygomatic arch is acute. The upper dentition is slightly smaller in total length and proportionally similar (Text-fig. 5). The M1 and M2 exhibit stronger protocone constriction, as well as a hypocone constriction. The ventral margin of the mandibular corpus is straight, quite similar to that of Kerassiá. Nevertheless, the mandibular ramus extends much higher above the alveolar level and it is rostrocaudally shorter in relation to its height. The coronoid process is also more prominent and is separated from the articular condyle by a narrower mandibular notch (Text-fig. 4). The p2 has a lingual cingulum, unlike K4/119.37. No description is provided by QIU et al. (1988) for the rest of the lower teeth. However, they appear to possess a much deeper labial groove compared to Kerassiá



Text-fig. 5. Comparative graph of the upper premolar and molar series dimensions. Own data and according to QIU et al. (1988), KAYA & HEISSIG (2001) and GERAADS & KOUFOS (1990). The data for Pentálophos refer to the specimen PNT-135, which is referred here to *Chilotherium*.



(QIU et al. 1988, pl. II, fig. 3). Metrically, the pre-molar-to-molar ratio is slightly lower than in K4/119.37, while the p3 and p4 appear markedly wide relatively to their length.

CERDEÑO (1996) referred to *A. zernowi* several well-preserved specimens from the Middle Miocene of the Tung-gur Formation, Inner Mongolia, China. These specimens exhibit some differences with respect to the typical sample of *A. zernowi* from Sebastopol (BORISSIAK 1914, pl. VI, fig. 1, pl. VII, figs 1a, 2), which led GERAADS & SPASSOV (2009) to regard them as distantly related to this species. The nasal bones are markedly longer and upturned, the nasal notch is less retracted (reaching the P3/P4 level), and the zygomatic arch is rostrally more slender (CERDEÑO 1996, figs 2A, 3A). The Kerassiá specimen differs from the Tung-gur skulls primarily by the significantly shorter nasals, the less concave dorsal profile, and the shape of the zygomatic arch, which is more robust rostrally and not caudally (Text-fig. 3). Further, the Kerassiá mandible possesses a narrower symphysis with shorter diastema and ventrally concave (not flat) surface, a much lower ramus, a wide (not V-shaped) mandibular notch, and a shorter coronoid process with rounded (not pointed) apex (at least when compared to AMNH-26215, CERDEÑO 1996, fig. 3B; see also Text-fig. 4). The configuration of the latter characters is not known in the type material of *A. zernowi* from Sebastopol (BORISSIAK 1914).

GAO & MA (1997) described the new species *Acerorhinus xiaoheensis* based on material discovered from the Late Miocene deposits of the Yuanmou Basin, China. The most salient cranial feature is the long and narrow nasal bones, which rise strongly upwards resulting to a markedly concave dorsal profile. The Kerassiá specimen differs from the Yuanmou material by the significantly shorter nasals and the less concave dorsal profile. In this aspect, the Yuanmou material exhibits some resemblance with the skull AMNH-26215 from Tung-gur described by CERDEÑO (1996), as also suggested by DENG (2000). According to DENG (2000), another species described from the same deposits of the Yuanmou Basin, *Acerorhinus yuanmouensis* ZONG, 1998, is a junior synonym of *A. xiaoheensis*.

DENG (2000) erected the species *Acerorhinus fuguensis* based on cranial and mandibular material from the latest Miocene of Wangdaifuliang (Fugu, Shaanxi, China). Compared to the Kerassiá specimen, the skull of *A. fuguensis* (DENG 2000, pl. 1, figs 1, 2, pl. 2, fig. 1)

is slightly smaller. In dorsal view, the nasal region in front of the orbits narrows abruptly, while in lateral view the nasal notch extends more caudally, at the level of M1 (Text-fig. 3). The occipital plane of *A. fuguensis* appears to be more vertically oriented than in Kerassiá, and the nuchal crest is notably notched (V-shaped) in dorsal view (DENG 2000, pl. 2, fig. 1). The paroccipital process is ventrally directed, not caudoventrally as in Kerassiá. There is no postorbital process in the zygomatic arch. The median valleys of P2 – P4 are wider than in Kerassiá, while P2, and in lesser degree P3, are characterised by the larger-sized hypocone relative to the protocone. The protocone of M1 is more constricted and has a larger antecrochet that almost closes its median valley. The mandible of *A. fuguensis* differs from K4/119.37 by its markedly convex ventral margin and the rostrally tapering mandibular corpus (much deeper behind m3 than at the p2/p3 level), which bends smoothly towards the symphyseal area (DENG 2000, pl. 2, fig. 3; see also Text-fig. 4). The symphysis is less upturned and narrower than in Kerassiá, and has a relatively longer diastema. Based on the figure provided by DENG (2000, pl. 1, fig. 3) the ratio  $L\ p2 - p4 / L\ m1 - m3$  is estimated to be about 80%, slightly larger than that of the Kerassiá specimen (77%). *Acerorhinus fuguensis* shares several notable cranial characters with *A. tsaidamensis*, including the presence of a sagittal crest, the markedly notched nuchal crest, and the prominent bilateral occipital crests, as well as a similar zygomatic morphology, relative positions of the orbit and the nasal notch. It differs from the latter in some mandibular features as the smoother ventral profile of the mandibular corpus and the less constricted symphysis.

DENG (2009) described recently the new species *Acerorhinus lufengensis*, based on a set of associated maxillary teeth and several isolated ones from the Late Miocene locality of Shihuiba in Lufeng (Yunnan, China). The holotype shows some dental characters that are atypical for the genus *Acerorhinus*, such as the presence of strong paracone and metacone folds in P3, and the faintly constricted protocone with virtually absent antecrochet in all molars (DENG 2009, fig. 1). In *Acerorhinus* the paracone fold is weakly developed, whereas the metacone fold is absent, and the molars feature at least a moderately constricted protocone with a notable antecrochet. Consequently we consider its assignment to *Acerorhinus* questionable.

### 6.2.3 Turkish and Bulgarian samples

The presence of *Acerorhinus* in Turkey was initially reported by HEISSIG (1975), in a short account on the Anatolian fossil faunas discovered during the joint German-Turkish expedition (SICKENBERG et al. 1975). In this preliminary report a phylogenetic, biostratigraphic and biogeographic scheme concerning the rhinocerotids is presented (HEISSIG 1975, tabs 6–8) without specimen descriptions. An extensive manuscript on these findings has been prepared but remains yet unpublished (HEISSIG pers. com. 2010). During the last decade additional material originating from Turkish localities has though been described.

KAYA & HEISSIG (2001) described a complete skull from Yulaflı (NW Turkey) as *Aceratherium incisivum*. The find is morphologically very close to *Acerorhinus* and in our opinion it is referable to this genus. The Yulaflı specimen is very similar to K4/119.37 in the relative position of the nasal notch and the orbit, the shortness of the nasals, the apparent absence of a marked facial crest, the robustness of the zygomatic arch, the unindented nuchal crest, the premolar/molar ratio, and the occlusal morphology of the cheek teeth. It differs, though, from the latter in being smaller and rather deeper in relation to its length: comparing the measurements and figures provided by KAYA & HEISSIG (2001, tab. 1, fig. 3), the two skulls have about the same height but the Kerassía one is 13% longer (see also Text-fig. 3). Moreover, its dental series is 29% longer than that from Yulaflı (Text-fig. 5), that is K4/119.37 has proportionally larger teeth in relation to its cranial dimensions (it should be noted, nonetheless, that the Yulaflı specimen belongs to a more aged individual). KAYA & HEISSIG (2001) referred to *A. zernowi* some fragmentary mandibular specimens from the same locality, but their incomplete preservation does not allow for any meaningful comparison with the corresponding Kerassía specimen. The locality of Yulaflı was initially considered as Turolian by KAYA & HEISSIG (2001), but its age has been recently revised to Vallesian (MN10), based on a more detailed faunal study (GERAADS et al. 2005).

FORTELIUS et al. (2003) referred to *A. zernowi* various remains from the Vallesian sites of Sinap Tepe in central Turkey. The best preserved specimen, a complete skull with associated mandible, from Sinap Loc. 1 (FORTELIUS et al. 2003, fig. 12.2) differs from both the Sebastopol and the Kerassía specimens mainly by its slenderer rostral part of the maxilla, slender zygomatic arch, and its shortened caudal part with the

postglenoid process very close to the occipital face in lateral view (Text-fig. 3). Furthermore, the orbit is positioned relatively more caudally, plausibly because of the shortened caudal part. Based on photographs kindly provided by DENIS GERAADS (pers. comm. 2010), this specimen's dentitions have relatively longer premolar sections than Kerassía. The upper molars have more constricted protocones, well-defined antecrochets and enlarged hypocones compared to the K4 skull. The mandible is slenderer than the Kerassía one, has a higher ramus and a smaller p2 (Text-fig. 4), but is similar to it in the very short and narrow symphysis.

A well-preserved skull from Upper Kavakdere (early Turolian) in Turkey was referred to as *Acerorhinus* sp. nov. by FORTELIUS et al. (2003, fig. 12.5). The specimen features a deep zygomatic arch, which remains robust in its caudal part unlike K4/119.37. The nasal notch seems to be deeper than in Kerassía, and the paroccipital processes are also more elongated (longer than the postglenoid ones). The teeth, with their folded enamel pattern, the markedly constricted protocone and hypocone in both molars and premolars, and the prominent antecrochet fusing with the hypocone in the premolars, are clearly different in morphology from both *A. zernowi* and the Kerassía samples and might indicate a closer taxonomic affinity with *Shansirhinus* (GIAOURTSAKIS 2009).

GERAADS & SPASSOV (2009) referred to *Acerorhinus* sp. various remains from the middle Turolian of Kalimantsi in Bulgaria. A probably deformed skull from Kalimantsi (K-595, GERAADS & SPASSOV 2009, pl. 2, figs A–C) is metrically smaller than the Kerassía specimen and, contrary to the latter, it features a sagittal crest and a caudally inclined occipital surface (Text-fig. 3). The relative positions of the nasal notch and the rostral margin of the orbit are similar in both specimens. Its upper toothrow is smaller in size than in the Kerassía specimen and the premolar-to-molar ratio (L P2 – P4 / L M1 – M3) is considerably higher (97% vs. 84%). Morphologically, though, they are quite similar, the K-595 presenting a stronger protocone constriction on P3, P4 and M1.

GERAADS & SPASSOV (2009, pl. 2, figs D, E) also referred a mandible from Kalimantsi-1 (K-608) to *Acerorhinus* sp. Its stratigraphic level is lower than that of the rest material from Kalimantsi and it is dated to the early Turolian (GERAADS & SPASSOV 2009). Although this specimen presumably belongs to a male individual, it has a markedly slenderer corpus than the Kerassía specimen (Text-fig. 4). The symphysis differs

from that of K4/119.37 by being almost horizontal and bearing strongly curved incisors. K-608 also has smaller cheek teeth and a proportionally somewhat longer premolar section (its premolar-to-molar ratio is 84%, vs. 77% in Kerassiá).

#### 6.2.4 *Acerorhinus* from Greek localities

Rhinocerotid findings with *Acerorhinus* affinities have been already noted from Greece (HEISSIG 1996, 1999, GIAOURTSAKIS 2003, 2009). The partially preserved mandible PIK-957 (MNHN) from Pikermi (Plate 3, Fig. 3), originally described by GAUDRY (1862–1867, pl. XXXIII, fig. 6) as *Acerotherium?* belongs to a male individual, as deduced by the size of its incisors. Its mandibular corpus' and symphyseal morphology (i.e. ventral margin, mandibular depth and symphyseal inclination and robusticity) is very similar to that of K4/119.37. The incisors, though stronger (maximum diameter of about 39 mm), present the same occlusal and cross-sectional morphology. The partially preserved cheek teeth do not differentiate from the Kerassiá ones, though PIK-957 has slightly stronger cinguli in m1 and m2. As far as the teeth of PIK-957 can be measured, the two specimens divert in terms of absolute dental dimensions, PIK-957 being about 15% – 17% smaller than K4/119.37 in pre-

molar and total toothrow length respectively and almost 19% in molar length (Table 4). The Pikermi specimen has also a slightly proportionally longer premolar section: an estimation of its premolar/molar ratio is 80%. Two slender metapodials described by GAUDRY (1862–1867, p. 214, pl. XXXIII, figs 4, 5) as belonging to a small rhinoceros have also *Acerorhinus* morphology.

A fragmentary skull from Chomaterí (AMPG 1992, originally unnumbered) was figured, but not described, by MARINOS & SYMEONIDIS (1975, p. 26, pl. VI, fig. 2), who referred it to *Diceros* aff. *pachygnathus*. It lacks the postorbital part, but the praeorbital and nasal regions, as well as the dentition, are adequately preserved. Its morphological characters are similar to those of the Kerassiá skull: the distal end of the nasal notch lies above the middle of P4; there are two infraorbital foramina, the larger one opening above the P3/P4 contact; the rostral margin of the orbit is situated above the M1/M2 contact and bears a lacrimal tubercle; the rostral part of the zygomatic arch is deep; the rostralmost part of the zygomatic arch is situated above the mesial root of M2; the rostral margin of the choanae is pointed and terminates at the level of the M2/M3 contact. The dentition of both sides is well preserved, except for the right P1,

Table 3. Upper teeth measurements (in mm) of the *Acerorhinus neleus* n. sp. skulls from Kerassiá and Chomaterí, compared to the skull PNT-135 from Pentálophos, which is referred here to *Chilotherium*.

	Kerassiá (K4/119.37)				Chomaterí (AMPG 1992)				Pentálophos (PNT-135)		
	sin.		dext.		sin.		dext.		L	sin.	W
	L	W	L	W	L	W	L	W			
P1	24.1	20.8	25.1	–	25.5	23.3	–	–	20.2		19.4
P2	42.2	46.6	45.1	51.3	39.4	44.5	39.4	42.0	29.1		33.3
P3	49.0	58.4	49.9	56.6	45.2	53.6	44.9	52.6	33.9		47.7
P4	51.1	60.5	49.6	–	46.1	56.0	45.4	55.2	35.1		48.6
M1	57.9	57.5	58.7	56.7	52.0	54.7	53.4	56.3	40.0		52.0
M2	60.8	61.6	60.5	58.8	53.8	55.8	53.8	54.2	43.5		48.8
M3	48.5	53.4	48.7	53.8	38.5	49.7	–	–	41.6		44.6
L P1–M3	304.0		–		262.5		–				230
L P2–M3	285.0		–		242.5		–				213.7
L P1–P4	150.5		–		133.7		–				104.7
L P2–P4	134.4		–		119.4		118.9				92.7
L M1–M3	159.8		(157.7)		141.0		–				120
L P1–P4 / L M1–M3	94 %		–		95 %		–				87 %
L P2–P4 / L M1–M3	84 %		–		85 %		–				77 %

which is lacking. The specimen is figured by MARINOS & SYMEONIDIS (1975, pl. VI, fig. 2) without M3s; however, the missing teeth (left M3 and labial part of the right M3) were found recently in the Chomaterí collection and restored in place (Plate 3, Fig. 1b). Morphologically the Kerassiá and Chomaterí upper dentitions are practically identical, exhibiting very similar labial and lingual walls, as well as occlusal pattern. As it is the case with the Pikermi specimen, the Chomaterí dentition is metrically somewhat smaller compared to K4/119.37, but the dental segment proportions are strikingly similar in both specimens (Table 3, Text-fig. 5).

The fragmentary mandible from Chomaterí (AMPG 19Π/1972), referred by MARINOS & SYMEONIDIS (1973) and MARINOS & SYMEONIDIS (1975, pl. X) to *Aceratherium* sp., preserves the left p3 – p4 and the right p4 – m3 (Plate 3, Fig. 2a, b). It belongs to a male individual, as deduced by the large diameter of its incisors' roots. This mandible and the above mentioned skull AMPG 1992 quite obviously belong to the same individual, as it can be inferred by the very good occlusion of their dentitions, the identical wear stage, and the equivalent state of preservation. The specimen from Chomaterí is ontogenetically some-

what older than the Kerassiá one, since its teeth are slightly more worn. The caudal margin of the symphysis is situated at the level of the distal half of p3. Its partly preserved dentition has smaller dimensions than K4/119.37. Relatively to the molar series the premolars are only slightly larger than in the Kerassiá specimen ( $L\ p3 - p4 / L\ m1 - m3 = 59\%$  and  $56\%$  respectively, Table 4). The dentition of the Chomaterí mandible is morphologically very similar to Kerassiá, as well. Only the premolars have a weaker paralophid, resulting in a less developed mesial valley, while their distal valleys open slightly higher in the crown. The molars are morphologically indistinguishable from the Kerassiá specimen.

GERAADS & KOUFOS (1990) described a vari-form aceratheriine sample from the Vallesian locality of Pentálophos, Macedonia, Greece, which they referred collectively to a new species, *Aceratherium kiliasi*. The sample comprises several cranial and mandibular specimens. The skull PNT-135 (GERAADS & KOUFOS 1990, pl. 2, figs 1–2, pl. 3, fig. 4), designated as the holotype of this species, is lacking most part of the right side and the occipital region, and it is skewed relative to the sagittal plane. The specimen shares only a few minor characters with K4/119.37, as the retract-

Table 4. Lower teeth measurements (in mm) of the mandibles from Kerassiá, Chomaterí and Pikermi. The i2 diameters were taken at the enamel base (in the case of i2s, L and W refer to the maximum and minimum diameters respectively).

	Kerassiá (K4/119.37)				Chomaterí (AMPG 1992)				Pikermi (PIK-957)			
	sin.		dext.		sin.		dext.		sin.		dext.	
	L	W	L	W	L	W	L	W	L	W	L	W
i2	23.4	17.1	22.0	17.5	–	–	–	–	–	–	(39)	(33)
p2	36.5	22.9	37.5	23.8	–	–	–	–	(32)	21.1	–	–
p3	43.5	30.0	43.2	31.6	40.2	28.0	–	–	41.2	–	–	–
p4	46.3	32.4	–	–	41.8	31.5	–	31.7	(42)	31.8	41.5	32.0
m1	52.1	30.9	51.3	31.0	–	–	48.2	30.8	–	–	–	–
m2	54.3	32.6	53.0	31.9	–	–	46.4	31.2	–	–	45.4	28.0
m3	49.4	27.5	48.9	28.5	–	–	45.4	27.4	44.0	27.1	43.5	26.8
L p2–m3	281.3		–		–		–		(233)		–	
L p2–p4	122.5		–		–		–		(104)		–	
L p3–p4	88.6		–		80.3		–		78.1		–	
L m1–m3	159.5		155.6		–		135.1		129.3		131.2	
L p2–p4 / L m1–m3	77 %		–		–		–		80 %		–	
L p3–p4 / L m1–m3	56 %		–		59 %*		–		60 %		–	

\* Calculated combining dental section measurements from both sides.

ed nasal notch and the rather high-positioned orbit, but differs clearly from it by its considerably smaller size, the flattened cranial roof and the more slender zygomatic arch (Text-fig. 3). Further, its premolar section is absolutely and proportionally shorter with respect to Kerassiá, as well as to all other *Acerorhinus* species (Table 3, Text-fig. 5), primarily due to an apparent size reduction of the second premolar. The dental morphology of PNT-135 cannot be easily assessed, because of the advanced stage of wear; still, the P2 demonstrates a notable abbreviation of its protoloph, while the somewhat less worn molars exhibit a more prominent antecrochet, a flattened ectoloph wall, and a squarish protocone (at least in M2), which are clearly different from the dental features described in the Kerassiá specimen. In fact, the dentition of PNT-135 shows close resemblance with that of the type specimen of *Aceratherium samium* (WEBER 1905, pl. IX, fig. 5), a species described from Samos, which was later revised and included in *Chilotherium* by RINGSTRÖM (1924) and HEISSIG (1975, 1996). Both specimens share the notable size reduction of the P2, resulting from the diminution of its protoloph. Functionally this exhibits a tendency towards a loph configuration that mimics the one of the already diminutive P1. Further, the M2s of both specimens have in common the squarish protocone, as well as an identical ectoloph profile with a flattened labial wall. Apart from the dental evidence, the marked cranial differences between PNT-135 and K4/119.37 described above refer indeed to significant characters that bring together "*Aceratherium*" *kiliasi* and *Chilotherium samium* (WEBER 1905, pl. X, figs 1–2).

In the same publication, GERAADS & KOUFOS (1990) referred two more skulls from Pentálophos to *A. kiliasi*, PNT-32 and PNT-122. Both are incomplete, especially the latter whose state of preservation does not allow detailed comparisons. PNT-32 is quite similar to the specimen from Kerassiá in several aspects, such as the short, though somewhat less retracted nasal notch, the high-placed orbit, the concave dorsal profile, the similar configuration of the processes at the periotic region, and the nearly bell-shaped occipital outline. In addition, most of these characters differentiate PNT-32 from PNT-135, the holotype of *A. kiliasi*, and signify its closer affinities to the genus *Acerorhinus*. PNT-32 differs from K4/119.37 by its less robust zygomatic arch, as well as by the wider and stouter nuchal crest. The incompletely preserved cheek teeth of PNT-32 lack their lingual parts. Their

labial walls, particularly in the molars, are characterised by the presence of a marked paracone fold, similar to Kerassiá and in contrast to PNT-135.

The evident differences between the holotype of *A. kiliasi* PNT-135 and the skull PNT-32 demonstrate the presence of two distinct aceratheriine taxa in the Pentálophos fauna, with *Chilotherium* and *Acerorhinus* affinities respectively. This taxonomic interpretation of the Pentálophos aceratheriine sample is further strengthened by the examination and re-evaluation of the mandibular specimens from the same locality. GERAADS & KOUFOS (1990) evaluated the symphyseal morphology of the Pentálophos mandibles with respect to *Aceratherium* (narrow symphysis, with flattened or slightly convex ventral face) and *Chilotherium* (wide symphysis, with concave ventral face), but not with *Acerorhinus* (narrow symphysis, with concave ventral face). All mandibles from Pentálophos feature a ventrally concave symphyseal surface at its rostral half, in-between the incisors' alveoli. This is a prominent character shared by *Acerorhinus* and *Chilotherium*, supporting thus further the inferred absence of *Aceratherium* sensu stricto in Pentálophos.

The mandible PNT-142 is characterised by a notably narrow mandibular symphysis, with a rostrally concave ventral surface in-between the alveoli of the second lower incisors (GERAADS & KOUFOS 1990, pl. 3, fig. 2), as in the Kerassiá specimen K4/119.37. Further, both specimens feature a straight ventral border and a comparable overall size. However, PNT-142 has a longer diastema, a less inclined symphysis, and a proportionally longer premolar series ( $L\ p2 - p4 / L\ m1 - m3 = 87\%$ ) (Text-fig. 4). The specimen PNT-142, originally included in the hypodigm of "*A. kiliasi*" by GERAADS & KOUFOS (1990), has been subsequently referred to *A. zernowi* by HEISSIG (1996, 1999) and to *Acerorhinus* by GIAOURTSAKIS (2003) and FORTELIUS et al. (2003). Later on GERAADS & SPASSOV (2009) excluded PNT-142 from their new subgenus *Chilotherium* (*Eochilotherium*), where they re-classified the rest of *A. kiliasi*'s hypodigm, implying a similar opinion. In accordance to these views, and based on the available morphological features described above, we conclude that PNT-142 fits perfectly within *Acerorhinus* and should be attributed to this genus.

In marked contrast to PNT-142 and K4/119.37, two other mandibular specimens from Pentálophos, PNT-31 and PNT-12, are characterised by a rostrally

widened symphyseal area without median constriction, combined with a notable size reduction in the premolar series, primarily on the p2. The right hemimandible PNT-31 has a deep corpus that does not taper rostrally, a steeply ascending symphysis, and a fairly long diastema (GERAADS & KOUFOS 1990, pl. 2, fig. 5). In dorsal view, it is clear that its maximal rostral width in life was at the level of i2s. The wide symphyseal region is better preserved in PNT-12; here the maximal rostral width of the symphysis surpasses even the maximal bilateral width between the labial walls of the p3s (GERAADS & KOUFOS 1990, pl. 2, fig. 4), which is an apomorphic feature of *Chilotherium*. Comparing these two chilothere mandibles with the sympatric PNT-142 *Acerorhinus* one, it is clear that the former feature an absolutely and relatively wider mandibular symphysis, despite the fact that the size of their premolar series is significantly reduced with respect to the latter (Text-fig. 6).

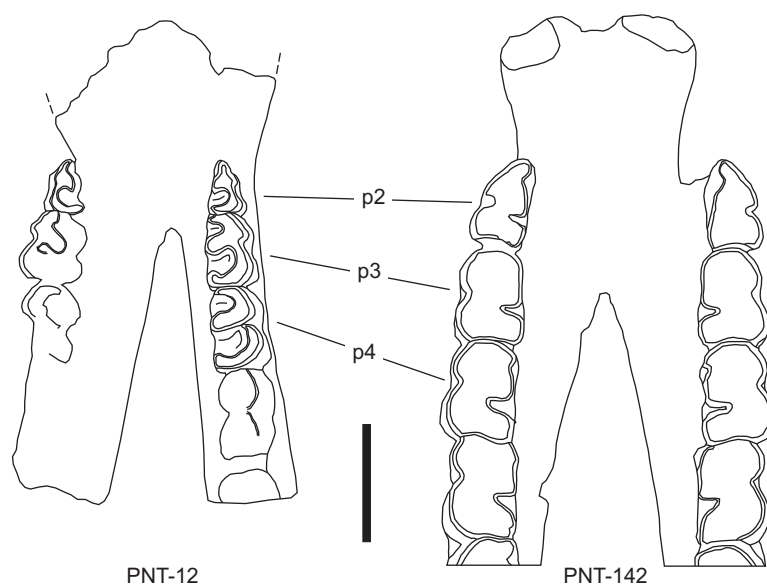
In conclusion, it is evident that the fauna of Pentálophos comprises two aceratheriine species, a smaller-sized *Chilotherium* and a larger *Acerorhinus*. The holotype of *Aceratherium kiliasi* is attributed to *Chilotherium*; though, regarding its specific assignment, it must be emphasized that the loss of the lectotype of *Chilotherium samium* obstructs presently a formal association, pending further comparisons with material from Samos. The apparent cranial and dental

similarities between “*Aceratherium*” *kiliasi* and *Chilotherium samium* have been also evaluated by GERAADS & KOUFOS (1990). However, their original differentiation was based primarily on the combined and thus misleading mandibular features of the Pentálophos mixed aceratheriine sample, as discussed above and also noted by HEISSIG (1996, 1999), GIAOURTSAKIS (2003) and FORTELIUS et al. (2003).

### 7. General systematic remarks and discussion

As evidenced by the comparison with already published aceratheriine samples, the Kerassiá cranium K4/119.37 belongs to the genus *Acerorhinus*; nonetheless, it clearly differentiates morphologically from the already described forms of this genus and is referred, together with the samples from Pikermi and Chomaterí, to the new species *A. neleus*, which is characterised by dolichocephaly, short hornless nasals, up-raised mandibular symphysis with very short diastema, low mandibular ramus and moderately long premolar series.

*Acerorhinus* is considered as a close relative of the genera *Chilotherium* and *Shansirhinus* (HEISSIG 1975, 1999, QIU et al. 1988, DENG 2005a). It appears to be the less derived genus of this group, as it lacks distinct autapomorphies, such as the marked widening of the mandibular symphysis in *Chilotherium*, or the more complex secondary enamel folding in *Shan-*



Text-fig. 6. Comparative drawing of mandibular specimens from Pentálophos (Macedonia, Greece) illustrating the differences in symphyseal morphology and premolar dimensions between the two distinct taxa included by GERAADS & KOUFOS (1990) in the hypodigm of *Aceratherium kiliasi*. The PNT-12 (on the left) is referred here to the genus *Chilotherium*, while the PNT-142 (on the right) to the genus *Acerorhinus*. The drawings are aligned according to the mesial margins of p2s. Graphical scale: 5 cm.

*sirhinus*. Regardless of the apparent conservatism of *Acerorhinus*, the various aceratheriine samples that have been classified to this genus exhibit considerable morphological and metrical variation, as discussed above (see Section 6 and the comparative outlines in Text-figs 3, 4). This may indicate the diversification of several temporal and/or spatial evolutionary lines within the genus. Nevertheless, based on our current state of knowledge, it is not feasible to trace these lines adequately, or define unequivocally the relevant evolutionary trends: samples that appear comparable in some characters are completely divergent in others. Particularly high variation is observed in the development of the nasal region, the dorsal profile, the symphyseal inclination, and the morphology of the mandibular ramus, as well as the overall size and proportions (Text-figs 3, 4). Since the majority of samples comprise only one or very few specimens, it is not yet known to what extent these differences may be attributed to intraspecific variation or which of them may be indeed taxonomically significant. This is a common situation among the Rhinocerotidae, where repeated-

Table 5. Updated taxonomy of the aceratheriine samples discussed in text.

Publication	original taxonomic assignment	updated classification
GAUDRY (1862–1867, pl. XXXIII, fig. 6)	<i>Acerotherium?</i>	<i>Acerorhinus neleus</i> n. sp.
BORISSIAK (1914)	<i>Aceratherium zernowi</i>	<i>Acerorhinus zernowi</i> (BORISSIAK, 1914)
KROKOS (1914)	<i>Aceratherium simplex</i>	<i>Acerorhinus simplex</i> (KROKOS, 1914)
PAVLOW (1914, pl. V, figs 1, 1a–c, 2)	<i>Aceratherium incisivum</i>	<i>Acerorhinus</i> sp.
RINGSTRÖM (1924)	<i>Diceratherium palaeosinense</i>	<i>Acerorhinus palaeosinensis</i> (RINGSTRÖM, 1924)
BOHLIN (1937)	<i>Diceratherium tsaidamense</i>	<i>Acerorhinus tsaidamensis</i> (BOHLIN, 1937)
MARINOS & SYMEONIDIS (1973, p.166)	<i>Aceratherium</i> sp.	<i>Acerorhinus neleus</i> n. sp.
MARINOS & SYMEONIDIS (1975, pl.6, fig. 2)	<i>Diceros</i> aff. <i>pachygnathus</i>	<i>Acerorhinus neleus</i> n. sp.
MARINOS & SYMEONIDIS (1975, pl. X)	<i>Aceratherium</i> sp.	<i>Acerorhinus neleus</i> n. sp.
QIU & YAN (1982)	<i>Chilotherium (Acerorhinus) cornutum</i>	<i>Shansirhinus</i> sp.
ZHENG (1982)	<i>Chilotherium (Acerorhinus) tianzhuense</i>	<i>Shansirhinus</i> sp.
QIU et al. (1988)	<i>Acerorhinus hezhengensis</i>	<i>Acerorhinus hezhengensis</i> QIU et al., 1988
GERAADS & KOUFOS (1990, pl. 2, figs 1–2, pl. 3, fig. 4)	<i>Aceratherium kiliasi</i>	<i>Chilotherium</i> cf. <i>samium</i> (WEBER, 1905)
GERAADS & KOUFOS (1990, text-fig. 1, pl. 3, figs 2, 3, 5)	<i>Aceratherium kiliasi</i>	<i>Acerorhinus</i> sp.
CERDEÑO (1996)	<i>Acerorhinus zernowi</i>	? <i>Acerorhinus</i> sp.
GAO & MA (1997)	<i>Acerorhinus xiaoheensis</i>	? <i>Acerorhinus</i> sp.
ZONG (1998)	<i>Acerorhinus yuanmouensis</i>	? <i>Acerorhinus</i> sp.
DENG (2000)	<i>Acerorhinus fuguensis</i>	<i>Acerorhinus fuguensis</i> DENG, 2000
KAYA & HEISSIG (2001, fig. 3)	<i>Aceratherium incisivum</i>	<i>Acerorhinus</i> sp.
FORTELIUS et al. (2003, fig. 12.2)	<i>Acerorhinus zernowi</i>	<i>Acerorhinus</i> sp.
FORTELIUS et al. (2003, fig. 12.5)	<i>Acerorhinus</i> sp.	aff. <i>Shansirhinus</i> sp.
DENG (2009)	<i>Acerorhinus lufengensis</i>	? <i>Acerorhinus</i> sp.
GERAADS & SPASSOV (2009, pl. 2, figs A–C)	<i>Acerorhinus</i> sp.	<i>Acerorhinus</i> sp.
GERAADS & SPASSOV (2009, pl. 2, figs D, E)	<i>Acerorhinus</i> sp.	<i>Acerorhinus</i> sp.

ly encountered evolutionary parallelism and convergence phenomena obscure their taxonomic and phylogenetic relationships. Bearing these drawbacks in mind, the following outline on the evolutionary and taxonomic affinities within the genus *Acerorhinus* must be regarded as provisional based on the morphological comparison of the available samples (see also Table 5).

Among the aforementioned *Acerorhinus*-like samples, the material from the Middle Miocene locality of Tung-gur retains the most primitive configuration of features. Its very long nasals, the markedly concave dorsal profile, and the low orbit (CERDEÑO 1996, fig. 3A) indicate close relationships with “*Aceratherium*” *depereti* BORISSIAK, 1927, from Turgai (BORISSIAK 1927, pl. I), as well as with samples referred to the Eurasian genus *Plesiaceratherium* YOUNG, 1937 (YAN & HEISSIG 1986, figs 1, 2). Further, according to CERDEÑO (1996), the ventral surface of the mandibular symphysis is flattened, which is a plesiomorphic feature and contrasts to the markedly concave ventral surface observed in the typical Late Miocene *Acerorhinus* samples. However, there is a significant difference in the postcranial anatomy between the Tung-gur and Turgai skeletons: “*A.*” *depereti* retains longer and more slender limb bones (especially metapodials; BORISSIAK 1927, pl. II), similar to the Middle Miocene *Plesiaceratherium* (YAN & HEISSIG 1986, figs 4, 16), whereas Tung-gur has shorter and more robust ones, as already pointed out by CERDEÑO (1996). This might indicate that a size reduction in the postcranial elements was already advancing during the Middle Miocene towards the more robust condition, also observed in Late Miocene *Acerorhinus*. The combination of these characters and the intermediate morphology of the Tung-gur sample suggest its placement close to the base of or marginally outside the *Acerorhinus* clade.

During the Late Miocene two regional groups appear to radiate from the ancestral stock typified by the Tung-gur morphology. The eastern group, which comprises the Chinese species, exhibits high diversity in the distribution and combination of morphological trends. As discussed in Section 6, *Acerorhinus fuguensis* and *A. tsaidamensis* appear to be more closely related, sharing several cranial characters (presence of a sagittal crest, notched nuchal crest, similar zygomatic morphology, relative positions of the orbit and the nasal notch, etc.), but also differ from each other in some mandibular features (ventral profile of the corpus,

constriction of symphysis). *Acerorhinus palaeosinensis* and *A. hezhengensis* differentiate both from the other two species and from each other. The former is characterised by a less dolichocephalic skull, a dorsally widened occiput, and an almost horizontal symphysis, while the latter features a comparatively wide cranial roof, deeper nasal incision and robust mandible. The taxonomic affinities of other *Acerorhinus* species from China (*A. xiaoheensis* GAO & MA, 1997, *A. lufengensis* DENG & QI, 2009) are uncertain, due to their incompletely documented hypodigms.

The western regional group comprises the samples of the Anatolian, Balkan and peri-Pontic regions. Within this group the samples from Ukraine and Moldova (Vallesian and Turolian localities Sebastopol 1 and 2, Tudora and Ciobruciu) are more closely related and may form a local temporal lineage (Sarmatian – Maeotian) of subspecific or specific rank, represented by the genotype *A. zernowi* and *A. simplex*, as discussed in Section 6.2.1. The Bulgarian and Anatolian representatives exhibit a variety of inconsistent morphological patterns and combination of features, which do not presently allow a firm assignment either to *A. zernowi*, or *A. neleus*. Despite the rather similar dental morphology and the resemblance in some cranial characters, such as the dorsal profile, the short nasals, the narrow praeorbital bar, and the configuration of the postglenoid, posttympanic and paroccipital processes, a notable degree of variation exists, e.g. in the cranial and dental proportions, in the robustness of the zygomatic arch, the nasal constriction, or in terms of mandibular morphology (symphyseal inclination and diastema length, condylar and coronoid morphology etc.) (Text-figs 3, 4).

The *Acerorhinus* samples from the Greek localities display much greater morphological homogeneity. The assessable cranial and mandibular differences between the Turolian *A. neleus* and the Vallesian *Acerorhinus* sp. from Pentálophos are rather few (zygomatic robustness, nuchal shape, symphysis inclination, length of diastema, dental segments proportion; compare also section 6.2.4) and may be well attributed to temporal variation within a single lineage. The Turolian samples from Kerassiá, Pikermi and Chomateri, which are included in *A. neleus*, are morphologically identical. The only apparent morphological difference is the substantial development of the second lower incisors in the latter samples, which is clearly considered as a male sexual character. The relative development of the premolar/molar segments is also very similar. On



morphological grounds all three samples are well referable to the same species, *A. neleus* n. sp. However, the Kerassiá specimen, which is referred to a female individual, is larger in dental dimensions than both the Chomaterí and Pikermi specimens (Section 6.2.4, Tables 3, 4). These metrical differences can be attributed either to spatial variation among more or less contemporaneous populations, or to potential size differences along an intraspecific temporal cline.

According to the available faunal data, Kerassiá and Chomaterí are biochronologically similar to Pikermi, which is commonly placed to the middle Turolian (MN12). Nonetheless, a comprehensive biostratigraphic correlation among these three localities is yet to be established, given the existence of several fossiliferous sites and levels in each one. Detailed stratigraphic data about the material originating from the old excavations at Pikermi is lacking, despite the fact that early authors had already recognised the occurrence of two or three fossiliferous horizons (GAUDRY 1862–1867, WOODWARD 1901, ABEL 1922, fig. 132). In the locality of Kerassiá seven sites have been discovered representing two different stratigraphic levels (see Section 1), but a clear biostratigraphic distinction between them is not recognizable based on their current faunal content. If there is actually a biochronological difference between Kerassiá and Pikermi / Chomaterí, then an intraspecific body size shift cannot be excluded. Nevertheless, the absence of fine stratigraphic resolution, as well as the small available number of specimens, are currently inadequate to firmly support such temporal trends.

The hypothesis of metrical variation among contemporaneous populations prerequisites (a) that we have come across a very large female individual in Kerassiá and two small male ones in Pikermi and Chomaterí, and (b) that there is no accentuated sexual size dimorphism resulting in considerably larger males. The extant rhinocerotid species have been generally considered as sexually monomorphic regarding their size, since they do not usually show any significant differences in body dimensions (at least in free-ranging populations) (POCOCK 1945, FREEMAN & KING 1969, LOOSE 1975, DINERSTEIN 1991). An exception is the African white rhino *Ceratotherium simum*, the male of which can be considerably more robust and heavier than the female, though the sexes don't differentiate from each other in withers height (OWEN-SMITH 1988, p. 10). Observed size differences between the sexes of extant species refer to individuals

raised in captivity (DINERSTEIN 1991). Size dimorphism has been evidenced in some Miocene species, the males generally being somewhat larger in mean values (OSBORN 1898, MEAD 2000, DENG 2005b, MIHLBACHLER 2007, CHEN et al. 2010). However, even in these cases, the intraspecific metrical variation can be considerably high, with overlapping values between males and females. Studies on a good statistical sample of *Teleoceras major* HATCHER, 1894, from the Miocene of North America have shown that maximum female dental measurements can be up to 21% higher than minimum male ones (MEAD 2000, tabs 1, 2). Moreover, dental measurements of recent rhinocerotid species frequently exhibit a maximum–minimum difference much higher than 20%, though no gender data are available (GUÉRIN 1980, tabs 5, 6). There are also several cases in the fossil record where female individuals may occasionally have longer tooththrows (PROTHERO 2005, p. 9, MIHLBACHLER 2007). These data show that if *A. neleus* exhibited a similar metrical variation, then the morphologically indistinguishable specimens from Kerassiá, Pikermi and Chomaterí could belong to the same palaeopopulation.

## 8. Palaeoecological and biogeographical remarks

The conservative occlusal morphology with simple, uncomplicated enamel pattern, which characterises the dentition of the studied specimen K4/119.37, implies barely specialised dietary habits. The dentition is brachyodont, according to the hypsodonty classes inducted by FORTELIUS & SOLOUNIAS (2000) and FORTELIUS et al. (2002), with non-prismatic crowns (i.e. with convergent lingual and labial walls), suggesting a diet based primarily on non-fibrous and non-abrasive food. Additional dental characters, such as the markedly concave upper occlusal surface, the absence of medifossette in the molars, the triangular shape of M3s and the convex labial walls of the lower teeth, the variable enamel thickness, the presence of cinguli, and the thin cement coating are also consistent with the low-crowned and functionally brachyodont dentition type (FORTELIUS 1982). Ungulates with brachyodont dentitions are practically always browsers that feed selectively on dicotyledonous plants (JANIS 2008), since a more abrasive diet comprising a higher percentage of grasses would have worn

down their teeth very rapidly and would require a more hypsodont dentition.

Examining further the specimen's dentition according to the mesowear method developed by FORTELIUS & SOLOUNIAS (2000), we observe a high intermediate relief on the ectoloph of the upper premolars and molars, and sharp metacone apices, which both suggest the predominance of attrition (tooth-to-tooth wear) during the comminution of bulky vegetation, such as soft plants, fruits, and twigs, that form a typical browsing diet. The paracone apex is more rounded due to the development of a paracone fold, which strengthens the shearing efficiency during the occlusal stroke. These features of the occlusal relief exclude the possibility of habitual feeding with grasses, which would have resulted in a flattened occlusal surface with low relief and blunt cusps.

In conclusion, on the basis of the crown morphology and the mesowear profile, *A. neleus* is palaeoecologically interpreted as a browser or at most a mixed feeder, ruling out the grazer option. Seasonal and/or geographical variations in diet resulting from opportunistic behaviour or seasonal availability of food resources are though quite probable and cannot be excluded based on the available data.

The Turolian rhinocerotid association in the Greco-Iranian (sensu DE BONIS et al. 1979, 1992) or Subparatethyan (sensu BERNOR 1984) zoogeographic province is generally characterised by the co-existence of the tandem-horned species "*Diceros*" *neumayri* and *Dihoplus pikermiensis*, combined with one or two aceratheriine species that are usually less frequent among the existing material (GAUDRY 1862–1867, WEBER 1904, 1905, GUÉRIN 1980, GERAADS 1988, HEISSIG 1996, GIAOURTSAKIS 2003, 2009, GIAOURTSAKIS et al. 2006). In addition, a massive elasmothere, *Iranotherium morgani* (MECQUENEM 1908), occurs in the Iranian locality of Maragheh (MECQUENEM 1908, 1924). Despite the apparent taxonomic resemblance of rhinocerotid taxa among the localities of the province, there is still a considerable variation in their distribution and their relative abundance. For instance, the available faunal data from the well-sampled localities of Pikermi and Samos support a differential interspecific dominance between the two horned species: *D. pikermiensis* predominates in Pikermi, while "*D. neumayri*" is far more abundant on Samos. Based on their relative abundance within Late Miocene communities and their differentiated palaeoecological adaptations, GIAOURTSAKIS

et al. (2006) proposed a niche and resource partitioning with limited competition between them. *Dihoplus pikermiensis* is commonly regarded as a selective browser favouring more closed habitats with denser vegetation cover, while "*D. neumayri*" as a dweller of more open and dry landscapes (HEISSIG 1996, GIAOURTSAKIS et al. 2006, GERAADS & SPASSOV 2009, GIAOURTSAKIS 2009). Concerning the hornless rhinocerotid taxa, there is a significant taxonomical difference between these two well-sampled localities: in Pikermi only *Acerorhinus* is present, while the Samos fauna comprises only *Chilotherium* (WEBER 1905, RINGSTRÖM 1924, GIAOURTSAKIS 2009). The marked differences observed in the relative distribution and abundance of rhinocerotid taxa among the Turolian localities of the Eastern Mediterranean and adjacent regions appear to be strongly associated with environmentally controlled provincial differences (GIAOURTSAKIS et al. 2006, GIAOURTSAKIS 2009). Localities situated at the western margin of the Greco-Iranian province, such as Pikermi, provided areas with denser tree coverage and more temperate conditions favoured by *D. pikermiensis*, which clearly dominates over "*D. neumayri*", as well as by the plesiomorphic *Acerorhinus*. In more eastern parts of the Greco-Iranian province (Samos, Turkish localities, Maragheh) *D. pikermiensis* becomes less common, whereas "*D. neumayri*" emerges as the dominant horned rhinoceros. Furthermore, the occurrence of derived *Chilotherium* becomes progressively more frequent over *Acerorhinus*, and it even turns up dominant at Maragheh, where we also encounter the grazer *Iranotherium morgani* (GIAOURTSAKIS 2009). These gradual changes observed in the rhinocerotid assemblages within the Greco-Iranian province are consistent with palaeoecological inferences based on dental hypsodonty and phytolith proxies, as well as on the faunal analyses as a whole (FORTELIUS et al. 2002, ERONEN et al. 2009, STRÖMBERG et al. 2007, KOUFOS et al. 2009), according to which there was an expansion of increasingly open and drier habitats towards the East during the Late Miocene.

The relative abundance between "*D. neumayri*" and *D. pikermiensis* in Kerassía cannot be evaluated for the moment, due to the small number of individuals (GIAOURTSAKIS et al. 2006). Nonetheless, the shared occurrence of *Acerorhinus* in Kerassía, Pikermi, and Chomaterí, as documented herein, combined with the absence of *Chilotherium* in these localities, suggest that the rhinocerotid association of Kerassía

resembles closer the one from Pikermi and Chomaterí, and it is clearly different from the assemblages of Samos and more eastern localities. Though there is still some debate over the palaeoenvironmental context of Pikermi, an interpretation as a sclerophyllous evergreen woodland is currently supported by several lines of evidence (dental microwear and mesowear analyses, masticatory morphology, stable isotopic, palaeobotanic and phytolith studies, faunal comparisons) and is considered plausible (see overview and discussion in SOLOUNIAS et al. 1999, 2010, but see also STRÖMBERG et al. 2007, who oppose to this theory, considering a more open environment with considerable presence of grasslands, at least for the part of the Greco-Iranian province situated to the east of the Aegean Sea). Palynological studies in the locality of Chomaterí (though not in direct association with the fossil mammal horizon) have also documented the predominance of subtropical trees (mainly Taxodiaceae with regular representation of the Mediterranean xerophytes) with herbaceous elements, indicating a forested region with open areas under warm and moist temperate climatic conditions (IOAKIM et al. 2005). Within this palaeoenvironmental context, the co-occurrence of *Dihoplus pikermiensis*, “*Diceros*” *neumayri*, and *Acerorhinus neleus* in Pikermi and Kerassiá may indicate mosaic habitat differentiations providing suitable dietary niches for each one of these species.

A further palaeoecological indication for a mosaic habitat is provided by the study of Giraffidae (ILIOPOULOS 2003a). Four species have been identified in the upper fossiliferous horizon (*Palaeotragus rouenii*, *Helladotherium duvernoyi*, *Bohlinia attica* and *Samotherium major*), and also four species in the lower horizon (*P. rouenii*, *Palaeotragus* sp., *H. duvernoyi*, and *S. major*). Based on their morphological features and the microwear studies by SOLOUNIAS et al. (1999, 2000), *H. duvernoyi* and *B. attica* are considered as browsers, whereas *S. major* as a grazer and *P. rouenii* as a mixed feeder.

The coexistence of numerous and dietarily diverse ungulates within the faunal association of Kerassiá is consistent with a heterogeneous vegetational regime, pointing to a mosaic habitat of extensive woodland with intermittent open, low vegetation landscapes.

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## Explanation of the plates

### Plate 1

*Acerorhinus neleus* n. sp. from Kerassía, AMPG K4/119.37

Fig. 1. The complete specimen as it was found (skull and mandible in articulation) in an early preparation stage.

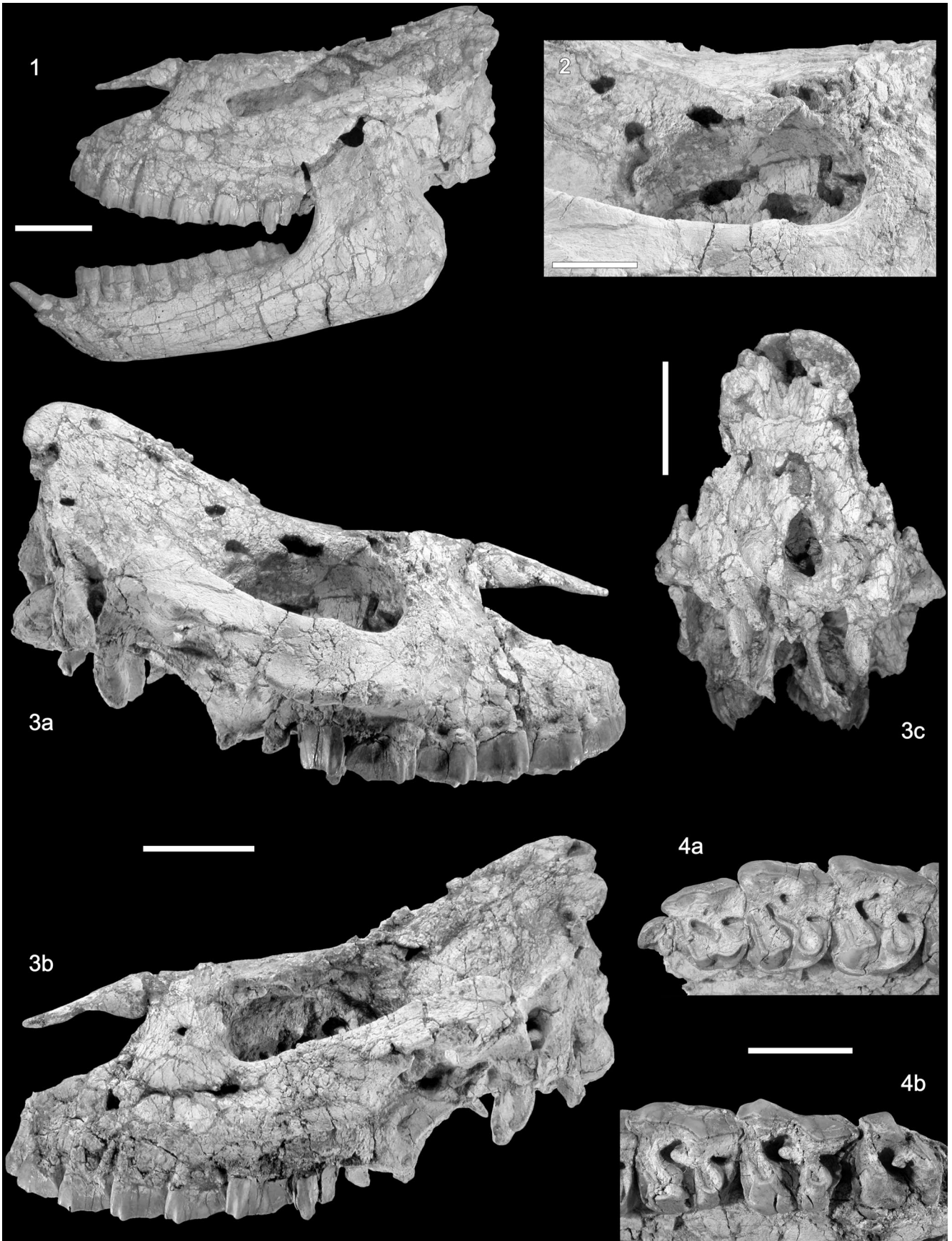
Fig. 2. Detailed view of the right-side orbital area, exhibiting considerable damage due to post-mortem biological activity.

Fig. 3. Skull. a: right lateral view, b: left lateral view, c: caudal view.

Fig. 4. Upper dentition, left side. a: premolar section, b: molar section.

Graphical scales of Figs 1 and 3: 10 cm; of Figs 2 and 4: 5 cm.





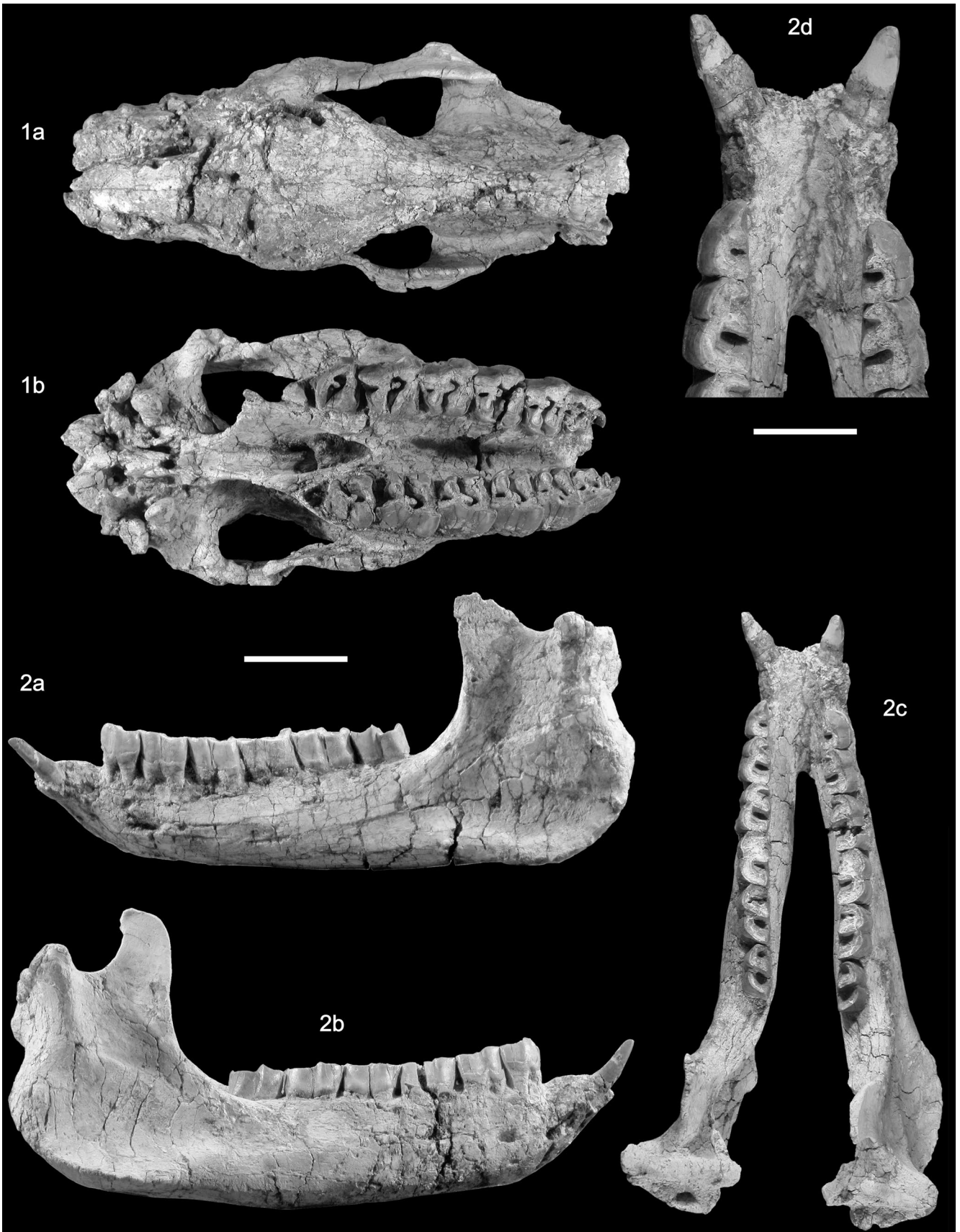
**Plate 2**

*Acerorhinus neleus* n. sp. from Kerassía, AMPG K4/119.37

Fig. 1. Skull. a: dorsal view, b: ventral view.

Fig. 2. Mandible. a: left lateral view, b: right lateral view, c: dorsal (occlusal) view, d: dorsal view of the symphyseal area.

Graphical scale of Fig. 2d: 5 cm; of all other Figs: 10 cm.



**Plate 3**

*Acerorhinus neleus* n. sp. from Chomaterí (AMPG)

Fig. 1. Skull fragment, AMPG 1992. a: right lateral view, b: ventral (occlusal) view.

Fig. 2. Mandibular fragment of the same individual, AMPG 19Π/1972. a: dorsal (occlusal) view, b: rostral view.

*Acerorhinus neleus* n. sp. from Pikermi (MNHN)

Fig. 3. Mandibular part (PIK-957), dorsal (occlusal) view.

Graphical scale: 10 cm.

