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UPPER MIOCENE RHINOCEROTIDAE (MAMMALIA) FROM PENTALOPHOS-1, MACEDONIA, GREECE

BY

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With 3 plates, 9 figures and 2 tables in the text

Zusammenfassung

Die neulich gefundene Lokalität von Pentalophos-1 hat mehrere Nashornschädel geliefert, und stellt deshalb für diese Gruppe die reichste Lokalität im Obermiozän des griechischen Mazedonien dar. Der zweihörnige *Ceratotherium neumayri* ist nicht so häufig wie eine neue *Aceratherium*-Art (*Aceratherium kiliasi* n. sp.). Wir vergleichen die letzte Art mit der Typus-Art der Gattung (*Aceratherium incisivum* von Eppelsheim), mit anderen europäischen und west-asiatischen Arten dieser Gattung (wir weisen nach, daß *Aceratherium* in Samos und Maragheh vorkommt) und mit der Schwestergattung *Chilotherium* aus Asien. Ein Kladogramm der obermiozänen *Aceratherium*-Arten wird erstellt.

Schlüsselwörter: Mammalia — Rhinocerotidae — *Aceratherium* — Obermiozän — Griechenland.

Summary

A newly discovered locality, Pentalophos-1, has yielded several skulls of Rhinocerotidae and represents for this group the richest locality known for the Upper Miocene of Greek Macedonia. The two-horned *Ceratotherium neumayri* is less common than a new species of Acerathere, *Aceratherium kiliasi* n. sp. The latter is compared with the type-species of the genus (*Aceratherium incisivum* from Eppelsheim), with other european and west-asiatic species of the same genus (*Aceratherium* is shown to occur at Samos and Maragheh), and with the sister-genus *Chilotherium* from Asia. A cladogram of upper Miocene *Aceratherium* is proposed.

Key words: Mammalia — Rhinocerotidae — *Aceratherium* — upper Miocene — Greece.

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I) Introduction

For over 15 years, a party of palaeontologists from the Universities of Thessaloniki, Paris and Poitiers, conducted by L. de Bonis, has been excavating numerous upper Miocene sites in the lower Axios valley (Macedonia, Greece). The most recent results and chief references can be found in Bonis et al. (1988).

Despite the wealth of large Mammals found in these localities, Rhinoceroses are usually scarce, except in a new site, named Pentalophos-1 (PNT), found in 1983 by Dr. Adamantios Kilias, from the University of Thessaloniki, during a mapping exercise with students. The fossiliferous beds are located at the bottom of the ravine bordering the eastern side of the village of Pentalophos, 15 km N-W of Thessaloniki. The deposits consist of hard red sandstones, possibly belonging to the formation cropping out, a few kilometers westwards, in the "Ravin de la Pluie", which yielded a Vallesian fauna, but no strong argument (neither direct stratigraphic correlation, nor biostratigraphy) can be put forward at the present time to support this datation for Pentalophos.

II) The horned Rhinoceros: *Ceratotherium neumayri* (Osborn, 1900)

This species has recently been revised (Geraads, 1988) and the cranial remains from Pentalophos provide few new data on the anatomy of this species. Therefore, they will not be described in detail, but only some points of difference with the specimens from the classic localities of Pikermi, Samos and Maragheh will be mentioned.

1) Sub-adult skull, PNT 143 (Pl. 1, Figs. 1–2)

This skull is crushed dorso-ventrally but complete except for the occipital crest. Unfortunately, as in most of the specimens from Pentalophos, the bone surface is extensively crackled so that details and sutures are not visible.

In lateral view, the upper outline of the nasals is bent as is usual in *C. neumayri*. In upper view, however, they are more pointed anteriorly, but this might be due to the young ontogenic age of the specimen. The posterior corner of the nasal notch is situated above P3/. The premaxillae are complete, edentulous, and short (the predental portion of the skull is only 65 mm long). The anterior border of the orbit is above the limit between M1/ and M2/. Among the typically Dicerotine characters of the skull (Geraads, 1988) one may mention the sloping inferior border of the orbit, the absence of any post-orbital process, the sloping posterior border of the pterygoid wings, the forwardly-directed post-tympanic process and the occiput which is clearly broader in its upper part than at the level of the post-tympanic processes. The basicranial region is not well preserved. The post-glenoid processes are bent forwards, and strongly flattened transversely.

M3/ is erupting but the dP4/ are not yet shed; this corresponds to stage VIII of Hitchins (1978). The left dP4/ has been removed in order to expose P4/. The foremost tooth, being completely worn out, is doubtless a persisting dP1/: the lateral wall of the maxilla has been excavated above the tooth and no trace of a true P1/ was found.

A crochet is present on P3/–M3/. A weak crista is present on P4/ but absent on all the other teeth. There is a clear groove on the posterior face of the protoloph, opposite the crochet, but not true antecrochet. The entrance to the median valley is narrow on M2/, wider on M3/, and blocked by the cingulum on M1/. This entrance pass is high on P3/ and very high on P2/ (20 mm) and P4/ (30 mm). The external wall of all the teeth is almost flat with only weak indications of the paracone and metacone folds. The cingulum is strong on all teeth. It completely surrounds the internal side of P3/ and P4/, the protocone of M2/, an it is also present lingually on P2/ and M1/.

2) Juvenile skull, PNT 144 (Pl. 1, Figs. 3–4)

All the milk-teeth are still present; M1/ is completely erupted but still unworn. This corresponds to stages IV–V of Hitchins (1978). The skull is transversely crushed but complete except for the occipital crest, the anterior part of the nasals and the premaxillae. Partly owing to numerous cracks on the surface, the sutures are not visible.

The posterior end of the nasal notch is situated above the limit between dP2/ and dP3/. There is a clear boss for the frontal horn. The orbit is low above the tooth-row, its floor is laterally sloping; the supra-orbital process is strong, but there is no post-orbital process. The post-glenoid process is similar to that of the adult skull. The paroccipital process is distant from it, slightly bent backwards and antero-posteriorly compressed. The post-tympanic process is long, forwardly directed, so as to partly overlap the post-glenoid process in side view, but without fusion, and even perhaps without contact between them. There is a strong median tubercle on the basi-occipital between the post-glenoid processes: this must be an individual variation since it is certainly absent on the sub-adult skull.

The milk-teeth need not be described in detail since they show all the typical characters of *C. neumayri* (cf. Geraads, 1988): dP1/ has no metaloph, dP2/ no post-fossette; there is an enclosed medifossette on all dP, a tubercle at the entrance of the median valleys, dP3/ and dP4/ are longer than broad. M1/ is almost identical with that of the sub-adult skull.

The dimensions of these two skulls are:

	PNT 143	PNT 144
Length from occipital crest to tip of nasals	#650	—
Length from occipital crest to front of orbit	#390	—
Length from occipital condyle to foremost tooth	540	480
Length from occipital condyle to front of orbit	365	330
Length from auditory meatus to front of orbit	257	210
Width over post-tympanic processes	240	179 +
Length dP^1–M^3	275	—
Length P^2–P^4/dP^1–dP^4	#120	138
Length M^1–M^3	160	—

3) Other remains of *Ceratotherium neumayri*

PNT 34 is an almost complete mandible. There were no incisors, but the anterior tip of the mandible is slightly broadened: the minimum width is located just in front of P/2 (61 mm). Posteriorly, the symphysis extends as far as the limit between P/3 and P/4; its upper side is concave. In lateral view, the horizontal rami are high and strong, their lower borders convex, especially below the premolars, where they curve strongly upwards. The articular condyles are large. All the teeth are present, but much worn. The main dimensions of this mandible are: Length from P/2 to rear of ascending ramus: 450; height of corpus below M/3: 115; height from condyle to lower border: 230; length of tooth row: 240; premolar length: 103; molar length: 137.

PNT 129 is a mandible with both rami, very incomplete. P/2–P/4 are preserved on the right side, P/3–M/1 on the left one. There is a vestigial external cingulum on all teeth. The valleys of the posterior lobes are noticeably deeper than those of the anterior ones. The symphysis reaches posteriorly the level of the limit between P/2 and P/3. Nothing can be said of the anterior part of the jaw, except that it was certainly less reduced than in *Diceros bicornis.*

PNT 130 is a left mandible with dP/1–dP/4. The posterior lobe of dP/2 is wide open; dP/3 has a well-developed third (anterior) lobe. The valleys of dP/3 and dP/4 are clearly U-shaped, instead of V-shaped on the definitive premolars.

PNT 89 is a right mandible with dP/1–dP/4. The posterior lobe of dP/2 is closed lingually, and a third (anterior) lobe is present on dP/3.

PNT 13 is a left mandible with the same characters. It possibly belonged to the same individual.

PNT 14 is a fragmentary right mandible, again with the same characters, but from a younger individual.

The dimensions of the teeth on these mandibles are:

	PNT 130	PNT 89	PNT 13	PNT 14
dP/1	20×10	18×9	18×9	—
dP/2	31×14.5	29×14.5	27.5×15	—
dP/3	45×23	45×23.5	—	46.5×24
dP/4	47.5×26	46×24	—	47× —
dP/1–dP/4	141	140	—	—

A few limb bones have also been recovered from Pentalophos, but none of them is well enough preserved to allow a detailed description. The only reasonably complete ones are a rather slender tibia, 400 mm long, associated with a calcaneus whose dimensions are: length 130 mm, width 93 mm.

4) Comparisons

Ceratotherium neumayri (formerly known as *Diceros pachygnathus*) is a widely spread species, known from several skulls in the eastern mediterranean area, with a local variant in North Africa (*"Diceros douariensis"* GUERIN, 1965). It is perhaps ancestral to *Ceratotherium praecox* HOOIJER & PATTERSON, 1972 from the Pliocene of Africa. GERAADS (1988) showed that *C. neumayri* is well distinct from a sympatric and synchronic species with which it has often been confused, *Dicerorhinus pikermiensis* (TOULA, 1906).

The specific identity of the Pentalophos specimens with those from Maragheh, Pikermi and Samos is not doubtful but it is more difficult to recognize within this species any geographic variation or evolutionary stages. The only attempt to do so was that of THENIUS (1955) who believed that the specimens from Maragheh and Samos belong to a subspecies (which should be called *C. neumayri neumayri*) different from that of Pikermi (for which no name is available, since the name *pachygnathus* should be restricted to the type specimen), but GERAADS (1988) showed that the distinctive characters put forward by THENIUS do not hold true when all the skulls are taken into consideration. Some other variable features, not mentioned by THENIUS, cannot be better correlated with the geographic and/or stratigraphic provenience. The cingulum, for instance, is strong at Pentalophos, as it is in one of the skulls from Pikermi in the MNHNP ("*Rhinocéros* d'espèce indéterminée" of GAUDRY, 1862–67), on the type skull from Maragheh, or on some of the Samos skulls (WEBER, 1904, pl. XV, fig. 1; SMNS skull B of GERAADS, 1988). However, it should be noticed that the cingulum is weaker on some skulls from the same localites (skull D from Pikermi in the MNHNP, and especially on the skull from Samos in Basel). The lingual closure of the median valley of the premolars, only partly correlated with the former feature (it is apparently always closed at Pikermi) does not provide a better criterion since both conditions occur at Samos.

When specifically compared with the incomplete skull from Saloniki (precise locality unknown: "Ravin X" or "Vathylakkos 3") described by ARAMBOURG & PIVETEAU (1929) as *R. pachygnathus*, it can be seen that this latter skull is slightly larger (but older, since P4/is already in use), that the cingulum is less prominent, and that the valleys of the premolars are open. These few visible differences do not allow us to draw any conclusion concerning the relative ages of the specimens.

III) The acerathere Rhinoceros: *Aceratherium kiliasi* n. sp.

1) Skull PNT 135 (Pl. 2, Figs. 1–2; Pl. 3, Figs. 4)

This skull is in fact a half-skull, since most of the right side is missing. Of the left side, the occipital is the main missing part. The skull is slightly crushed obliquely. It belongs to a rather old individual with all the teeth well worn (M1/ almost to the roots, the fossettes being completely circled with enamel). The only visible suture is the mid-nasal one.

Seen from above, the cranial roof is roughly lozengic, broadest at the supra-orbital processes (much stronger than the post-orbital ones) and only slightly concave antero-posterior in lateral view. The rearmost part is missing, but it is most unlikely that the fronto-parietal crests fused in the sagittal plane: they probably remained separated by several centimeters. There is no indication of a frontal horn, but its absence cannot be definitely established, since the bone surface is eroded. The same can be said about a possible terminal nasal horn, as the tips of the nasals are missing. These bones are broad and short, since they do not extend in front of the first premolar.

Not much can be said about the premaxillae, as this part is missing; we do not know whether any incisor was present.

The posterior border of the nasal notch is situated above the limit between P4/ and M1/. This notch is triangular when seen from the side, that is, it narrows regularly from front to back, and ends to a point. There are at least two infra-orbital foramina. The anterior one assumes the shape of a gutter along the margin of the nasal opening; the posterior one is very large, almost 2 cm in vertical diameter. The ante-orbital area is depressed, but it is difficult to ascertain how far this is due to crushing. The area of insertion of the labial muscles, so conspicuous in the asiatic genus *Chilotherium* Ringström, 1924, is not clearly visible here.

The zygomatic arches, though stronger than in the horned rhinoceroses, are more slender than in *Chilotherium*, and in contrast to this genus, they curve upwards behind the orbit, but this is probably accentuated by crushing.

The squamosal does not fundamentally differ from that of horned rhinos. The glenoid articular area is transversely directed, and very slightly convex anteriorly. The post-glenoid process is almost straight and perhaps slightly flattened antero-posteriorly. It remains separated from the post-tympanic process. In all these features, the skull from Pentalophos is similar to *Diceros bicornis*, but an important difference can be seen in the mastoid area.

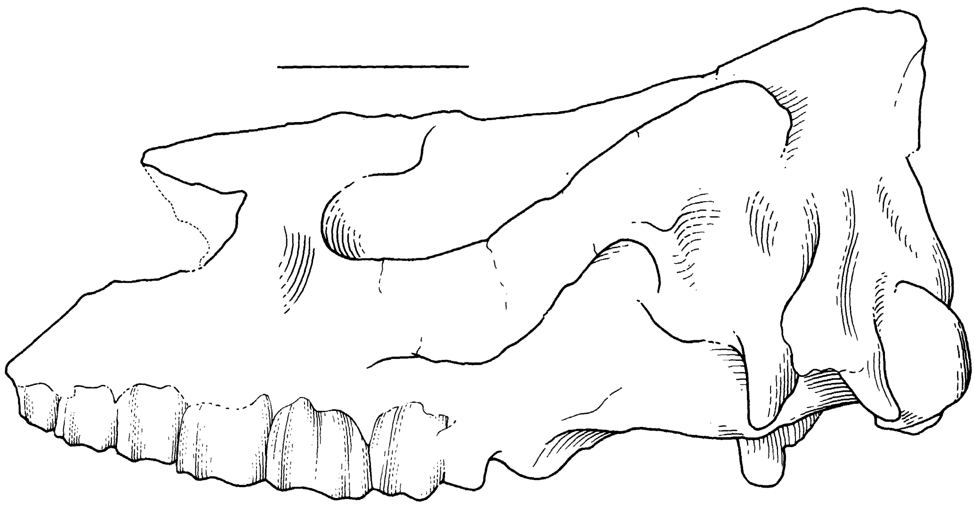
In many Mammals, the mastoid exposure separates, at the postero-lateral corner of the skull, the post-tympanic and paroccipital processes. Often, however, the petrosal becomes concealed within the skull and is no longer visible externally. This is the case in all horned Rhinos. In the intermediate condition, the post-tympanic and paroccipital processes come into contact, but the mastoid exposure is still visible higher up. This intermediate condition can be observed, for instance, in some Ruminants and in *Tapirus*. In this genus, the mastoid appears as a narrow tongue of bone, at the floor of a depression between the lateral side of the occipital crest and the buttress drawn upwards from the paroccipital process. A similar, but broader, depression can be observed on the Pentalophos skull; its central part is slightly raised exactly as the mastoid exposure of *Tapirus*. Although the identity of the bone cannot be formally established, since all the sutures are fused and no longer traceable, the close morphological similarity with *Tapirus* leaves no doubt as to the homology of the bones of this area. We therefore suspect that the horned Rhinos are united by an important synapomorphy: the loss of the mastoid exposure. This is probably linked with the shortening of the skull in this group. The same disappearance of the mastoid could probably be found in the very brachycephalic Brachypotheres (s.l.), but the sutures are still less easily traceable.

All the teeth (Pl. 3, Fig. 4) are well-worn and the degree of hypsodonty cannot be determined; they were all covered with cement. The foremost tooth is not more worn than P2/; it is therefore probably a true P1/, rather than a persisting dP1/ which would have been completely worn out. It has the normal pattern of a rhino premolar, with two transversal lophs.

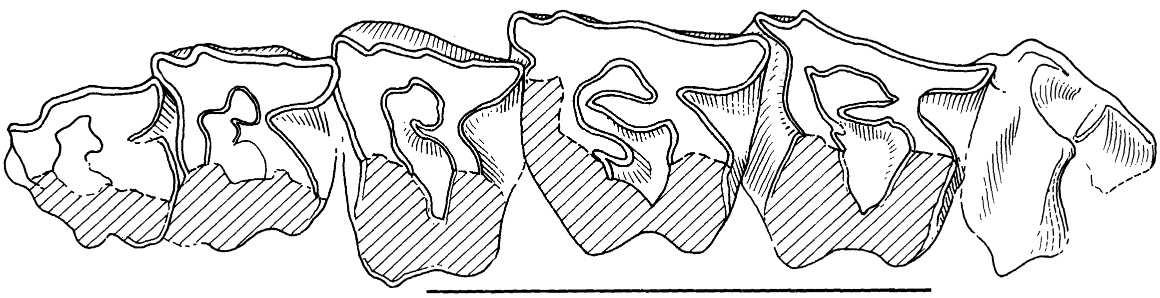
A moderately long crochet was present on all teeth (except perhaps M1) but only the premolars bore a crista. The antecrochet was absent on P2/, doubtfully present on P3/–M1/, present but moderate on M2/–M3. There is no groove on the anterior face of the protoloph, so that the protocone does not appear as a special entity, as it does in many Aceratheres. Its lingual side is flattened, especially on M2/ and M3/. The external wall of the teeth is gently undulating, the paracone fold being only slightly prominent at this level of the crown. The cingulum is remarkably weak on the lingual and labial sides of the teeth.

2) Skull PNT 32 (Text-figs. 1–2)

This is the skull of a younger individual, since M3/ is not yet touched by wear. The tips of the nasals and the premaxillae are missing but otherwise the left side of the skull is almost complete, as well as most of the posterior half of the right side. There are only a few differences from skull PNT 135. There is a shallow anteorbital depression, with a well-defined posterior border, 31 mm in front of the orbit; the lateral profile of the skull-roof is slightly more concave, but this may be due to crushing; the post-glenoid and paroccipital processes are more divergent. Although transversely crushed, the specimen shows that the occipital face was trapezoidal, with a clear constriction above mid-height, and a well rounded upper occipital crest. The occipital was certainly much narrower than in any horned Rhinocerotid.



Text-fig. 1. *Aceratherium kiliasi* n. sp. Skull PNT 32, lateral view. Scale = 10 cm.

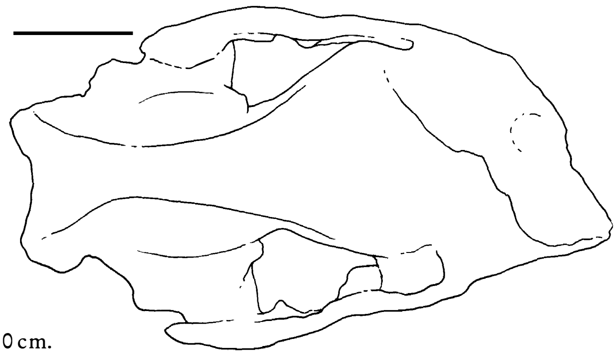


Text-fig. 2. *Aceratherium kiliasi* n. sp. Skull PNT 32, occlusal view of upper tooth-row P^2–M^3. Scale = 10 cm.

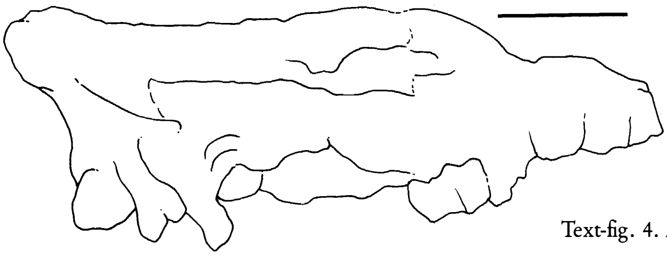
The teeth are little worn, but unfortunately incomplete in their lingual part; no cement is preserved. The crochet is present on all teeth, complex on P3/, and very long on the molars; on M1/ it reaches the protoloph. There is only a minute crista on the premolars. The antecrochet was probably present on the molars; this area is missing on the premolars. In the higher part of the crown, the external wall is well undulating with a paracone-fold underlined by two depressions.

3) Skull PNT 122 (Text-figs. 3–4)

This is an incomplete skull; the nasals, the premaxillae and most of the maxillae are broken away. It is morphologically similar to skulls PNT 135 and PNT 32.



Text-fig. 3. *Aceratherium kiliasi* n. sp. Skull PNT 122. Upper view. Scale = 10 cm.



Text-fig. 4. *Aceratherium kiliasi* n. sp. Skull PNT 122. Lateral view. Scale = 10 cm.

The cranial roof is flat and lozengic, with its maximum width (178 mm) at the supra-orbital processes. It narrows posteriorly, but the parieto-temporal crests remain separated throughout their length. The zygomatic arches are strong, still less clearly directed upwards than in PNT 135. The anterior border of the choanae reaches the level of the limit between M2/ and M3/. Their distance to the anterior border of the foramen magnum is 275 mm. What remains of the teeth does not differ from PNT 135.

Table 1. Cranial measurements of *Aceratherium kiliasi* n. sp.

	PNT 135 (type)	PNT 32	PNT 122
Skull length, from occipital crest to tip of nasal	500	—	—
— d° — to P2/	~ 520	~ 525	500 to P3/
— d° — to front of orbit	340	336	340
Skull length, from occipital condyle to front of orbit	—	345	310
Skull length, from auditory meatus to front of orbit	225	240	240
Occipital height	—	180–	141
Width over occipital crest	—	120	140
Width over post-tympanic processes	—	—	215
Length of upper tooth-row	~ 210	—	—
Premolar length	94	—	—
Molar length	122	130	130

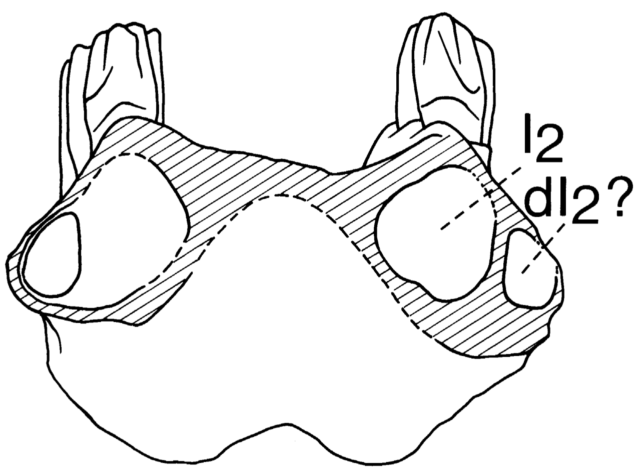
4) Mandible PNT 142 (Pl. 3, Figs. 2, 3, 5)

This mandible is not associated with any of the skulls or maxillae, and does not fit any of them (from the size, state of wear and peculiar wear of P/2 and M/3). All the teeth, except the incisors, are retained, and the right half of the jaw is complete except the coronoid process and the condyle. The occlusal plane and the lower border of the mandible are only slightly convergent forwards. The anterior border of the vertical ramus ascends less steeply than in most Rhinos. Although the condyle is missing, it can be seen that the vertical ramus was not very high. The lower border of the mandible is but weakly convex, but is strongly bent upwards below P/2. The teeth are much worn. There is a well-marked cingulum along the labial side of P/2, but it is weaker on the other premolars, and reduced to the antero-labial corner on the molars. Anteriorly, the mandible consists chiefly of the two weakly divergent sheaths of the lower tusks, themselves absent. Nothing suggests that more than one tooth was present in each alveolus. The section of these alveoli is ovoid, the long axis (30 mm) being oblique (medio-superior to latero-inferior). The two alveoli are only 36 mm apart. From these alveoli it can be seen that the tusks were little recurved and directed at an angle of about 30° above the horizontal plane. The diastema is short, the distance between the anterior root of P/2 and the posterior margin of the alveolus of I/2 being only 60 mm. There is no indication of any alveolus for I/1, and these teeth were certainly absent.

There are two lower incisors in the collection from Pentalophos which, although not exactly symmetrical, might well belong to the aforementioned mandible. The transversal diameter of the left one is 29 mm; that of the right one 27.5 mm. The dorso-ventral diameters are 18.3 and 18 mm, respectively. These tusks are only slightly curved, not very long (132 mm for the right one, which is complete) and the crown itself is short (45 mm; from its conical shape, it is clear that it was not much longer when unworn). The crown is ovoid in section, with a keeled mesial angle, a well-rounded inferior (labial) angle and a weakly convex mesio-labial face. The base of the crown is completely circled with enamel (a difference with most *Chilotherium*).

5) Mandible PNT 12 (Text-fig. 5; Pl. 2, Fig. 3–4)

This is the mandible of a young adult, with P/2–M/1 more or less complete, and only moderately worn. There is no P/1, as in the other specimens, and the diastema is also rather short (less than 60 mm), but its precise length cannot be given, since the alveolar margin of the anterior dentition is not well preserved. Most interesting is this area. The symphysis is broader than on PNT 142; two minute I/1 were probably present near the midline. Lateral to I/1 is a single large ovoid alveolus, transversely elongated. It appears that in fact two teeth were present in each, since the lateral half of the right one is filled by the root, bean-shaped in section, of a tooth leaving mesially a large circular room for the root of a second tooth, of which nothing remains.



Text-fig. 5. *Aceratherium kiliasi* n.sp. Mandible PNT 12. Schematic anterior view. Scale = 10 cm.

6) Maxilla and right mandible PNT 31 (Pl. 2, Fig. 5; Pl. 3, Fig. 1)

These are the remains of a very old individual, since all the teeth are extremely worn. On the maxilla, the predental region is reduced, but we cannot assert the absence of incisors. The posterior border of the nasal notch is located high above the posterior border of P4/. There is a clear, but still relatively shallow, depression in front of the orbit. The only visible features of the teeth are the presence of a crochet and absence of crista on M2/ and M3/, and the presence of an antecrochet on M3/. The horizontal ramus of the mandible is deep and of a regular height, similar to that of PNT 12, and is strongly bent upwards below P/2. The premolars are moderately long. M/3 is not too much worn, and it can be seen that the paralophid was long. The symphysial area is similar to that of PNT 12. Three incisors were present on the right half of the mandible. I/1 was a minute tooth; what remains of the crown is conical, without enamel. Lateral to is is a large I/2 (diameters: 26,5 × 23), well preserved and similar to the isolated teeth that we have tentatively associated above with the mandible PNT 14, but less compressed. Another difference is the apparent absence of enamel on the upper face. Laterally and slightly ventrally to it is the section of another tooth (diameters: 20 × 14), bean-shaped with its concave side along I/2. The shape and position of this tooth leave no doubt as to its homology with the external tooth of PNT 12.

It appears, then, that the *Aceratherium* of Pentalophos, in two of the three known symphysis, bore 6 front teeth, a case normally unknown in the Rhinocerotidae (sensu Radinsky, 1969; Prothero et al., 1986) which it doubtless belongs to. The 4 central incisors pose no problem, since they are similar, in size and morphology, to those of other *Aceratherium* species. The absence of the minute I/1 on the third mandible can also easily be explained by intraspecific variation.

Table 2. Mandibular measurements of *Aceratherium kiliasi* n. sp.

	PNT 31 (paratype)	PNT 142	PNT 12
Length of diastema	70	60	50
Length from rear of jaw to P/2	—	445	—
Height below M/3	114	100	—
Height between P/4 and M/1	~ 110	95	80
Greatest anterior width	~ 122	90	110
Length of lower tooth-row	212	255	—
Premolar length	93	120	90
Molar length	120	138	—
Diameters of I/2	26×23	(29×18 ?)	—

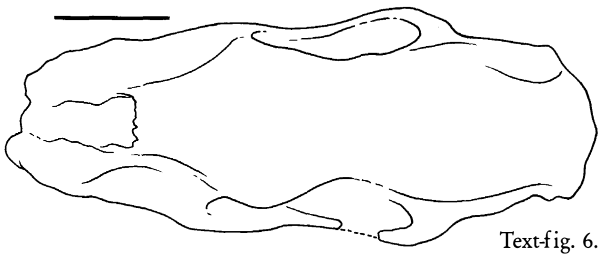
This leaves us with the most external tooth. We believe that it is impossible to consider it as an I/3 or canine for two reasons. First, this tooth was probably absent on PNT 142, and it seems most unlikely that an I/3 or C, which was certainly less tusk-like than I/2, would have been more affected by sexual dimorphism; on the other hand, it is too large (contrary to I/1) to be suppressed just by intraspecific variability. Secondly, the occurrence of an I/3 or canine in a well-characterized Rhinocerotidae would imply either a complete upsetting of the phylogeny of the family, or the atavistic reappearance of a tooth lost 10 million years earlier, both events that we consider unnecessary or unlikely.

We thus believe that this external tooth is in fact a persisting dI/2, even though it is still present in a very old individual. Examination of the recent asiatic species (the only ones with functional anterior dentition) shows that the relative position of the incisors is exactly the same: when I/2 erupts, the alveolus of dI/2 is bean-shaped in section, lateral and slightly inferior to that of I/2.

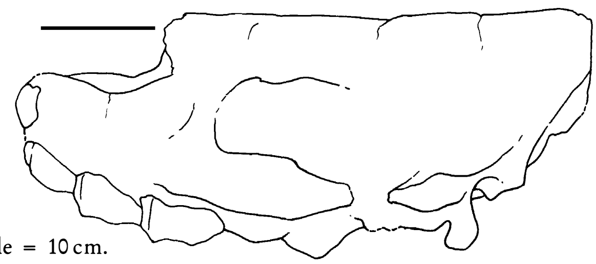
The reasons for this late persistance of dI/2 remain to be established. Since, unfortunately, this tooth is known only by its alveolus, it is impossible to suggest any functional interpretation, all the less than we do not even know whether the upper incisors were present or not. The meaning of the difference between the mandibles PNT 12 and 31, on the one hand, PNT 135 on the other, can neither be satisfactorily explained; sexual dimorphism would be a likely hypothesis but only a more abundant material could confirm it.

7) Associated skull and mandible PNT 95 (Text-fig. 6–7)

These specimens are from a very young animal. Only the milk molars are visible; dP4/ is very little worn, its metaloph still unworn, as is the posterior lobe of dP/4. The occipital condyles, the maxillae and most of the nasals are missing. The posterior end of the nasal opening is situated above the posterior half of dP3/. The supra-orbital processes are strong; there is no post-orbital process. The fronto-parietal area is flat. The post-glenoid process is transversely flattened and bent forwards.



Text-fig. 6. *Aceratherium kiliasi* n.sp. Juvenile skull PNT95. Upper view. Scale = 10 cm.



Text-fig. 7. *Aceratherium kiliasi* n.sp. Juvenile skull PNT95. Lateral view. Scale = 10 cm.

The maxilla is broken in front of dP2/, but the germ of a P1/ can be seen, embedded in bone. DP2/ to dP4/ are well preserved on both sides. At the lingual end of the protoloph, the protocone assumes the shape of an antero-posteriorly directed lingual wall, tending to close the median valley. On dP2/ only, the protocone is isolated. On dP4/ only, an antecrochet can be seen parallel and labial to it, but still lingual to the long crochet. There is no crista, but since the crochet is long enough to reach the protoloph, the medifossette is closed.

On the mandible, dP/1 is very small and conical. The valleys are U-shaped; the posterior valley is deeper than the anterior one. There is a well developed cingulum at the antero-external corner. There is no third (anterior) lobe on dP/3.

8) Comparisons

The systematics and evolution of the acerathere Rhinoceroses is extremely confused, no cladistic analysis of them having ever been attempted. Few skulls have been adequately described, many species and even genera have been named after only a few teeth or even limb bones and the validity of the characters used is seldom discussed. As a result, many species (not to talk of the specimens themselves) have been wandering among several ill-defined genera. At the present time, we do not know what are *Plesiaceratherium*, *Dromoaceratherium*, *Mesaceratherium*, because these genera have never been correctly defined. Because of this confusion, we believe that it would be meaningless to insert the

Pentalophos *Aceratherium* in a complete cladogram or evolutionary scenario, and we will only compare it with the genera said to occur in the european upper Miocene, *Aceratherium* s. str. and *Chilotherium.*

Aceratherium is represented in the upper Miocene by 3 species, *A. incisivum*, *A. tetradactylum* and *A. simorrense.*

The species *Rhinoceros incisivus* was erected by CUVIER (1822) for an upper I1/ from Germany. The precise locality is unknown but according to HEISSIG (1969), it might be the locality of Weisenau, which contains two fossil sites, belonging to zones MN 1 and MN 9 (GUÉRIN, 1980: 374). The genus *Aceratherium* KAUP, 1832 was founded on this species. Whatever the type-locality is, it is clear that no other specimen can confidently be assigned to this species, and not even to this genus. However, a long use has consecrated this binomial, with the material from Eppelsheim described by KAUP (1832, 1834) as chief reference. Since no direct comparative description of the Eppelsheim material can be found in the literature, we will start with it.

a) Comparison with *A. incisivum* from Eppelsheim

1 — Skull

Most of the Rhinoceroses from Eppelsheim are housed in the Hessisches Landesmuseum, Darmstadt, and there are also some specimens in other museums. The first important point, which seems not to have been previously noticed, is that KAUP's figures of the skulls are grossly incorrect, in spite of their apparent accurateness. It is astonishing and pitiful that these misleading drawings have repeatedly been used, for more than 150 years, to illustrate two of the most central Rhinoceroses species of the upper Miocene (the other one being *Dihoplus schleiermacheri*).

Not all the specimens figured by KAUP are still preserved. Only a few limb-bones remain, and D. G. could not find the skull figured by KAUP, 1834, pl. X, fig. 2 a. The skull figured by KAUP, pl. X, fig. 2 b, is still in good condition, except for the maxillary area, which has been very imperfectly restored. The tooth characters are well observable on a tooth-row from Eppelsheim in the BM (NH), M233.

From the Vienna basin a beautiful skull from Prottes is housed in the NHMW as well as a complete palate from Inzersdorf but they have not been published and their specific identity with the Eppelsheim species is doubtful.

The skull from Eppelsheim is about the same size as those from Pentalophos. The skull roof is similar, in lateral as well as in upper view. GUÉRIN (1980: 207) doubted the presence of a frontal horn first mentioned by OSBORN (1899) but a horn, at least in a rudimentary form, was indeed certainly present, as shown by a roughened area, located, as in the two-horned Rhinoceroses, at the anterior end of the frontal bone, slightly extending onto the nasals. In upper view, the nasals of the Eppelsheim skull are shorter; they sharply decrease in width immediately in front of the supra-orbital processes and then assume an almost regular width for about half their length, before tapering to their tips, completely devoid of any trace of horn. In the Pentalophos skulls, instead, the width of the nasals decreases regularly forwards. The nasal notch is not V-shaped as in the Pentalophos skulls and in KAUP's incorrect drawing, but U-shaped, and is as much internal as anterior relative to the orbital margin (about 45 mm in both directions); between them is a deep ante-orbital depression (similar to the canine fossa of the anthropologists).

There are some other differences between the skulls. At Eppelsheim, the post-orbital processes are better developed, the supra-orbital ones less so; the anterior part of the zygomatic arch is much higher: about 85 mm instead of less than 60 at the level of the lower post-orbital process. The mastoid area is similar: a true mastoid exposure is almost certainly present. The position of the anterior border of the orbit cannot be determined on the Eppelsheim skull. On the BM(NH)M233 maxilla, it was certainly more anterior (above the limit between M1/ and M2/) than at Pentalophos.

The same characters can be seen on an incomplete maxilla with very worn teeth, HLMD 96–1–96 in Darmstadt, erroneously labelled *R. schleiermacheri* (as shown by the shape of the root of the zygomatic arch and by the angular lower border of the orbit). The maximum height of the zygomatic arch is 86 mm, and the beginning of a deep depression can be seen in front of the orbit.

2 — Mandible

In Darmstadt there are two mandibles from Eppelsheim showing some very clear-cut differences. The following are the main ones which distinguish *A. incisivum* from *Dihoplus schleiermacheri:* the symphysial portion and the incisors are much stronger; the tooth-row is shorter, but the premolars are relatively longer; the horizontal ramus is of regular height, the ascending ramus is narrow and high, the condyle is much more elevated above the level of the occlusal plane (a feature correlated with the different shape of the skull, and especially the direction of the zygomatic arch). In both species the lower border of the mandible is gently convex (and not at all concave as in KAUP's figure of *D. schleiermacheri*).

Unfortunately, these features are not so well segregated in the other, less complete, mandibles, housed in Darmstadt or in the BM(NH). Several constant differences could probably be found, should more numerous complete mandibles become available, but at the present time, the only reliable ones seem to be the relative proportions of the premolars and molars and perhaps the height of the vertical ramus. We are unable to confirm the validity of some often-mentioned criterions, such as the external cingulum, or the length of the paralophid, but they may well be valid as a rule. It is likely that the sexual dimorphism plays an important role in such features as the height of the horizontal ramus, the proportions of the symphysis, or strength of the tusks. We did not observe a single specimen reminding the very peculiar front dentition of the Pentalophos *Aceratherium*, but this area is but seldom preserved.

3 — Dentition

To be meaningful, the comparisons must be limited to those dentitions which are reliably specifically determined. They are the ones which can be distinguished from *Brachypotherium*, from *D. schleiermacheri* and from the dwarf Rhino present at Eppelsheim.

The upper front teeth are not known with certainty (except, of course, the type-specimen of *Aceratherium incisivum*), since none was found in association with a skull. One can even question their occurrence.

On the mandible figured by KAUP (1834, pl. XIV, fig. 9), 4 incisors were present. Only the alveoli of the minute central ones are retained. The I/2 are probably almost 300 mm long, and their maximum diameters are 44×33 mm. They are thus much longer than those from Pentalophos. The enamel is thin, but present on the lingual (upper) face. An isolated specimen, Din 1921, almost as strong (length: 235 mm; 38×25 in section), shows no enamel on this face, as in *Chilotherium*. In Darmstadt and London, there are several other incisors, but we cannot tell whether the smaller ones represent the females of *A. incisivum*, or *D. schleiermacheri*, or both species.

The upper premolars of *A. incisivum* always bear a well-developed crochet and usually also a crista, which can however be almost absent (BM M233). There may be an enclosed medifossette on P4/: this appears to be the case on the skull, assuming that KAUP's figure 5, pl. XIV (1834), is correct (the teeth can no longer be studied). The internal tubercles may remain separated until late in wear, or they main be joined by a narrow bridge (KAUP, 1834, pl. XIV, fig. 5; and several isolated teeth), but they are never fused, contrary to *D. schleiermacheri*. The metaloph is about as long as the protoloph, and the cingulum is usually weak on the internal side, being chiefly present at the entrance of the median valley.

On the molars, the antecrochet is always present, although sometimes weak. It is never recurved lingually as in *Chilotherium*, but in one specimen (HLMD Din 2159) a low crest, produced from its posterior end, runs along the bottom of the median valley as far as its lingual entrance. The flattening of the lingual wall of the protocone is a well-known feature of *A. incisivum*, but is not peculiar to this species. In sum, only the front teeth are noticeably different from those of Pentalophos.

b) Comparisons with other sites

From Montredon (MN 10), GUÉRIN (1980) has described and illustrated as *A. incisivum* an incomplete skull with complete upper dentition (GUÉRIN, 1980, pl. VIII, fig. A). All the features of the Eppelsheim species are present, and there is no reason to doubt GUÉRIN's determination.

On the contrary, *Dicerorhinus belvederensis* WANG, 1929, included into *A. incisivum* by GUÉRIN (1980), differs from the Eppelsheim and Pentalophos species by several features of the premolars: the cingulum is strong and continuous on the lingual side, the metaloph is decidedly shorter than the protoloph. These features recall more the earlier species of *Aceratherium*.

From Pikermi, we have seen the only known specimen from this site, a mandible in the MNHNP, figured by GAUDRY (1862–67, pl. 33, fig. 6). The diastema is rather short (length between P/2 and I/2: 35 mm). The I/2 are very close to each other, and there was no I/1. The outline of the section of the large I/2 at the crown-root junction is less flattened (39×33 mm) than in the Pentalophos specimens, but more similar to the Eppelsheim ones (compare Mermier, 1895, figs. 7 and 8). We believe that this material is too poor for a specific determination.

From Samos no *Aceratherium* is currently recognized and all the specimens that we have seen belong to *Chilotherium* or to horned species. However, the associated skull and mandible figured by Weber (1905, pl. X, figs 1–2) as *Aceratherium samium* (which we hereby select as lectotype) may well have been correctly generically identified by him, although this species was included in *Chilotherium* by Ringström (1924) and Heissig (1975). The specimen is now probably lost, but the following features, taken from Weber's description and figures, seem to preclude an assignment to *Chilotherium*:

— the frontal is "etwas gewölbt", and not flat or even concave as in *Chilotherium*; as a result, the orbit is not quite so high as in this genus.
— Weber's figures clearly show the presence of a supra-orbital process, and the weakness of the post-orbital one. This is in sharp contrast to *Chilotherium*, where the latter are always strong.
— the front part of the lower jaw is missing, but 32 mm forward of P/2 there is no trace of the root of any incisor, suggesting that the specimen "nur sehr kleine Incisiven hatten". On the contrary, the I/2 of *Chilotherium* are always strong, their minimum length being about 15 cm (Ringström, 1924: 38). Weber did not mention any broadening of the mandibular symphysis, so conspicuous in *Chilotherium*.
— the teeth are much worn, but they show no important difference from those of *Aceratherium*. None of the autapomorphic features of *Chilotherium* is visible.

We thus believe that *Aceratherium samium* Weber is a true *Aceratherium*, showing numerous similarities with the Pentalophos species, although the loss of the lectotype forbids a formal specific identification.

From Maragheh only 3 Rhinoceros species have been described. *Ceratotherium neumayri* (Osborn, 1900), a Dicerotine, and *Iranotherium morgani* (de Mecquenem, 1905), an Elasmothere, are rare, but *Chilotherium persiae* (Pohlig, 1886) is a common species. Furthermore, in the NHMW is housed the lower part of a Rhinocerotid skull not belonging to any of the previous species. It is not numbered, but according to its label originates from Kopran, that is, from the lower levels of the Maragheh succession (Bernor, 1986). All the teeth are present, except the right foremost one. The M3/ are not erupted yet, nor the dP4/ shed. The teeth are completely different from those of *Iranotherium* or *Chilotherium* and need only be compared with those of *C. neumayri*.

The premolars are broad relative to their length, and relative to the molars (P3/ is broader than M1/). There is a vertical groove on the anterior wall of the protoloph of P3/, P4/, DP4/, M1/, M2/, and also on the posterior wall of DP4/–M2/: the protocone is thus well recognizable as a distinct entity. These teeth (except perhaps P4/, on which this area is still hidden by DP4/) bear a clear antecrochet, much shorter, however, than in *Chilotherium*. On M1/ and especially M2/, the crochet is stronger than in any upper Miocene horned Rhinoceros. The basicranial area is shorter than in *Ceratotherium neumayri* but is also very narrow: the width (167 mm, perhaps slightly underestimated) over the post-tympanic processes (little expanded laterally) is not much greater than the estimated length M1/–M3/: this single character shows that the skull cannot belong to a horned Rhinoceros.

There are some differences from most *Aceratherium incisivum* and from the *Aceratherium* of Pentalophos: The cingulum is strong all around the lingual side of the premolars and is also well marked on the molars; the metaloph of P3/ and P4/ is much shorter lingually than the protoloph. These characters recall *"Dicerorhinus" belvederensis* Wang, but this species is slightly smaller, and the premolars are narrower.

In sum, we can say that a previously unrecorded species of *Aceratherium* is present at Maragheh, but that its precise specific identification cannot be given at the present time.

A. tetradactylum Lartet, 1836, is chiefly known from Sansan, but has also been mentioned in other localities, many of them belonging to zone MN 9. The fronto-parietal profile is concave (Guérin, 1980, pl. 3); there is a vestigial sagittal crest; the nasals extend much forward of P1/; there is no ante-orbital depression; the orbit is not much elevated above the tooth-row; the zygomatic arch is strong; on the well-preserved skulls from Sansan (Guérin, 1980, pl. 3–4), the post-glenoid and post-tympanic processes come into contact, but probably without fusion. *A. tetradactylum* is thus very different from the Pentalophos specimens, and more primitive by most of its features.

For *A. simorrense*, no type-specimen was designated by Lartet (1851) but Guérin (1980, pl. 7) figured an incomplete skull from Simorre as lectotype. Some disagreement exists concerning the occurrence of this species at Sansan but according to Guérin (1980), the species ranges from MN 6 to MN 10 and Ginsburg & Guérin (1979) state that the species (or at least its ancestor) immigrated in Europe "au début de la zone MN 3".

The best figures of the upper teeth of this species are of Guérin (1980, pl. 7) from Simorre and of Alberdi et al. (1981) from Spain, and we have also seen the fine incomplete skull from Villefranche d'Astarac in London (BM

M 33525). The species was given sub-generic rank by GINSBURG & GUÉRIN (1979), chiefly on the basis of the upper cheek-teeth characters, but we were unable to find many significant differences from *A. tetradactylum*. The "net pli du paracône" is indeed rather weak on all the above-mentioned specimens; the broad hypocone and the crochet are not different from those of *A. tetradactylum* or *A. incisivum*; a bridge is present on the premolars of BM M 33525 (which therefore do not fit the sub-generic diagnosis of GINSBURG & GUÉRIN, 1979), but sometimes absent, on the contrary, on *A. tetradactylum*; the hypsodonty has been checked on a few specimens only and is a poor basis for sub-generic distinction.

Two possible differences are the overall size (smaller in *A. simorrense*, but this could perhaps be explained by intraspecific variation) and the position of the orbit, more backwardly situated in the London specimen of *A. simorrense* than in *A. tetradactylum*. Not much can be said of the limb characters. *A. simorrense* is said by GINSBURG & GUÉRIN (1979) to have a tridactyl fore-foot, and by GUÉRIN (1980) to have short metapodials, what is, however, at variance with LARTET's original description "membres grêles et os des pieds très-longs".

Chilotherium RINGSTRÖM, 1924, is chiefly known from China, Maragheh and Samos. Its main differences from the above-mentioned species are:

— there is a strong post-orbital process
— the upper border of the orbit is at the same level as the skull roof
— the articulation between skull and mandible is rather low
— there are no upper incisors
— the cheek-teeth are high and covered with cement
— the lower incisors are strong and very wide apart
— the antecrochet is very strong.

The first character is plesiomorphic.

The last two characters are autapomorphic among the Rhinocerotidae and suffice to define the genus.

The other characters are more or less present in the *Aceratherium* of Pentalophos. They probably indicate a close phyletic relationship between the two taxa, which are, however, clearly distinct in the morphology of the front lower teeth. RINGSTRÖM (1924) has shown that the tusks of *Chilotherium* are permanent I/2, since they are preceded by milk teeth; therefore, they are not homologous with the most external tooth of some mandibles of *Aceratherium* from Pentalophos, and the latter cannot be taken as a forerunner of *Chilotherium* for this character.

Finally, according to RINGSTRÖM (1924), only the subspecies *Chilotherium habereri laticeps* had a mastoid exposure located very low, between the post tympanic and paroccipital processes. We have not seen the Chinese material, but the *Chilotherium* skulls from Maragheh and Samos do not seem to differ fundamentally from *Aceratherium* in this respect: they show a long narrow depression on the occipital.

9) Conclusion on *Aceratherium*

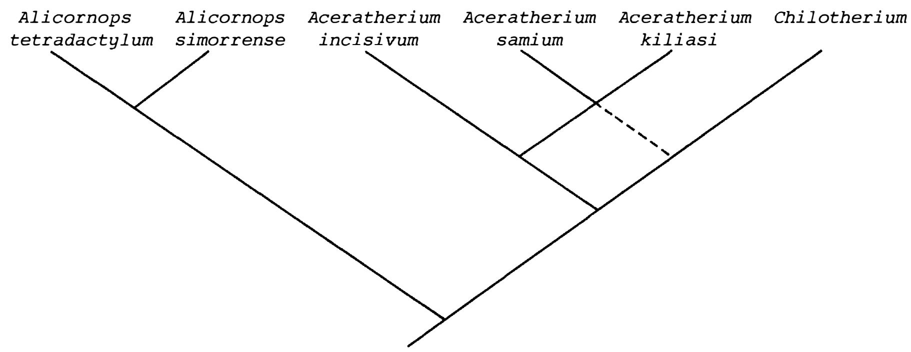
Text-fig. 8 gives the distribution of the main characters in the above-mentioned taxa, which form a monophyletic group, defined by the following apomorphies:

— cranial profile flat or weakly concave;
— nasals short, nasal notch retracted backwards;
— anterior border of orbit more posterior than M^1;
— upper incisors reduced or lost;
— antecrochet present;
— crochet long.

This *Aceratherium-Chilotherium* group, as well as the Aceratheriinae, were both recognized as monophyletic by PROTHERO et al. (1986). Although a revision of the systematics of the Rhinocerotidae is beyond the scope of this paper, we must note that most of the characters used by these authors to define the Aceratheriinae are either doubtful or of very limited value (strength of the parasagittal crests, of the firth metacarpal, loss of I1/) or even erroneous (we can see no difference between the Aceratheriinae and the horned Rhinoceroses in the flange of I/2, nor in the divergence of these teeth, nor in the fusion of the nasals, which is completed only in old horned Rhinoceroses with strong nasal horns, nor in the possession of a terminal horn, which has recently been discovered in a *Chilotherium* by QIU & YAN, 1982, nor in the length of the diastema, which, as we have seen above, can be very short in some *Aceratherium*).

	Al. tetradactylum	*Ac. incisivum*	*Ac. samium*	*Ac. kiliasi*	*Chilotherium*
Nasals shortened	□	■	■	■	■
Nasal notch shifted backwards	□	◩	◩	■	■
Nasal horn present	□	□	○	○	◩
Premaxilla reduced	□	■	■	■	■
Ante-orbital depression present	□	■	◩	◩	□
Orbit shifted backwards	□	◩	■	■	■
Orbit high above tooth-row	□	□	◩	◩	■
Supra-orbital process developped	□	◩	◩	■	□
Post-orbital process reduced	□	◩	■	■	□
Sagittal crest lost	□	◩	■	■	■
Sub-aural fusion	◩	□	○	□	□
Articulation skull/mandible low above occlusal plane	□	□	□	◩	■
Antecrochet very long	□	□	□	□	■
Lower incisors reduced	□	□	■	■	□
dI/2 long persisting in ?males	□	□	○	■	□
Symphysis broadened	□	□	□	□	■

Text-fig. 8. Distribution of the apomorphic characters among the upper Miocene eurasiatic Aceratheriinae. Black squares: derived condition; black and white squares: partially derived or variable condition; open squares: primitive conditions; open circle: condition unknown.



Text-fig. 9. Hypothesis of phylogenetic relationships among the upper miocene eurasiatic *Aceratherium*.

The cladogram of Fig. 9 suggests the possible relationships between the various species of *Aceratherium* and *Chilotherium*. We include in *Aceratherium: A incisivum* CUVIER, *A. samium* WEBER and *A. kiliasi* n. sp. Since the branching order is somewhat doubtful, this genus might be paraphyletic; it shares with *Chilotherium* many synapomorphies whose ancestral conditions are retained in *"A." tetradactylum*. This latter species should, in our opinion, be kept in a separate genus, together with the doubtfully distinct *"A." simorrense*. The name of this genus is therefore *Alicornops* GINSBURG & GUÉRIN, 1979.

The diagnosis of *Aceratherium* and of *A. kiliasi* n. sp. are given below.

Genus *Aceratherium* KAUP, 1832

Type-species: *Rhinoceros incisivus* CUVIER, 1822.

Diagnosis (the genus being perhaps paraphyletic, the diagnosis includes some characters shared by *Chilotherium*): Rhinocerotidae without horns, or with a small median horn, on the frontal or tips of nasals. Skull narrow in its posterior part, but broad at the supra-orbital processes. Cranial profile usually weakly concave. Nasal notch deep, nasal bones moderately long. Ante-orbital depression present, of variable depth. Zygomatic arch strong, primitively directed upwards, the glenoid cavity being much higher than the occlusal plane. Post-glenoid and post-tympanic processes separate. Upper incisors not well known, moderate, perhaps sometimes absent. Molars usually with strong crochet, no crista, antecrochet always present but not exaggerated. Premolars rather large, with weak crochet and crista, internal tubercles well separated but often with a bridge between them. Cingulum reduced. Main lower incisors not widely separated, symphysis not much enlarged. Horizontal ramus usually of regular depth.

Aceratherium kiliasi n. sp.

Holotype: skull No PNT 135, described above, housed in the Department of Geology and Physical Geography, University of Thessaloniki, Greece.

Paratype: mandible and maxilla, No PNT 31, described above, same whereabouts.

Type-locality: Pentalophos-1, the fossiliferous beds at the bottom of the ravine which marks the south-eastern limit of the village of Pentalophos, 15 km N-W of Thessaloniki, Greece.

Derivatio nominis: From Dr. ADAMANTIOS KILIAS, who found the locality of Pentalophos-1.

Diagnosis: an *Aceratherium* of relatively large size. Cranial profile almost flat, upper border of orbit at the same level as the frontal. Nasal notch V-shaped, ante-orbital depression shallow. Zygomatic arches relatively weak, glenoid cavity not much elevated above tooth-row. Upper incisors unknown, probably reduced or lost. Cement present on premolars and molars. Mandibular symphysis (sexually ?) dimorphic, either of the normal *Aceratherium*-type, or slightly broadened, with long-persisting dI/2, resulting in an hexaprotodont dentition even in old individuals. I/2 small. Diastema short.

Chronologic and geographic extension of the genus *Aceratherium*

The genus *Aceratherium* s. str. as defined above is not known with certainty before the Vallesian. On the other hand, we are aware of no skull of the primitive *Alicornops*-type during the upper Miocene, and it is likely that all the late representatives of these hornless Rhinoceroses belong to *Aceratherium* s. str. or *Chilotherium*, but the west-european specimens are poorly known, although common. The latest specimens are late turolian (Lubéron: GAUDRY, 1893).

From Spain to Greece and the Vienna basin, the genus is widespread in Europe, and we have shown above that it even reached Samos and Maragheh, but probably not much further eastwards, since the Siwalik hornless Rhinoceroses are certainly different. The genus has also often been mentioned from Africa, but GENTRY (1987) has recently questioned these determinations. We fully agree with GENTRY's opinion.

IV) General conclusions

The Rhinocerotid fauna from Pentalophos includes only two species, but their remains are quite numerous compared with the other mammals. This family alone contributed probably to more than half of the total biomass at the worked locality, but the latter is of a very limited extent, and no general conclusion can be drawn, since taphonomic biases might well have resulted in an apparent overrepresentation of this group.

Ecologically, the Rhinoceroses do not provide us with much precise information regarding the amount of tree cover. Both species were probably grazers, but not strictly specialized; the limb-bones are unfortunately virtually absent. Nothing suggests that the environment was different from the open woodland or savannah common in the other greek localities.

Rhinoceroses make a limited contribution to the datation of the site of Pentalophos. *Ceratotherium neumayri* is not known with certainty before the Turolian, but well-preserved vallesian Rhinocerotid skulls have yet to be published outside Germany. The Aceratheres most akin to those of Pentalophos are from an unknown level of Samos (according to WEIDMANN et al., 1984, all the Samos localities are turolian but this is unlikely), and from Prottes in Austria, a locality whose precise age is unknown (F. RÖGL, pers. comm.). Since *Aceratherium kiliasi* n. sp. is more evolved by almost all its characters than *A. incisivum* from Eppelsheim, it can be reasonably assumed that it is more recent. The "best fit", although very imprecise, is between middle Vallesian and middle Turolian, inclusive.

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References

ALBERDI, M. T., GINSBURG, L. & MORALES, J. (1981): Rhinocerotidae del yacimiento de los Valles de Fuentidueña (Segovia). — Estudios geol., **37**: 439–465.

ARAMBOURG, C. & PIVETEAU, J. (1929): Les Vertébrés du Pontien de Salonique. — Ann. Pal., **18**: 59–138.

BERNOR, R. L. (1986): Mammalian biostratigraphy, geochronology and zoogeographic relationships of the late Miocene Maragheh fauna, Iran. — J. Vert. Pal., **6**, 1: 76–95.

BONIS, L. DE, BOUVRAIN, G. & KOUFOS, G. (1988): Late Miocene mammal localities of the lower Axios valley (Macedonia, Greece) and their stratigraphic sigificance. — Modern Geol., **13**: 141–147.

CUVIER, G. (1822): Recherches sur les ossements fossiles. — Dufour et d'Ocagne éd., Paris.

GAUDRY, A. (1862–67): Animaux fossiles et géologie de l'Attique. — Savy éd., Paris.

—,— (1873): Animaux fossiles du Mont Lébéron (Vaucluse). — Savy éd., Paris.

GENTRY, A. W. (1987): Rhinoceroses from the Miocene of Saudi Arabia. — Bull. Br. Mus. nat. Hist. (Geol.), **41**, 4: 409–432.

GERAADS, D. (1988): Révision des Rhinocerotinae (Mammalia) du Turolien de Pikermi. Comparaison avec les formes voisines. — Ann. Pal., **74**, 1: 13–41.

GINSBURG, L. (1974): Les Rhinocerotidés du Miocène de Sansan (Gers). — C.R. Acad. Sc., Paris, (D), **278**: 597–600.

GINSBURG, L. & GUÉRIN, C. (1979): Sur l'origine et l'extension stratigraphique du petit Rhinocerotidé miocène *Aceratherium (Alicornops) simorrense* (LARTET, 1851), nov. subgen. — C.R. somm. Soc. géol. Fr., **1979**, 3: 114–116.

GUÉRIN, C. (1966): *Diceros douariensis* nov. sp., un Rhinocéros du Mio-Pliocène de Tunisie du Nord. — Docum. Lab. Géol. Lyon, **16**: 1–50.

—,— (1980): Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. — Docum. Lab. Géol. Lyon, **79**: 1–1184.

Heissig, K. (1969): Die Rhinocerotidae (Mammalia) aus der oberoligozänen Spaltenfüllung von Gaimersheim bei Ingolstadt in Bayern und ihre phylogenetische Stellung. — Abh. bayer. Akad. Wiss., Math. Nat. Kl., (N.F.), **138**: 1–133.

—,— (1973): Die Unterfamilien und Tribus der rezenten und fossilen Rhinocerotidae (Mammalia). — Säugetierk. Mitt., **21**, 1: 25–30.

—,— (1976): Rhinocerotidae aus dem Jungtertiär Anatoliens. — Geol. Jb., **15**: 145–151.

Hitchins P.M. (1978): Age determination of the black Rhinoceros (*Diceros bicornis* L.) in Zululand. — S. Afr. J. Wildl. Res., **8**: 71–80.

Hooijer, D.A. & Patterson, B. (1972): Rhinoceroses from the Pliocene of Northwestern Kenya. — Bull. Mus. Comp. Zool., **144**, 1: 1–26.

Kaup, J.J. (1832): Über *Rhinoceros incisivus* Cuv. und eine neue Art, *Rhinoceros schleiermacheri.* — Isis, **8**: 898–904.

—,— (1834): Description d'ossements fossiles de Mammifères ... — Heyer, Darmstadt, 3ème cahier: 33–64, atlas: pl. 1–25 + 2.

Lartet, E. (1836): Nomenclature des Mammifères et des coquilles trouvés dans un terrain d'eau douce près de Simorre et de Sansan. — Bull. Soc. géol. Fr., **7**: 217–220.

—,— (1851): Notice sur la colline de Sansan ... Portes, Auch, 42 pp.

Mecquenem, R. de (1905): Le gisement de Vertébrés fossiles de Maragha. — C.R. Acad. Sci., Paris, **141**: 924–925.

Mermier, E. (1895): Sur la découverte d'une nouvelle espèce d'*Aceratherium* dans la molasse burdigalienne du Royans. — Ann. Soc. Linn. Lyon, (N.S.), **42**: 163–169.

Osborn, H.F. (1899): Frontal horn of *Aceratherium incisivum.* Relation of this type to *Elasmotherium.* — Science, (N.S.), **9**, 214: 161–162.

—,— (1900): Phylogeny of the Rhinoceroses of Europe. — Bull. Ann. Mus. Natur. Hist., **13**: 229–267.

Pohlig, H. (1886): On the Pliocene of Maragha, Persia ... — Quart. J. Geol. Soc. London, **42**: 177–182.

Prothero, D., Manning, E. & Hanson, C.B. (1986): The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla). — Zool. J. Linn. Soc., **87**: 341–366.

Qiu Zhan Xiang & Yan Defa (1982): A horned *Chilotherium* skull from Yushe, Shansi. — Vert. Palasiat., **20**, 2: 130–132.

Radinsky, L.B. (1969): The early evolution of the Perissodactyla. — Evolution, **23**, 2: 308–328.

Ringström, T. (1924): Nashörner der *Hipparion*-Fauna Nord-Chinas. — Pal. sin., (C), **1**, 4: 1–156.

Thenius,, E. (1955): Zur Kenntnis der unterpliozänen *Diceros*-Arten (Mammalia, Rhinocerotidae). — Ann. Naturhist. Mus. Wien, **60**: 202–211.

Toula, F. (1906): Das Gebiss und Reste der Nasenbeine von *Rhinoceros (Ceratorhinus* Osbsorn) *hundsheimensis.* — Abh. k. k. Geol. Reichs-Ausz., **20**, 2: 1–38.

Wang, K.M. (1929): Die fossilen Rhinocerotiden des Wiener Beckens. — Mem. Inst. Geol. Shanghai, **7**: 53–59.

Weber, M. (1904–05): Ueber tertiäre Rhinocerotiden von der Insel Samos. — Bull. Soc. Imp. Natur. Moscou, **17**, 4: 477–501 (1904); **18**, 4: 344–363 (1905).

Weidmann, M., Solounias, N., Drake, R.E. & Curtis, G.H. (1984): Neogene stratigraphy of the eastern basin, Samos Island, Greece. — Geobios, **17**, 4: 477–490.

Explanations of the plates

Plate 1

Ceratotherium neumayri

1: sub-adult skull, PNT 143, basal view. 2: same specimen, lateral view. 3: juvenile skull, PNT 144, basal view. 4: same specimen, lateral view. Scale: 10 cm for all figures.

Plate 2

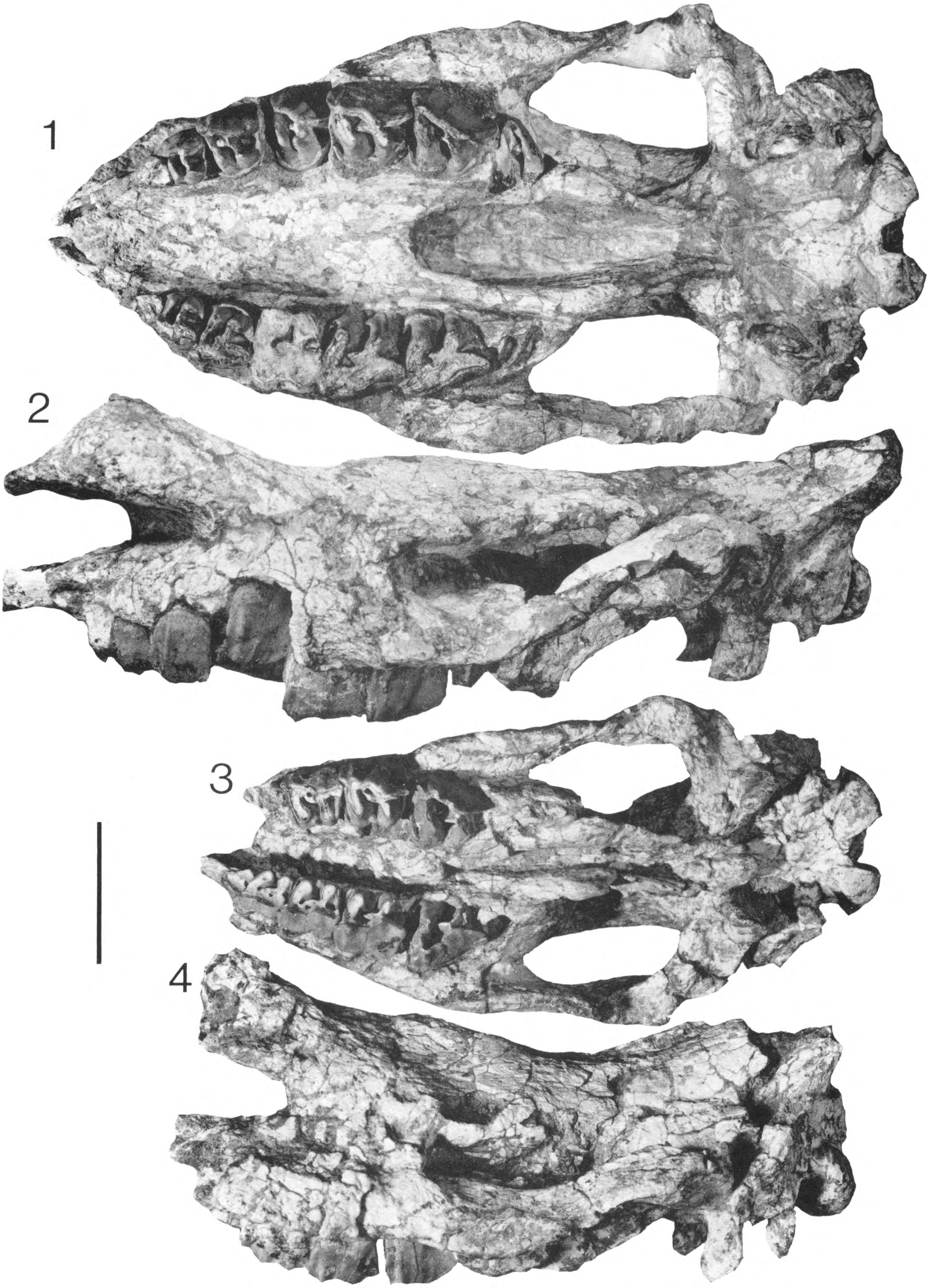
Aceratherium kiliasi n. sp.

1: skull PNT 135 (holotype), upper view. 2: same specimen, lateral view. 3: mandible PNT 12, lateral view. 4: same specimen, occlusal view. 5: mandible PNT 31 (part of paratype), lateral view. Scale: 10 cm for all figures.

Plate 3

Aceratherium kiliasi n. sp.

1: mandible PNT 31 (part of paratype), oblique anterior view; c. a. nat. size. 2: mandible PNT 142, antero-superior view. 3: same specimen, occlusal view. 4: upper tooth-row of skull PNT 135 (holotype), occlusal view. 5: same specimen as fig. 2 and 3, lateral view. Scale: 5 cm for each figure.



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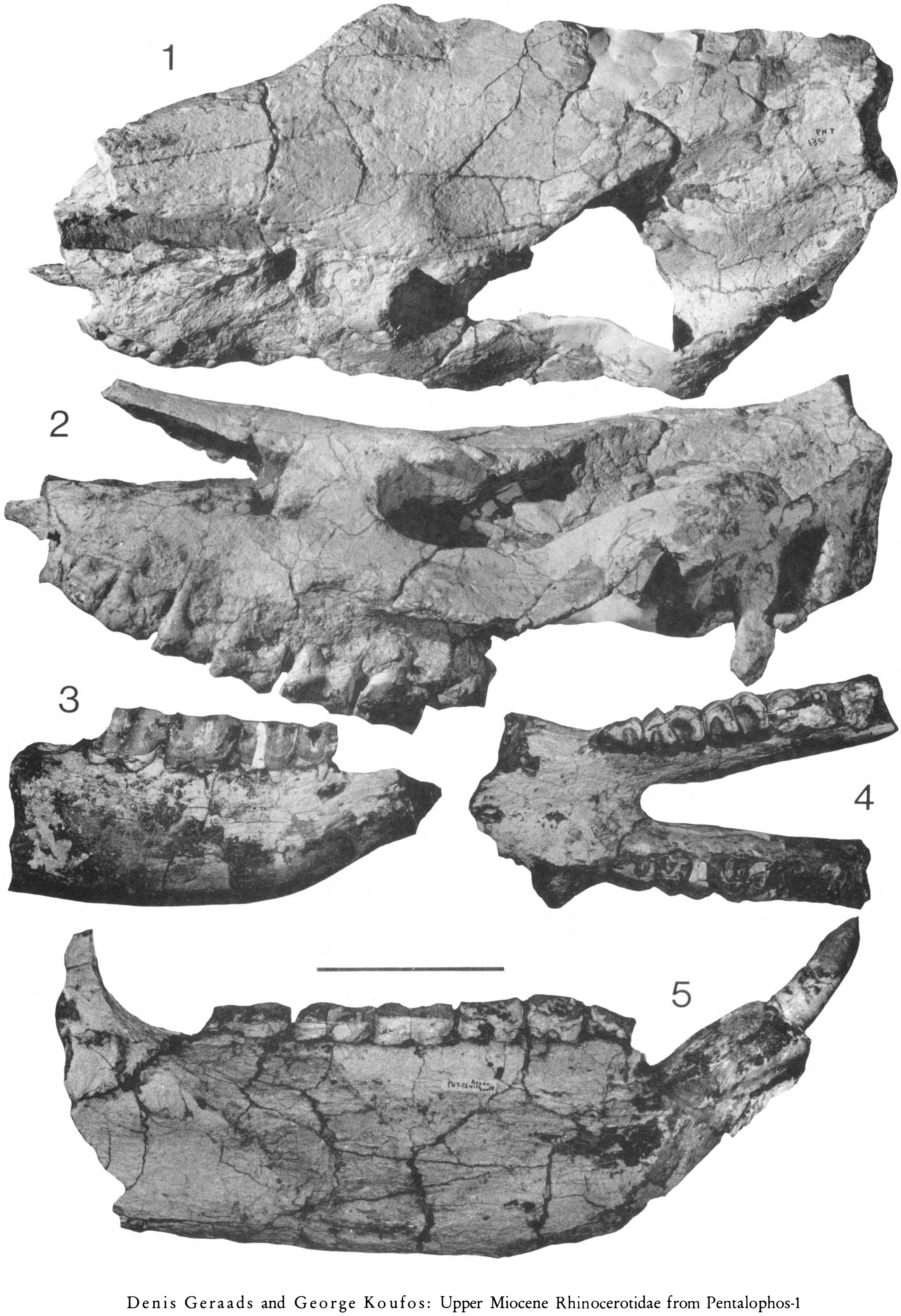

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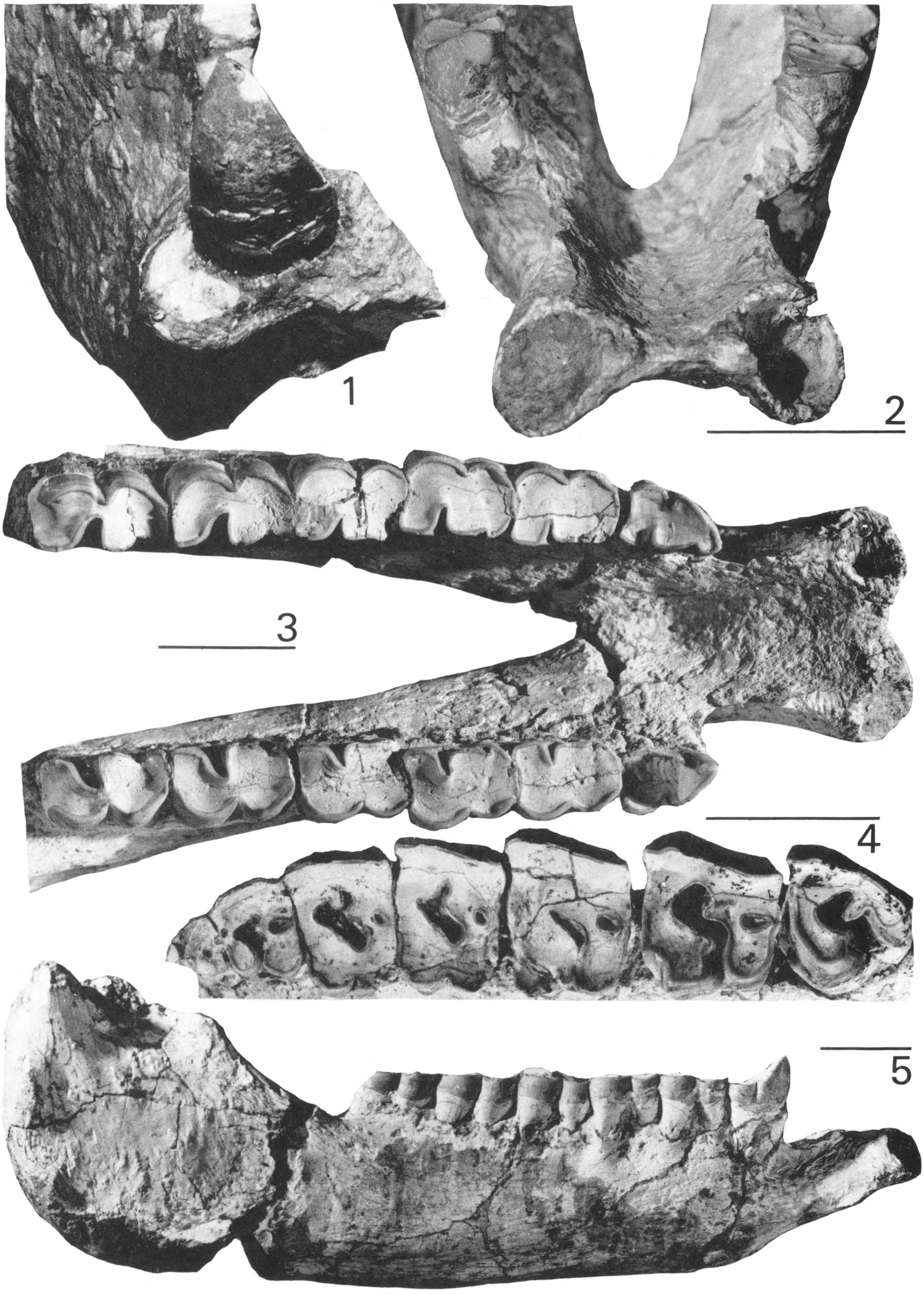

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