

Late Miocene horned rhinoceroses (Rhinocerotinae, Mammalia) from Kerassia (Euboea, Greece)

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With 4 figures and 5 tables

GIAOURTSAKIS, I., THEODOROU, G. ROUSSIAKIS, S., ATHANASSIOU, A. & ILIOPOULOS, G. (2006): Late Miocene horned rhinoceroses (Rhinocerotinae, Mammalia) from Kerassia (Euboea, Greece). – N. Jb. Geol. Paläont. Abh., **239**: 367–398; Stuttgart.

Abstract: Recent systematic excavations near the village of Kerassia (Northern Euboea) have yielded a diverse mammal fauna of Late Miocene age. Among the most complete and prominent findings are a juvenile skull and an adult mandible that belong to two different horned rhinoceros species. The juvenile skull from the site Kerassia-3 (K3) is assigned to *Ceratotherium neumayri*, while the adult mandible from the plausibly isochronous site Kerassia-4 (K4) belongs to *Dihoplus pikermiensis*. These new specimens are compared with the known Eastern Mediterranean rhinocerotid record, which is briefly reviewed and updated. The potential interspecific interaction of both species is discussed. Most Eastern Mediterranean localities have yielded only one tandem-horned rhino. In localities with ample material (Pikermi, Samos), where both species are present, one of them is more abundant, signifying a clear interspecific dominance. *D. pikermiensis* must have preferred temperate forested habitats, whereas the more specialized *C. neumayri* more open habitats. For the cases of sympatry, a marked resource partitioning is suggested, not excluding some territorial interaction by water resources or at the boundaries of mixed habitats. A partial dietary competition in these cases cannot be excluded, as well.

Key words: Rhinocerotidae, Rhinocerotinae, *Ceratotherium*, *Dihoplus*, Late Miocene, Kerassia, Euboea, Greece.

Zusammenfassung: Systematische Ausgrabungen, die während den letzten Jahren in der Nähe des Dorfes Kerassia (Nördliches Euböa) ausgeführt wurden, haben eine artenreiche obermiozäne Säugetierfauna geliefert. Unter den am besten erhaltenen

Funden befinden sich der Schädel eines juvenilen und der Unterkiefer eines erwachsenen Tieres, die zu zwei verschiedenen Nashornarten gehören. Der juvenile Schädel aus der Fundstelle Kerassia-3 (K3) wird als *Ceratotherium neumayri* bestimmt, während der Unterkiefer aus der etwa gleichzeitigen Fundstelle Kerassia-4 (K4) zu *Dihoplus pikermiensis* zu stellen ist. Die neuen Funde werden mit dem bekannten Material aus dem östlichen Mittelmeerraum verglichen. Die potentielle paläoökologische Wechselwirkung beider Arten wird besprochen. Die meisten ostmediterranen Fundstellen haben nur eine doppelhornige Nashornart geliefert. An Fundstellen mit reichem Material wie Pikermi und Samos, wo beide Arten anwesend sind, ist eine der beiden Arten häufiger, so dass eine klare artliche Dominanz anzunehmen ist. *D. pikermiensis* hat wohl gemäßigte Wälder vorgezogen, während das stärker spezialisierte *C. neumayri* mehr offene Lebensräume bevorzugt haben muss. Wo beide Arten sympatrisch vorkommen, ist eine unterschiedliche Ernährungsweise anzunehmen, ohne dass eine beschränkte territoriale Wechselwirkung und Nahrungskonkurrenz ausgeschlossen werden kann.

Schlüsselwörter: Rhinocerotidae, Rhinocerotinae, *Ceratotherium*, *Dihoplus*, Obermiozän, Kerassia, Euböa, Griechenland.

1. Introduction

Euboea is a large island of central Greece, which is separated from the mainland by a narrow sea channel. The island is covered by extensive Neogene, primarily continental, deposits that overlay Mesozoic sedimentary and igneous rocks of the Pelagonian geotectonic unit. KATSIKATSOS et al. (1981) group the main occurrences of the Neogene deposits of Euboea in three major sedimentary basins: the Aliveri-Kymi basin, the Paliouras-Gides basin and the Limni-Istiea basin. The locality of Kerassia is situated in the middle of the Limni-Istiea basin, which occupies the northernmost part of the island (Fig. 1). The fossil bone beds of Kerassia were tracked down by R. W. KÖHLER in 1981, during geological fieldwork in the area (KÖHLER 1983). However, fossil bones have been known to local people since 1966, after a new road was cut north of the village. The first excavation was carried out in 1982 by HANS DE BRUIJN, ALBERT VAN DER MEULEN (University of Utrecht) and CONSTANTIN DOUKAS (University of Athens). This was not followed by other fieldwork until 1992, when the University of Athens began new systematic field studies in the locality (THEODOROU et al. 1995, 2003). Until now, seven fossil mammal sites have been discovered at Kerassia, namely K1-K7. The site of the 1982 excavation (KER) quite plausibly

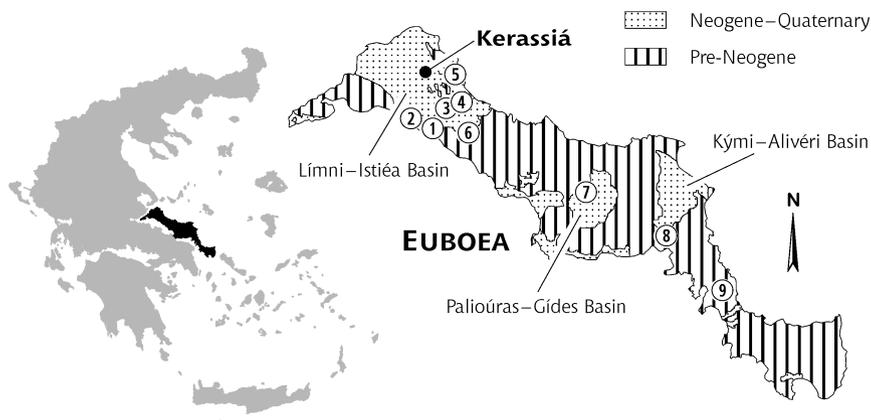


Fig. 1. Simplified geological map of Euboea Island (based on KATSIKATSOS et al. 1981), showing the three major Neogene sedimentary basins of the island, as well as the geographical position of the Kerassia and the other known Neogene mammal localities of Euboea: 1: Limni, 2: Rhovies, 3: Palaeovrissi, 4: Hagia Anna, 5: Achladi, 6: Prokopi, 7: Eria, 8: Aliveri, 9: Halmyroptamos.

coincides with K1. The bone bearing layers are reddish-brown fluvial deposits that belong to the upper sequence of the Limni-Istiea Basin (METTOS et al. 1991). The lower sequence, as well as the ophiolitic basement, are exposed NE of the village Kerassia. The reddish-brown fluvial deposits include clays, conglomerates, sands, and siltstones in succession. Based on sedimentological and geochemical data, two fossiliferous horizons were identified in Kerassia, an upper one and a lower one. The upper fossiliferous level comprises the sites K1 (including KER) and K6 and the lower one the sites K2, K3, and K4. The relative position of K5 and K7 is currently under study. Additional information about the excavation history and the geological setting of the locality is provided by THEODOROU et al. (2003) and ILIOPOULOS (2003).

The fossil fauna of Kerassia is rich and diversified, comprising (sites K1-K7, both levels) Carnivora (*Machairodus giganteus*, *Metailurus parvulus*, *Adcrocuta eximia*, cf. *Ictitherium pannonicum*, *Plioviverrops* sp.), Proboscidea (*Deinotherium* sp., *Tetralophodon* cf. *longirostris*, *Choerolophodon* sp.), Artiodactyla (*Microstonyx major erymanthius*, *Palaeotragus rouenii*, *Palaeotragus* sp., *Helladotherium duvernoyi*, *Bohlinia attica*, *Samootherium major*, *Tragoportax* cf. *amalthea*, *Gazella* sp., *Dorcatherium* sp.), Perissodactyla (*Hipparion* sp., *Ceratotherium neumayri*, *Dihoplus pikermiensis*, *Ancylotherium* sp.), Tubulidentata (*Orycteropus* sp.) and Aves indet. (THEODOROU et al. 2003, ILIOPOULOS 2003, ROUSSIAKIS et al. in press).

Among the most complete and impressive findings are a juvenile skull and an adult mandible that belong to two different horned rhinoceros species described here. The presence of fossil Rhinocerotinae in Kerassia was previously indicated in two preliminary reports (THEODOROU et al. 1995, 1998), as well as in a more detailed overview on the herbivores of the locality (THEODOROU et al. 2003).

2. Material and Methods

The material from Kerassia, including that of the 1982 excavation, is stored in the collections of the Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens (AMPG). Comparative study with material from Pikermi and Samos (Greece) was conducted in the collections of AMPG, BSPG, SMF, HLMD, SMNK, NHMW, IPUW, and NHML. The material from Halmyropotamos (Euboea, Greece) is housed in AMPG, from Pentalophos-1 (Macedonia, Greece) in LGPUT, from Eppelsheim (Germany) in HLMD and from Maragheh (Iran) in NHMW. Material of the extant rhinoceros species was also used for comparison at the zoological collections of the aforementioned Museums and Institutes.

The skull and mandibular measurements follow GUÉRIN (1980). Dental measurements and terminology follow PETER (2002). Width measurements include, however, the anterior (W_A) as well as the posterior (W_P) maximal width of each tooth. On the first upper and lower teeth only one maximal width (W_P) is measured. Measurements ranging 0-150 mm were taken with a digital calliper to 0.01 mm and rounded to the nearest 0.1 mm. For larger measurements a linear calliper with a precision of 0.1 mm was applied. All measurements are given in millimetres (mm).

Suprageneric taxonomy follows partly HEISSIG (1999) in recognizing two tribes within the subfamily Rhinocerotinae OWEN, 1845: Rhinocerotini OWEN, 1845 and Elasmotheriini BONAPARTE, 1845. Within the tribe Rhinocerotini we recognize, however, three subtribes, Dicerorhinina RINGSTRÖM, 1924, Rhinocerotina OWEN, 1845 and Dicerotina RINGSTRÖM, 1924, fol-

lowing partly PROTHERO & SCHOCH (1989); the latter authors consider otherwise Elasmotheriina as a fourth subtribe within Rhinocerotini and not as a separated tribe. Suprageneric arrangements and cladistic analyses proposed for rhinoceroses during the last 25 years are conflicting and controversial. For alternative views compare GUÉRIN (1980, 1989), GROVES (1983), GERAADS (1988), PROTHERO et al. (1989), PROTHERO & SCHOCH (1989), HEISSIG (1989, 1996), CERDEÑO (1995), ANTOINE et al. (2003).

A comment, on the nomenclature of the species is necessary. After ROTH & WAGNER (1854) and GAUDRY (1862-1867), all authors recognize the presence of two different horned rhinoceros species during the Late Miocene in Greece. Here they are referred provisionally to as *Ceratotherium neumayri* (OSBORN, 1900) and *Dihoplus pikermiensis* (TOULA, 1906), following the specific concept and accustomed usage established since GERAADS (1988) (e.g. CERDEÑO 1995, HEISSIG 1996, 1999, KAYA & HEISSIG 2001, GIAOURTSAKIS 2003). The first species has been commonly treated as a close relative of the extant African species *Diceros bicornis* and *Ceratotherium simum*, whereas the second one as a relative of the living Sumatra rhino *Dicerorhinus sumatrensis* (GAUDRY 1862-1867, BRANDT 1878, OSBORN 1900, WEBER 1904, RINGSTRÖM 1924, KRETZOI 1942, THENIUS 1955, HEISSIG 1996, GUÉRIN 1980, 1989, GERAADS 1988, GIAOURTSAKIS 2003). Both species suffer though from complicate nomenclatural issues caused by misidentifications and repeated errors in the past and mainly because the type specimen of *Rhinoceros pachygnathus* WAGNER, 1848, a fragmentary juvenile mandible from Pikermi housed at the BSPG in Munich, belongs actually to "*Stephanorhinus pachygnathus*" (here *Dihoplus pikermiensis*), as noted by HEISSIG (1975). *Rhinoceros pachygnathus* WAGNER, 1848 was the first specific name made available for a fossil rhinoceros from Pikermi, at a time when the presence of two species was not obvious. However, GAUDRY (1862-1867) used WAGNER's name to describe a wealth of complete skulls and postcranial material that belonged primarily to *Ceratotherium neumayri* and not to *Dihoplus pikermiensis* as WAGNER's holotype mandible. Based on GAUDRY's descriptions, later authors have used repeatedly the specific name *pachygnathus* (under the generic names *Rhinoceros*, *Atelodus*, *Pliodiceros* or *Diceros*) to refer to "the extant African rhino relative" from Pikermi (e.g. BRANDT 1878, OSBORN 1900, WEBER 1904, RINGSTRÖM 1924, KRETZOI 1942, THENIUS 1955, PROTHERO et al. 1989, GUÉRIN 1980, 1989). GERAADS (1988) suggested restricting the specific name *Rhinoceros pachygnathus* WAGNER, 1848 only to its type mandible and abandoning it. However, in our opinion a formal nomenclatural act is required to resolve the problem permanently, since the binomen *Diceros pachygnathus* still remains in use (e.g., PROTHERO et al. 1989, GUÉRIN 2000), following the former accustomed usage. Moreover, if priority rules are strictly applied (HEISSIG 1975,

1989), the specific name *Rhinoceros pachyganthus* threatens the stability of *Dihoplus pikermiensis*. A review of these issues is provided by GERAADS (1988) and GIAOURTSAKIS (2003).

Abbreviations of institutions and collections:

AMPG: Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece.

LGPOT: Laboratory of Geology and Palaeontology, Aristotelian University of Thessaloniki, Greece.

BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, München Germany.

SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany.

IPGUH: Institut für Paläontologie und Geologie der Universität Hamburg, Germany.

SMNK: Staatliches Museum für Naturkunde Karlsruhe, Germany.

HLMD: Hessisches Landesmuseum, Darmstadt, Germany.

MNHN: Muséum National d'Histoire Naturelle, Paris, France.

NHML: The Natural History Museum London, United Kingdom.

NHMW: Naturhistorisches Museum Wien, Austria.

IPUW: Institut für Paläontologie der Universität Wien, Austria.

3. Systematic description

Family	Rhinocerotidae OWEN, 1845
Subfamily	Rhinocerotinae OWEN, 1845
Tribe	Rhinocerotini OWEN, 1845
Subtribe	Dicerotina RINGSTRÖM, 1924

Genus *Ceratotherium* GRAY, 1867

Ceratotherium neumayri (OSBORN, 1900) Figs. 2, 3a, b

Description of the skull: K3.111 is a well-preserved, nearly complete juvenile skull retaining the full deciduous dentition on both sides (Fig. 2).

Fig. 2. *Ceratotherium neumayri* from Kerassia (AMPG: K3.111), juvenile skull, (a) lateral, (b) dorsal and (c) ventral view.



Fig. 2 (Legend see p. 372)

Only the small premaxillary bones are missing, since they have not been yet fused with the maxilla. A very small part of the nasals' anterior tip is also missing. The basioccipital part of the occipital bone has not been fused to the rest of the skull either. Fortunately, this bone was found in fine condition separately in the same fossiliferous layer (K3.3, Fig. 3 b). The postglenoid and posttympanic processes are better preserved on the left side of the skull, but they are also incompletely fused. The cranial measurements of the skull are given in Table 1 and the dental measurements in Table 2.

The nasal horn boss is well developed, with extensive vascular impressions. The nasal bones terminate abruptly and their rostral end is very broad. The internasal groove is deep and marked along the horn boss but narrows backwards as the nasal suture reaches the frontal one. In adult animals of *C. neumayri* the nasal bones remain separated only anteriorly, since this suture fuses behind the horn boss. The ventral surface of the nasals is transversally concave. In lateral view, the nasal incision is U-shaped and extends backwards to above the middle of D². There is a single large infra-orbital foramen situated over the middle of D³. The facial crest is smooth and not marked. There is no contact between the lacrymal and the nasal bone. The maxillary bone interferes between them and gains contact with the frontal one. The median frontal horn boss is placed above the level of the supraorbital processes. The zygomatic arc is slender and rather low. The transition between the maxillary bone and the anterior end of the zygomatic arch is smooth. Parts of the zygomatic process of the temporal bone are missing, probably because they were not fully ossified. The orbit is low and its anterior border is situated over the anterior half of D⁴. The floor of the orbit (dorsal surface of the zygomatic bone) is sloping laterally. A strong lacrymal process with two *foramina lacrymalia* is present on the lacrymal bone, but its tip is partly broken on both sides. The supraorbital process is very strong and prominent. On the contrary, there is no postorbital process developed. In lateral view, the dorsal profile of the skull is quite concave

Fig. 3. (a) *Ceratotherium neumayri* from Kerassia (AMPG: K3.111), left upper deciduous tooththrow of the juvenile skull with D¹-D⁴ in occlusal view. (b) Unfused isolated basioccipital bone (AMPG: K3.3) of the same individual in occipital view. (c) *Dihoplus pikermiensis* from Kerassia (AMPG: K4.387), symphysis of the adult mandible in dorsal view.

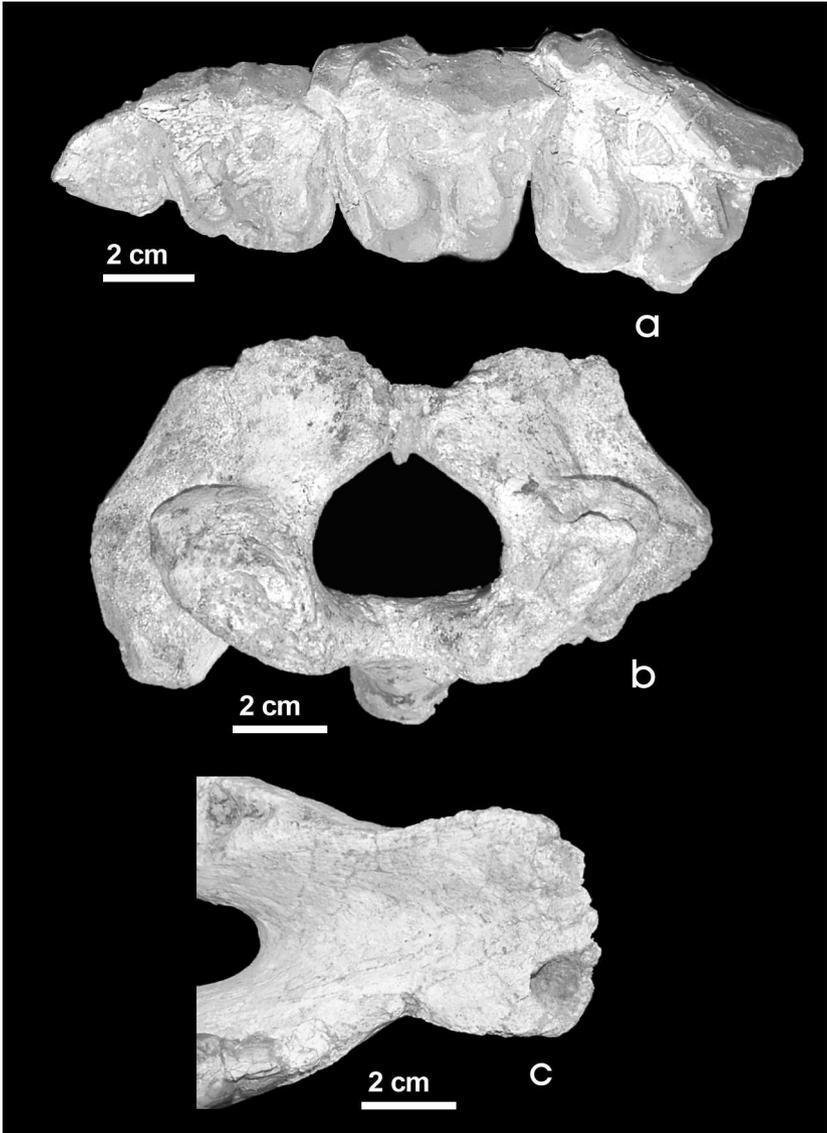


Fig. 3 (Legend see p. 374)

Table 1. *Ceratotherium neumayri* from Kerassia. Cranial measurements (in mm) of the juvenile skull. Measurement numbers follow GUÉRIN (1980).

<i>Ceratotherium neumayri</i> Kerassia, AMPG, K 3.111		
3.	Distance between occipital crest and nasal tip	453
4.	Distance between nasal tip and nasal notch	94.5
5.	Minimal width of the braincase	123.0
7.	Distance between occipital crest and supraorbital process	303
8.	Distance between occipital crest and lacrymal process	265
9.	Distance between nasal notch and orbit	94.6
14.	Distance between nasal tip and orbit	183
15.	Width of occipital crest	153.5
19.	Width between supraorbital processes	212
20.	Width between lacrymal processes	200
21.	Maximal width between zygomatic arches	268.5
22.	Width of nasals	108.3
28.	Width of palate in front of D ²	64.7
29.	Width of palate in front of M ¹	77.0
31.	Maximal width of foramen magnum	43.8
32.	Maximal width of occipital condyles	120.4

anteroposteriorly, but not as concave as observed in adult specimens. The two oblique frontoparietal crests are well separated and the *os interparietale* between them remains wide and transversally slightly convex. They diverge backwards smoothly into the nuchal crests.

The occipital face appears to be almost vertical, considering the original anatomical position of the unfused basioccipital. The external occipital protuberance is only slightly concave, but this might be influenced by the early ontogenetic stage. The *fossa squamae occipitalis* is rather deep. The *tuberculum nuchale* is well developed. In lateral view, there is no contact between the postglenoid and the posttympanic processes. The distance between them is in fact fairly large, leaving the subaural channel widely open. The separately found basioccipital part of the occipital bone (K3.3, Fig. 3b) bears the occipital condyles, the paroccipital processes and the

Table 2. Comparative dimensions (in mm) of the upper deciduous teeth.

	<i>Ceratotherium neumayri</i>				<i>Dihoplus pikermiensis</i>		
	Kerasia AMPG K3.111	Pental-1 LGPUT PNT-144	Pikermi AMPG PA33/91	Samos N=4	Pikermi N=9	Samos NHMW 1911.V30	Samos NHMW 1911.V41
D ¹ L	24.6	21.3	21.0	22.5-24.6	24.0-30.3	26.9	29.1
W _P	22.6	22.2	19.4	21.8-23.5	22.5-26.5	24.0	23.7
D ² L	39.2	33.7	38.8	32.1-36.5	33.5-39.0	37.3	39.0
W _A	35.8	32.7	32.8	33.8-35.9	33.3-41.5	37.1	37.0
W _P	38.3	34.3	35.1	34.3-37.2	32.6-39.8	36.8	36.9
D ³ L	46.0	42.2	44.9	44.5-45.7	39.3-44.3	43.1	45.2
W _A	44.8	41.8	38.8	43.8-45.8	37.4-46.4	46.2	43.4
W _P	43.1	41.4	37.9	41.7-45.4	35.2-42.3	43.2	40.5
D ⁴ L	54.7	49.4	—	50.4-55.4	45.4-49.7	49.4	49.5
W _A	47.6	47.5	—	46.2-51.6	40.9-50.1	49.1	47.3
W _P	46.4	46.6	—	47.9-49.3	36.9-46.9	47.5	44.8
D ¹ -D ⁴	150.2	138.7	—	140.8-146.5	136.3-150.9	144.5	148.2
D ² -D ⁴	131.8	121.3	—	123.1-126.3	114.0-127.4	121.6	122.7
D ³ -D ⁴	94.7	90.0	—	90.5-93.4	82.7-93.3	89.8	90.0

foramen magnum. The paroccipital processes lack their tips, since they have not yet been ossified. The *foramen magnum* is bell shaped. The occipital condyles are not well preserved due to the incomplete co-ossification.

In ventral view, the posterior palatine margin is placed just behind the level of the posterior part of D⁴. The small *foramina palatina majus* lie at the same level. The vomer has the form of a blunt ridge. The pterygoid plates slope evenly forward, their posterior margin being nearly horizontal. The alar canal is placed well behind the hamulus level of the pterygoid.

Description of the dentition: The first upper milk molar is a small subtriangular tooth with rounded sides. The occlusal surface of both D¹ is more worn and fragmented than any other teeth (Fig. 3 a). The protoloph is very long and bends backwards posterolingually almost blocking the en-

trance of the medisinus. The metaloph, on the other hand, is extremely short and reduced. In front of and below the angle between protoloph and parastyle, a small but deep prefossette is surrounded by a shallow anterior cingulum, which merges lingually with the protoloph at the base of the protocone. No other lingual or labial cingula are present; a posterior one however might have been, but this area is not well preserved. A weak paracone rib is developed on the ectoloph, situated one-third from the anterior tip, just above a small depression between the roots. The parastyle is long and rounded, the parastyle groove smooth, not deep. The remaining of the outer wall, behind the paracone rib, is broad and slightly convex.

By juvenile rhinoceroses, D^2 is the most characteristic tooth of the upper deciduous dentition due to its particular shape and function. The protoloph is long and slender and bends slightly lingually. The metaloph is broader and forms a right angle with the ectoloph. The hypocone is larger and more round than the protocone. Both the protocone and the hypocone are not constricted. The occlusal surface of the tooth is not well preserved. At least a single crista connects with the long crochet to form a closed medifossette. The anterior cingulum is well developed and extends slightly lingually, reaching the middle of the protocone. A strong isolated cingular pillar is developed in front of the entrance of the medisinus. The posterior cingulum does not project lingually. A postfossette is not developed behind the metaloph and, if present during an earlier stage of wear, it must have been very narrow. On the ectoloph, the parastyle is very long since the paracone rib has been shifted backwards. The paracone rib is thick and prominent and is followed by another stronger vertical rib. This second rib, found in many *Dicerotina* directly after the first rib and some times merging with it, is effectively a doubled paracone rib rather than a mesostyle. A metacone rib is not developed and the remaining of the ectoloph is wide and slightly convex.

The D^3 and D^4 are quite similar in morphology, the last milk molar being distinctly larger and its transverse lophs more oblique. Both teeth have a well-developed crista, which merges with a long crochet forming a medifossette. There is no protocone constriction; both anterior and posterior protocone grooves are virtually absent. The same is true for the hypocone. The anterior cingulum is strong, but it does not project lingually. Only some faint cingular traces are present lingually at the base of D^4 . Similar to D^2 , an isolated cingular cusplet is developed in front of the entrance of the medisinus. It is weaker on D^3 . On D^4 this pillar was also present but broken as indicated by fragmentary traces. The posterior cingulum is well developed in both teeth and a postfossette is present. The postfossette of D^4 is larger and still open from behind as the posterior cingulum lowers at the base of the tooth and has not yet been reached by wear. Some cement traces are still visible on the ectoloph. The parastyle is of normal width, narrower than in

the first two milk molars. The parastyle groove is marked but shallow. The paracone rib is strong and prominent. No metacone rib is developed. Posteriorly, the ectoloph turns up slightly concave, especially near the top of the crown.

Discussion and comparisons: This is one of the most complete juvenile skulls of *Ceratotherium neumayri* found in Greece. Juvenile skulls are reasonably present in Pikermi and Samos collections but they are partly damaged or deformed. We have compared our material with three juvenile skulls of *C. neumayri* from Samos (HLMD: SS192, SMF: M3602, NHMW: 1911V45) and two skulls of *Dihoplos pikermiensis* from Pikermi (BSPG: ASII285, NHMW: A4672). As it will be discussed later, this is no coincidence, since *C. neumayri* dominates in Samos whereas *D. pikermiensis* in Pikermi. The juvenile skull PNT-144 of *C. neumayri* from Pentalophos-1 (GERAADS & KOUFOS 1990: pl. 1, figs. 3-4) was also used for comparison. Moreover, numerous isolated maxillae of both species with complete deciduous dentition, which are quite frequent in Pikermi and Samos collections (AMPG, NHMW, IPUW, BSPG, SMF, HLMD, NHML), were metrically compared with the studied specimen (Table 2).

The cranial differences between the juvenile skulls of both species are effectively the same as between the adult ones, which are sufficiently documented by GERAADS (1988). They are roughly the same that distinguish the extant African species from the Sumatra rhino (GUÉRIN 1980, GROVES 1983, GERAADS 1988). Some of the most notable differences are: the abrupt and broad termination of the nasals of *C. neumayri*, more smooth and pointed in *D. pikermiensis*; the loss of the contact between lacrymal and nasal bones in *C. neumayri*, present in *D. pikermiensis*; the particularly strong and prominent supraorbital process of *C. neumayri*, much weaker in *D. pikermiensis*; the absence of postorbital process in *C. neumayri*, present in *D. pikermiensis*; the lower border of the orbit is sloping laterally in *C. neumayri*, flat (regular) in *D. pikermiensis*; the posttympanic processes are laterally less developed in *C. neumayri* (occipital outline in posterior view nearly rectangular), enlarged and transversally expanded in *D. pikermiensis* (occipital outline trapezoid); the external auditory pseudomeatus is open in *C. neumayri* (postglenoid and posttympanic processes separated), partially closed in *D. pikermiensis* (processes in contact, however separated in the extant Sumatra rhino).

Isolated upper deciduous tooththrows and even single upper milk teeth of *C. neumayri* and *D. pikermiensis* can be easily distinguished. There are several morphological differences between the deciduous dentition of both species (GERAADS 1988). A detailed comparison, including some additional characters, is provided in Table 3. Some size differences are also observable

in Table 2, although more specimens are necessary to enhance the sample. The last two deciduous molars of *C. neumayri* are quite longer than *D. pikermiensis*, the overlapping being rather small. On the other hand, the first deciduous molar of *D. pikermiensis* is longer, or rather the D^1 of *C. neumayri* is shortened due to the reduction of metaloph and postfossette in this species. The second deciduous molars of both species have similar dimensions. The greater ranges observed in width measurements, especially in *D. pikermiensis*, can be explained by the variable strength of the vertical ribs on the ectoloph.

After this comparison, it would be very useful to review and revise all published juvenile skulls and deciduous dentitions related to our material. The first juvenile rhino skull from Pikermi was described but not figured by ROTH & WAGNER (1854: 61-62) as *Rhinoceros schleiermacheri*. This partly damaged skull with complete deciduous dentition is housed in Munich (BSPG: ASII285) and belongs to *Dihoplus pikermiensis*. It features all typical dental characters described in Table 3. GAUDRY (1862-1867) mentioned the presence of numerous juvenile rhino skulls and maxillae among his material from Pikermi, which is housed at MNHN in Paris. He has figured though only one right upper deciduous tooththrow under the name of *Rhinoceros pachygnathus* (pl. 26, fig. 1). As correctly noted by RINGSTRÖM (1924), this particular maxilla belongs however to *Dihoplus pikermiensis*. Its specific characters are clearly demonstrated in GAUDRY's fine illustration: D^1 with a long metaloph, D^2 with a large postfossette, D^2 - D^4 with slightly constricted protocone, D^3 - D^4 without a crista and medifossette. Two additional unnumbered deciduous upper tooththrows from GAUDRY's collection have been figured by GERAADS (1988: fig. 5) to demonstrate the dental differences between *C. neumayri* and *D. pikermiensis*.

WEBER (1904, 1905) studied a remarkable sample of fossil rhinoceroses from Samos. In his first contribution he studied remains of the horned rhinoceroses, while in his second work he studied the aceratheres of the locality. This material was housed in the collections of the BSPG in Munich, but unfortunately it has been entirely destroyed during World War II. WEBER (1904, pl. 16) discussed and figured two juvenile specimens, which he assigned to horned taxa. In the first figure, WEBER (1904: pl. 16, fig. 1) figured the maxilla of a juvenile skull with complete deciduous dentition and described it as *Rhinoceros schleiermacheri*. This maxilla belongs however to a *Chilotherium*, as shown by the complicated structure of the second milk molar, the particularly oblique transverse lophs, the presence of strong anterior cingula on all teeth and the well constricted protocone and hypocone cusps. In the second figure, WEBER (1904: pl. 16, fig. 2) described a complete left upper deciduous dentition as *Rhinoceros pachygnathus*. This specimen belongs though to *Dihoplus pikermiensis*. All typical characters of

D. pikermiensis are exceptionally illustrated in WEBER's figure: D¹ with a long metaloph, D² with a large postfossette, D²-D⁴ with slightly constricted protocone, a well-developed metacone rib on the ectoloph and a small but clear hypostyle arising from the posterior cingulum, D³-D⁴ without a crista and medifossette.

Two more juvenile skulls from Samos have been figured in brief reports. Both belong to *Ceratotherium neumayri*. DREVERMANN (1930) briefly documented the Samos collection of the SMF illustrating the most prominent specimens. A juvenile skull with associated mandible was figured as *Atelodus pachygnathus* (DREVERMANN 1930, fig. 7). The specimen (SMF: M3602) is ontogenetically older than the skull from Kerassia, since the first molar is fully erupted. The occipital and basioccipital region are missing and the frontal horn is slightly damaged. As in the Kerassia specimen, the nasal horn boss is strong with extensive vascular impressions and the broad nasals terminate abruptly. The nasal suture is, however, fused behind the nasal horn boss since it is an older juvenile specimen. But even in adults, the nasal bones remain anteriorly always separated. The nasal notch extends posteriorly to the middle of D² and the anterior border of the orbit is situated above the fully erupted M¹. The lower border of the orbit is sloping laterally and the zygomatic arch is slender. The lacrymal and especially the supra-orbital processes are very strong and prominent. The dorsal profile is slightly concave in lateral view and the frontoparietal crests widely separated. LEHMANN (1984) documented briefly the most prominent specimens of the Samos collection housed in IPGUH. Among them, he described a fairly complete juvenile rhino skull with broken nasals as *Diceros neumayri*. This specimen (IPGUH: Nr.3018) has similar age and morphology to the skull from Kerassia and features also a slender zygomatic arc and a slightly concave dorsal profile. The strong and prominent supraorbital process and the sloping lower border of the orbit, characteristic for the species, are markedly evident in the accompanying figure of LEHMANN (1984: pl. 1, fig. 3).

ALEXEJEW (1916: pl. 8, fig. 9) described a complete right upper milk toothrow from the village of Novo Elisavetovka (Ukraine) as *Rhinoceros pachygnathus*. We refer this specimen to *Dihoplus* sp., based on the morphological characters observed in the accompanying photograph: D¹ large, with a long metaloph, the protoloph does not bend lingually; D² with a large postfossette, D²-D⁴ with apparently slightly constricted protocone and no cingular pillar developed in front of the entrance of the medisinus; D³-D⁴ without a crista and medifossette. This toothrow does not show any significant morphological difference in respect to the Eastern Mediterranean specimens of the genus but we will avoid a specific assignment until more cranial and postcranial material from this region is made available. The

Table 3. Morphological differences between the upper deciduous teeth of *Ceratotherium neumayri* and *Dihoplus pikermiensis*.

	<i>Ceratotherium neumayri</i>	<i>Dihoplus pikermiensis</i>
D¹ Overall size	Slightly reduced	Normal
Protoloph	Very long, bends posterolingually blocking up the entrance of medisinus.	Regular, vertical, does not bend
Metaloph	Reduced, very short	Regular, long
D² Lingual cingular pillar	Present in front of the entrance of medisinus	Absent
Protocone constriction	Not constricted	Slightly constricted
Size of postfossete	Very small and narrow, if present	Large, wide
Hypostyle	Not developed or distinct from posterior cingulum	Present, distinct from posterior cingulum
Paracone rib	Very strong, usually double	Strong, always single
Metacone rib	Absent or faint only at the top of the crown, then fades out and disappears	Present, clearly marked and continuous down to the basis of the crown
D³ Lingual cingular pillar	Present in front of the entrance of medisinus	Absent
D⁴ Protocone constriction	Not constricted	Slightly constricted
Crista	Always present	Always absent
Mediofossete	Usually present	Always absent
Metacone rib	Absent or faint only at the top of the crown, then fades out and disappears	Present, clearly marked and continuous down to the basis of the crown

measurements of the deciduous teeth given by ALEXEJEW (1916: 310) are more than 10 % larger than the largest specimen we have measured from Pikermi and Samos and may indicate a closer relationship to the Asian *Dihoplus ringstroemi*. A subspecific arrangement of these local populations of the genus *Dihoplus* cannot be excluded and might be actually more appropriate.

MELENTIS (1970: pl. 10, figs. 2-3) described as *Dicerorhinus orientalis* an incomplete left upper deciduous tooththrow with D²-D⁴ from the locality of Halmyropotamos in Southern Euboea. *D. orientalis* is a junior synonym of *D. pikermiensis* and this specimen (AMPG: HAL1967/13) belongs undoubtedly to this species (GERAADS 1988). The teeth bear all typical dental characters described in Table 3.

TSISKARISHVILI (1987: text-fig. 2b, pl. 8, figs. 1-2) assigned an isolated complete upper deciduous dentition to his new species *Diceros gabunia* from Kazakhstan. *Diceros gabunia* was described as a close relative of *Diceros pachygnathus* (here *Ceratotherium neumayri*), but their specific or subspecific affinities must be further investigated. The tooththrow is very similar with the Eastern Mediterranean specimens and, based on the figures, bears at least the following key features: cingular pillar on D²-D⁴ in front of the entrance of the medisinus, no protocone constriction on any teeth, small postfossette on D², crista present on D²-D⁴ merging with a long crochet to form a closed medifossette.

GERAADS & KOUFOS (1990: pl. 1, figs. 3-4) described in detail a juvenile skull of *Ceratotherium neumayri* from the locality of Pentelophos-1 in North Greece. The skull (LGPUT: PNT-144) is transversally compressed with numerous cracks on the surface, but is quite complete. It has the same morphology but is ontogenetically slightly older than the skull from Kerassia, its first permanent molar being fully erupted but still unworn. The dental characters of its deciduous dentition are the same, as described in Table 3.

GERAADS (1994: fig. 1) described a complete upper deciduous tooththrow of *Ceratotherium neumayri* from the Turkish locality of Kemiklitepe-A, which bears also all typical dental features of the species mentioned above.

Recently, FORTELIUS et al. (2003: fig. 12.16) described as *Stephanorhinus pikermiensis* a complete right upper deciduous tooththrow from the Turkish locality of Kavakdere in the Sinap Formation. The following features of the accompanying figure leave however no doubt that this specimen belongs to *Ceratotherium neumayri*. The D¹ has a short metaloph and a long protoloph that bends backwards blocking lingually the entrance of the medisinus. The characteristic prominent cingular pillar is present on D²-D⁴ in front of the entrance of the medisinus. There is no protocone constriction in any teeth and cement appears to be present on their ectoloph. The postfossette of D² is small. A crista is present on D³ and merges with a long crochet forming a closed medifossette. On D⁴ the small crista does not merge with the crochet and probably they would have further remained separated by additional wear. We have seen again this trait in two specimens of *C. neumayri* from Samos (HLMD: SS192, SMF: M3602). In *D. pikermiensis* however, a crista is completely absent on D³ and D⁴.

Genus *Dihoplus* BRANDT, 1878

Dihoplus pikermiensis (TOULA, 1906)

Figs. 3c, 4

Description of the mandible: K4.387 is a virtually complete, well-preserved mandible, which belongs to an old individual (Fig. 4). Only the two coronoid processes and portions of the right condyle are missing. Unfortunately the specimen is lacking the incisors (Fig. 3c) and both P₂. Some portions of the posterior dentition, especially on the left side, are damaged as well. The right side of the mandible is slightly distorted resulting to smaller measurements on this side. For this reason, measurements of the mandibular rami (Tab. 4) are based on the left side.

The horizontal ramus is long and quite slender. The lower margin of the mandible is nearly straight. Below the first molar, the horizontal ramus bends gradually upwards to the anterior tip of the symphysis. The mental foramen is located in front of the P₂ alveolus. The vertical ramus of the mandible is rather low and at a straight angle with the horizontal one. The mandibular foramen is placed well below the level of the alveolar arc. The condyle, better preserved on the left side, is not particularly strong. The distance between the posterior border of the condyle and the anterior margin of the mandible is 571 mm.

The symphysis is long and narrow. In lateral view, it forms a smooth angle with the horizontal ramus. Its dorsal face is concave and delimited by marked bilateral ridges along the *margo interalveolaris*. The ventral face is convex. The posterior margin of the symphysis extends back to the middle of the P₂ roots. In front of the P₂ alveoli the symphysis gradually narrows down, forming a slight median constriction. At this point the minimum symphyseal width is 64.2 mm. The symphysis widens again smoothly to the front, reaching a maximum width of 76.3 mm near the incisors alveolar level. There are two well-formed, oval-shaped alveoli in the anterior part of the symphysis that suggest the presence of two functional I₂ (Fig. 3c). There are no visible alveoli for I₁, but the symphysis is slightly damaged in this area. The small distance between the two I₂ alveoli (min. width 21 mm) does not exclude the possibility that two very small I₁ actually existed. If present, these teeth must have been diminutive.

Description of the dentition: The trigonid and the talonid of the last molar are worn down to the same level, but their dentine is not yet confluent. This implies that the mandible belongs to an older adult individual. The left toothrow of the mandible lacks completely the second premolar and from the rest of the teeth only P₄ and M₃ are still in good condition. For this reason the description of the lower dentition is based mainly on the better-preserved right toothrow (Fig. 4c).

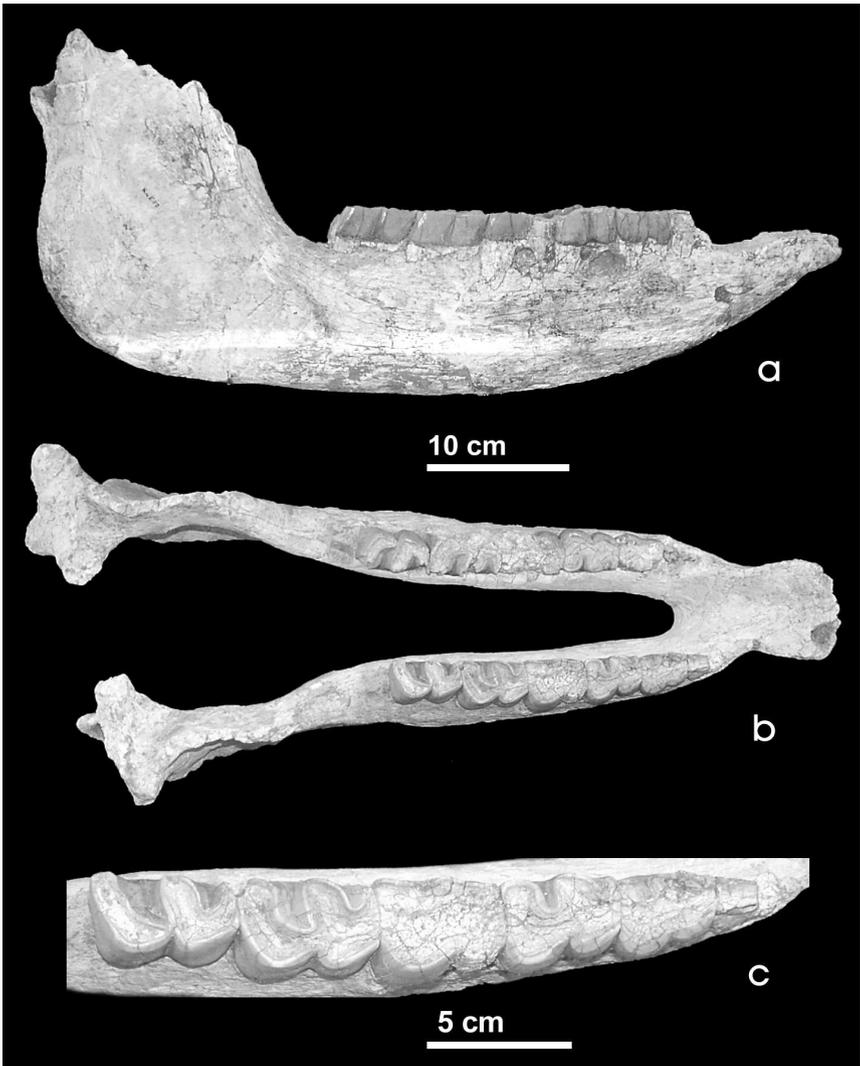


Fig. 4. *Dihoplus pikermiensis* from Kerassia (AMPG: K4.387). Adult mandible in (a) lateral and (b) dorsal view. (c) The same specimen, lower right toothrow with P₃-M₃ in occlusal view.

Table 4. Comparative dimensions (in mm) of the mandible.

	<i>Dihoplus pikermiensis</i>			<i>Dihoplus</i>	<i>C.</i>
	Kerassia AMPG K4D387	Pikermi IPUW Nr.342red	Pikermi AMPG PA3691/91	Eppelsheim HLMD DIN 1929	Maragha NHMW A 4791
1. Length	566.8	532	—	538.9	—
2. Length symph.- angulus	443.5	426.0	415.0	413.1	402.0
3. Corpus H in front of P ₃	75.7	74.3	76.2	—	54.9
4. Corpus H in front of P ₄	85.3	84.6	85.6	—	77.3
5. Corpus H in front of M ₁	90.1	89.2	91.6	90.0	88.0
6. Corpus H in front of M ₂	93.2	94.7	96.8	94.0	93.0
7. Corpus H in front of M ₃	96.8	99.4	101.2	99.3	98.1
8. Corpus H behind M ₃	101.4	106.2	107.6	105.4	106.2
9. Corpus W in front of M ₁	49.8	44.9	57.2	47.4	36.9
10. Corpus W behind M ₃	51.3	46.3	61.2	47.8	46.2
11. Length of symphysis	123.8	>108	—	142.2	—
13. Depth vertical ramus	162.6	—	—	150.4	148.3
14. Width of condyle	94.9	—	—	114.9	99.4
15. Ramus H at condyle	230.2	—	—	264.9	—
16. Ramus H at coronoid	—	—	—	278.4	286

There are no visible alveoli of the first lower milk molar (D₁). This small tooth must have been lost during an earlier ontogenetic stage and its alveolus was subsequently filled. The P₂ of the right toothrow is heavily damaged. Only the roots and a very small piece of the posterior part of its talonid are still present. No measurements and description can be given for this fragmentary tooth, however the total length of the whole toothrow can be approximately estimated (Tab. 5). All preserved cheek teeth have a deep and well-marked labial groove (ectoflexid), continuous down to the crown basis. Only on P₃ the ectoflexid is somewhat shallower. There are neither lingual nor labial cingula nor crenulated rugosities present on any tooth. Cement is also absent. Metaconid and entoconid are not constricted. Due to wear, the metaconid is larger than the entoconid and the trigonid valleys considerably smaller and narrower than the talonid ones. The transversal paralophid is markedly long in all teeth, reaching lingually the level of metaconid and entoconid. It forms a right angle with the horizontal axis of the mandibular

corpus, whereas the lingual branches of the metalophid and the hypolophid are inclined backwards, especially on the molars. Besides the shallower ectoflexid, P₃ differs from P₄ mainly by the smaller size of its anterior part, because the trigonid is narrower and the paralophid shorter. All molars are considerably larger than the premolars. The right M₁ is a heavily worn tooth and no additional features can be described. Its length is smaller but its maximal width is greater than that of M₂. The second molar is the longest tooth. The trigonid and talonid valleys of the last two molars have a V-shaped lingual transverse profile. The shape of the talonid valley of the last molar is however more rounded without turning though into a U-shaped. On M₃, the hypoconulid forms a faint but distinct fold in the hypolophid, projecting slightly into the talonid valley. Due to the stage of wear, it is not clear if this feature is present in the preceding molars as well.

Discussion and comparisons: Well-preserved adult rhinocerotid mandibles are among the scarcest bones in Pikermi and Samos collections. Juvenile mandibles are quite frequent, but they are not useful for comparison; their symphysis is usually broken too. For instance, in the AMPG collection of over 700 rhino specimens from Pikermi, less than 10 adult mandibular fragments are present and only one was complete enough (AMPG: PA3691/91) to be used for comparison. All other specimens lack the valuable symphysis, the vertical rami are broken and the dentition is quite incomplete. A complete adult mandible of *Dihoplus pikermiensis* from Pikermi, which preserves intact the second lower incisors, is housed in the collections of the NHML (NHML: M10150). Another useful one of the same species was found at the Pikermi collections of the IPUW (IPUW: Nr.342red). It retains a great part of the symphysis but the incisors are broken off. The well-preserved type mandible of *C. neumayri* from Maragheh (NHMW: A4791) has been studied directly for comparison, but complete specimens of this species from the Eastern Mediterranean were not present in the collections we have examined.

Due to the limited available material and since the lower dentition of Rhinocerotinae is quite uniform, we cannot discuss at present about constant dental differences between both species. However, the type mandible of *C. neumayri* from Maragheh shows some clear differences in respect to the mandibles of *D. pikermiensis* from Kerassia and Pikermi: the teeth are more hypsodont; there are some notable traces of cement, especially on the outer wall; the trigonid is more angular and to some extent the talonid as well, the trigonid and talonid valleys are broader, clearly U-shaped; the labial groove (ectoflexid) is deeper and angular. The most helpful distinguishing characters between adult mandibles of *D. pikermiensis* and *C. neumayri* concern the morphology of the symphyseal region and to a lesser degree the

Table 5. Comparative dimensions (in mm) of the lower teeth.

		<i>Dihoplos pikermiensis</i>			<i>Dihoplos schleiermacheri</i>	<i>Ceratotherium neumayri</i>
		Kerasia AMPG K4D 387	Pikermi IPUW Nr.342red	Pikermi AMPG PA 3691/91	Eppelsheim HLMD DIN 1929	Maragha NHMW A 4791
P₁	L	–	–	–	–	–
	W	–	–	–	–	–
P₂	L	–	–	33.2	31.2	31.7
	W _A	–	–	19.4	17.6	15.5
	W _P	–	–	22.9	21.0	16.7
P₃	L	37.3	37.5	37.4	36.5	41.5
	W _A	25.6	–	25.0	24.5	23.8
	W _P	29.5	24.2	–	27.2	28.2
P₄	L	40.2	38.2	44.3	42.3	46.0
	W _A	29.4	26.7	31.6	28.7	29.3
	W _P	33.1	28.5	33.5	30.2	31.0
M₁	L	46.0	43.2	46.5	45.4	49.1
	W _A	–	29.6	32.3	31.4	31.7
	W _P	37.2	29.8	35.8	33.6	33.3
M₂	L	48.4	47.9	52.3	47.8	54.1
	W _A	32.9	31.4	33.8	32.0	33.5
	W _P	35.5	34.3	35.4	34.8	35.3
M₃	L	47.6	44.3	51.3	46.9	56.2
	W _A	31.4	32.8	34.2	31.7	31.6
	W _P	30.3	31.4	32.6	30.8	33.8
P₁- M₃	–	–	–	–	–	
P₂- M₃	c.252	–	270.5	250.1	278.0	
P₂- P₄	c.110	–	116.8	109.6	116.3	
M₁- M₃	141.4	135.8	150.4	143.8	158.9	
I_{P/M}	c.0.78	–	0.78	0.76	0.73	

curvature of the mandibular corpus. In *D. pikermiensis* the symphysis is long and bears two small but functional permanent second lower incisors. The presence of diminutive permanent first lower incisors cannot be excluded; at least deciduous ones are documented in a well-preserved juvenile mandible

from Pikermi (AMPG: PA3690/91). The posterior margin of the symphysis terminates before P_3 or even P_2 . The horizontal ramus inclines gradually upwards to the anterior tip of the symphysis. Its lower border remains almost straight or slightly convex below the toothrow. The mandibular angle is regular, neither strongly ridged nor too convex. On the other hand, the symphysis of *C. neumayri* is anteriorly abbreviated and edentulous, permanent lower incisors are absent. Its posterior margin terminates usually at the level of P_3 or even behind it. The horizontal ramus bends upwards more abruptly to the symphysis. The lower border of the mandibular corpus remains slightly convex and becomes very convex as it turns to the ascending ramus. However, this might be not as intensively convex as in the extant African species or *Elasmotherium*. OSBORN (1900: 262) and THENIUS (1955: 205) described this curvature as “Jaw without distinct angle” and “Mandibel besitzt keinen Angulus mandibulae”, which technically seen might be exaggerated.

GAUDRY (1862-1867) described and figured two adult mandibles from Pikermi, both as *Rhinoceros pachygnathus*. GAUDRY's figures are not very informative about their dentition as they belong to old individuals and we have not seen the originals specimens yet. The first mandible was found associated with a skull (GAUDRY 1862-1867: pl. 27, fig. 1) and consequently belongs undoubtedly to *Ceratotherium neumayri*. The figure shows all characteristic features described above for this species, in particular the short edentulous symphysis and the markedly convex lower border of the mandibular corpus near the symphysis and the mandibular angle. The second mandible (GAUDRY 1862-1867: pl. 28, fig. 1) was found separately and belongs actually to *Dihoplus pikermiensis*, as correctly noted by RINGSTRÖM (1924: 19-21). It has quite the same morphology and size with the mandible from Kerassia. The symphysis is long with a small median constriction and its posterior margin lies in front of P_2 . The horizontal ramus inclines gradually upwards to the anterior tip of the symphysis and the lower border of the mandibular corpus is slightly convex. The mandibular angle is normally formed but partly broken. A main feature of this mandible is that it preserves intact a small, but functional second lower incisor. The complete mandible of the WOODWARD collection in NHML (NHML: M10150) has exactly the same morphology. The second lower incisor is small, but fully functional. The size of the empty alveolus in Kerassia mandible suggests that the missing I_2 could have been slightly stronger than in these two mandibles. The mandible from Pikermi housed in IPUW (IPUW: No.342red) has also an empty alveolus of similar size as the mandible from Kerassia. Sexual dimorphism of the second lower incisor is well established among rhinoceroses and may explain these small differences.

WEBER (1904) cited the presence of four complete adult mandibles among his material from Samos, most of them found in association with the skulls of *Rhinoceros pachygnathus* (here *Ceratotherium neumayri*). As mentioned, this material has been unfortunately destroyed. WEBER'S excellent illustrations do not include any mandibles, but his detailed descriptions (p. 482-483) demonstrate indeed all typical features of *C. neumayri* described above (translated from German): "the mandibles have not a prominent *angulus mandibulae*, but only a convex curvature that bends over from the horizontal ramus to the ascending one... the posterior margin of the symphysis extends back to the level of P₃ and sometimes even back to the first half of P₄ ... the plump horizontal rami raise rapidly up to the symphysis forming a short hollow beak ... in all adult individuals there is nowhere a sign of incisors or canines".

The well-known type mandible of *Dihoplus schleiermacheri* (HLMD: DIN1929) from Eppelsheim (KAUP 1832, KAUP 1834: pl. 11, fig. 8) has been directly studied for comparison with *Dihoplus pikermiensis* from Kerassia and Pikermi (Tab. 4). The key differences between both species concern the strength of the symphysis and the anterior dentition. The type mandible of *D. schleiermacheri* has a more robust symphysis and bears additionally two little but well-formed alveoli for the small peg-like I₁, which have been unfortunately broken off. We have confirmed the presence of these small alveoli in two more unpublished mandibles from Eppelsheim housed at SMF and NHML. In the mandibles from Kerassia and Pikermi there is no trace of permanent I₁ alveoli. The I₂ of *D. schleiermacheri* are furthermore fairly stronger. KAUP'S mandible belongs possibly to a male, taking into consideration several isolated lower incisors from Eppelsheim housed in HLMD. These are usually stronger when compared to the few known female Pikermi specimens discussed earlier: the mandible figured by GAUDRY (1862-1867: pl. 28, fig. 1) and the mandible NHML: 10150. Male lower incisors from the Eastern Mediterranean are still undocumented. We can only assume that the empty alveoli of the Kerassia mandible may indicate a male individual. Similar differences exist in the upper anterior dentition of both species, too. The type skull of *D. schleiermacheri* has fully-developed functional I¹ as well as small but well-formed I² (KAUP 1834: pl. 10, fig. 1, 1a; GIAOURTSAKIS & HEISSIG 2004: fig. 1.4). In two complete skulls of *D. pikermiensis* that we have examined (unnumbered specimens in AMPG and NHMW), the I¹ are very small, practically not functional, and only slightly rising outside the premaxillary bone. Furthermore, there is no sign of permanent I² in these skulls. We consider all these differences observed in the anterior dentition of both species to be of specific and perhaps stratigraphic value. The Vallesian *D. schleiermacheri* of Western and Central Europe is more primitive than its Turolian relative *D. pikermiensis*

from the Eastern Mediterranean. *D. schleiermacheri* continues to be present during the Turolian in Western and Central Europe, but information on its anterior dentition is still incomplete for this time of period. GUÉRIN (1980) has recognized several evolutionary stages for this species during the Upper Miocene based on the available dental and postcranial material.

RINGSTRÖM (1924) described as *Dicerorhinus orientalis* (a junior synonym of *Dihoplus pikermiensis*) a well-preserved adult mandible from the Locality 11 of the Honan Province in China. This mandible retains the symphysis but, according to RINGSTRÖM, only rudimentary permanent incisors could have been present. RINGSTRÖM (1924: pl. 1, fig. 4) documents the presence of diminutive deciduous incisors, both dI_1 and dI_2 , in a complete juvenile mandible. These small teeth are also present in Eastern Mediterranean specimens of *D. pikermiensis*, as demonstrated by a well-preserved juvenile mandible from Pikermi (AMPG: PA 3690/91). The adult mandible from Honan (RINGSTRÖM 1924: text-figs. 3-4) is morphologically similar to the mandible from Kerassia. The symphysis is long and slightly constricted in the middle; its posterior margin terminates below P_2 . The mandibular corpus is nearly straight or slightly convex (this cannot be accurately judged, since the drawing is simplified) and rises gradually upwards to the anterior tip of the symphysis. The mandibular angle is regular, not very prominent. The total length of the mandible according to RINGSTRÖM (1924: 12) measures 745 mm, which is more than 1/3 larger than the mandibles we have measured (Table 4). The larger size of the Chinese specimens was one of the main diagnostic characters used by ARAMBOURG (1959) when he established the new species *D. ringstroemi* to separate them from the Eastern Mediterranean and Central European forms. We retain here this name for the Chinese specimens, but further material is necessary to establish more accurately the specific or subspecific variation between the local populations.

THENIUS (1956) described as *Diceros pachygnathus* a pathologic mandibular fragment affected by actinomycosis from the locality of Hauskirchen in Lower Austria. Previously, the author had assigned the same specimen to *Brachypotherium* (THENIUS 1951) but he revised his initial determination and interpreted it as the first evidence of the presence of *Diceros pachygnathus* (here *C. neumayri*) in the Pannonian of the Vienna Basin. The specimen is housed in the collections of IPUW. A close re-examination revealed that this mandibular fragment belongs indeed to *Brachypotherium*. The actinomycosis has not only affected the alveoli of the premolars, but the alveoli of the incisors, as well. The fragmented symphysis bears a large alveolus for a strong second lower incisor and a smaller one for a well-formed permanent first incisor, both typical of a hornless Late Miocene rhino. The assignment to *Brachypotherium* is supported by the large size of

the teeth and the rather shallow labial groove (ectoflexid). Based on the available data, *Ceratotherium neumayri* has never reached the Vienna Basin.

TSISKARISHVILI (1987: text-fig. 2a, pl. 5, figs. 1-2) assigned an incomplete mandible to his new species *Diceros gabunia* from Kazakhstan. The vertical ramus and most part of the mandibular angle are missing. The mandibular corpus with P₃-M₃ and the symphyseal region are well preserved. The symphysis is short and edentulous. It looks long in the illustration, because the left P₂ is missing. The mandibular corpus bends rather abruptly upwards to the symphysis. The lower border of the mandibular corpus is only slightly convex behind P₃ and seems to become more convex again just before the mandibular angle where the bone is broken. As with the *C. neumayri* mandible from Maragheh, this specimen shows that the mandibular corpus in the Miocene Dicerotina might be not as extremely convex as seen in many mandibles of the extant African genera, especially *C. simum*. The curvature remains markedly strong only near the symphysis and the mandibular angle.

KAYA & HEISSIG (2001: fig. 5.5) described recently a mandibular fragment from the Turkish locality of Yulafli as *Dihoplus schleiermacheri*. Only a small part of the mandibular corpus with the last two molars is preserved. The specimen belongs undoubtedly to a horned species as shown by the long vertical paralophid and the angular trigonid and talonid valleys. It is however too incomplete to be assigned to *D. pikermiensis* or *C. neumayri*. A similar mandibular fragment of *Acerorhinus zernowi* from the same locality (KAYA & HEISSIG 2001: fig. 5.4) demonstrates the marked dental differences observed in hornless species.

4. Biostratigraphic and palaeoecological remarks

Sedimentological and geochemical analyses showed that at least two fossiliferous horizons occur in Kerassia, an upper and a lower one (ILIOPOULOS 2003, THEODOROU et al. 2003: fig. 3). The site K3, where the juvenile skull was found, and the site K4, where the mandible was recovered, are possibly isochronous and belong to the lower fossiliferous horizon of Kerassia. The available biochronological data suggest an MN12 age for the Kerassia fauna (ROUSSIAKIS & THEODOROU 2003, THEODOROU et al. 2003, ILIOPOULOS 2003).

The co-existence of *Ceratotherium neumayri* and *Dihoplus pikermiensis* is well established in Pikermi and Samos (ROTH & WAGNER 1854, GAUDRY 1862-1867, OSBORN 1900, WEBER 1903, GUÉRIN 1980, GERAADS 1988, GIAOURTSAKIS 2003). The ongoing revision of the Pikermi and Samos rhinoceroses (GIAOURTSAKIS, in preparation) documents, however, a significant detail: at least 70 % of the bones studied in several Pikermi collections

belong to *D. pikermiensis*, whereas the majority of Samos specimens represent *C. neumayri*, signifying thus a clear interspecific dominance in these two localities with ample material (more than 1500 specimens). Most other Eastern Mediterranean sites have yielded only one horned rhino species (HEISSIG 1975, 1996, GIAOURTSAKIS 2003, FORTELIUS et al. 2003). The reasons for this differentiated dispersal or dominance can be stratigraphic, palaeoecological or both.

A simple stratigraphic boundary between these two rhinoceros species seems improbable, at least during the Late Miocene. Based on the available data from Greece (GIAOURTSAKIS 2003), both *C. neumayri* and *D. pikermiensis* are present constantly throughout the Turolian. However, this does not exclude the possibility of a differentiated stratigraphic distribution within particular localities. Different stratigraphic layers within the same formation may also represent different or intermediate environmental conditions that favour the presence of the one or the other species, or even of both. The known geographic distribution of these species in the Eastern Mediterranean suggests such a palaeoecological differentiation, even in localities where both species are sympatric. *C. neumayri* is dominant in Iran, Turkey, Northern Greece and Samos. *D. pikermiensis* remains dominant in Pikermi and Halmyropotamos in Southern Greece. Important faunal differences with similar palaeoecological implications are well known between Pikermi and Samos, as well as between other Eastern Mediterranean localities (BONIS et al. 1993, BERNOR et al. 1996, SOLOUNIAS et al. 1999).

The palaeoecological and dietary preferences of *C. neumayri* and *D. pikermiensis* are still not sufficiently documented. Most of the dietary implications proposed so far for the Miocene Eurasian rhinoceroses have been primarily based on the relative hypsodonty or some anatomical adaptations (body size, position of the head). Although there might be no objection that the low crowned *D. pikermiensis* was a true browser, it remains doubtful if the more hypsodont *C. neumayri* was a true grazer (HEISSIG 1975, 1996, GERAADS & KOUFOS 1990). The dentition of *C. neumayri* resembles more that of the browsing black rhino *Diceros bicornis*, than the highly specialised dentition of the extant grazing white rhino *Ceratotherium simum*. However, the lowering and prolongation of the head, similar to *C. simum*, and several dental tendencies, such as the weakening of the protocone followed by strengthening of the mesostyle, may indicate an increasing adaptation to harder and lower bush vegetation (HEISSIG 1999). Compared to the conservative *D. pikermiensis*, *C. neumayri* was obviously a more specialised rhino and has preferred open and drier environments, as testified by its dominance in Samos, Turkey and Maragheh. *D. pikermiensis*, probably a selective browser, must have favoured more forested habitats. In the cases of sympatry, the clear interspecific dominance of one of both species suggests a

marked resource partitioning, not excluding the possibility of territorial interaction by water resources or at the boundaries of mixed habitats. In these cases, a limited dietary competition could also have been possible. However, a more detailed dietary analysis based on modern methods (dental microwear and mesowear analysis, carbon isotopes in tooth enamel etc.) is still necessary to further evaluate the palaeoecological preferences of the Eastern Mediterranean Late Miocene rhinoceroses.

The presence of a mosaic environment in Kerassia is documented by the study of Giraffidae (ILIOPOULOS 2003). 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 (*Palaeotragus rouenii*, *Palaeotragus* sp., *Helladotherium duvernoyi*, and *Samotherium major*). Based on their morphological features and the microwear studies of SOLOUNIAS et al. (1999, 2000), *Helladotherium duvernoyi* and *Bohlinia attica* are considered as browsers, whereas *Samotherium major* as a grazer and *Palaeotragus rouenii* as a mixed feeder. This implies that the species coexisting in each site occupied different niches and exploited different food resources. The available palaeoecological data of Kerassia support the hypothesis that evergreen sclerophyllous woodland with C₃ undergrowth dominated the Pikermian Biome (SOLOUNIAS et al. 1999).

Acknowledgements

We wish to thank Prof. E. VELITZELOS (University of Athens) for providing us with information concerning the existence of fossil mammals close to the Kerassia village in Northern Euboea. Since 1992, the excavations have been financed by the University of Athens Special Account for Research Grants (Project 70/4/1397), the Municipality of Niveas and the Local Council of Northern Euboea (Project 70/3/2842), and the General Secretary of Research and Technology (Project 95 ΣΥΝ 107, 70/3/3922). For providing access to material under their care, as well as for their valuable help, we would like to thank Prof. K. HEISSIG and Prof. R. LEINFELDER (BSPG), Dr. O. SANDROCK, Dr. G. GRUBER and Dr. K. KURZ (HLMD), Prof. F. SCHRENK, Dr. J. FRANZEN, Dr. G. PŁODOWSKI and Dr. O. KULLMER (SMF), Dr. R. FREY, D. SCHREIBER and W. MUNK (SMNK), Prof. G. KOUFOS and Dr. D. KOSTOPOULOS (LGPOT), Dr. G. HÖCK, Dr. F. SPITZENBERGER and Dr. HERZIG (NHMW), Prof. G. RABEDER, Prof. D. NAGEL and W. RABA (IPUW) and Dr. J. HOOKER, A. CURRANT, R. SABIN, D. HILLS (NHML). The first author wishes also to thank the Deutsche Akademische Austauschdienst (DAAD), the European Science Foundation (ESF-EEDEN/2003/EX05) and the NHML (EU-SYNTHESIS GB-TAF-574) for financial support. Special thanks are ought to the reviewers of this paper, Dr. D. GERAADS and Prof. K. HEISSIG, whose suggestions greatly improved the manuscript.

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Manuscript received: June 3rd, 2005.

Revised version accepted by the Stuttgart editor: October 17th, 2005.

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