

Late Neogene Rhinocerotidae of Greece: distribution, diversity and stratigraphical range

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The present contribution provides a comprehensive overview of the Neogene rhinoceroses of Greece and evaluates their affinities with the European and Asian species. The distribution, diversity and dispersal of the family in the Eastern Mediterranean are discussed in detail. Knowledge of rhinos during the Middle Miocene in Greece is still very limited, because of the scarce material. During the Late Miocene the family was diverse and abundant in Greece. The dominant form, *Ceratherium neumayri*, was probably an African immigrant that invaded Southeastern Europe, Anatolia and the Middle East during the Late Miocene. This rather subhypisodont tandem-horned rhino has already achieved most of the apomorphic characters of the living Dicerotina. The contemporary species *Dihoplus pikermiensis* is also common, but the origin and evolutionary relationships among its Miocene and Plio-Pleistocene relatives are still controversial. The Greek Late Miocene representatives of the subfamily Aceratheriinae are obviously closer related to the Asian genera *Chilotherium* and *Acerorhinus*, than to the typical aceratheres *Aceratherium*, *Alicornops* and *Hoploaceratherium* found in Central and Western Europe at the same time. *Chilotherium* and *Acerorhinus* migrated into Greece from Central Asia through Anatolia at the beginning of the Vallesian. *Chilotherium* dominated Samos, where it was represented by at least three species: *Ch. samium*, *Ch. kowalevskii* and *Ch. schlosseri*. In continental Greece, the richest aceratheres material comes from the recently discovered locality of Pentalophos-1, where the species *Aceratherium kiliasi* has been described. Later, this material was assigned partly to *Chilotherium* and partly to *Acerorhinus*. The Late Miocene rhino assemblages of Greece are in conformity with the ones from Southeastern Europe and the Eastern Mediterranean, especially with the ones from Anatolia. By the end of the Turolian, all these species became extinct in Greece, unable to survive the paleoenvironmental changes and the faunal turnover at the Miocene-Pliocene boundary. Pliocene rhinoceroses are poorly documented in Greece. *Stephanorhinus* cf. *etruscus* has been reported with more or less certainty from several localities, but the available material is not sufficient for useful comparisons.

Correspondence: Ioannis X. Giaourtsakis, Institut für Paläontologie und Historische Geologie, Ludwig-Maximilians-Universität München, Richard-Wagner-Str. 10, D-80333 Munich, Germany, i.giaourtsakis@lrz.uni-muenchen.de

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INTRODUCTION

The study of fossil Rhinocerotidae in Greece has already begun at the middle of the last century. The first remains of a fossil rhinoceros from Greece were mentioned by Goldfuss (1841) in a brief note announcing the discovery of fossil mammals at a new locality north of Athens, Pikermi. A few years later,

Wagner (1848) described and illustrated the first rhino specimens from Pikermi introducing a new species, *Rhinoceros pachygnathus*. In subsequent studies, Roth & Wagner (1854) and Wagner (1857) recognised the presence of a second species at Pikermi, *Rhinoceros schleiermachi*. Gaudry's (1862-67) monumental monograph on the Pikermi fauna

documented adequately both species. In addition, Gaudry described an adult mandible with well developed incisors as *Aceratherium* sp. Weber (1904, 1905) was the first one who studied thoroughly rhino material from Samos, although the island was known long ago for its wealth of Neogene mammals. In his first contribution, Weber studied the remains of *Rhinoceros pachygnathus* and *Rhinoceros schleiermachersi*, while in his second work he published a remarkable sample of aceratherium material and described two new species, *Aceratherium schlosseri* and *Aceratherium samium*. Andree (1920) later created two additional species based on material from Samos, *Aceratherium wegneri* and *Aceratherium angustifrons*. Arambourg & Piveteau (1929) documented the presence of *Rhinoceros pachygnathus* and *Aceratherium* sp. at the Neogene deposits of the Axios Valley, near Thessaloniki. Naturally, modern workers have gradually modified the generic and some of the specific names used by these first authors.

During the years after the Second World War and up to the beginning of the 1980's very little systematic work was undertaken on the fossil rhinoceroses of Greece. However, during this period quite a few occasional papers and many references in faunal lists of preliminary reports revealed in silence the presence of the family in numerous Neogene localities of Greece. The rhinoceroses of Pikermi and Samos continued to be mentioned frequently in major reviews and global works on the family, but in most cases neither new material was introduced nor was the old one properly revised. A bright exception to the aforementioned was the important contribution of Geraads (1988), who reviewed a lot of the known Rhinocerotinae material of Pikermi and Samos. Geraads established excellent criteria for distinguishing cranial and dental remains of *Ceratotherium neumayri* and *Dihoplus pikermiensis*. Two years later, Geraads & Koufos (1990) studied in detail the rich material discovered at the locality Pentalophos-1, near Thessaloniki, and

created the species *Aceratherium kiliasi*. These two papers mark also the last significant contributions on the Neogene fossil Rhinocerotidae of Greece.

More details on the research chronicle as well as on the geological setting and the faunal history of each locality (Fig. 1) are given in the author's Diploma Thesis, which has been accomplished at the University of Athens (Giaourtsakis 1999). A Ph.D. study dealing with an extensive systematic revision of the fossil rhinoceroses of Greece, including old and new unpublished material, is currently in progress at the University of Munich. The essence of this contribution is to provide a comprehensive updated overview of the present knowledge on the Neogene rhinoceroses of Greece and to evaluate their affinities with the European and Asian record. Errors often repeated in the past are emended, while some new aspects on old controversies are introduced.

During the Neogene we can recognise three successive rhino assemblages in Greece and the Eastern Mediterranean, which are interrupted by major faunal turnovers at the Middle/Late Miocene and at the Miocene/Pliocene boundary.

MIDDLE MIOCENE

Middle Miocene localities with large mammals are poorly documented in Greece (De Bonis & Koufos 1999). The richest and best known site from this time period is the locality of Thymiana on the island of Chios. From the older excavations on Chios, the presence of Rhinocerotidae indet. has been reported only in a preliminary report (Tobien 1968). A recent Greek-French field campaign has yielded many new specimens, but no rhinoceros was present (De Bonis & Koufos 1999). In an overview of the family Rhinocerotidae, Heissig (1989) stated the presence of "early Dicerotini specimens from the Middle Miocene of Anatolia and Chios". The author considered these specimens as being earlier even than the first named species of this lineage, the African *Paradicerus mukirii* HOOIJER,

1968. During a conversation, Prof. K. Heissig explained that the referred specimens from Chios belong to the collections of Prof. H. Tobien, but their present status is uncertain (K. Heissig, pers. comm. 2001). Thus these references will be considered here as Rhinocerotidae indet.

Two lower premolars from a lignite mine near the village of Chrysavgi (Mygdonia basin, N. Greece) were described as "*Diceros pachygnathus*" by Psarianos (1958). Dimopoulos (1972) studied also these teeth together with three upper molars and some ribs and placed them to "*Dicerorhinus orientalis*". Both authors implied a Late Miocene age for the fossils. In our opinion, these few teeth remains are insufficient to establish an accurate taxonomic ascription at the present. De Bonis & Koufos (1999), in their review of the Miocene large mammal succession in Greece, considered also this material as Rhinocerotidae indet., but they proposed a late Middle Miocene age (MN7-MN8) for Chrysavgi. This age is based on a micromammalian association, which has been collected much later and studied by Koliadimou (1996). It is not clear however, if the rhino remains and the micromammals come from the same stratigraphic level.

The last reference of a Middle Miocene rhinoceros from Greece is better documented, but until now was overlooked. Symeonidis (1974) described some interesting remains from a small lignite pit near the city of Atalanti as *Aceratherium* sp. The presence of a thin, hornless nasal fragment and portions of two well-developed second lower incisors, one of a male and one of a female, leave no doubt that the rhino from Atalanti belongs to the subfamily Aceratheriinae. The few dental remains with strong lingual cingula in the premolars, combined with marked paracone ribs and constricted protocones speak also for this opinion. The morphology and the size of the teeth exclude an ascription to *Brachypotherium*, too. Moreover, these specimens lack features such as the prominent antecrochet, the weaker paracone rib combined with more

constricted protocones and the wider, oblique ectometaloppe in M3, often observed in *Chilotherium*. The affinities of this material recall the morphology of the "West European" aceratheres, which were present in the Eastern Mediterranean region at that time (Heissig, 1976). This work was published before the modern revision that separated the various "*Aceratherium*" species in several new genera and therefore Symeonidis (1974) used provisionally the name "*Aceratherium* sp." for the remains of Atalanti.

Currently three genera (*Aceratherium* KAUP, 1832; *Alicornops* GINSBURG & GUÉRIN, 1979; *Hoploaceratherium* GINSBURG & HEISSIG, 1989) with about six species are considered valid from the later Middle and Late Miocene of Western Europe (MN6 – MN13). Cerdeño (1996) proposed a synonymy between *Hoploaceratherium* and *Acerorhinus* KRETZOI, 1942, but we believe this view needs further investigation. Regarding the Eastern Mediterranean region, Heissig (1976) reported the presence of *Hoploaceratherium* aff. *tetradactylum* and *Alicornops simorreense* in several Middle Miocene localities of Turkey. Ginsburg & Guérin (1979) argued that some of the teeth of *A. simorreense* belong to *H. aff. tetradactylum*, but Cerdeño & Sánchez (2000) partly supported Heissig's determinations. This case demonstrates the difficulty of ascribing isolated teeth to these genera. Another unresolved problem among these taxa is the association of postcranial material from different localities with the dental remains and the few available skulls. A simple comparison between the measurement tables of recent publications (Guérin 1980, 1988; Cerdeño & Alcalá 1989; Cerdeño 1989, 1997; Cerdeño & Sánchez 2000; Heissig in press) reveals that there is no common approach among the specialists. This issue became more evident, when two nearly complete acerathere skeletons from the Early Vallesian locality of Höwenegg (Hegau, Germany) were described as *Aceratherium incisivum* by Hünemann (1989). The fact that Eppelsheim, the type locality of

Aceratherium incisivum, may actually compromise more than one acerathere species has been previously discussed by Heissig (1972a, 1996b), but not further investigated.

Moreover, Guérin (1980) has also reported the presence of two different aceratheres in Höwenegg. Revision of old and new material from Eppelsheim and Höwenegg confirms the presence of two different acerathere types in these two important localities (Giaourtsakis, under study). In this case, an interesting, but puzzling question may arise: which remains would correspond to the type skulls of *Aceratherium incisivum* (Kaup 1832, 1834)? Keeping these circumstances in mind, we retain provisionally the rhinoceros of Atalanti as *Aceratheriini* indet.

The Eastern Mediterranean record of Middle Miocene Rhinocerotidae is better documented in Anatolia. Apart from the aceratheres *Hoploaceratherium* aff. *tetradactylum* and *Alicornops simorreense* mentioned above, Heissig (1976) documented the presence of one brachypothere, *Brachypotherium brachypus* and two primitive elasmotheres, *Hispanotherium grimmii* and 'Beliajevina' *tekkayai* (but for different opinions on the elasmotheres compare Cerdeño 1996 and Antoine 2000). *Brachypotherium* and elasmotheres have not been recorded in Greece, probably due to the poor fossil record during this time period. The end of the Middle Miocene marks an important faunal turnover caused by climatic changes that favoured the expansion of more open and arid habitats (Janis 1989). These events affected also the rhino assemblages of the region. The elasmotheres, together with *Brachypotherium* and the aforementioned acerathere genera disappeared from the Eastern Mediterranean and were gradually replaced by new immigrants from Central Asia and Africa at the beginning of the Late Miocene.

LATE MIOCENE

During the Late Miocene rhinoceroses were diverse and abundant in Greece. During this

time period, we find representatives of both subfamilies Rhinocerotinae and Aceratheriinae.

Subfamily Rhinocerotinae

Two species of the subfamily Rhinocerotinae are present during the Late Miocene in Greece: *Ceratotherium neumayri* (OSBORN, 1900), formerly known as *Diceros pachygnathus*, and *Dihoplus pikermiensis* (TOULA, 1906). Both species suffer from complicated nomenclature problems due to false determinations and repeated errors in the past, but mainly because the holotype of *Rhinoceros pachygnathus* WAGNER, 1848, a fragmentary juvenile mandible housed at the Paleontological Museum of Munich, belongs actually to *Dihoplus pikermiensis*. Heissig (1975), who discovered the mistake, proposed to switch the names of the taxa ('*Stephanorhinus pachygnathus*' for '*Dicerorhinus pikermiensis*') and abandon the specific name '*pikermiensis*', but this brought more chaos to the already confused literature. To avoid further confusion we will follow provisionally the concept used by Geraads (1988): *Ceratotherium neumayri* (OSBORN, 1900) for *Diceros pachygnathus* (WAGNER, 1848) and '*Dicerorhinus*' *pikermiensis* (TOULA 1906) for '*Dicerorhinus*' *orientalis* (SCHLOSSER, 1921), a younger synonym often used in the literature. However, we prefer to place '*Dicerorhinus*' *pikermiensis* within the genus *Dihoplus* BRANDT, 1878 and argue for this decision.

Ceratotherium neumayri was probably an African immigrant that invaded Southeastern Europe, Anatolia and the Middle East during the Late Miocene. *C. neumayri* was widespread in many Greek localities and is the best known species from this time period. This subhypsodont tandem-horned rhino has already achieved most of the apomorphic characters of the living Dicerotina. A large number of skulls, sometimes with associated mandibles, as well as ample postcranial material have been described from Pikermi (Wagner 1848; Gaudry 1862-67; Guérin 1980; Geraads 1988), Samos (Weber 1904; Thenius 1955;

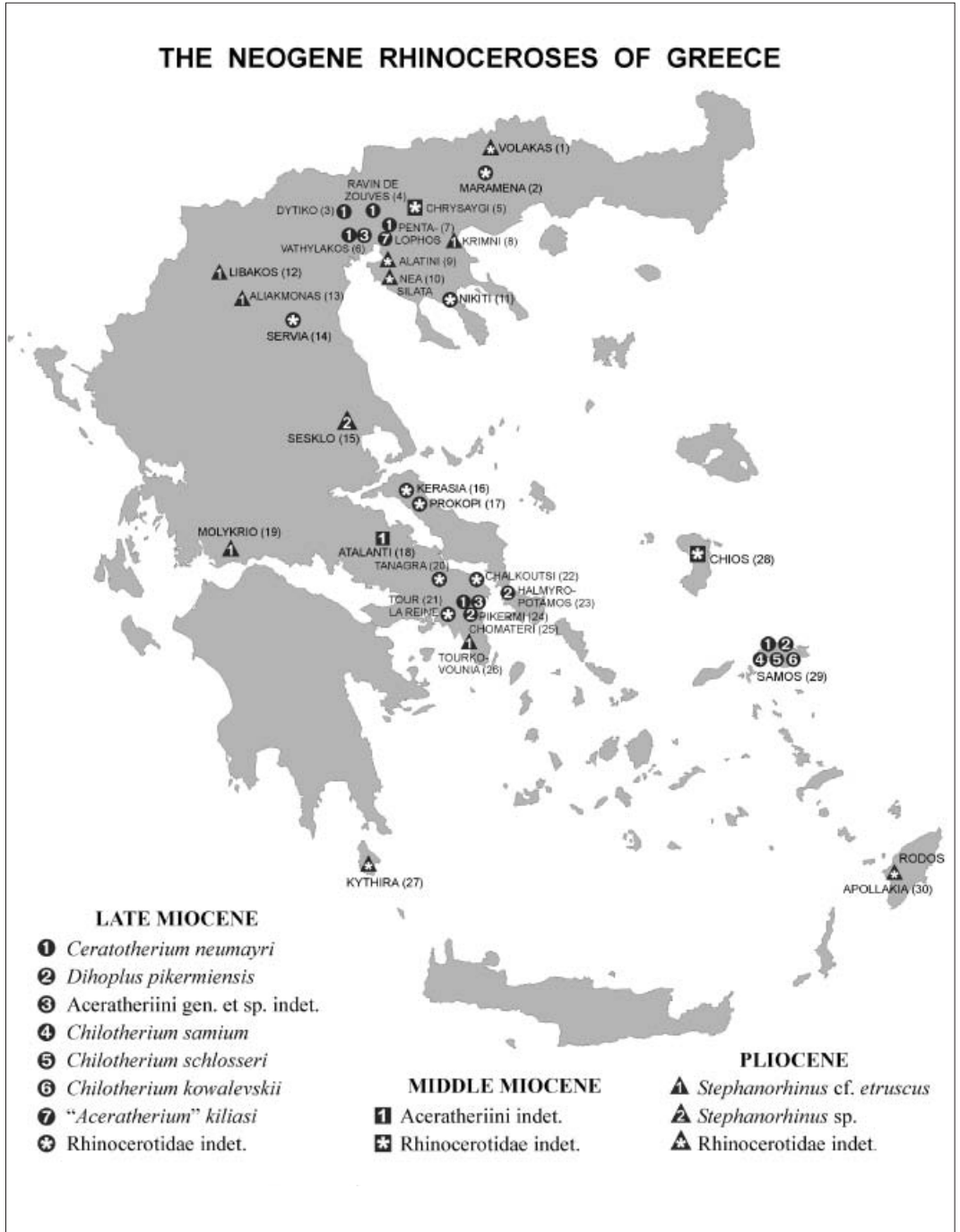


Figure 1 Distribution of the family Rhinocerotidae in Greece during the Neogene.

Geraads 1988), Vathylakkos (Arambourg & Piveteau 1929), Ravin de Zouaves (Koufos 1980), and Pentalophos (Geraads & Koufos 1990). Some of the references about Pikermi and Samos are partly incorrect and currently, together with new unpublished material, under revision. The presence of this species has been reported at a few more Greek localities, as well (see Figure 1 and Appendix).

C. neumayri is very common in the Eastern Mediterranean. Its occurrence is very well documented in Anatolia (Heissig 1975; Geraads 1994; Kappelman *et al.* 1996). The published record of the species in other Balkan countries (Bulgaria, former Yugoslavia) is sufficient only to confirm its presence and has not been studied in detail. *C. neumayri* has been also reported in a few localities of the former USSR, but the available data are inadequate. Tsiskarishvili (1987) described the new species *Diceros gabunia* from a Vallesian locality in Caucasus as being a regional variant. A few poorly documented and somewhat doubtful references from Hungary, Italy and Austria may outline the Western margin of the species. From these, only Thenius (1956) described and illustrated properly some mandibular fragments from the Vienna basin, Austria, but this assignment must be re-examined. Still, this does not exclude the possibility that some populations of *C. neumayri* might have wandered in these regions. Eastern elements have been often reported in some West European localities. A few Spanish remains reported as *Diceros pachygnathus* by Guérin (1980) were later assigned to *Dihoplus schleiermacheri* by Cerdeño (1989, 1992). In the Middle East, *C. neumayri* is undoubtedly present at Maragheh, Iran (Thenius 1955), but the rhino material from this locality still lacks its dedicated monograph. This occurrence marks the Eastern margin of the species.

Several authors have discussed the occurrence of different geographic or temporal subspecies of *C. neumayri*. Osborn (1900) originally created "*Atelodus*" *neumayri* as a separate species from "*Atelodus*" *pachygnathus*,

based on a few dental differences found in a skull from Maragheh. Thenius (1955) re-examined carefully the type skull from Maragheh and questioned the value of Osborn's dental differences. He introduced however some new features and proposed the existence of two separate subspecies: *Diceros pachygnathus pachygnathus* at Pikermi and Thessaloniki and *Diceros pachygnathus neumayri* at Maragheh and Samos. Geraads (1988) rejected Thenius' opinion with the argument that the proposed differences disappear, when additional skulls from the several localities were taken into consideration.

In our opinion, a certain degree of variation is expected among the various populations due to temporal evolution and/or local environmental factors. The question is how good we can document these habitual differences and if they are enough to establish distinct species or subspecies. Heissig (1975) observed a progressive size increasing as well as some morphological specialisations for *C. neumayri* at the Late Miocene sequences of Anatolia (e.g. diminution of the fibular facet at astragalus, increase of gracility at metapodials etc.). The advantage of Heissig's observations is that they are based on stratigraphically well calibrated localities. On the other hand, the number of the available specimens from these localities is too limited to test the variability and constancy of the suggested features (Heissig, unpublished data; author's personal observations). For instance, a small, but anatomical almost complete sample from the Turkish locality of Mahmutgazi housed at Museum für Naturkunde Karlsruhe shows a remarkable stability near the maximum values observed in much greater samples from Pikermi. Only a few interesting morphological differences could be observed between the two localities. Unfortunately the great bulk of the fossils from the classical locality of Pikermi has no stratigraphic data and it is not clear yet, if it occurs in significantly distinct horizons (Theodorou & Nicolaides 1988, Bernor *et al.* 1996). Such 'contaminated' samples may tolerate a greater variability

when used for statistical purposes. In any case, only careful investigations on both morphological and metrical variability between well defined population samples can clarify, whether some of the expected evolutionary trends are sufficient to support the distinction of geographic or temporal subspecies. Until then, it is better to avoid the application of different specific or subspecific names.

The oldest and most plesiomorphic representative of the subtribe Dicerotina is *Paradiceros mukirii* HOOIJER, 1968 from the Middle Miocene of Fort Ternan, Kenya. The species has also been reported in North-eastern Africa at Beni Mellal, Morocco (Guérin 1976) and in the Kisegei Formation in Uganda (Guérin 1994). As stated earlier, Heissig (1989) cited the presence of "early Dicerotini specimens from the Middle Miocene of Anatolia and Chios", but this unpublished material appears to be inadequate for any useful comparison at the present (K. Heissig, pers. comm. 2001). Late Miocene representatives of Dicerotina are poorly documented in Africa compared to the richness of the Eastern Mediterranean localities. Only three African sites have yielded some interesting Dicerotina material and in each case a new species has been described. The first species comes from the Vallesian of Algeria and was originally described as *Dicerorhinus primaevus* by Arambourg (1959), but it was later recognised as *Diceros primaevus* by Geraads (1986). The second species was found in the Turolian site of Duaria (Tunisia) and was described as *Diceros douariensis* by Guérin (1966). Recently, Guérin (2000) assigned the rhino remains from Arrisdrift (Sperrgebiet, Namibia) to a third species, *Diceros australis*. All three species appear to be more primitive than *Ceratotherium neumayri*.

Due to the existing complicated nomenclature issues, which require a formal request at the International Commission, the generic status of these species as well as their relationships with the two living genera will not

be discussed further here. In any case, the synapomorphies within the group of the Dicerotina are remarkable constant and clear. It is enough to mention that the monophyly of this group is probably the only one within the family which is unequivocally supported by all modern phylogenetical hypotheses proposed so far (Heissig 1973, 1989; Guérin 1982, 1989; Groves 1983; Prothero *et al.* 1986; Prothero & Schoch 1989; Geraads 1988, Cerdeño 1995; McKenna & Bell 1997).

The contemporary species *Dihoplus piker-miensis* is also common in Greece and has been described in Pikermi (Roth & Wagner 1854; Gaudry 1862-67; Geraads 1988), Samos (Weber 1904; Geraads 1988) and Halmyropotamos (Melentis 1968, 1969). Its presence in other sites, such as the well known *Graecopithecus* locality of Tour la Reine (Paraskevaidis 1977), is not sufficiently documented. This large tandem-horned rhino recalls in many features the smaller living Sumatra rhino *Dicerorhinus sumatrensis*. In the past they have been often treated as congeneric. This was also the case for all fossil tandem-horned species apart from *Coelodonta* and the Dicerotina. In time, quite a few new generic names were introduced for some of these species. In most cases though, a suprageneric arrangement for the group has been retained, without always a general agreement. Currently the origin and evolutionary relationships among the Miocene and Plio-Pleistocene representatives of this lineage are extremely controversial among the specialists and even their suprageneric status has been challenged. In the following discussion, only the most recent opinions will be reviewed with emphasis on the Miocene species. We believe this discussion is necessary in order to establish some stability, at least at generic level.

Guérin (1980, 1982, 1989) follows the 'traditional' view for the Miocene and Early Pliocene species without an ossified nasal septum and includes them within the genus *Dicerorhinus* GLOGER, 1841. For the rest of the Plio-Pleistocene species with partly ossified

nasal septum he creates the new subgenus *Brandtorhinus*. The generic names *Lartetotherium* GINSBURG, 1974 and *Stephanorhinus* KRETZOI, 1942 are considered as synonyms. All the species are ranked together with *Coelodonta* BRONN, 1831 under the Subfamily Dicerorhininae.

Prothero & Schoch (1989), following basically the phylogeny proposed by Prothero *et al.* (1986), include the genera *Dicerorhinus*, *Lartetotherium*, *Stephanorhinus* and *Coelodonta* within the subtribe Dicerorhinina, but they don't discuss the specific context of each genus. Alternative phylogenetical hypotheses for some species were also proposed by Heissig (1981), Groves (1983), Geraads (1988) and Fortelius *et al.* (1993). Groves (1983) suggests that the genus *Dicerorhinus* must be restricted only to the living Sumatra rhino. He supports the use of the generic names *Lartetotherium* and *Stephanorhinus* for some fossil species and states the availability of the name *Dihoplus* for *D. schleiermacheri*.

Heissig (1989, 1996a, 1999) regards the medium sized Middle Miocene *Lartetotherium sansaniense* as clearly plesiomorphic and recognises two evolutionary lineages during the Late Miocene and Pliocene: The first evolves successively through the species *Dihoplus schleiermacheri*, '*Dicerorhinus*' *megarhinus* and '*Dicerorhinus*' *jeanvireti*, while the other one through *Stephanorhinus pikermiensis* and *Stephanorhinus etruscus*. Heissig's arguments uniting '*Stephanorhinus*' *pikermiensis* with *Stephanorhinus etruscus* and separating it from *Dihoplus schleiermacheri* are the following: the 'medium size' of '*S.*' *pikermiensis* (compared to the 'large' *D. schleiermacheri*), the narrower skull, the loss of all the enlarged incisors and the strong interior cingula in the upper premolars. The size of the many skulls from Pikermi and Samos that we know is about the same as the size of the only known complete skull of *Dihoplus schleiermacheri*, the lectotype from Eppelsheim. The differences in the postcranial skeleton are also insignificant. *Stephanorhinus etruscus* is considerably

smaller than both species. A mandible, originally figured as *Rhinoceros pachygnathus* by Gaudry (1862-67, Pl. xxviii, fig. 1, 2), as well as adequate material under study, shows that '*S.*' *pikermiensis* has a weak, but still functional anterior dentition. *Stephanorhinus etruscus* lacks completely this feature. The appearance of internal cingulum at the premolars is not always constant in '*S.*' *pikermiensis* and in no case as strong as in *Stephanorhinus etruscus*. Moreover, '*S.*' *pikermiensis* lacks many of the apomorphic characters shared by the species included in *Stephanorhinus* (Fortelius *et al.* 1993), especially the absence of a partially ossified nasal septum. The affinities of '*S.*' *pikermiensis* are indeed closer to *Dihoplus schleiermacheri* than to *Stephanorhinus etruscus*. Some morphological and metrical differences are expected, since *Dihoplus schleiermacheri* is better documented in the Vallesian of Western Europe, while *Dihoplus pikermiensis* in the Turolian of Eastern Mediterranean, but these can be treated at specific or even subspecific level. The same is also true for the larger *Dihoplus ringstroemi* (ARAMBOURG, 1959) of Eastern Asia.

Cerdeño (1995) presents a cladistic analysis of the whole family Rhinocerotidae and introduces some new ideas. The author (Cerdeño 1995, 1998) ranks all the Miocene species into a single genus, *Lartetotherium*, while the Plio-Pleistocene species are all placed within the genus *Stephanorhinus* (including also the species with no partially ossified nasal septum, such as the Early Pliocene '*Dicero-*' *rhinus*' *megarhinus*). Apart from the stratigraphic separation there are not many arguments offered to support this arrangement, since the analysis considers most of the taxa at generic level. Another interesting result of Cerdeño's analysis is that the subtribe Dicerorhinina was not supported. Instead of this, *Stephanorhinus* and *Coelodonta* were placed together with *Elasmotherium* and *Ninxiatherium* (= *Parelasmotherium*) under the subtribe Elasmotheriina. It is obvious (Cerdeño 1995: Tab. 4, node 20; Tab. 5, node

24) that the only character practically supporting this ‘monophyly’ was the presence of a partially or totally ossified nasal septum, a fact also admitted by the author, since the rest of the apomorphic characters gathered at these nodes were also shared by other groups. Out of the 45 taxa, only these four genera had states 1 or 2 for character 4, i.e. partially or totally ossified nasal septum (ibid. Tab. 2, 3). Erroneously, this character state was interpreted by the analysis as a synapomorphy (Cerdeño 1995: p. 20), although it is clear from the paleontological record that the acquisition of an ossified nasal septum has been achieved at least twice independently within the groups of *Stephanorhinus-Coelodonta* and *Elasmotherium-Ninxiatherium* as a result of parallelism. This view is also supported by another cladistic analysis (Antoine 2000), in which the presence and the development of an ossified nasal septum were coded as two separate binary characters instead of a single multiple one. Cerdeño (1995) discussed also the possibility of an independent acquisition of the ossified nasal septum but did not adopt it in her final classification. For these reasons, we do not favour the classification of *Stephanorhinus* and *Coelodonta* within the *Elasmotheriina* (sensu Cerdeño 1995).

The genus *Lartetotherium* has been erected by Ginsburg (1974) for the species *Rhinoceros sansaniensis* LARTET, 1851 from the Middle Miocene locality of Sansan in France. There are many primitive and autapomorphic characters found in this species (Ginsburg 1974, Groves 1983, Heissig in press), but the presence or not of a frontal horn tends to be the most significant and controversial one. Ginsburg (1974) did not discuss the horn arrangement in his generic diagnosis, while the original specific diagnosis (Lartet 1851) was also somehow undecided, because of the craniocaudal distortion of the type skull. Guérin (1980) and Cerdeño (1989) favour the presence of a frontal horn in the type material from Sansan. Heissig (in press) believes that the French specimens could lack a frontal

horn. Skulls found in Sandelzhausen (Bavaria, Germany) unequivocally have only one nasal horn (Heissig 1972b; Groves 1983; author’s personal observations).

The subject requires certainly further study and discussion. Regarding the Miocene taxa concerned here, we can note the following conclusions: We follow Heissig (1972b, 1989, in press) and Groves (1983) in considering *Lartetotherium sansaniense* as a primitive Rhinocerotinae, separate, and near the base of the subfamily. The phyletic position of more primitive forms, such as ‘*Dicerorhinus*’ *abeli* in Southeast Asia is poorly documented. The same is true for the Spanish ‘*Dicerorhinus*’ *montesi* and the small ‘*Dicerorhinus*’ *steinheimensis* in Europe. If the African ‘*Dicerorhinus*’ *leakeyi* or the Chinese ‘*Dicerorhinus*’ *cixianensis* belong also to *Lartetotherium* or to *Dihoplus* cannot be decided at the present. We believe though that the large Late Miocene species: ‘*Dicerorhinus*’ *schleiermachersi* in Central and Western Europe, ‘*D.*’ *pikermiensis* in Southeastern Europe and the Eastern Mediterranean and ‘*D.*’ *ringstroemi* in Eastern Asia are morphologically and metrically very closely related. We propose therefore the generic name *Dihoplus* BRANDT, 1878, originally erected for *Rhinoceros schleiermachersi* KAUP, 1832, to include all of them. *Dihoplus* has in any case the priority over all the alternative generic names mentioned above (*Stephanorhinus*, *Lartetotherium*) and may be convincingly extended to include other Neogene species, as well. A stable and persuading phylogeny for the whole group, from the Miocene forms to the highly specialised *Coelodonta* and the living Sumatran rhino, is yet to be given.

Subfamily Aceratheriinae

The Greek representatives of the subfamily Aceratheriinae during the Late Miocene are obviously closer related to the Asian genera *Chilotherium* and *Acerorhinus* than to the typical aceratheres *Aceratherium*, *Alicornops* and *Hoploaceratherium* found in Central and

West Europe at the same time. *Chilotherium* and *Acerorhinus* migrated into Greece from Central Asia through Anatolia at the beginning of the Vallesian. *Chilotherium* has dominated Samos, where it was represented by at least three species: *Ch. samium*, *Ch. schlosseri* and *Ch. kowalevskii*. The richest acerathere material in continental Greece comes from the recently discovered locality of Pentalophos-1, where the species *Aceratherium kiliasi* has been described. Later, this material was partly assigned to *Chilotherium* and partly to *Acerorhinus*. The few references on 'Aceratherium sp.' from Pikermi, Vathyakos and Chomateri that are based on scanty finds could also belong to these genera.

The island of Samos has been known for its wealth of Miocene mammals since the middle of the last century. Weber (1905) studied a remarkable sample of acerathere material including several skulls with associated mandibles as well as partly articulated limb bones and described two new species, *Aceratherium schlosseri* and *Aceratherium samium*. Andree (1920) created later two additional species based on material from Samos: *Aceratherium wegneri* and *Aceratherium angustifrons*. Unfortunately, Weber's entire material as well as many specimens of Andree's material have been destroyed during the Second World War. At present, only a skull housed at the Geological Institute of Padova and referred to *Ch. wegneri* by Leonardi (1947) as well as another one with associated mandible at the Paleontological Institute of Hamburg described as *Ch. schlosseri* by Lehman (1984) comprise the intact published chilothere material from Samos. However, a wealth of unpublished material is expected to be available at the numerous museums where fossils from Samos are stored (Solounias 1981a,b). Ringström (1924) placed rightfully all these species to his new genus *Chilotherium*. Heissig (1975) published a preliminary report on the Miocene rhinoceroses of Anatolia. In this report, Heissig considered *Ch. wegneri* synonymous with *Ch. schlosseri* and *Ch. angustifrons* with *Ch. kowalevskii* (PAVLOW,

1913).

The smaller and less hypsodont *Ch. samium* is the most primitive of the three species. In Anatolia, *Ch. samium* first appears in Vallesian (MN10/11) about at the same time, but not together, with the more hypsodont *Ch. habereri* (Heissig 1975). *Acerorhinus*, another acerathere genus that lacks the specialization of *Chilotherium*, was also present at that time in Anatolia with the species *Acerorhinus zernowi* (BORISSIAK, 1914). Unfortunately, many of Samos' classical collections are missing accurate stratigraphic data for comparison with Anatolia (compare Solounias 1981a,b and Bernor *et al.* 1996). *Ch. kowalevskii* with semimolariform molars was found on material from Grebeniki (Ukraine). It is probably a later immigrant (MN 12) that represents a divergent evolutionary lineage. The larger and high crowned *Ch. schlosseri* is the typical Turolian chilothere. The advanced stage of *Ch. schlosseri* is very similar to the contemporary Chinese genotype *Ch. andersoni* and both species can be possibly traced back to *Ch. habereri* (Heissig 1975, 1996a). All these chilothere forms indicate diverse ecological preferences, which explain their parallel existence. Additional studies on the unpublished material from Samos are necessary to establish clear affinities for all species.

In continental Greece, the richest acerathere material comes from the recently discovered locality of Pentalophos-1, where the species *Aceratherium kiliasi* has been described by Geraads & Koufos (1990). The material comprises of several skulls and mandibles, but no postcranials. Heissig (1996a, 1999) designated the material from Pentalophos partly to *Chilotherium kiliasi* and partly to *Acerorhinus zernowi*, with the remark that the first one could be specifically identical with *Chilotherium samium*. Heissig did not provide any arguments for this separation. Judging from the description and the illustrations of 'Aceratherium' *kiliasi*, part of the material reveals many similarities with *Chilotherium samium*. This point has been also evaluated

by Geraads & Koufos (1990), but they considered *Chilotherium samium* as *Aceratherium*. The low and broad holotype skull with flattened dorsal profile and elevated orbita (upper border at the same level as the frontal) shows more affinities to the *Chilotherium* cranial type (Ringström 1924) than to the Vallesian '*Aceratherium*' skulls from Eppelsheim (Kaup 1832, 1834) and Höwenegg (Hünnerman 1989). The upper dentition of the type skull (Geraads & Koufos 1990, pl. 3, fig. 4) appears also to be identical with the (destroyed) type material of *Ch. samium* from Samos figured by Weber (1904, Pl. II, Fig. 5) and the unpublished material from Turkey housed at the Paleontological Museum of Munich and referred to the same species by Heissig (1975). Some important diagnostic characters are based on the mandible, especially on the symphyseal part. The absence of an anteriorly broadened mandibular symphysis, a synapomorphy of the true chilothers, led Geraads & Koufos (1990) to exclude an ascription to *Chilotherium* (only one of the three mandibles was "slightly broadened"). On the other hand, a narrower symphysis often combined with a concave labial side is considered as diagnostic for the genus *Acerorhinus*. This condition, unknown to the three 'West European' acerathere genera discussed earlier, is documented among others in *Acerorhinus paleosinensis* (RINGSTRÖM, 1924), *Acerorhinus tsaidamensis* (BOHLIN, 1937), *Acerorhinus fuguensis* (DENG, 2000) and the genotype *Acerorhinus zernowi* (Borissiak 1914; Heissig 1975; Cerdeño 1996). Geraads & Koufos (1990) offer many other interesting characters in their detailed description and it is quite possible that at least some part of the material belongs indeed to a new species. Since a close re-examination of the original material from Pentalophos is necessary for final conclusions, we prefer to keep the acerathere remains from this site temporary under their original name '*Aceratherium*' *kiliasi*.

Gaudry (1862-67) described an acerathere mandible from Pikermi as *Aceratherium* sp.

at a time where no other generic name was available, because it clearly differed from the mandible of *Aceratherium incisivum* from Eppelsheim. Since then, this reference has been frequently repeated in numerous publications, sometimes also as *Aceratherium incisivum* and others as *Aceratherium* cf. *incisivum*. It appears that only Geraads & Koufos (1990) have examined the mandible again, but they also considered the material too poor for a specific determination. This is indeed a puzzling specimen. Gaudry's description offers some interesting characters but the accompanying figure is not very informative (ibid., pl. 33, fig. 6). The short distance between the second lower incisors, mentioned also by Geraads & Koufos, excludes an ascription to *Chilotherium*. The large size of the mandible, the short diastema combined with a long and upraised symphysis could speak for an *Acerorhinus* determination. However it is not clear if the symphysis is labially concave. The small metapodials identified by Gaudry as "Rhinocéros indéterminé de petite taille" may actually be more useful. They belong also to an acerathere and probably to the same species. Their size and gracility index correspond well to the values found for *Acerorhinus* (Bohlin 1937, Cerdeño 1996). Unpublished material under study supports these observations, but a re-examination of Gaudry's collection is required to establish final conclusions. For this reason these specimens are temporary considered as *Aceratheriini* indet.

Arambourg & Piveteau (1929) described a strong second lower incisor from Vathilakos 3 (Axios Valley, N. Greece) as '*Aceratherium* sp.'. An acerathere mandible from the locality of Chomateri near the classical Pikermi was cited as '*Aceratherium* sp.' by Marinos & Symeonidis (1974) in a preliminary faunal list. Both specimens are here referred to as *Aceratheriini* indet., since they could belong to any of the aforementioned genera. The present status of the tribe *Aceratheriini* in Southeastern Europe and Asia is extremely complicated and in fact badly needs a revi-

sion. Three genera, *Chilotherium*, *Subchilotherium* and *Acerorhinus* are currently recognised during the terminal Middle and the Late Miocene, but their context and even their suprageneric affinities are still debatable and not very well understood (Heissig 1975, 1989, 1996a; Qiu *et al.* 1988; Bayshashov 1993; Cerdeño 1996; Deng 2000). More than twenty species have been assigned to these genera, ranging from Portugal to Japan. The limits within these forms are not always evident and the distinguishing characters designated are rather confusing than convincing. Many of the newly introduced species lack a differential diagnosis from older species. In a preliminary report, Heissig (1975) presented a table summarising many of the known species together with an initial phylogenetical hypothesis for the group, but not enough arguments were presented to support this. The number of new species has been doubled since Heissig's summary. It is clear that a basic phylogenetical framework, not to speak for a solution, can be discussed only when regional revisions in Greece, Turkey and the rest of the Balkans as well as in the former USSR, the Middle East and especially in China and Mongolia are completed.

Conclusions

The Late Miocene rhino assemblages of Greece are in conformity with the ones from Southeastern Europe and the Eastern Mediterranean, especially with the ones from Anatolia. From a biogeographical aspect, these results correspond to the Eastern regional block of Fortelius *et al.* (1996) or, in a closer approach, to the Greco-Iranian or sub-Paratethyan mammalian province of Bernor (1984) and De Bonis *et al.* (1993, 1999). By the end of the Turolian, all these species became extinct in Greece, unable to survive the paleoenvironmental changes and the faunal turnover at the Miocene-Pliocene boundary. The aceratheres disappeared completely from Europe and Western Asia, while the subtribe Dicerotina was restricted to Africa, where it survived until nowadays. In

Europe, only the less specialized *Dicerorhinina* managed to resist into the Pliocene.

PLIOCENE

During the Early Pliocene (Ruscinian), the localities with large mammals in Greece are extremely rare (Koufos & Kostopoulos 1997). The presence of Rhinocerotidae indet. has been cited in the faunal lists of three localities (Apollakia, Nea Silata, Alatin), but no specimens were published. The Apollakia Formation, placed near the south-west coast of the island Rhodes, is the best known of these three. Apollakia features a typical Ruscinian micro- and macromammalian local fauna, which has been described by van de Weerd *et al.* (1982). The presence of Rhinocerotidae indet. is referred only in the faunal list of the site. Syrides (1990) noted the presence of Rhinocerotidae fragments among the few remains of large mammals found at Nea Silata (Chalkidiki). The micro-mammals of this site were originally dated to basal Pliocene (Syrides 1990). New studies on the rich micromammalian fauna of Nea Silata indicate a transitional Turolian/Ruscinian character for the locality (K. Vassiliadou, pers. comm. 2001). Marinos (1965) mentioned in a short comment the presence of several mammals including '*Rhinoceros* sp.' at the locality of Alatin, near Thessaloniki. A few years later, Sickenberg (1972) described the carnivore *Nyctereutes donnezani* from the same locality suggesting a Ruscinian age. In all three cases, we can assume that the available material was too scarce to support any further investigation.

The scantiness of large mammal faunas during the Ruscinian characterises the whole Eastern Mediterranean region. The most common rhino in Western Europe during this period is the large '*Dicerorhinus*' *megarhinus*. Only recently Guérin & Sen (1998) documented adequately the presence of this species at the Early Pliocene locality of Çalta, near Ankara (Turkey). '*Dicerorhinus*' *megarhinus* probably represents the terminal

evolutionary stage of the large Miocene Dicerorhinina, here placed under the genus *Dihoplos*. As discussed above, the origin and evolutionary relationships among the Miocene and Plio-Pleistocene representatives of this subtribe are still controversial.

Middle and Late Pliocene localities with large mammals are rather frequent in Greece. Despite the numerous localities, knowledge of rhinos during this time period is also very limited, because of the scarce material. It is notable that the published material exceeds the number of five specimens in one site only, Sesklo (Thessaly, Central Greece). Symeonidis (1992), in a brief description, assigned the few postcranial materials from Sesklo to *Dicerorhinus cf. etruscus*. Later, Athanasiou (1998) re-examined the Sesklo fauna and observed some significant differences from the standards established for *Stephanorhinus etruscus* by Guérin (1980) and Fortelius *et al.* (1993). Therefore he referred the material temporarily to *Stephanorhinus* sp. Further isolated remains of Rhinocerotidae have been reported with more or less certainty as *Stephanorhinus* sp. or *Stephanorhinus cf. etruscus* from several other Late Pliocene sites (Fig. 1, Appendix), but the available material is not sufficient for useful comparisons.

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APPENDIX Neogene localities with rhinoceroses in Greece. (fl)= cited only in a faunal list (no description/specimens published). Chronostratigraphic units after Steininger et al. (1996).

Nr.	Locality	Species	References	Age
(28)	Chios (fl)	Rhinocerotidae indet.	Heissig (1989)	MN 5
(5)	Chrysaugi	Rhinocerotidae indet.	Psarianos (1958), Dimopoulos (1972)	MN 7-8
(18)	Atalanti	Aceratheriini indet.	Symeonidis (1974)	MidMio
(-)	Ravin de la Plui (fl)	Rhinocerotidae indet.	Bonis & Koufos (1999)	MN 10
(-)	Xirochori 1 (fl)	Rhinocerotidae indet.	Bonis & Koufos (1999)	MN 10
(7)	Pentalophos 1	<i>Ceratotherium neumayri</i> <i>Aceratherium kiliasi</i>	Geraads & Koufos (1990)	MN 10
(11)	Nikiti 1 (fl)	Rhinocerotidae indet.	Bonis & Koufos (1999)	MN 10/11
(4)	Ravin de Zouaves 5	<i>Ceratotherium neumayri</i>	Koufos (1980)	MN 11
(6)	Vathylakos 2 (fl)	Rhinocerotidae indet.	Bonis & Koufos (1999)	MN 11/12
(6)	Vathylakos 3	<i>Ceratotherium neumayri</i> Aceratheriini indet.	Arabourg & Piveteau (1929),	MN 11/12
(20)	Tanagra (fl)	Rhinocerotidae indet.	Mitzopoulos (1960)	MN 11-12
(23)	Halmyropotamos	<i>Dihoplus pikermiensis</i>	Melentis (1968, 1969)	MN 11-12
(29)	Samos (various localities)	<i>Dihoplus pikermiensis</i> <i>Ceratotherium neumayri</i> <i>Chilotherium samium</i> <i>Chilotherium kowalevskii</i> <i>Chilotherium schlosseri</i>	Wagner (1848), Roth & Wagner (1854), Gaudry (1862-67), Osborn (1900), Weber (1904, 1905), Andree (1921), Thenius (1955), Heissig (1975), Guérin (1980), Geraads (1988)	MN 11-13
(24)	Pikermi	<i>Dihoplus pikermiensis</i> <i>Ceratotherium neumayri</i> Aceratheriini indet.		MN 11-12
(25)	Chomateri	Aceratheriini indet.	Marinos & Symeonidis (1974)	MN 12
(3)	Dytiko	<i>Ceratotherium neumayri</i>	Koufos (1980)	MN 13
(14)	Servia (fl)	Rhinocerotidae indet.	Paraskevaïdis (1977)	LatMio
(21)	Tour la reine	Rhinocerotidae indet.	Paraskevaïdis (1977)	LatMio
(16)	Kerasia (fl)	Rhinocerotidae indet.	Theodorou et al. (1995)	LatMio
(22)	Chalkoutsis (fl)	Rhinocerotidae indet.	Theodorou et al. (1995)	LatMio
(17)	Prokopi (fl)	Rhinocerotidae indet.	Woodward (1901)	LatMio
(2)	Maramena (fl)	Rhinocerotidae indet.	Schmidt-Kittler et al. (1995)	MN 13/14
(10)	Nea Silata (fl)	Rhinocerotidae indet.	Syrides (1990)	MN 13/14
(30)	Apolakia (fl)	Rhinocerotidae indet.	Van de Weerd (1982)	MN 15
(9)	Alatini (fl)	Rhinocerotidae indet.	Marinos (1965)	EarPlio
(26)	Tourkovounia	<i>Stephanorhinus cf. etruscus</i>	Symeonidis & deVos (1976)	MN 16/17
(15)	Sesklo	<i>Stephanorhinus sp.</i>	Athanasïou (1998)	MN 17
(1)	Volakas	Rhinocerotidae indet.	Sickenberg (1968)	MN 17
(27)	Kythira	Rhinocerotidae indet.	Bartsïokas (1998)	LatPlio
(13)	Aliakmonas	<i>Stephanorhinus sp.</i>	Psarianos (1958)	LatPlio
(8)	Krimni	<i>Stephanorhinus cf. etruscus</i>	Sakelariou-Mane et al. (1979)	LatPlio
(19)	Molykrio	<i>Stephanorhinus cf. etruscus</i>	Symeonidis et al. (1985-86)	LatPlio

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