

Rhinocerotidae from the Late Miocene and Late Pliocene of Macedonia, Greece. A revision of the Neogene - Quaternary Rhinocerotidae of Greece

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Abstract

Rhino fossils have been found in 65 localities in Greece, spanning the biozones MN 5 to MNQ 26. Some specimens represent the first occurrence of their species in Greece (such as *Stephanorhinus jeanvireti* in Milia, West Macedonia) while others are new species identified first in Greece (e.g. *Dihoplus pikermiensis*, *Acerorhinus neleus* at Pikermi, Kerassia, etc.). We provide an updated overview of the Neogene - Quaternary Rhinocerotidae of Greece. We describe herein Late Miocene rhinos from two sites in Eastern Macedonia: Thermopigi (Serres) and Platania (Drama). At Thermopigi, *Dihoplus pikermiensis* is represented by maxillas with teeth, a few complete long bones with special taphonomic remarks, metapodials and phalanges. At Platania, remains of *Ceratotherium neumayri* consist of a mandible of a juvenile, some dental fragments and postcranial elements, mainly carpals, tarsals and metapodials. Some of the metapodials appear to have been gnawed by a large scavenger, as indicated by the presence of tooth-marks and special fragmentation. We also report well-preserved limb bones of *Stephanorhinus jeanvireti* from Angelon Beach at Angelochori (Megalo Emvolo, Thessaloniki); these point out to a Late Pliocene age of the site.

Keywords

Neogene rhinoceroses, Platania, Thermopigi, Angelochori, revision, Greece.

1. INTRODUCTION

In 1841 Goldfuss (Giaourtsakis, 2003 and ref. therein) first reported the presence of rhinoceros fossils in Greece at the Late Miocene site of Pikermi. More synthetic work on Neogene rhinoceroses of Greece was done by Giaourtsakis (2003, 2009) and Athanassiou *et al.* (2014). Astonishingly, systematic palaeontological excavations conducted over decades at Kryopigi (Kassandra, Chalkidiki peninsula) uncovered more than ten thousand Turolian mammalian remains (including *Mesopithecus pentelicus*) but did not provide any remain of rhinoceros in this site.

We present herein newly recovered rhino fossils from systematic excavations in Macedonia, Northern Greece, specifically from the Upper Miocene sites of Thermopigi (Sidirokastro, Serres) and Platania (Paranesti, Drama), and from the Upper Pliocene site of Angelon-Angelochori (Thessaloniki) (Fig. 1A). We added an update of the Neogene-Quaternary Rhinocerotidae of Greece in the Appendix, with Miocene rhinos in Table A1 and Plio-Pleistocene rhinos in Table A2.

Abbreviations

Abs: absolute; anat.: anatomical; ant.: anterior; art.: articulation; B: breadth; cond.: condyle; D/d: upper/

lower deciduous premolars; D: dextra, right; DAP: antero-posterior diameter; Dist. 2 brims: distance between the two brims of astragalus; dist., d.: distal; DT: transversal diameter; H: height; I: index; L: length; M/m: upper/lower molars; max: maximal; md: mandible; Mp: metapodial, Mc: metacarpal, Mt: metatarsal; min: minimal; olec.: olecrani; Ph: phalanx; P/p: upper/lower premolars; post.: posterior; prox.: proximal; S: sinistra, left; sust.: sustentaculum; troch.: trochlea.

2. GEOLOGY AND PALEONTOLOGY

The site of Thermopigi (SIT: Sidirokastro Thermopigi; N 41°17'16", E 23°21'51") is located in the Serres Basin (Prefecture of Serres, Eastern Macedonia), 4 km from the Sidirokastro municipal center and 18 km from the Bulgarian border (Fig. 1). Paleontological research began in 1998, and systematic excavations have been undertaken in 1999. Between 2011-2015, the research in this site was done with the collaboration of Vienna University (Prof. D. Nagel) (Fig. 1B).

We have unearthed hundreds of fossils preserved in consolidated reddish sandstones. The fossils are generally in good condition but some specimens are marked by neotectonic events such as faults and

joins (Fig. 3L, M, O), which resulted in fractures and deformations. The recovered fossils are stored in the Municipal Paleontological Museum in Thermopigi village, established in 2005. Preliminary faunal list includes, in addition to the rhino *Dihoplus pikermiensis*, *Felis attica*, *Paramachairodus* sp., *Machairodus* sp., *Adcrocuta eximia*, *Hipparion* cf. *dietrichi*, *Hipparion* cf. *matthewi*, *Ancylotherium pentelicum*, *Microstonyx major*, *Propotamochoerus* cf. *hysudricus*, *Tragoportax* cf. *amalthea*, *Palaeoreas lindermayeri*, *Prostrepsiceros* cf. *axiosi*, *Criotherium* ? sp., and *Gazella* sp. (Geraads et al., 2007), and the giraffids *Samotherium major*, *Palaeotragus rouenii*, *Helladotherium duvernoyi*, and *Palaeotragus* sp. nov. (Xafis, 2015).

The site of Platania (PLD: Platania, Drama; N 41°11'48.4", E 024°23'42.0", altitude 257 m a.s.l., Hellenic Grid, EGSA '87) is located in the Municipality of Paranesti (Drama Prefecture, Eastern Macedonia), 14 km from the Paranesti municipal center (Fig. 1).

We began our research there in 2013, with systematic excavations carried out from 2014 onwards, and still in progress (Fig. 1C, D).

A few hundred well-preserved fossils have been collected from yellow–brownish fine sandy mud, indicative of a rather lacustrine environment. These fossils are stored in the Paleontological Museum of Aristotle University. The preliminary faunal list of species includes, in addition to the rhinoceros *Ceratotherium neumayri*, *Adcrocuta eximia*, hipparions, the giraffid cf. *Samotherium major* (Xafis, pers. comm.), suid, the bovids *Prostrepsiceros rotundicornis*, *Miotragocerus* cf. *pannoniae*, *Trago-reas* aff. *onyxoides*, cf. *Palaeoryx*, Cervidae indet (Kostopoulos & Vasileiadis, pers. comm), *Konobelodon atticus* (Konidaris, pers. comm.) and *Testudo* cf. *graeca* (Vlachos & Tsoukala, 2014).

The fossil assemblage and the stratigraphic context indicate a Late Miocene age. Several fossils are almost complete and have a blackish color easily recognizable

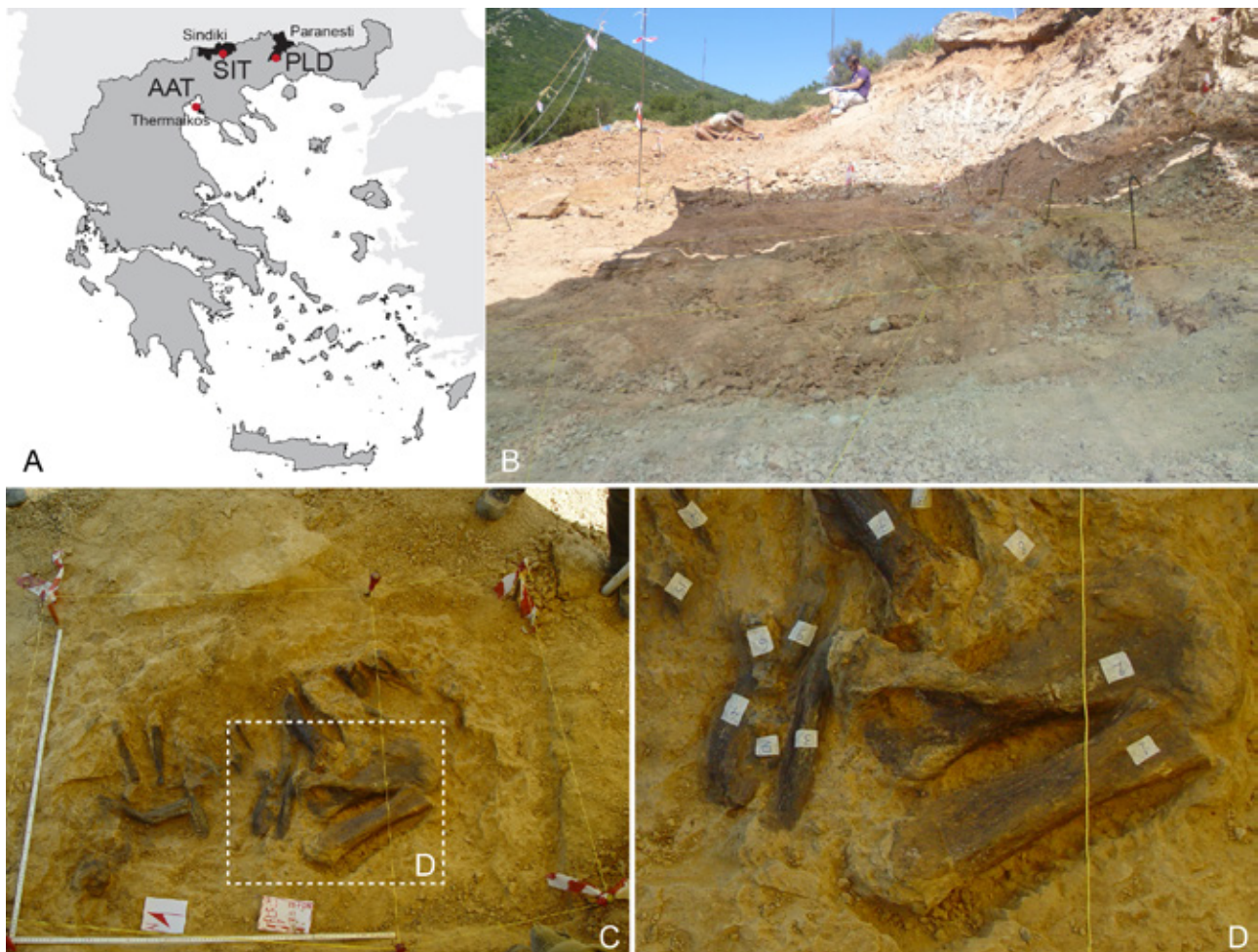


Fig. 1: A. Map of Greece with the location of the Upper Miocene sites of Platania Drama - PLD and Thermopigi, Serres – SIT and the Pliocene site of Angelon Angelochori Thessaloniki – AAT; B. The Thermopigi excavation of 2011 in the reddish cohesive sandstones, with the orientated block of squares; C. D. The Platania excavation of 2016 in the yellowish sandy mud, with the orientated block of squares; D. Detail of the excavation square with an almost complete left tibia of rhino (1-PLD 608) and a complete left humerus (2- PLD 609) *in situ*.

in the light colored sediments (Fig. 1C); the black color is associated with the presence of high concentrations of manganese (Mn) during the fossilization processes. Fossil remains and sediments from Platania contain high levels of natural radionuclides (Zougrou, 2017).

The site of Angelochori, Angelon Beach (AAT: Thermaikos Gulf; N 40°63'09", E 22°96'48", 72 m above sea level) is located in the Municipality of Nea Michaniona (Central Macedonia), 30 km from Thessaloniki (Fig. 1). Fossil specimens from this locality were collected by A. Tzanoudakis. Fossils are hosted in grey fine-granulated sandy sediments. The broader area is known as Cape Megalo Emvolo. According to the map of this broader area in Koufos *et al.* (1991: fig. 1, p. 284) the site MEV, at which was recorded a *Dolichopithecus ruscinensis* mandible among several vertebrate remains, is relatively close to the AAT site.

3. SYSTEMATIC PALEONTOLOGY

Order Perissodactyla Owen, 1848
 Sub-order Ceratomorpha Wood, 1937
 Family Rhinocerotidae Gray, 1821
 Subfamily Rhinocerotinae Gray, 1821
 Tribe Rhinocerotini Gray, 1821
 Subtribe Rhinocerotina Gray, 821
 Genus *Dihoplus* Brandt, 1878

Dihoplus pikermiensis (Toula, 1906)

Locality: Thermopigi (SIT), Municipality of Sindiki, Prefecture of Serres, Eastern Macedonia, Greece.

Material: Right maxilla with P4-M3 SIT 1325; left maxilla with P2-P4 SIT 660; right P2 SIT 661; right D4 SIT 650; right scapula SIT 670; right humerus complete SIT 250; left humerus SIT 251; left humerus proximal + diaphysis SIT 877; metapodials: 2 right Mc II SIT 860, SIT 663; 2 right Mc III SIT 1423, SIT 990; left Mc III SIT 1366; 2 right Mc IV SIT 1245, SIT 662; left Mc IV SIT 888; right Mt II SIT 973; left Mt IV SIT 1236; phalanges: axial proximal Ph I SIT 664; left abaxial proximal Ph I for Mp IV SIT 669; left abaxial medial Ph II SIT 667.

Description: The right maxilla SIT 1325 preserves the worn tooth-row P4-M3, which is labially eroded (Fig. 2A-B, Table 1). The left maxilla SIT 660 preserves in good condition the middle worn P2-P4 (Fig. 2C, Table 1). The isolated teeth are well preserved: the middle worn P2 SIT 661 (Fig. 2D, Table 1) and the unworn D4 SIT 650 (Fig. 2E, Table 1). The squarish P2 SIT 660 and SIT 661, left and right respectively, show similar dimensions, wear stage and state of preservation; therefore it cannot be excluded that they belong to the same individual. At this stage of wear the parastyle is developed, anteriorly followed by a strong mesial cingulum. The protocone is slightly notched close to the parastyle fold and protocone and hypocone are lingually fused. P3 and P4 are middle

worn, similarly constructed: at this stage of wear the ectoloph shows a strong parastyle, a well-distinct fold of the paracone and a slight fold of the metacone. The protocone and hypocone are confluent. The mesial cingulum below the inner half of the protocone is strong and the protocone presents a slight constriction. The fourth premolar and the molars on the maxilla SIT 1325 are poorly preserved. The ectolophs of the worn P4, M1 and M2 and the labial cones are destroyed, whereas part of the ectometaloph of middle worn M3 is missing. In all teeth, a strong mesial cingulum is present, whereas lingual cingula are absent and the protocone is constricted more mesially than distally. In the worn M1, the mesial groove at this stage of wear is well marked, still preserving the mesial constriction of the protocone. The sub-triangular M3 shows a strong crochet and a small anticrochet that never meet each other; therefore, they do not close the fossette. The unworn D4 has a strongly undulated ectoloph with the strong fold of paracone, and the protocone shows a strong constriction, whereas the hypocone is slightly constricted. There is no lingual but a strong mesial cingulum. The medi-fossette is absent, whereas the post-fossette is present. Crochet is also present and there is a rudimentary cusp on the base of the crown instead of crista. The maximum height of the ectoloph is 31.5 mm, and the index of hypsodonty 67. Of the right robust scapula SIT 670 only the distal part with the glenoid cavity is preserved.

The right humerus SIT 250 is robust and well preserved, better than the other SIT rhino humeri (Fig. 3A-F), which makes it possible reliable measurements (Table 2). The caput humeri is rather oval in shape with well-distinct collum, the sulcus intertubercularis is deep and wide, the crest joins tuberositas deltoidea (the tip of which is broken) and the intermediate indentation of caput is not strong. The fossa olecrani is wide and the trochlea is also wide and quite oblique. The tip of the epicondylus lateralis is broken, whereas epicondylus medialis is well developed. The fossa coronoidea is deep and elongated above the proximal lip of trochlea. The left almost complete humerus SIT 251 is transversally compressed (Fig. 3G-K). Its length can be estimated as 425 mm, the minimum breadth of diaphysis 63 mm and the depth of that point 69 mm. The left almost complete humerus SIT 877 shows a remarkably high *in situ* deformation due to neotectonic events in the excavation site, where the sense of movement is strike-slip with horizontal displacement. The bone has been affected by faults and joints (Fig. 3L-O). The proximal breadth is c. 162.5 mm and at the tuberositas deltoidea 136 mm, whereas the proximal depth is about 122 mm.

The complete Mc II SIT 663 only lacks the lateral part of the proximal end (Fig. 4A; Table 6), whereas the SIT 860 is more complete but deformed, dorsal and ventral sides flattened (Fig. 4B; Table 6). They are rather long and slender. The proximal end of the latter has not strong lateral projection as observed often in rhinos.

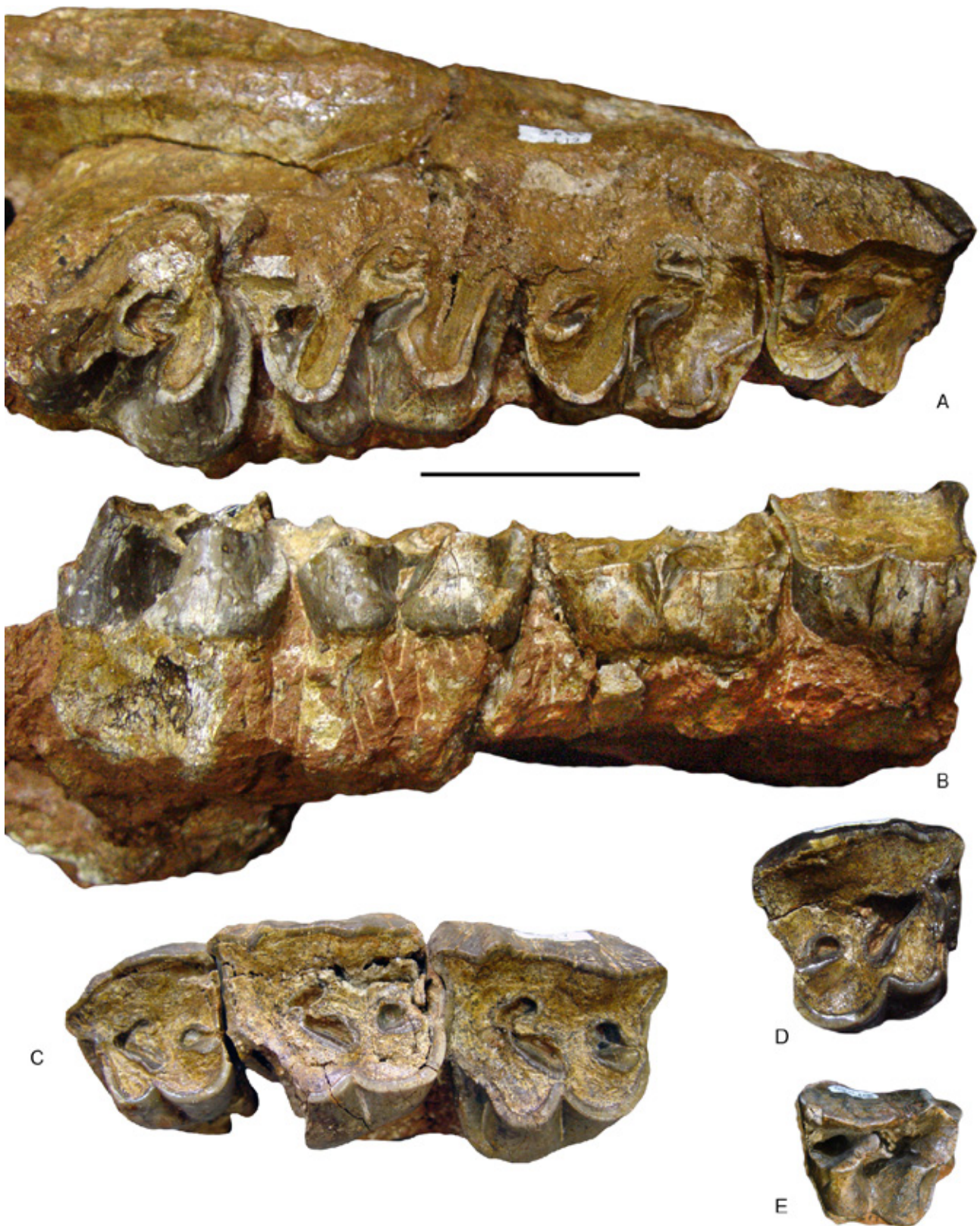


Fig. 2: The Thermopigi *Dihoplus pikermiensis*: A, B. Right maxilla with P4-M3, SIT 1325; C. Left maxilla with P2-P4 SIT 660; D. Right P2 SIT 661; E. right D4 SIT 650. A, C-E: occlusal view; B: lingual view. Scale-bar: 50 mm.



Fig. 3: The Thermopigi *Dihoplus pikermiensis*: A-F. Right humerus SIT 250. G-K. Left humerus SIT 251. L-O. Left humerus SIT 877, which exhibits high deformation. A, G: dorsal view; B, H, L: caudal view; C, I, M: lateral view; D, J: medial view; E, N: proximal view; F, K: distal view; O: detail of the deformation. Scale-bar: 50 mm.

The proximal articulation bears a weakly convex dorsal border. The lateral articular surfaces for Mc III are well preserved, with wide contact between them, the palmar facet being smaller than the dorsal one. The lateral groove of trochlea is deep. In palmar side, there is a rounded articular facet for the trapezium and a longitudinal crest. The Mc III SIT 1423 is the most complete and well preserved. It is long and slender, with an almost straight diaphysis. The distal trochlea is robust, its posterior crest is eroded, and the supra-trochlear tubercles are well developed (Fig. 4H-J; Table 6). Of the articular surfaces for Mc IV, the dorsal one is elliptical, whereas the palmar one is rounded (Fig. 4I). SIT 990 has similar characters

(Fig. 4K; Table 6), and SIT 1366, which preserves the proximal end with upper half of diaphysis, has also the same morphology (Fig. 4L; Table 6). The Mc IV SIT 662 (Fig. 4C; Table 7), SIT 888 (Fig. 4D, Table 7) and SIT 1245 (Fig. 4E; Table 7) are complete and almost well preserved. They are long and slender, with diaphysis slightly curved laterally. The tuberosity on the medial proximal half of diaphysis is developed along the longitudinal axis of the bone on the first two specimens, whereas the latter is deformed, dorsally and ventrally widened. The two articular surfaces for Mc III are very close each other, the dorsal being elliptical and the palmar one circular. On the distal-palmar diaphysis there is depression above



Fig. 4: The Theropigi *Dihoplus pikermiensis*. Metapodials (Mp): A. Right Mc II SIT 860; B. Right Mc II SIT 663; C. Right Mc IV SIT 662; D. Left Mc IV SIT 888; E. Right Mc IV SIT 1245; F. Right Mt II SIT 973; G. Left Mt IV SIT 1236, dorsal view. H-J. Right Mc III SIT 1423, H. dorsal view, I. lateral view, J. palmar view; K. Right Mc III SIT 990; L. Left Mc III SIT 1366. Phalanges: M. Axial proximal phalange for Mp III SIT 664. N. Abaxial proximal phalange for left Mp IV SIT 669; O. Abaxial medial phalange for Mp IV SIT 667, dorsal view. Scale-bar: 50 mm.

the medial condyle of SIT 662, whereas this character is not observed on the other two specimens. The distal Mt II SIT 973 is well preserved (Fig. 4F; Table 7). The distal trochlea is relatively narrow and rounded in cross section and the medial crest is eroded. The lateral groove is very deep and these characters are similar in *D. pikermiensis* from Nikiti (Koufos *et al.*, 2016). The complete Mt IV SIT 1236 is well preserved, only the distal mid-medial part of diaphysis is missing. The proximal articulation is wider than longer. The ovoid longitudinal protuberance in the mid-proximal medial part of diaphysis is weak. The diaphysis is laterally curved. On distal plantar diaphysis, there is a slight depression above the lateral condyle (Fig. 4G; Table 7). The phalanges are well preserved: they consist of the axial proximal phalange SIT 664 (Fig. 4M; Table 5), the left proximal phalange for Mp IV SIT 669 (Fig. 4N; Table 7) and the middle phalange SIT 667 (Fig. 4O; Table 7). On the axial phalange, the proximal articulation is elliptical and slightly concave, whereas the dorsal border of the distal articulation is slightly curved. On the plantar diaphysis there is a strong middle crest and little developed medial and lateral grooves above trochlea. The abaxial phalange is voluminous, the proximal articulation is slightly concave and rather rounded, whereas the distal articulation is rather flat, plantarly developed. The abaxial middle phalange is short, the proximal face is trapezoid and its slightly concave articulation facet covers the proximal end, whereas the distal articulation is concave and caudally developed.

Subtribe Dicerotina Ringström, 1924
Genus *Ceratotherium** Gray, 1867

***Ceratotherium neumayri* (Osborn, 1900)**

*After Geraads, 1988; Heissig, 1999; Giaourtsakis, 2003; Giaourtsakis *et al.*, 2006; Pandolfi, 2016

Locality: Platania (PLD), Municipality of Paranesti, Drama Prefecture, Eastern Macedonia, Greece.

Material: Right mandible with d2-d4 PLD 300; ~20 tooth fragments PLD 83, PLD 84 and PLD 727; left humerus complete, male PLD 609; left humerus diaphysis PLD 640; right humerus distal part and diaphysis of juveniles PLD 641, 729, 730; right radius complete PLD 392; right patella PLD 502; left tibia, almost complete, male PLD 608; left tibia, distal, male PLD 754; right scaphoid PLD 409; 2 left scaphoids PLD 77, PLD 78; right semilunaris PLD 400; left semilunaris PLD 82; 2 right magnums PLD 80, PLD 81; 2 right unciforms complete PLD 79, PLD 504; left astragalus PLD 76; left distal calcaneum PLD 501; left navicular complete PLD 505; left Mc II PLD 669; right Mc II proximal and diaphysis PLD 728; right Mc III PLD 302 (in connection with Mc IV PLD 301); right Mc III, almost complete PLD 303; right Mc III proximal PLD 618; left distal Mc III PLD 304; right Mc IV PLD 75; right Mc IV PLD 301 (associated with

Mc III PLD 302); right Mc IV proximal PLD 503; left Mc IV PLD 74; left Mc IV proximal PLD 668; left Mc IV distal + dia. PLD 375; left Mt IV PLD 670.

Description: The right mandible PLD 300 is well preserved and bears d2-d4, part of diastema and ramus up to mandibular condyle. It shows convex ventral border and brachygnathism towards symphysis (Fig. 5A, B; Table 1), because it narrows abruptly in front of d2. The mylohyoid line is well distinguished along the lingual side of corpus. There is a small mental foramen below the talonid of d2. The deciduous teeth are well preserved except the talonid of d4. There are no labial and lingual but only mesial and distal cingula. The second deciduous premolar d2 is little worn. At this stage of wear the paralophid is slightly worn and double. The V-shaped talonid valley is much deeper than the trigonid (Fig. 5B). The ectoflexid is moderate, oblique and distally slightly inclined and terminates before the dental collum. The height of the crown at the protoconid is at least 24.9 mm, with the hypsodonty index 81.9. The d3 is little to medium worn with V-shaped deep trigonid and talonid valleys (Fig. 5B). In the former, there is a blunt protoconid fold. It shows closed paralophid groove (Fig. 5C). The buccal wall of talonid is more curved than the trigonid. The ectoflexid is well marked, oblique, mesially slightly inclined and terminates before the dental collum. There are distal and stronger mesial cingula. Of the d4 only the trigonid and the entoconid of the talonid are preserved. It is slightly worn and has molar-like morphology. There is a strong distal cingulum. The trigonid valley is V-shaped and deep, whereas the talonid valley is U-shaped (Fig. 5B). The paralophid is single, and the protoconid fold is weak. The height of the crown at the protoconid is at least 34 mm, giving a hypsodonty index 72.34. The rest dental material PLD 83 and 84 comprises tooth fragments.

The left humerus PLD 609 is complete and almost well preserved (Fig. 6A-D; Table 2). The caput humeri is rather rounded with less-distinct collum, the tuberculi are eroded, maybe by the action of carnivores, the sulcus intertubercularis is little deep and narrow, the crest that joins tuberositas deltoidea (the tip of which is broken) and the intermediate indentation of caput humeri is well developed. The flattened part of dorsal diaphysis, below the caput humeri, seems to be compressed. The fossa olecrani is very wide and the trochlea is also wide and quite oblique. The distal part of the epicondylus lateralis is broken, whereas epicondylus medialis is well developed.

The left humerus PLD 640 preserves the distal half of diaphysis and it belongs to a robust male individual (DT dia. min=73, DAP dia.=79), and it presents gnawing marks. The PLD 641 preserves half of diaphysis and distal epiphysis of a slender juvenile individual (DT dia. min=53, DAP dia.=59); it is poorly preserved due to deformation, and has gnawing marks. The PLD 730 is also of juvenile (DT dia. min=49, DAP dia.=51.5), whereas PLD 729 is probably of neonate. The right radius PLD



Fig. 5: The Platania *Ceratotherium neumayri*: A, C. Right mandible with d2-d4, PLD 300; A, labial view; B: tooth-row, lingual view; C: occlusal view. Scale-bar: 50 mm.

392 is complete and robust (Fig. 6E, F; Table 3). Only its distal part is slightly damaged. The insertion of the biceps brachii is not well distinguished and not shifted medially. The proximal articulation is broad, distinctly undulating on its dorsal border, with strong medial re-entrant on the caudal edge forming an obtuse angle; on the lateral side the facet slightly extends outwards, whose front edge is recessed from the front edge of the medial facet. The distal epiphysis is robust and distal articulation is broad. The right patella PLD 502 is well preserved and robust (Fig. 6G). The almost complete left tibia PLD 608 is rather long and slender (Fig. 6H, I; Table 2). The proximal epiphysis is missing, probably gnawed by carnivores. Laterally, the longitudinal interossea crest is strong and ends in a triangular incisura fibularis. The distal left tibia PLD 754 is robust but eroded. The preserved distal DAP is ~70 mm and corresponds to a male individual. The scaphoids PLD 409, PLD 77 and PLD 78 (Fig. 6J, K; Table 4) are complete and well preserved. Only a small part of the latero-palmar side of the PLD is missing. Of the two semilunaris, the PLD 400 is complete (Fig. 6L, M), whereas on the PLD 82 the palmar part is missing (Table 4). The magnums PLD 80, PLD 81 are complete and well preserved. The former (Fig. 6O) is more robust than the latter, the dorsal side is wider and bears a concave articular surface for the scaphoid, whereas this surface

on the latter is slightly curved (Fig. 6N; Table 4). The complete right unciforms are large. The PLD 504 is eroded so no reliable measurements can be taken. On the other hand PLD 79 is well preserved and robust (Fig. 6P, Q; Table 4). Compared with that from Nikiti (*C. neumayri*/*D. pikermiensis*; Koufos *et al.*, 2016) it is larger, the ventral apophysis is larger, and the articulation for pyramidal is slightly more elongated than on the Nikiti specimens. The complete astragalus PLD 76 is well preserved (Fig. 6R-T; Table 5), probably associated with the calcaneum PLD 501. Compared with the astragalus of *D. pikermiensis* from Nikiti (Koufos *et al.*, 2016), it shows similar morphology and dimensions, except the articular surface for the cuboid, which is little wider in the latter than in the former. Of the distal calcaneum PLD 501 only the area of the sustentaculum tali is preserved (Fig. 6U; Table 5). It is as wide as the calcaneum of *D. pikermiensis* from Nikiti (Koufos *et al.*, 2016) and has a similar morphology. The left navicular PLD 505 is complete and semi-circular in shape (Fig. 6V; Table 4). Compared with the navicular of *D. pikermiensis* from Nikiti (Koufos *et al.*, 2016), it shows similar morphology and dimensions, except the height of the bone which is a little higher in the latter than in the former.

Of the metapodials, the almost complete Mc II PLD 669 lacks some portions, perhaps due to predator's action. It



Fig. 6: The Platania *Ceratotherium neumayri*: A-D. Left humerus PLD 609, A: dorsal view, B: caudal view, C: distal view, D: lateral view; E, F. Right radius PLD 392, E: dorsal view; F: proximal view. G. Right patella PLD 502, caudal view; H, I. Left tibia PLD 608, H: lateral view; I: distal view; J, K. Left scaphoid PLD 78, J: dorsal view, K: proximal view; L, M. Right semilunaris PLD 400, L: palmar view, M: medial view; Right magnums: N. PLD 81, lateral view; O. PLD 80, distal view; P, Q. Right unciform PLD 79, P: dorsal view, Q: distal view; R-T. Left astragalus PLD 76, R: dorsal view, S: plantar view, T: distal view, U. Left calcaneum distal, PLD 501, dorsal view; V. Left navicular PLD 505, distal view. Scale-bar: 50 mm.

is rather short and robust, probably belonging to an early adult according to the presence of the epiphyseal line. On the proximal end it bears a prominent lateral projection (Fig. 7O; Table 6).

The Mc II PLD 728 preserves the proximal epiphysis and diaphysis (Table 6). The lateral projection is smaller than that of PLD 669. The articular surfaces for Mc III are well preserved, the palmar one being larger than the dorsal one. The complete Mc III PLD 302 associates with Mc IV PLD 301 (Fig. 7A-C; Table 6). Another almost complete Mc III PLD 303 is also well preserved (Fig. 7D, E; Table 6); both are relatively short and robust, the diaphysis laterally curved, more intensely on the latter, which has the lateral portion of trochlea missing. The supra-trochlear tubercles are developed and the crest of trochlea is eroded. The articular surfaces for Mc IV are rounded (Fig. 8E, F). The PLD 618 preserves the proximal end with upper half of diaphysis (Fig. 7H; Table 6), whereas the PLD 304 preserves the axial distal end, on the palmar side of which there is a lateral well-distinguished concavity above the trochlea (Table 6). The Mc IV PLD 301 is well preserved, short and robust. Its diaphysis is laterally concave (Fig. 7A, B; Table 7).

The crest of trochlea is prominent, and there is a little depression above the medial condyle on the palmar face. Of the fourth metacarpals, the Mc IV PLD 74 is complete and well preserved (Fig. 7F; Table 7). The Mc IV PLD 75 is almost complete except the posterior portion of the proximal articulation, and it is of the same morphology and dimensions as PLD 75 (Fig. 7G; Table 7). They are longer than PLD 301, but robust, with laterally curved diaphysis. The tuberosity on the medial proximal half of diaphysis is strong. The two articular surfaces for Mc III are distinct, the dorsal one elliptical and the caudal one circular. On the distal-caudal diaphysis there is a deep depression above the medial condyle. The Mc IV PLD 668 preserves the proximal half with the epiphysis and shows taphonomical marks such as bites of a large predator that can be *Adcrocuta eximia* (Fig. 7I; Table 7). The Mc IV PLD 503 is also the proximal half, which also presents taphonomical interest as there is special break on the lateral part of diaphysis due to hyena action (Fig. 7N; Table 7). On the Mc IV PLD 375 the proximal epiphysis is missing, probably due to the action of scavengers. In the cross section of diaphysis, two medullary cavities are distinguished, interpreted here as probably due to

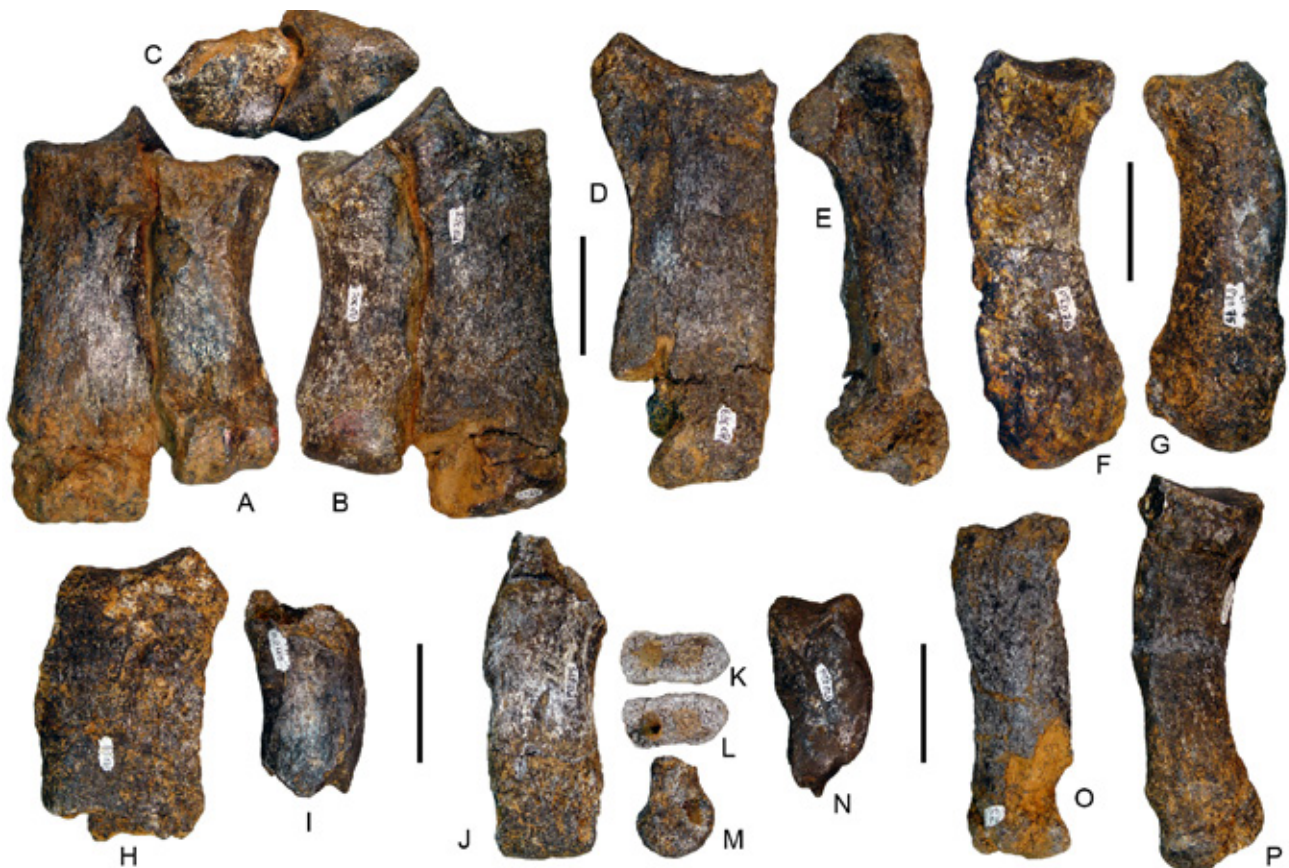


Fig. 7: The Platania *Ceratotherium neumayri*, metapodials (Mp): A-C. Right Mc III+Mc IV (in situ) PLD 302 +301; D, E. Right Mc III PLD 303; F. Left Mc IV PLD 74; G. Right Mc IV PLD 75; H. Left Mc III proximal PLD 618; I. Left Mc IV PLD 668; J-M. Left Mc IV PLD 375; N. Right Mc IV PLD 503; O. Left Mc II PLD 669; P. Left Mt IV PLD 670. A: plantar view; B, D-J, N-P: dorsal view. C: proximal view; E: lateral view, K, L: cross section of diaphysis; M: distal-medial view. Scale-bar: 50 mm.

paleopathology, as well as a deep hole ($D=9.3$ mm) which is apparently the mark of a carnivore tooth (Fig. 7 J-M; Table 7). The complete Mt IV PLD 670 is well preserved. The proximal part is robust, the two articular surfaces for Mt III are separated, and a strong ovoid protuberance is longitudinally developed on the mid-proximal medial part of diaphysis. The diaphysis is laterally little curved. On the distal plantar diaphysis, there is a deep depression above the medial condyle (Fig. 7P; Table 7).

Discussion on the Miocene rhinos from Thermopigi (SIT) and Platania (PLD)

Comparisons between SIT *D. pikermiensis* and PLD *C. neumayri* are mainly based on Geraads (1988), Giaourtsakis *et al.* (2006), Giaourtsakis (2009). Further comparisons of postcranial material (Pandolfi *et al.*, 2016) have been made with the latest Miocene "*Dihoplus*" *megarhinus* (de Christol, 1834) from Kávás (Pannonian Basin, Hungary). The upper permanent teeth from SIT show characteristics that distinguish the former species from the latter: paramolariform premolars, strong paracone fold, presence of a slight metacone fold, constricted protocone, cingulum only present on the mesial face. The *C. neumayri* skulls from Ravin des Zouaves 5 (RZO, Axios valley; Koufos, 1980) are different because the lingual cingulum is absent in SIT, whereas it is present in the RZO specimen. The protocone and hypocone of the SIT premolars are fused forming a closed valley, whereas in RZO this channel is open. The P4 is larger in SIT and narrower in RZO, whereas the parastyle is larger in RZO than in SIT. Permanent teeth are more brachydont indicating a true browser rhino at SIT while the RZO teeth are higher crowned. Compared to rhinoceroses from Bulgaria (Geraads & Spassov, 2009), the dimensions of the upper tooth-rows are close to *D. pikermiensis* from Hadjidimovo, but closer to *Brachypotherium* sp. from Ahmatovo, one of the latest representatives of the genus in Europe.

The D4 SIT 650 shows a constricted protocone, lacks the lingual cingulum, crista and medial fossette, it has a well-developed fold of paracone, a weak metacone fold, more marked in the middle of the height down to the basis of the crown, thus pointing out *C. neumayri* (Giaourtsakis *et al.*, 2006; Giaourtsakis, 2009). Since the morphology of the lower cheek teeth of diverse species of rhinoceroses is very monotonous, the species distinction is mainly based on their dimensions. Concerning the morphological differences between the d3 of *C. neumayri* and *D. pikermiensis* (Giaourtsakis *et al.*, 2006), the PLD 300 shows hypsodonty, no traces of cement on the outer wall and, at this stage of wear, clearly closed paralophid groove, similar in that to the former species.

In comparison with the humerus of Thermopigi, the Platania humerus is stouter, with more voluminous caput, less distinct collum, shallower and narrower sulcus intertubercularis, a more developed crest that joins tuberositas deltoidea, a wider fossa olecrani, a more developed epicondylus medialis and less developed fossa

coronoidea. On the rhino humerus of Kávás, the distal part is much larger than on the humeri from both SIT and PLD.

On the PLD radius, the proximal part is much smaller in depth compared to that of the Kávás rhino, even though they are of about the same width. The PLD scaphoids are larger than that of the Kávás rhino. The two PLD semilunaris are larger and the caudal apophysis more developed in comparison with those from Nikiti (*C. neumayri*/*D. pikermiensis*; Koufos *et al.*, 2016).

Of the metapodials, the Mc II PLD 669 is short and robust (little less robust than in *C. neumayri* from Nikiti; Koufos *et al.*, 2016), the proximal end is well preserved only in PLD 728 and it has a strong lateral projection, compared with those characters from SIT Mc II, which are longer and slenderer, without strong proximal projection. These characters are similar for PLD and Nikiti *C. neumayri* (Koufos *et al.*, 2016). The proximal articulation for trapezoid carpal bone is larger and rather semi-circular in SIT whereas it is trapezoid-shaped in PLD. Compared to Mc II of the Kávás rhino, its proximal width is much larger than that from SIT.

Comparison of the metacarpals Mc III from SIT (Fig. 8A-C) and PLD (Fig. 8D-F) shows that no significant difference is observed between the sizes of the crest of trochlea. In the former, the bone is slender, its diaphysis rather straight and the dorsal articular surface for Mc IV is elliptical. The Mc III from PLD is rather short and robust, its diaphysis laterally curved, the supra-trochlear tubercles less developed and trochlea less robust and the dorsal articular surface for Mc IV rounded. The dimensions of SIT Mc III are close to *D. pikermiensis* from Hadjidimovo (Geraads & Spassov, 2009).

The studies of Geraads (1988), Giaourtsakis (2009) and Pandolfi *et al.* (2015) add some characteristics helpful to distinguish *D. pikermiensis* from *C. neumayri* on their metapodials. Concerning Mc III from Thermopigi (SIT) and Platania (PLD), the outline of the lateral margin of diaphysis presents striking difference, which is markedly concave in the latter than in the former (Fig. 8A, D, see arrow). Also, on the dorso-proximal side, the rugose attachment for the carpal extensor muscle is more pronounced in the former than in the latter (Fig. 8A, D, see arrow). On the lateral articular surfaces for Mc IV, the palmar one is more rounded in the former, whereas the dorsal articular facet is clearly rounded in the latter than in the former, in which it is elliptical (Fig. 8B, C, E, F, see arrow). Generally the metapodials from SIT are clearly more elongated and relatively slender than those from PLD, which are shorter and more robust. In Mc II, according to Geraads (1988) and Giaourtsakis (2009), the presence of the articular facet for the trapezium and the longitudinal crest in the palmar side of the Mc II SIT 860, which are missing on Mc II PLD 728, are reliable differences between *D. pikermiensis* and *C. neumayri*. In PLD Mt IV the proximal end is more robust, the ovoid protuberance which is longitudinally developed on the mid-proximal medial part of diaphysis

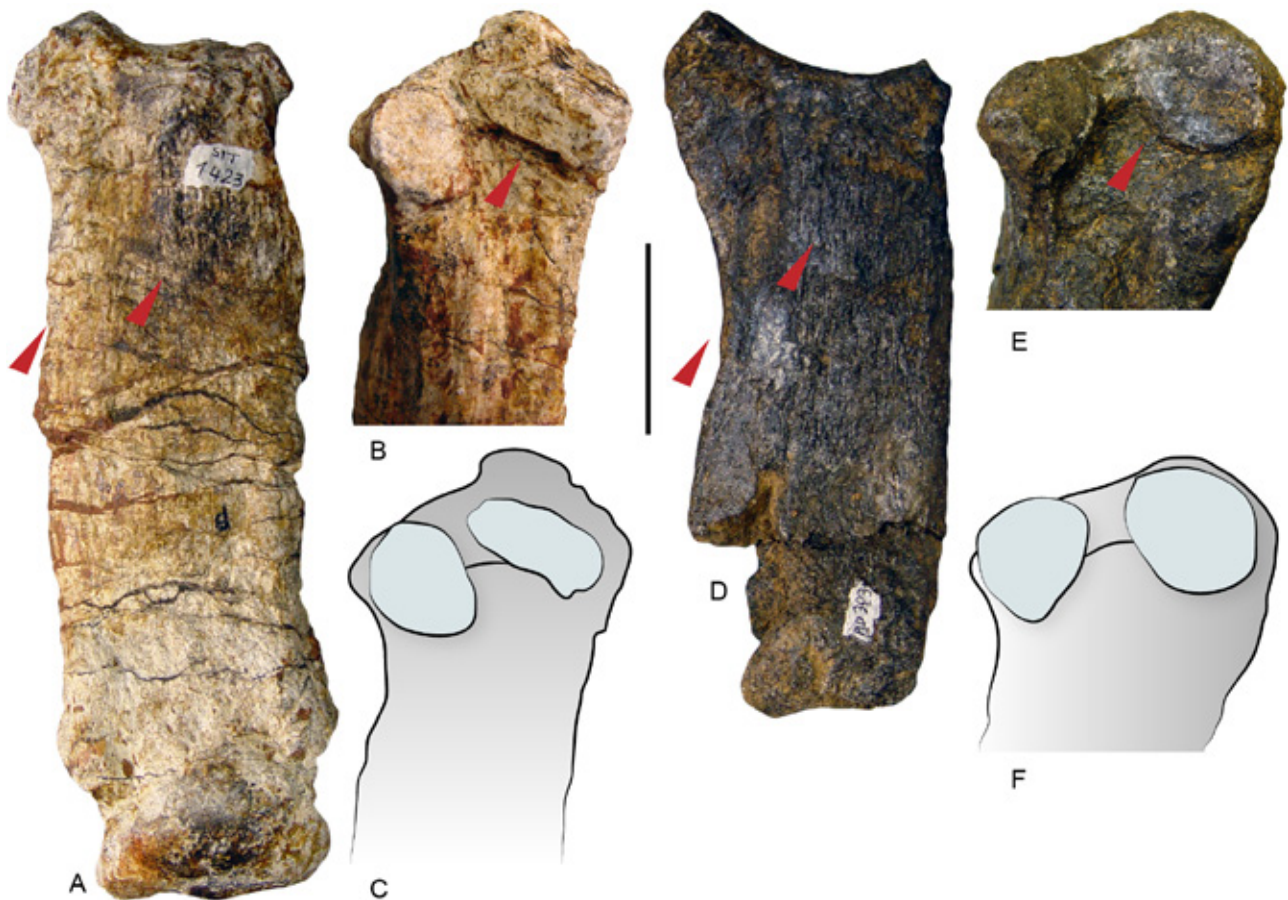


Fig. 8: Comparison between the right third metacarpals Mc III from the Thermopigi *Dihoplus pikermiensis* SIT 1423 (A-C) and the Platania *C. neumayri* PLD 303 (D-F). For discussion see text. A, D: dorsal view; B, C, E, F: lateral view with the articular facets for Mc IV. Scale-bar: 50 mm.

is stronger, the diaphysis is laterally less curved, and on the distal caudal face, there is a deep depression above the medial condyle, whereas the lateral depression is missing, different in that from from SIT Mt IV. Compared to Mt IV of the Kávás rhino, which is much longer than that from SIT and little longer than that from PLD, the distal width is quite similar in all specimens. These comparisons led to the conclusion that the Thermopigi rhinoceros can be attributed to *Dihoplus pikermiensis*, whereas the Platania rhino to *Ceratotherium neumayri*.

It is worthy to note that these two rhino species, the true browser *D. pikermiensis* and the not strict grazer with adaptations to feed on low-level vegetation for *C. neumayri*, are separately observed in the two sites studied here: SIT and PLD, whereas they co-occurred in the well-known sites of Pikermi, Samos and Kerassia, indicating mosaic habitat differentiations. According to Solounias *et al.* (2010), both species from Pikermi are suggestive of grazing habits, since *D. pikermiensis* has an unexpected grazing microwear pattern, but it is very possible that the browsing phase in this taxon is missed because of the seasonal variability in the microwear signal. On the other hand, according to Geraads (1988),

C. neumayri may indicate a trend toward grazing and open habitats at the very beginning of this lineage.

Subtribe Rhinocerotina (Gray, 1821) Dollo, 1885
Genus *Stephanorhinus* Kretzoi, 1942

***Stephanorhinus jeanvireti** (Guérin, 1972)**

* Ballatore & Breda (2016) proposed the conservation of the old name of the species *S. elatus*. Guérin in Guérin & Tsoukala (2013: 455) refers to the sentence in brackets that we follow: “*Rhinoceros elatus* Croizet & Jobert, 1828: 144-154, in pursuance of the article 23.12 of the International Code of Zoological Nomenclature, is nomen oblitum because explicitly rejected by Guérin (1972), i.e. between 6th November 1961 and 1st January 1973, following the article 23b then in force between those dates”. For the generic name we follow Fortelius *et al.*, 1993; Lacombe & Mörs, 2008; Pandolfi *et al.*, 2015.

Locality: Angelochori (AAT), Thermaikos Gulf, Municipality of Nea Michaniona, Central Macedonia, Greece.

Material: Part of left anterior leg: radius AAT 1; ulna AAT 2; axial metacarpal Mc III AAT 3; abaxial metacarpal Mc II AAT 4; axial proximal phalange Ph I AAT 5; abaxial proximal phalange for the second metacarpal Ph I AAT 6.

Description and discussion: All these bones most likely belong to the same individual, because they were found together, they are at the same state and color of preservation and fit in size. This individual is an early adult, based on the presence of the distal epiphyseal line on the well-preserved radius (Fig. 9C).

The left radius AAT 1 is long and slender (Fig. 9C-G; Table 3); the proximal articulation undulates on its dorsal border, the palmar edge forms an obtuse angle, and the lateral facet slightly extends outwards (Fig. 9F). In dorsal view, the strong lateral tuberosity of the proximal epiphysis below the articulation, the convex medial border of the epiphysis, and the strong insertion of the biceps brachii shifted slightly medially are the main features to be mentioned. The distal articulation is narrow. On the left ulna AAT 2, the tuber olecrani and part of the distal epiphysis are missing (Fig. 9A, B; Table 3). The olecranon presents taphonomic interest as it shows marks of gnawing. The metapodials and phalanges are complete and well preserved. The Mc III (AAT 3; Fig. 9H-K;

Table 6) displays characters similar to *S. jeanvireti* from Milia (Guérin & Tsoukala, 2013): a long and relatively slender bone; proximal articulation with clearly convex dorsal border, slightly more convex than that from Milia; proximo-lateral palmar facet a little higher than wider; diaphysis mid-section elliptical with slightly depressed palmar border; and well-developed tuberosity on the dorsal medial proximal half of diaphysis. The supra-trochlear tuberosities are well developed. The dimensions are very close to the updated mean value of *S. jeanvireti* after Guérin & Tsoukala (2013) and a little larger than that from Milia Mc III. The Mc II AAT 4 only lacks the proximal part of the palmar crest of trochlea (Fig. 9L-O; Table 6). It is long and slender. The proximal articulation bears a clearly convex dorsal border. On the proximal epiphysis there is a developed palmar tuberosity, as well as a lateral projection for the ovoid well-developed articulation facet for the Mc III. The facet for magnum is also well developed. The plantar area of the shaft bears a median and a lateral longitudinal crest between the trochlea and nutrient foramen. The lateral groove of trochlea is deep. Compared with *S. jeanvireti* from Dusino and Roatto in Italy (Campanino *et al.*, 1994), the dimensions of the AAT bones are closer to that of the former site,

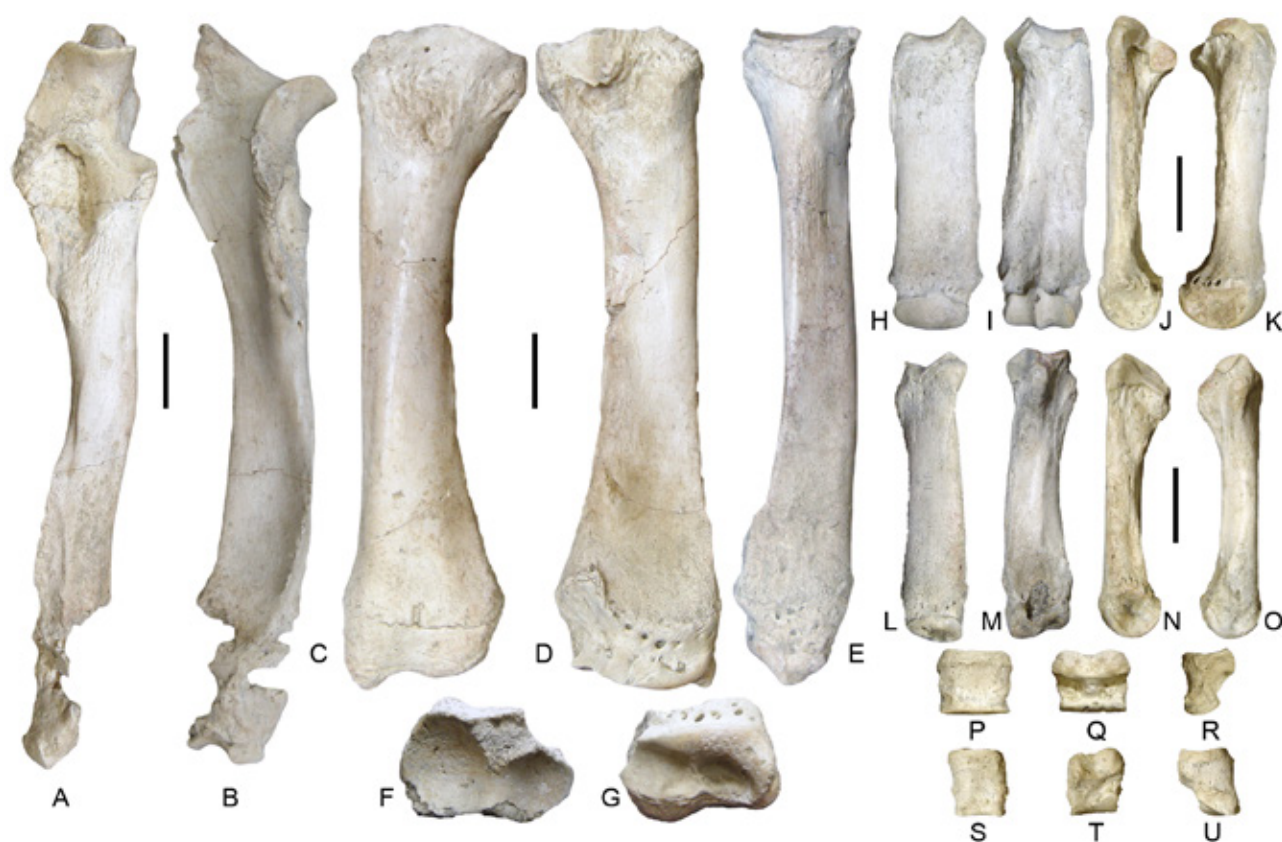


Fig. 9: The Angelochori *Stephanorhinus jeanvireti*. A, B. Left ulna AAT 2; C-G. Left radius AAT 1. Left metapodials and phalanges: H-K. Mc III AAT 3; L-O. Mc IV AAT 4; P-R. Proximal phalanx, axial, for Mc III AAT 5; S-U. proximal phalanx, abaxial, for Mc IV AAT 6; A, C, H, L, P, S: dorsal view; D, I, M, Q, T: palmar view; B, E, K, O, U: medial view; J, N, R: lateral view; F: proximal view; G: distal view. Scale-bar: 50 mm.

whereas the rhino of the latter site is larger, even though the flattening of diaphysis of the Mc III is the same for all specimens. Ďurišová (2004) gives the dimensions of two Mc III of early Villanyan *S. jeanvireti* from Hajnačka (Czech Republic), which correspond perfectly to those of AAT. These dimensions are clearly larger than those of *S. etruscus etruscus* and close to the mean value of *S. megarhinus* according to the updated values given by Guérin & Tsoukala (2013). The axial proximal phalange AFT 5 (Fig. 9P-R; Table 5), and the abaxial AFT 6 for Mc II (Fig. 9S-U; Table 6) are well preserved. On the axial phalange, the proximal articulation is ovoid and slightly concave, whereas the distal articulation is a rather flat parallelogram. On the palmar diaphysis there is a strong transversal tuberosity below the proximal articulation, followed by a middle strong crest and well-developed medial and lateral grooves above trochlea. The abaxial phalange is voluminous; the proximal articulation is slightly concave, whereas the distal articulation is asymmetrically concave, and caudally developed.

The Angelon Angelochori is the second site in Greece with remains of *S. jeanvireti* (Guérin, 1972). Geologically, this site belongs to the Gonia Formation (Syrides, 1990). It is located in Megalo Emvolon Cape that is known since the beginning of last century for its vertebrate fossils. Koufos *et al.* (1991) suggested an Early

Pliocene (Ruscinian, MN 15) age, based on the presence of *Dolichopithecus rusciniensis*. We would like to point out, based on the rhino material presented herein, that the AAT site is Upper Pliocene (MN 16 biozone). The preferential habitat of *S. jeanvireti* is a woodland with grassy areas including gramineae and ferns, in a humid climate (Guérin, 1980).

4. CONCLUSIONS

More than 65 sites throughout Greece yielded rhinocerotid fossils to date: new excavation sites are constantly providing additional material, such as the Late Miocene sites of Thermopigi (SIT) and Platania (PLD) and the Late Pliocene site of Angelochori (AAT). These sites yielded *Dihoplus pikermiensis*, *C. neumayri* and *Stephanorhinus jeanvireti*, identified respectively.

The minimum number of individuals for SIT is MNI=3: two adults, based on post cranial bones, and a juvenile individual based on a deciduous tooth. For PLD the MNI=6: three adults and three juveniles based on post the cranial bones. The rhino remains from AAT should belong to a single young adult individual as indicated by the presence of the epiphyseal line on the radius. The two former sites are correlated to middle Turolian (MN 12) according

Tables of measurements according to methodology of Guérin, 1980

Table 1: Measurements (in mm) of maxilla and teeth of the Thermopigi *Dihoplus pikermiensis* and mandible and teeth of the Platania *Ceratotherium neumayri*.

Maxilla <i>D. pikermiensis</i>				Mandible		<i>C. neumayri</i>	
Teeth	SIT 1325	SIT 660	SIT 661	Tooth	SIT 650	PLD 300	
	D	S	D		D		D
LP2		36.1	36.9	LD4	47	Ld2	30.4
BP2		40	37.6	BD4	41	Bd2	15.8
LP3		44.1		HD4	31.5	Hd2	25
BP3		52.6				Ld3	41
LP4	50.3	49.5				Bd3	21.4
BP4	57	55				Ld4	47
LM1	57.4					Bd4	24.1
BM1	60.9						
LM2	60.7					Ld2-d4	118
BM2	64						
LM3	49.4					Lmd cond.-d2ant.	250
BM3	56.4					H md labial	
HM3	40					H md at d2 ant.	37
L P-M	289					H md at d2,d3	48
LM	163					H md at d3,d4	54.6
LP	126	127				H md at d3 post.	59.5

to geological and stratigraphical remarks on the paleofaunal assemblage, but the definition of a precise biozone is difficult based on these rhinos, because they expand through all Late Miocene biozones. On the other hand, the attribution of Angelochori rhino to the *S. jeanvireti*, second reference in Greece, provides evidence for the correlation to MN 16 biozone for the site of Angelochori.

The presence of the rhino *C. neumayri* in Platania indicates the existence of an open and dry environment (Giaourtsakis *et al.*, 2006). The presence of the more conservative selective browser rhino *D. pikermiensis* in Thermopigi indicates the presence of forested areas, in agreement with the presence of *Ancylotherium pentelicum*, interpreted as a browser on arboreal vegetation (Geraads *et al.*, 2007). In addition, four different species of giraffes, classified mostly as browsers or mixed feeders, have been identified, and these plot very close to the browsing morphospace (Xafis, 2015).

The identification of the taxon Rhinocerotidae and the presence of numerous rhinoceroses species contributes significantly to the interpretation of the stratigraphy and paleoenvironment of Greece during the early Middle Miocene (MN 5) to the Late Pleistocene (MNQ 26).

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Table 2: Measurements (in mm) of humerus of the Thermopigi *Dihoplus pikermiensis* and of humerus, tibia and patella of the Platania *Ceratotherium neumayri*.

	<i>D. pikermiensis</i>		<i>C. neumayri</i>		Patella	PLD 502	
	Humerus	SIT 250	PLD 609	Tibia			PLD 608
		D	S		S	D	
L		450	c435		~390	L	90
DT prox.		210	199		>(103)	DT	97
DAP prox.		114	105		>(108)	DAP	58
DT dia. min		70	70		64		
DAP dia.		76.5	76		59		
DT distal		146	157		~85		
DAP distal		122	119		65		
DT tuber deltoidea		154	157				
DT trochlea		105	102				
H trochlea max		95.8	91				
H trochlea min		57	52.3				
H cond.		75	68				
DT fossa olec.		55					

Table 3: Measurements (in mm) of radius and ulna of the Angelochori *Stephanorhinus jeanvireti* and radius of the Platania *Ceratotherium neumayri*.

Radius	<i>C. neumayri</i>		<i>S. jeanvireti</i>		Ulna	AAT 2
	PLD 392		AAT 1			
	D		S			
L	382		410		L	a495
DT prox.	121		104		DT olec.	
DAP prox.	73		68		DAP olec.	89
DT dia.	74		58		DT art. prox.	89.3
DAP dia.	47		39		DAP prox.	116.7
DT distal	113		101		DT dia.	37
DAP distal	76.5		73		DAP dia.	49.9
DT dist. art.	99		87		DT distal	
DAP dist. art.	56		45.5		DAP distal	

Table 4: Measurements (in mm) of carpal and tarsal bones of the Platania *Ceratotherium neumayri*.

Scaphoid	Semilunaris			Magnum			Unciform		Navicular				
	PLD	PLD	PLD	PLD	PLD	P L D	PLD	PLD	PLD				
	77	78	409	400	82	80	81	79	505				
	S	S	D	D	S	D	D	D	S				
L	95.5	84	82.5	L	76.5		L	93	91	L abs.	90	L	63
DT	63.5	64	57	DT	53.7	53	DT	53	47	L anat.	67.5	DT	54
H	70	62	58	H	52.5	48	H	67	62	DT	68	H	29
L art. prox.	50	45	43	H ant.	54	49	H art.	64	60	H	53		
DT art. prox.	55.5	57	52										
L dist. art.	71	67.8	67.5										
DT dist. art.	39	32.5	32.8										

Table 5: Measurements (in mm) of astragalus and calcaneum of the Platania *Ceratotherium neumayri* and of phalanges of the Angelochori *Stephanorhinus jeanvireti* and the Thermopigi *Dihoplus pikermiensis*.

<i>C. neumayri</i>	Calcaneum		<i>S. jeanvireti</i>			<i>D. pikermiensis</i>			
Astragalus	PLD		Proximal phalange	axial	abaxial	axial	abaxial	Middle phalange	abaxial
	76 S		PLD	AAT 5	AAT 6	SIT 664	SIT 669		SIT 667
			501 S	->Mc3 S	->Mc2 S	->Mp3	->Mp4 S		->Mp4 S
DT	95	DAP sust. tali	92	L	49.7	47	48.5	54	38
H	82			DT prox.	56.9	43.3	55.8	48.9	40
DAP int.	62			DAP prox.	39.1	42.2	38.1	43.5	27
DT dist. art.	73			DT dia.	51.5	40	46.7	45.3	32.6
DAP dist. art.	49			DAP dia. min	22.7	29.7	22.7	33.9	26
Dist. 2 brims	73			DT distal	52	42.2	48.5	40.8	36.8
DT dist. max	87.5			DT dist. art.	50.3	37.1	46.3	39.2	28
				DAP dist. art.	26.3	28.5	24.2	33.6	29

Table 6: Measurements (in mm) of metacarpals of the Angelochori *Stephanorhinus jeanvireti*, the Thermopigi *Dihoplus pikermiensis* and the Platania *Ceratotherium neumayri*.

	Mc II					Mc III								
	<i>S. jeanv.</i>	<i>D. pikermiensis</i>		<i>C. neumayri</i>		<i>S. jeanv.</i>	<i>D. pikermiensis</i>		<i>C. neumayri</i>					
	AAT	SIT	SIT	PLD	PLD	AAT	SIT	SIT	SIT	PLD	PLD	PLD	PLD	
	4	860	663	669	728	3	1423	990	1366	302	618	303	304	
	S	D	D	S	D	S	D	D	S	D	S	D	S	
L	195.6	163	167	144	-	L	222	218	201	-	170	-	171	
DT prox.max	53.2	50.5	-	51.7	45.3	DT prox.	62.7	69	66.5	71	64.3	66.5	69	
DT prox.	47.1	47	-	41.3	41	DAP prox.	52.5	56	52	52.3	53.6	48	53.7	
DAP prox.	46.7	41.5	41.2	-	40.7	DT dia.	55.6	62	58.7	65	54	66	56.5	
DT dia.	39	(44.6)	38.2	41.3	38.5	DAP dia.	24	28.5	24.5	25	28	21.5	26	
DAP dia.	25.1	(19.4)	23.6	23.5	21	DT distal	66.5	68.6	66.6		64.2		62.5	
DT dist. max	48.9	(55.5)	49.5	47	-	DT dist. art.	51.8	57.3	52.5		54.5		50.1	
DT dist. art.	42.4	(44.3)	41	40	-	DAP dist. art.	48.1	51.5	46.5		46		49	
DAP dist. art.	43	(36.7)	46.5	42.6	-	I DT prox/L	28.2	31.6	33.1		37.8		40.3	
I DT d art/L	21.7	-	24.5	27.8	-	I DT d art/L	23.3	26.3	26.1		32			

Table 7: Measurements (in mm) of metacarpals and metatarsal of the Thermopigi *Dihoplus pikermiensis* and the Platania *Ceratotherium neumayri*.

	Mc IV						Mt II				Mt IV		
	<i>D. pikermiensis</i>			<i>C. neumayri</i>			<i>D. pik.</i>				<i>D. pik.</i>		
	SIT	SIT	SIT	PLD	PLD	PLD	PLD	PLD	PLD	SIT	SIT	PLD	
	1245	888	662	301	74	75	668	503	375	973	1236	670	
	D	S	D	D	S	D	S	D	S	D	S	S	
L	151.5	159.5	152.5	135	163	159					151.5	164.5	
DT prox. max	46.5	48.3	45.8	51	50.7	49.2	47	42			55.4	52.7	
DAP prox.	45			43.7	50.8	49.2					41	48.4	
DT dia.	38	41.6	40	41	40.2	40.3	40		38.6		36	34.7	
DAP dia.	25	26	18.7	24.1	24.3	25	24		21.8		23.7	25	
DT dist. max	51	52	54	49.3	51	52.4			43	39	41	45	
DT dist.art.	48.6	47.5	48	42	45	45.9			41	37	38.3	41	
DAP dist.art.	48	45.2		43.5	47	47.3			40.3	39	43.5	44	

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APPENDIX

The Rhinocerotidae of Greece through time (Miocene, Pliocene and Pleistocene)

Greece yielded abundant remains of fossil rhinos with a remarkable variety through time: the older ones from Middle Miocene of Chios island (MN 5 after Mein, 1990) were mentioned in a reference list of Heissig in 1989, and *Brachypotherium* sp. from Chrysavgi (MN 7-8), Mygdonia Basin, described by Koufos & Kostopoulos (2013); the youngest rhinos are recorded in Late Pleistocene (MNQ 26). In 1958, Psarianos referred to rhinos some remains from Macedonia: *D. pachygnathus* from Chrysavgi – Lagada and *S. etruscus* from Aliakmon Valley. The former species was previously reported by Arambourg & Piveteau (1929) from the Thessaloniki area. More than 65 main localities all over Greece revealed rhino remains. In well-known sites, some new species are recognized (e.g. *Dihoplus pikermiensis*, *Acerorhinus neleus* in Pikermi and Kerassia), as well as first noted occurrence in Greece: *Stephanorhinus jeanvireti* in Milia and now in Angelochori. The presence of rhinos in Paleolithic sites is also mentioned here. E: Early; M: Middle; L: Late; Lst: latest; Mio.: Miocene; indet: indeterminate.

Table A1: Miocene sites of Greece with rhino remains with stratigraphical biozones, chronology and references.

Localities	Biozone/ Age	Taxon/Genus	Species	Abs Age- Ma	References
1 Achmet Aga (AHG) -Euboia	MN 11-13	Rhinocerotidae	indet.		Koufos, 2006a
2 Atalanti-Phtiotida	M Mio.	Aceratheriini	indet		Symeonidis, 1974
3 Chalkoutsis-Attiki	L Mio.	Rhinocerotidae	indet.		Theodorou <i>et al.</i> , 1995
4 Chios Island	MN 5	Rhinocerotidae	indet.		Heissig, 1989; Giaourtsakis, 2003
5 Chomateri (CHO) -Attiki	MN 12	<i>Acerorhinus</i>	<i>neleus</i>		Athanassiou <i>et al.</i> , 2014; Marinos & Symeonidis, 1974
6 Chrysavgi (CHR) -Lagada	MN 7-8	<i>Brachypotherium</i>	<i>brachypus</i>		Koufos & Kostopoulos, 2013; Psarianos, 1958; Dimopoulos, 1972
7 Dytiko 1 (DTK)-Thessaloniki	MN 13	<i>Ceratotherium</i>	<i>neumayri</i>		Koufos, 1980
8 Halmyropotamos (HAL) -Euboia	MN 11-12	<i>Dihoplus</i>	<i>pikermiensis</i>		Melentis, 1968; 1969
9 Kerassia (KRS-3) - Euboia	MN 11-12	<i>Ceratotherium</i>	<i>neumayri</i>		Giaourtsakis <i>et al.</i> , 2006; Athanassiou <i>et al.</i> , 2014
10 Kerassia (KRS-4) - Euboia	MN 11-12	<i>Dihoplus</i> <i>Acerorhinus</i>	<i>pikermiensis</i> <i>neleus</i>		Giaourtsakis <i>et al.</i> , 2006; Athanassiou <i>et al.</i> , 2014

Localities	Biozone/ Age	Taxon/Genus	Species	Abs Age- Ma	References
11 Kerassia (KRS-5) - Euboia	MN 11-12	<i>Dihoplus</i>	cf. <i>pikermiensis</i>		Theodorou <i>et al.</i> , 1995; Koufos, 2006a
12 Mytilinii - 3 (MYT) - Samos	E MN12	<i>Dihoplus</i>	<i>pikermiensis</i>	~7.3	Giaourtsakis, 2009
13 Mytilinii - 3 (MYT) - Samos	E MN12	" <i>Diceros</i> "	<i>neumayri</i>	~7.3	Giaourtsakis, 2009
14 Mytilinii - 4 (MLN) - Samos	Lst MN11	" <i>Diceros</i> "	<i>neumayri</i>	~7.5	Giaourtsakis, 2009
15 Mytilinii-1A (MTLA) -Samos	MN 12	<i>Dihoplus</i>	<i>pikermiensis</i>	~7.1	Giaourtsakis, 2009
16 Mytilinii-1A (MTLA) -Samos	M MN12	" <i>Diceros</i> "	<i>neumayri</i>	~7.1	Giaourtsakis, 2009
17 Mytilinii-1B (MTLB) -Samos	M MN 12	" <i>Diceros</i> "	<i>neumayri</i>	~7.1	Giaourtsakis, 2009
18 Mytilinii-1C (MTLC) -Samos	MN 12	Rhinocerotidae	indet.	~7.1	Koufos, 2006a
19 Mytilinii-1D (MTLD) -Samos	M MN12	<i>Dihoplus</i>	<i>pikermiensis</i>	~7.1	Giaourtsakis, 2009
Mytilinii-1D (MTLD) -Samos	M MN12	" <i>Diceros</i> "	<i>neumayri</i>	~7.1	Giaourtsakis, 2009
20 Nikiti 1 (NKT)	MN 10	Rhinocerotidae	indet.	9.3-8.7	De Bonis & Koufos, 1999; Koufos, 2006a
21 Nikiti 2 (NIK)	MN11	" <i>Diceros</i> "	<i>neumayri</i>		Koufos, 2016
22 Pentalophos 1 (PNT)	MN 9-10	<i>Aceratherium</i> <i>Chilotherium</i> <i>Acerorhinus</i>	<i>kiliasi</i> cf. <i>samium</i> sp.		Geraads & Koufos, 1990 Athassiou <i>et al.</i> , 2014
23 Perivolaki (PER)	MN 12	<i>Ceratotherium</i>	cf. <i>C. neumayri</i>		Koufos, 2006c
24 Pikermi (PIK) - Attiki	MN 12	<i>Acerorhinus</i> <i>Ceratotherium</i> <i>Dihoplus</i>	<i>neleus</i> <i>neumayri</i> <i>pikermiensis</i>		Athassiou <i>et al.</i> , 2014 ; Marinos & Symeonidis, 1974
25 Prokopi - Euboia	L Mio.	Rhinocerotidae	indet.		Giaourtsakis, 2003 and ref. therein
26 Pyrgos Vassilissis (PYV)	MN 9-13	? <i>Ceratotherium</i>	<i>neumayri</i>		Paraskevaidis, 1977; Koufos, 2006a
27 Ravin de la Pluie (RPI)	MN 10	Rhinocerotidae	indet.	~9.3	De Bonis & Koufos, 1999; Koufos, 2006a
28 Ravin des Zouaves 5 (RZO)	MN 11	<i>Ceratotherium</i>	<i>neumayri</i>	~8.2	Koufos, 1980, 2006a
29 Ravin X (R-X)	MN 12	<i>Ceratotherium</i>	<i>neumayri</i>		Koufos, 2006a
30 Samos PMMS	M MN12	<i>Ceratotherium</i>	<i>neumayri</i>	~7.1	Giaourtsakis 2009
31 Samos-Q5	MN 12	<i>Dihoplus</i>	<i>pikermiensis</i>	6.7-7.0	Koufos, 2006a
32 Samos		<i>Chilotherium</i>	<i>schlosseri</i>		Pandolfi, 2016 and ref. therein
33 Servia (SRV)	MN 9-13	Rhinocerotidae	indet.		Paraskevaidis, 1977; Koufos, 2006a
34 Silata - Chalkidiki	MN13end	Rhinocerotidae	indet.		Syrides, 1990; Koufos, 2006b
35 Tanagra (TNG) -Boeotia	MN 9-13	Rhinocerotidae	indet.		Mitzopoulos, 1960
36 Vathylakkos 2 (VTK) -Thessaloniki	MN 12	Rhinocerotidae	indet.	~7.5	Koufos, 2006a
37 Vathylakkos 3 (VAT) -Thessaloniki	MN 12	<i>Ceratotherium</i>	<i>neumayri</i>		Koufos, 2006a
38 Xirochori 1 (XIR) -Thessaloniki	MN 10	<i>Ceratotherium</i>	<i>neumayri</i>	~9.6	De Bonis & Koufos, 1999; Koufos, 2006a
39 Thermopigi (SIT) - Serres	L Mio.	<i>Dihoplus</i>	<i>pikermiensis</i>		Present study
40 Platania (PLD) - Drama	L Mio.	<i>Ceratotherium</i>	<i>neumayri</i>		Present study

Table A2: Plio-Pleistocene sites of Greece with rhino remains with stratigraphical biozones and references. It must be noted that the rhino fossils in the sites of Aliakmon River, Angitis Cave (Drama), Asprochaliko (Epirus), Kalamakia and Lakonis Cave (Peloponnese) and Penios (Thessaly) are possibly associated with Palaeolithic artefacts. E: Early; M: Middle; L: Late; Lst: latest; Plioc.: Pliocene; Pleist.: Pleistocene; Villafr.: Villafranchian; y.: years; indet: indeterminate.

	Localities	Biozone/Age	Taxon/Genus	Species	References
1	Aivaliki -Serres	E Pleist.	<i>Stephanorhinus</i>	cf. <i>etruscus</i>	Symeonidis <i>et al.</i> , 2006
2	Aliakmon Valley	L Plioc.	<i>Stephanorhinus</i> Rhinocerotidae	sp. indet.	Psarianos, 1958 Harvati <i>et al.</i> , 2008; Panagopoulou <i>et al.</i> , 2006
3	Allatini -Thessaloniki	E Plioc.	Rhinocerotidae	indet.	Marinos, 1965
4	Angelochori -Thessaloniki	MN 16a	<i>Stephanorhinus</i>	<i>jeanvireti</i>	Present study
5	Angitis cave, Drama		<i>Coelodonta</i>	<i>antiquitatis</i>	Koufos, 1981; Trantalidou, 1996; 2013
6	Apolakkia -Rodos (APK)	MN 15	Rhinocerotidae	indet.	Van de Weerd <i>et al.</i> , 1982
7	Apollonia -Mygdonia	MNQ 20	Rhinocerotidae	indet.	Koufos & Kostopoulos, 1997
8	Asprochaliko, Epirus		<i>Stephanorhinus</i>	<i>kirchbergensis</i>	Bailey <i>et al.</i> , 1983
9	Gefira (G.A.) – Axios Valley	MNQ 24	<i>Coelodonta</i>	<i>antiquitatis</i> <i>praecursor</i>	Tsoukala, 1991b
10	Halykes, Volos	MNQ 18-20	Rhinocerotidae	indet.	Athanassiou, 1998
11	Kalamakia, Peloponnese		<i>Stephanorhinus</i>	sp.	Gardeissen & Trantalidou, 1996; Harvati <i>et al.</i> , 2013
12	Kalamoto 1 (KAL) -Mygdonia	Lst Villafr.	<i>Stephanorhinus</i>	<i>etruscus</i>	Tsoukala & Chatzopoulou, 2005
13	Kalamoto 2 (KLT) - Mygdonia	L Villafr.	<i>Stephanorhinus</i>	<i>etruscus</i>	Tsoukala & Chatzopoulou, 2005
14	Krimni -Mygdonia	L Villafr.	<i>Stephanorhinus</i>	<i>etruscus</i>	Sakellariou-Mane <i>et al.</i> , 1979; Koufos & Kostopoulos, 1997
15	Kythera island	Plioc.?	Rhinocerotidae	indet.	Bartsiokas, 1998 (p. 96)
16	Lakonis Cave, Peloponnese	38.240-43.335 y.	Rhinocerotidae	indet.	Panagopoulou <i>et al.</i> , 2002-2004
17	Libakos -Kozani	MN 17	<i>Stephanorhinus</i> <i>Stephanorhinus</i>	<i>etruscus</i> sp.	Steenma, 1988
18	Maramena (MAR) - Serres	MN 13/14	Rhinocerotidae	indet.	Schmidt-Kittler <i>et al.</i> , 1995
19	Marathousa - Peloponnese	E Biharian	<i>Stephanorhinus</i>	<i>etruscus</i>	Sickenberg, 1975
20	Megalopolis - Peloponnese	M - L Pleist.	<i>Stephanorhinus</i> <i>Stephanorhinus</i> <i>Coelodonta (?)</i>	<i>kirchbergensis</i> <i>hemitoechus</i> <i>antiquitatis</i>	Melentis, 1966
21	Milia (MIL) - Grevena	MN 16a	<i>Stephanorhinus</i>	<i>jeanvireti</i>	Guérin & Tsoukala, 2013
22	Molykrio Etoloakarnania	L Plioc.	<i>Stephanorhinus</i>	cf. <i>etruscus</i>	Symeonidis <i>et al.</i> , 1985-86
23	Penios, Thessaly		<i>Stephanorhinus</i>	cf. <i>hemitoechus</i>	Boessneck, 1965; Athanassiou, 2002 and refer. therein
24	Petralona (PEC) -Chalkidiki	early M Pleist.	<i>Stephanorhinus</i>	<i>hemitoechus</i>	Tsoukala, 1991a Tsoukala & Guérin, 2016
25	Platanochori (PLN) -Mygdonia	Lst Villafr.	<i>Stephanorhinus</i>	<i>hundsheimensis</i>	Konidaris <i>et al.</i> , 2015
26	Sesklo (SES) - Thessaly	MN 17	<i>Stephanorhinus</i>	sp.	Symeonidis, 1992; Athanassiou, 1998; 2002
27	Tourkovounia - Attiki	MN 16/17	<i>Stephanorhinus</i>	cf. <i>etruscus</i>	Symeonidis & de Vos, 1976
28	Tsotra (TSR) - Mygdonia	Lst Villafr.	<i>Stephanorhinus</i>	sp.	Konidaris <i>et al.</i> , 2015
29	Vatera (VTR-DS) - Lesbos	MN 17	<i>Stephanorhinus</i>	cf. <i>etruscus</i>	De Vos <i>et al.</i> , 2002
30	Volax (VOL) - Drama	MN 17	Rhinocerotidae	indet.	Sickenberg, 1968