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FIRST OCCURRENCE OF PLIORHINUS CF. MEGARHINUS (PERRISSODACTYLA, RHINOCEROTIDAE) IN GREECEKrystalia Chitoglou^{1*}, Luca Pandolfi², Dimitris S. Kostopoulos¹¹Laboratory of Geology and Palaeontology, School of Geology, Aristotle

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luca.pandolfi@unibas.it***Corresponding author****Abstract**

Pliocene rhinoceros' bearing fossiliferous localities are very limited in Greece. The rhinocerotid from the locality of Allatini, near Thessaloniki presented here, has long been cited in the literature but has never been studied in detail up to now. This taxon is represented by a single specimen, a radius of a sub adult individual, which is herein studied in detail to clarify its systematic position. Both morphological and metrical data suggest its assignment to the genus Pliorhinus, and more specifically to the species P. megarhinus. Pliorhinus megarhinus thrived in Eurasia from the latest Miocene to the Late Pliocene, however its records are restricted so far to a few localities, mainly in Italy and France. This is the first known occurrence of Pliorhinus in Greece resulting a slight enrichment of the local and European Pliocene Rhinocerotidae record.

Keywords: Pliocene, Pliorhinus, Greece

ΠΕΡΙΛΗΨΗ

Οι Πλειοκαινικές απολιθωματοφόρες θέσεις με ευρήματα ρινόκερων στην Ελλάδα είναι πολύ περιορισμένες. Στην παρούσα εργασία επανεξετάζεται ο ρινόκερος της θέσης Αλλατίνη, εντός του αστικού ιστού της Θεσσαλονίκης, γνωστός στην βιβλιογραφία εδώ και καιρό, αλλά χωρίς ποτέ να έχει μελετηθεί συστηματικά. Το άξιο εκπροσωπείται από ένα μόνο δείγμα, μια κερκίδα νεαρού ατόμου, η οποία μελετήθηκε λεπτομερώς προκειμένου να προσδιοριστεί με σαφήνεια η συστηματική της θέση. Τα μορφολογικά και βιομετρικά δεδομένα που προέκυψαν υποδεικνύουν την αναγωγή του δείγματος στο γένος *Pliorhinus* και στο είδος *P. megarhinus*. Το είδος *Pliorhinus megarhinus*, ήκμαζε στην Ευρασία από το ανώτατο Μειόκαινο μέχρι το Άνω Πλειόκαινο. Ωστόσο, το αρχείο του περιορίζεται μέχρι στιγμής σε θέσεις που βρίσκονται κυρίως στην Ιταλία και τη Γαλλία. Η πρώτη εμφάνιση του *Pliorhinus* στην Ελλάδα επεκτείνει την γεωγραφική του κατανομή και ενισχύει μερικώς το τοπικό αλλά και Ευρωπαϊκό αρχείο των Πλειοκαινικών ρινόκερων.

Λέξεις - Κλειδιά: Πλειόκαινο, *Pliorhinus*, Ελλάδα

1. Introduction

During the Pliocene, the European Miocene rhinocerotids (e.g., *Dihoplus*, *Miodiceros*, *Brachypotherium*, *Aceratherium*) are replaced by the genera *Stephanorhinus* and *Pliorhinus*, known in this period by four species, *P. megarhinus*, *P. miguelscrusafonti*, *S. jeanvireti* and *S. etruscus*. *Pliorhinus megarhinus*, and *S. jeanvireti* are large sized species, especially *P. megarhinus*, which preserves a massive skull and wide thick nasal bones without a nasal septum (Pandolfi and Rook, 2017). Its first appearance in Kánás (Hungary), is recorded in Mammal Neogene Zone MN12-MN13 (Turolian), and the species survived until the late Early Pliocene in Europe (MN14-MN15; Ruscinian) and probably until the latest Pliocene (MN15-MN16; early Villafranchian) in Russia (Guérin, 1980; Fukuchi et al., 2009; Pandolfi, 2013; Pandolfi et al., 2015, 2016).

The species *P. miguelscrusafonti* is chronologically restricted, limited to a few Spanish French, and Georgian localities (Guérin, 1980; Pandolfi et al., 2021; Pandolfi et al., 2022). This medium to small sized Pliocene taxon, which is larger than *S. etruscus* but smaller than the rest of the Pliocene species, was found along with *P. megarhinus*. There hadn't been any new records of the species since the 1900's, until the recent findings in the locality of Kvabebi in Georgia and in Spain (Guérin and Santafe-Llopi, 1978;

Pandolfi et al., 2021; Pandolfi et al., 2022). The Kvabebi (Georgia) record of *Pliorhinus* in MN16a (early Villafranchian) also represents the last known European occurrence of the genus (Pandolfi et al., 2021), which did not survive into the Pleistocene. During the same time, the genus *Stephanorhinus* initially represented by *S. jeanvireti* and *S. etruscus*, made its appearance and continued into the Pleistocene with several species, i.e., *S. kirchbergensis*, *S. hemitoechus*, *S. hundsheimensis*. To these species that roamed Europe the genus *Coelodonta* was later added; it arrived in Western Europe from Asia during the Middle Pleistocene (Kahlke and Lacombat, 2008, Uzunidis et. al., 2022).

Although Late Miocene Greek rhinoceroses are well diversified and known by rich material as that from Pikermi, Axios Valley and Samos, they are poorly represented in the Greek Pliocene, recorded in only six sites. Two localities, Maramena in Serres Basin and Nea Silata in Chalkidiki, dated at the Miocene-Pliocene boundary, provided a few specimens referred to Rhinocerotidae indet. *S. jeanvireti* has been reported from the Upper Pliocene localities of Milia and Saint George Priporos (Grevena), as well as from Angelochori (Thessaloniki) (Guérin and Tsoukala, 2013; Tsoukala, 2018). *Stephanorhinus* sp. has been reported from the Upper Pliocene lower fossil layers of Sesklo, and Rhinocerotidae indet. from the Lower Pliocene site of Apolakkia in Rhodes Island (Symeonidis, 2006; Athanassiou 2018; Giaourtsakis, 2022). Here we report the first Greek occurrence of a single specimen of *Pliorhinus* from the Lower Pliocene site of Allatini, nowadays, within the urban fabric of Thessaloniki and discuss the geographic distribution of the genus.

1.1 Geological Setting and Age of the Site

The site of Allatini is located in East Thessaloniki and was named after a private company that exploited clay pits (Syrides, 1990; Vlachos et al., 2015 and references there in). The deposits nowadays are either fully exploited or covered and turned into urban landscapes. The stratigraphy of western Chalkidiki, including the area of Thessaloniki was described by Syrides (1990), who divided the Neogene deposits into six formations (Fm) (Fig. 1). The local stratigraphy of Allatini site was summarized by Sickenberg (1972), based on unpublished data provided by Prof. Gardikas and those by Stevanovic (1964). According to these lines of evidence, the stratigraphy of Allatini starts with a unit of brown-grey sandy clays with brown sandstone intercalations. It continues with clays, marls, and sands characterized by the presence of fossil invertebrates of Paratethyan origin. The succession continues with a unit of sandy clays where the poor vertebrate fossil remains of Allatini most likely come from and ends with a unit of brownish cross-stratified sands with conglomerate intercalations. The

local data are well-correlated with the upper layers of Trilophos Fm and the lower layers of Gonia Fm (Syrides 1990) representing the gradual transition between these two formations. Syrides (1990) dated this transition at the end of the Upper Miocene-lowermost Pliocene. Studies on the vertebrate fauna recovered from Allatini are very few. Marinos (1965) reported findings of *Elephas* sp., *Rhinoceros* sp. and *Vulpes* sp., all taxonomic definitions are considered outdated today. Further studies were only focused on the Canidae, more specifically on the mandible of *Eucyon odessanus* which is, along with the *Nyctereutes* from Megalo Emvolon, the earliest evidence of canids in Greece (Sickenberg, 1972; Koufos, 1997; 2022). As for the single Rhinocerotidae specimen known from this site, no meticulous research has been done and the findings were simply assigned to Rhinocerotidae indet. (Sickenberg, 1972; Symeonidis et al., 2006; Giaourtsakis, 2022).

2. Materials and methods

The studied specimen belongs to the historical collections of the Museum of Geology-Palaeontology-Palaeoanthropology of the Aristotle University of Thessaloniki (LGPOT) where it is housed. It is morphologically compared with rhinoceros' radii from Pliocene Eurasian localities, including Vialette (France), Montpellier (France), Layna (Spain), Alcalá (Spain), Kvabebi (Georgia), Udunga (Russia), Angelochori (Greece), Les Etouaries (France), Upper Valdarno (Italy), and Perpignan (France) (Guérin, 1972; Guérin and Santafe-Llopis, 1978; Mazo, 1997; Fukuchi et al., 2009; Pandolfi et al., 2017, 2022; Tsoukala, 2018).

The morphological nomenclature is based on Mazza (1988). Measurements were taken by a digital caliper at 0.01 mm precision. Photographs and illustrations were proceeded with GIMP Development Team. Biometrical comparative data are from Guérin (1972); Guérin and Santafe-Llopis (1978); Mazo (1997); Fukuchi et al. (2009); Pandolfi et al. (2017), (2021); and Tsoukala (2018). Data were analyzed with the software Rstudio (R Core Team, 2020).

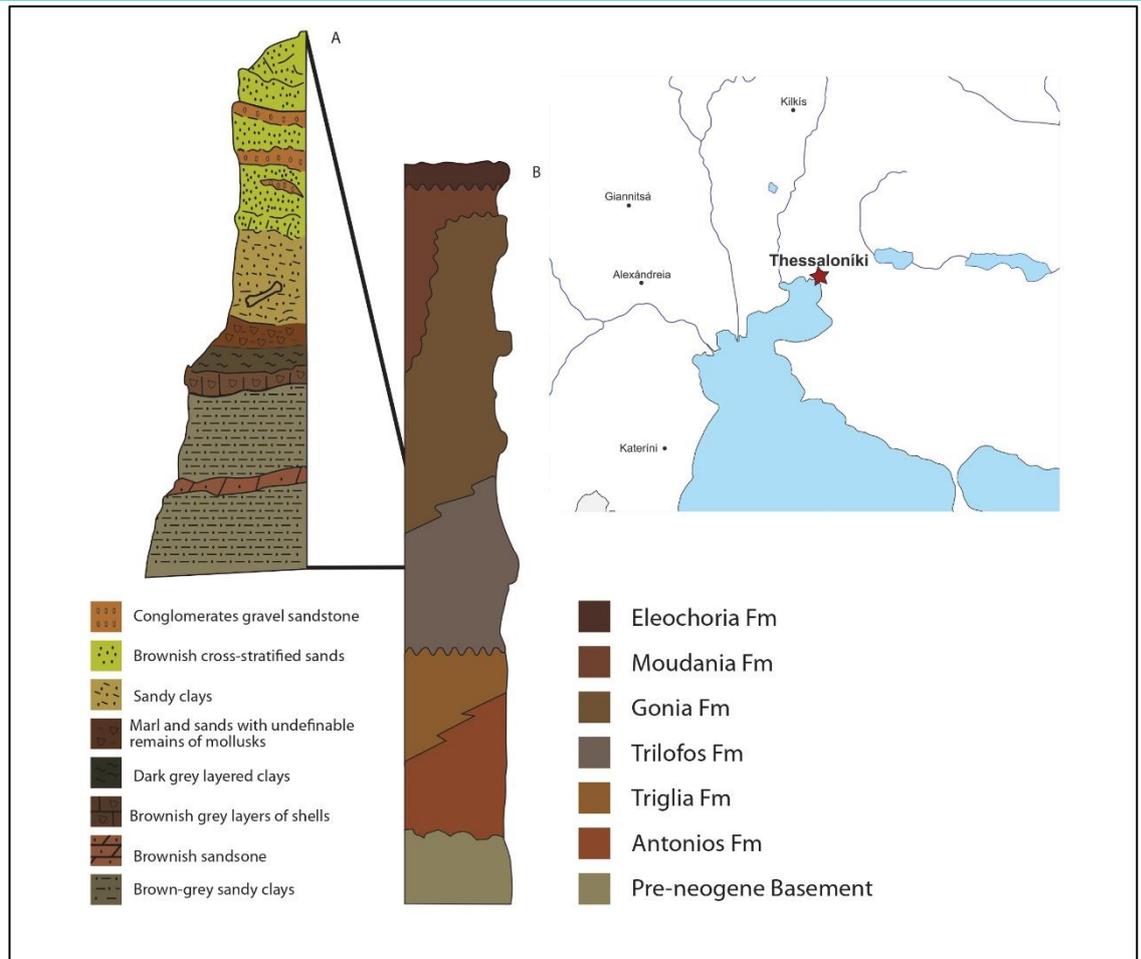


Fig. 1: Geographic location and local stratigraphy of Allatini site, Thessaloniki, based on Sickenberg (1972) and Syrides (1990).

3. Systematic Paleontology

Order **Perissodactyla** Owen, 1848

Family **Rhinocerotidae** Gray, 1821

Subfamily **Rhinocerotinae** Gray, 1821

Tribe **Rhinocerotini** Gray, 1821

Subtribe **Rhinocerotina** Gray, 1821

Genus ***Pliorhinus*** Pandolfi, Pierre-Olivier, Bukhsianidze, Lordkipanidze, Rook, 2021

Type species: *Pliorhinus megarhinus* (de Christol, 1834)

Remarks: The species *Rhinoceros megarhinus* de Christol 1841 is one of the first extinct Plio-Pleistocene rhinoceroses described ever by paleontologists. It is repeatedly included into the genus *Dicerorhinus* Gloger, 1841, represented by the extant species *Dicerorhinus sumatrensis* Fisher 1814; however, the two species differ in various

diagnostic characteristics (i.e., Pandolfi et al., 2016). The species is also referred to the genus *Dihoplus* based on Heissig's (1999) hypothesis of an evolutionary lineage from the Late Miocene *Dihoplus schleiermacheri* to the Late Pliocene *Dihoplus megarhinus*. Besides, Fortelius et al. (1993) and Cerdeño (1995) included the latter species into *Stephanorhinus*, though there are no important morphological characters in common (i.e., Pandolfi et al., 2016). The present study follows the most recent review by Pandolfi et al. (2021) according to which the species is included in a new genus, namely *Pliorhinus* along with the species *P. miguelcrusafonti* from Spain.

Material:

A complete radius, LGPUT-ALL OP(7) 131-133.

Description

The specimen from Allatini is a well-preserved right radius (Fig. 2), belonging to a sub-adult individual; the suture between the distal epiphysis and the diaphysis is not completely fused. In anterior view (Fig. 2A), the coronoid process is prominent forming an obtuse angle with the proximal border. In the same view, the radial and lateral tuberosities are evident; the posterior process is damaged; the proximo-medial border is convex and the proximo-lateral border is straight and slightly shorter than the medial one. In anterior view, the medial border is longer and more downwards directed than the lateral one.

In posterior view (Fig. 2, B), a triangular lateral articular surface for the ulna is present, while the medial one is not preserved. In proximal view (Fig. 2C), the medial articular surface is sub-squared, with a convex anterior border and a roughly convex medial one. The anterior border of the proximal articulation is slightly concave at the level of the coronoid process. The posterior-lateral border of the proximal epiphysis is roughly straight forming a $\sim 45^\circ$ angle with the postero-medial one.

On the distal epiphysis and in anterior view, the styloid process is prominent. The distal border of the articular surface for the semilunar is convex, with a convex distal outline. In distal view (Fig. 2D), the posterior portion of the articular surface for the scaphoid extends backwards. The anterior border of the epiphysis is concave at the level of the extensor carpi radialis. The articular surface for the semilunar is mediolaterally concave; that for the scaphoid has a rather concave anterior portion and a convex posterior one. The medial border of the articular surface for the scaphoid is straight, and the lateral border of the articular surface for the semilunar is slightly concave. Measurements are given in Table 1.

Comparison

The radius from Allatini differs from that of *S. jeanvireti* which has, in anterior view, a straight medial border, and in posterior view, a less protruding posterior process (Tsoukala, 2018). Additionally, the radius of *S. jeanvireti* from Angelochori, has in proximal view a more marked concavity on the anterior border in comparison with the studied specimen. In distal view, the radius from Allatini differs from the radius of *S. jeanvireti* from Vialette by the more convex posterior border of the articular surface for the scaphoid (Guérin, 1972; Tsoukala, 2018). In anterior view, the radius of *P. miguelcrusafonti* differs from that of Allatini in the less developed lateral tuberosity and concave lateral and straight medial proximal borders (Guérin and Santafe-Llopis, 1978; Pandolfi et al., 2021).

The studied specimen differs from *S. etruscus* which has a less developed brachii biceps in anterior view and a weakly concave posterior border, as well as a straight posterior-medial border in proximal view. The specimen from Allatini shares several common characters with *P. megarhinus*, such as an enlarged posteriorly articular surface for the scaphoid in distal view; a convex medial-proximal border and a straight lateral-proximal border in anterior view (Pandolfi et al., 2016, 2021).

The proximal transversal diameter (PTD) and proximal anteroposterior diameter (PAPD) (Fig. 3) of the radii of *S. jeanvireti* and *P. megarhinus* are strongly overlapping. The specimen of Allatini is closer to the smaller known values for *P. megarhinus*, though it is a sub-adult individual. Considering only the biometrical comparison, it is not possible to discriminate between *P. megarhinus* and *S. jeanvireti* by the proportions of the proximal epiphysis.

The proportions of the distal epiphysis (Fig. 4) clearly distinguish the range of *S. etruscus* radius from that of the other species in comparison. The specimen from Allatini is close to the minimum values of *P. megarhinus* and *S. jeanvireti*, and larger than the specimens of *P. miguelcrusafonti*.



Fig. 2: *Pliorhinus megarhinus* radius from Allatini, in A. anterior, B. posterior, C. proximal and D. distal views. Scale bar 50 mm.

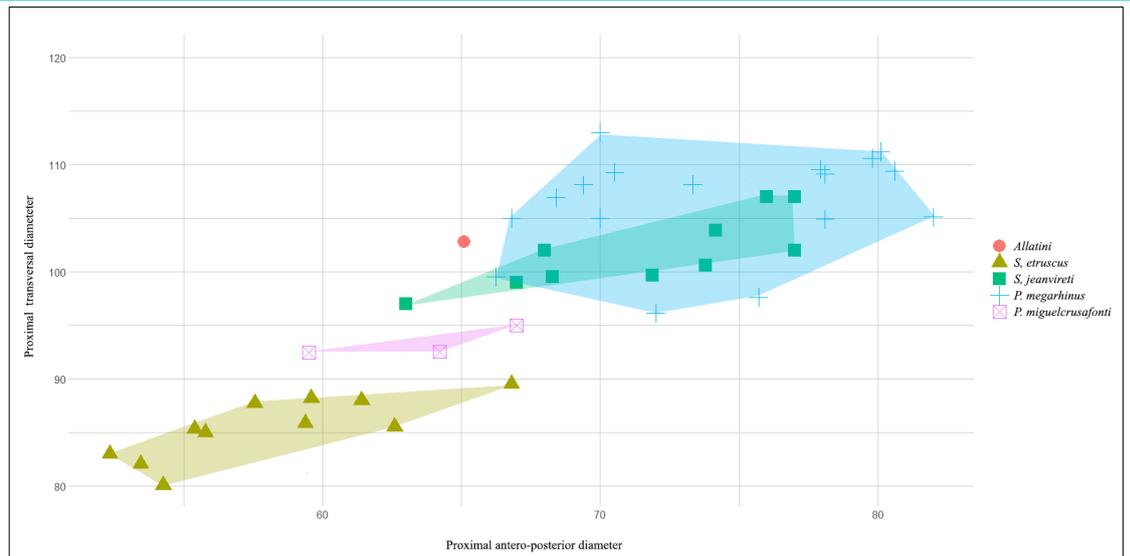


Fig. 3: Scatter plot of PTD (proximal transverse diameter) and PAPD (proximal antero-posterior diameter) (in mm) of the radius from Allatini; data from: Guérin (1972); Guérin and Santafe-Llopis (1978); Mazo (1997); Fukuchi et al. (2009); Pandolfi et al. (2017), (2021); Tsoukala (2018).

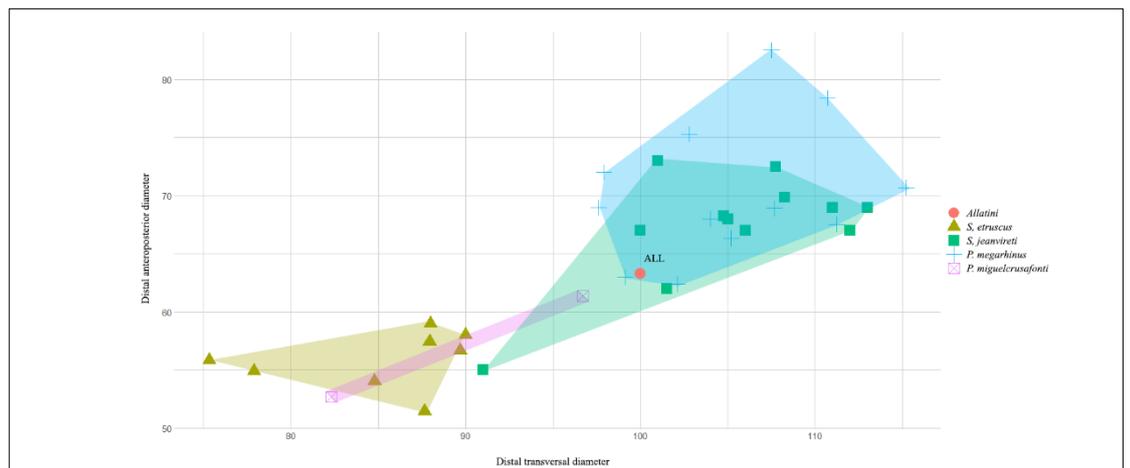


Fig. 4: Scatter plot of DTD (distal transverse diameter) and DAPD (distal anteroposterior diameter) (in mm) of the radius, data from: Guérin (1972); Guérin and Santafe-Llopis (1978); Mazo (1997); Fukuchi et al. (2009); Pandolfi et al. (2017), (2021); Tsoukala (2018).

4. Discussion & Conclusion

Based on the combination of morphological and metrical data, the Allatini rhino radius may quite safely be attributed to the species *P. megarhinus*, though the absence of adequate material and the poor stratigraphy and chronology of the site require a more open nomenclature, i.e., *Pliorhinus* cf. *megarhinus*. Based on our knowledge, this is the first record of this species and genus in Greece. Given the available stratigraphic and

biochronologic evidence (Koufos 2006), the Allatini rhino radius should be chronologically placed into Ruscinian and more likely in its early part. European sites with *P. megarhinus* and of more or less the same age as Allatini are Venta del Moro, Spain, dated to the Miocene-Pliocene transition (Cerdeño, 1992; Pandolfi et al., 2022), and Montpellier, France dated to the Lower Pliocene (MN14) (Guérin, 1980), Alcoy Mina, Spain, dated to the Lower Pliocene (Montoya et al., 2006; Pandolfi et al., 2022), Vera Basin, Spain dated to the Lower Pliocene (Pandolfi et al., 2022), and Val di Pugna, Italy dated to the late Lower Pliocene as well (base MN15; Pandolfi, 2013).

Based on the younger occurrence of *P. megarhinus* in Russia, Fukuchi et al. (2009) suggested that the taxon dispersed directly from Europe to Asia. Conversely, Pandolfi et al. (2015) advocate that *P. megarhinus* could have spread from Asia to Eastern Europe and the youngest occurrence in Udunga is the consequence of the persistence of this species in the area. However, this record has not been recently revised in the light of the record of *P. miguelsalvadori* in Georgia. *P. megarhinus* firstly occurred in Hungary during the Late Miocene, in Italy at the end of the Miocene (MN13) and during the Mio-Pliocene transition and the Early Pliocene (MN14/base MN15) it spread in Western Europe. Additionally, in Turkey it is present during the second half of the Pliocene (Guérin, 1980; Guérin and Sen, 1998; Pandolfi, 2013; Pandolfi et al., 2015). Hence, the Allatini record enforces with a E-SE European distribution of the species at the beginning of the Pliocene.

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5. References

- Athanassiou, A., 2018. A Villafranchian hipparion-bearing mammal fauna from Sésklo (E. Thessaly, Greece): implications for the question of hipparion–Equus sympatry in Europe. *Quaternary* 1(2),1–25.
- Cerdeño, E. 1992. Spanish Neogene rhinoceroses. *Palaeontology* 35 (2): 297–308.
- Cerdeño, E., 1995. Cladistic Analysis of the Family Rhinocerotidae (Perissodactyla). *Am. Museum Novit.* 3143, 1–25.
- Fortelius, M., Mazza, P., Sala, B., 1993. *Stephanorhinus* (Mammalia: Rhinocerotidae)

of western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). *Palaeontogr. Ital.* 80, 63–155.

Fukuchi, A., Nakaya, H., Takai, M., Ogino, S., 2009. A preliminary report on the Pliocene rhinoceros from Udunga, Transbaikalia, Russia. *Asian Paleoprimatology* 5, 61–98.

Giaourtsakis, I.X., 2022. The Fossil Record of Rhinocerotids (Mammalia: Perissodactyla: Rhinocerotidae) in Greece, in: E. Vlachos (ed.) *Fossil Vertebrates of Greece Vol. 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics*. Springer International Publishing, 409–500 pp.

Guérin, C., 1972. Une nouvelle espèce de rhinocéros (Mammalia, Perissodactyla) à Vialette (Haute-Loire, France) et dans d'autres gisements du Villafranchien inférieur européen : *Dicerorhinus jeanvireti* n. sp. *Doc. des Lab. Géologie la Fac. des Sci. Lyon* 49, 53–150.

Guérin, C., 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles., *Doc. Lab. Geol. Fac. Sci. Lyon*.

Guérin, C., Santafe-Llopis, J.V., 1978. *Dicerorhinus miguelcrusafonti* nov. sp., une nouvelle espèce de rhinocéros (Mammalia, Perissodactyla) du gisement pliocène supérieur de Layna (Soria, Espagne) et de la formation pliocène de Perpignan (Pyrénées-Orientales, France). *Geobios* 11, 457–491.

Guérin, C., Sen, S., 1998. Rhinocerotidae. In: Sen, S. (Ed.), *Le gisement de vertébrés pliocènes de Calta, Ankara, Turquie*. *Geodiversitas* 20, 397–407.

Guérin, C., Tsoukala, E., 2013. The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Geodiversitas* 35, 447–489.

Heissing, K., 1999. Family Rhinocerotidae, in: Rössner, G.E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Munich, 175–188 pp.

Kahlke, R.D., Lacomat, F., 2008. The earliest immigration of woolly rhinoceros (*Coelodonta tologojensis*, Rhinocerotidae, Mammalia) into Europe and its adaptive evolution in Palaearctic cold stage mammal faunas. *Quat. Sci. Rev.* 27, 1951–1961.

Koufos, G.D., 1997. The canids "*Eucyon*" and "*Nyctereutes*" from the Ruscinian of Macedonia, Greece. *Paleontologia i Evolució*, (30), 39–48.

Koufos, G.D., 2006. The Neogene mammal localities of Greece: faunas, chronology

and biostratigraphy. *Hellenic Journal of Geosciences*, 41(1), 183–214.

Koufos, G.D., 2022. The Fossil Record of Canids (Mammalia: Carnivora: Canidae) in Greece., in: E. Vlachos (ed.) *Fossil Vertebrates of Greece Vol. 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics*. Springer International Publishing, 577–594 pp.

Marinos, G., 1965. Beitrage zur Kenntnis der Verbeitung des Pleistozans in Mazedonien. *Scient.. Annals, Fac. Phys & Math. Univ. Thessaloniki*, 9, 96–111.

Mazo, A. V, 1997. El yacimiento Rusciniense de Alcalá del Júcar (Albacete). *Taxonomía y bioestratigrafía. Estudios Geológicos* 53 (5–6): 275–286.

Mazza, P., 1988. The Tuscan Early Pleistocene rhinoceros *Dicerorhinus etruscus*. *Palaeontog. Ital.* 75, 1–87.

Montoya, P., L. Ginsburg, M.T. Alberdi, J. van der Made, J. Morales J., and M.D. Soria. 2006. Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas* 28(1): 137–173.

Pandolfi, L., 2013. New and revised occurrences of *Dihoplus megarhinus* (Mammalia, Rhinocerotidae) in the Pliocene of Italy. *Swiss J. Palaeontol.* 132, 239–255.

Pandolfi, L., Rook, L., 2017. Rhinocerotidae (Mammalia, Perissodactyla) from the latest Turolian localities (MN 13; Late Miocene) of central and northern Italy. *Boll. della Soc. Paleontol. Ital.* 56, 45–56.

Pandolfi, L., Gasparik, M., Piras, P., 2015. Earliest occurrence of “*Dihoplus*” *megarhinus* (Mammalia, Rhinocerotidae) in Europe (Late Miocene, Pannonian Basin, Hungary): Palaeobiogeographical and biochronological implications. *Ann. Paleontol.* 101, 325–339.

Pandolfi, L., Gasparik, M., Magyar, I., 2016. Rhinocerotidae from the Upper Miocene deposits of the Western Pannonian Basin (Hungary): Implications for migration routes and biogeography. *Geol. Carpathica* 67, 69–82.

Pandolfi, L., Cerdeño, E., Codrea, V., Kotsakis, T., 2017. Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae). *Comptes Rendus - Palevol* 16, 762–773.

Pandolfi, L., Pierre-Olivier, A., Bukhsianidze, M., Lordkipanidze, D., Rook, L., 2021. Northern Eurasian rhinocerotines (Mammalia, Perissodactyla) by the Pliocene–Pleistocene transition: phylogeny and historical biogeography. *J. Syst. Palaeontol.* 19, 1031–1057.

- Pandolfi, L., Sendra, J., Reolid, M., Rook, L., 2022. New Pliocene Rhinocerotidae findings from the Iberian Peninsula and the revision of the Spanish Pliocene records. *Pal. Z.* 96(2), 343–354.
- Sickenberg, O., 1972. Ein Unterkiefer des Caniden *Nyctereutes donnezani* (Dep.) aus der Umgebung von Saloniki (Griech. Mazedonien) und seine biostratigraphische Bedeutung. *Ann. Naturhistor. Mus. Wien* 76, 499–513.
- Stevanovič, P., 1964. Contribution à la connaissance de l' étage Pontien de Grèce avec une remarque spéciale sur le Pontien de la Mer Noire., *Curs. Conf. Inst. Lucas Mallada*, vol. 9, 93–100.
- Symeonidis, N.K., Giaourtsakis, I.X., Giannopoulos, V.I., 2006. Aivaliki, a New Locality with Fossil Rhinoceroses near Alistrati (Serres, Greece). *Beiträge zur Paläontologie* 30, 437–451.
- Syrides, G.E., 1990. Lithostratigraphic, biostratigraphic and palaeogeographic study of the Neogene–Quaternary sedimentary deposits of Chalkidiki Peninsula, Macedonia, Greece. *Sci. Ann. Sch. Geol. Aristotle Univ. Thessaloniki*, 11, 243.
- Team, R.C., 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Tsoukala, E., 2018. Rhinocerotidae from the late Miocene and late Pliocene of Macedonia, Greece. A revision of the Neogene - Quaternary Rhinocerotidae of Greece. *Rev. Paleobiol.* 37, 609–630.
- Uzunidis, A., Antoine, P.O., Brugal, J.P., 2022. A Middle Pleistocene Coelodonta antiquitatis praecursor (Mammalia, Perissodactyla) from Les Rameaux, SW France, and a revised phylogeny of Coelodonta. *Quat. Sci. Rev.*, 288, 107594.
- Vlachos, E., Kotsakis, T., Delfino, M., 2015. The chelonians from the Latest Miocene–Earliest Pliocene localities of Allatini and Pylea (East Thessaloniki, Macedonia, Greece). *Comptes Rendus - Palevol* 14, 187–205.