



## PRIMATES AND CARNIVORES FROM LATE MIOCENE AND EARLIEST LATE PLIOCENE SITES OF MACEDONIA, NORTHERN GREECE

EVANGELIA TSOUKALA<sup>1</sup>, DORIS NAGEL<sup>2</sup>, DIONISIOS YOULATOS<sup>3,4,\*</sup>, EVELYNE CRÉGUT-BONNOURE<sup>5,6</sup>,  
EVANGELOS VLACHOS<sup>7</sup>, NIKOLAI SPASSOV<sup>8</sup>

<sup>1</sup> Aristotle University of Thessaloniki, School of Geology, 54124 Thessaloniki, Greece; e-mail: lilits@geo.auth.gr.

<sup>2</sup> Department of Paleontology, University of Vienna, 1090 Vienna, Austria; e-mail: doris.nagel@univie.ac.at.

<sup>3</sup> Aristotle University of Thessaloniki, School of Biology, 54124 Thessaloniki, Greece; e-mail: dyoul@bio.auth.gr.

<sup>4</sup> International Center for Biodiversity and Primate Conservation, Dali University, 671003 Dali, Yunnan, China.

<sup>5</sup> Muséum Requiens, Avignon.

<sup>6</sup> TRACES, UMR 5608 (CNRS) – Université Toulouse Jean Jaurès, Toulouse, France; e-mail: evelyne.cregut1313@orange.fr.

<sup>7</sup> CONICET and Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Chubut, Argentina; e-mail: evlacho@mef.org.ar.

<sup>8</sup> National Museum of Natural History at the Bulgarian Academy of Sciences, Sofia, Bulgaria; e-mail: nspassov@nmnhs.com.

\*corresponding author

Tsoukala, E., Nagel, D., Youlatos, D., Crégut-Bonnouire, E., Vlachos, E., Spassov, N. (2024): Primates and carnivores from Late Miocene and earliest Late Pliocene sites of Macedonia, Northern Greece. – Fossil Imprint, 80(2): 362–389, ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

**Abstract:** Four sites in northern Greece, presented here, are of particular interest, due to the presence of fossil primates and carnivores in Late Miocene and Pliocene assemblages. The Thermopigi site in eastern Macedonia is particularly important, due to its demonstrable Late Miocene assemblage of more than twenty different species of large mammals, including the postcranial remains (humerus, tibia, calcaneus) of the colobine *Mesopithecus delsoni*. Carnivores from this site, represented by hyenids, felids, and mustelids, are also described here. Among them, the hyper-carnivorous and widely spread *Adcrocuta eximia*, an important biostratigraphic marker of Late Miocene, is compared with the single skull from the nearby site of Platania (Drama), both of great taphonomic interest. The site of Milia (Grevena), in Western Macedonia, is also of particular importance, as it includes the earliest Villafranchian age assemblage. New primate material, an ulna and tibia attributed to aff. *Dolichopithecus* sp. are also described here. Among the new carnivore finds, an incomplete distal tibia belongs to a new felid for the Milia locality, most likely attributable to either a female *Megantereon* or a new species of *Puma*. Further investigations are necessary to confirm either attribution. Finally, the new Pliocene site at Promachonas (Serres), mentioned here for the first time, yielded dental material, most likely belonging to cf. *Dolichopithecus balcanicus*. This study of new material from these sites contributes to a better knowledge regarding the occurrence of primates and carnivores and their paleoenvironments in northern Greece.

**Key words:** *Adcrocuta*, Cercopithecidae, *Dolichopithecus*, Felidae, *Mesopithecus*, Milia, Neogene, Platania, *Plesiogulo*, Promachonas, Thermopigi

Received: June 18, 2024 | Accepted: October 21, 2024 | Issued: December 20, 2024

Zoobank: <http://zoobank.org/urn:lsid:zoobank.org:pub:53D565CF-581F-4682-B79D-31E74ED35543>

### Introduction

In Europe, Miocene primates are uncommon, and Miocene carnivores are relatively rare compared to herbivores. Therefore, their presence in European fossil sites is of particular scientific interest for understanding the diversity and evolution of European mammals. In this context, several studies and revisions of the Neogene primates and carnivores of Greece have been provided by Koufos (2006a, 2009a, b, 2011, 2013, 2022a–d). This report aims to complement previous studies by presenting new primate and

carnivore fossil material deriving from four sites in Northern Greece: Thermopigi, Platania, Milia, and Promachonas, spanning from MN 11 to MN 15/16a – the beginning of the Villafranchian. Among primates, fossil cercopithecids are quite common in the Greek Miocene sites, mainly represented by the colobine genera *Mesopithecus* WAGNER, 1839 and *Dolichopithecus* DEPÉRET, 1889 (Koufos 2022d). *Mesopithecus pentelicus* WAGNER, 1839, of biozone MN 12, is reported from Pikermi, Chomateres (Koufos 2022d), and Kryopigi (Lazaridis et al. 2018). Rarer are the older

*Mesopithecus delsoni* BONIS et al., 1990 of biozone MN 11 reported from Ravin des Zouaves (Axios), and the younger *Mesopithecus monspessulanus* GERVAIS, 1849 of biozone MN 13 from Dytiko. *Mesopithecus* sp. of biozone MN 13/14 is reported from Maramena (Küllmer and Doukas 1995). The other colobine, *Dolichopithecus* was first attributed to the species *D. rusciniensis* DEPÉRET, 1889 (Koufos et al. 1991) and subsequently to *D. balcanicus* SPASSOV et GERAADS, 2007 of biozone MN 15 from the Megalo Emvolo and Ptolemais sites. Among the carnivores studied here, the most widespread hyper-carnivore scavenger *Adcrocuta eximia* is of interest due to its distribution in Northern Greece and the taphonomic marks on the bones of the associated fauna, followed by *Plesiogulo*, another largely scavenger, and finally felines, among which some were identified for the first time in Greece. In this context, this report presents the first evidence and initial taxonomic diagnosis on the Miocene and Pliocene primates and carnivores of northern Greece, contributing to our knowledge on the evolution of the paleodiversity and paleoenvironment of southeastern Europe.

## Material and methods

The fossil material from four excavation sites in northern Greece is described here: Thermopigi (SIT) and Platania (PLD) from the Late Miocene, with the former providing the first description of newly recovered primate postcranial material, as well as Milia (MIL) and Promachonas (PRC) from the Pliocene, both sites yielding the first reference to primates. Additionally, we describe 15 carnivore remains recovered from Thermopigi, one from Platania, and one from Milia.

## Studied fossil material

The material studied here belongs to the collections of the Museum of Geology, Palaeontology, Palaeoanthropology (M-GEPAPAL), Aristotle University of Thessaloniki. The SIT carnivore material is stored in the municipal Museum Natural History – Paleontological exhibition in Thermopigi, Serres, established in 2005 and recognized as a Peripheral Unit of M-GEPAPAL. We use taxonomical hierarchy according to McKenna and Bell (1997).

## Abbreviations

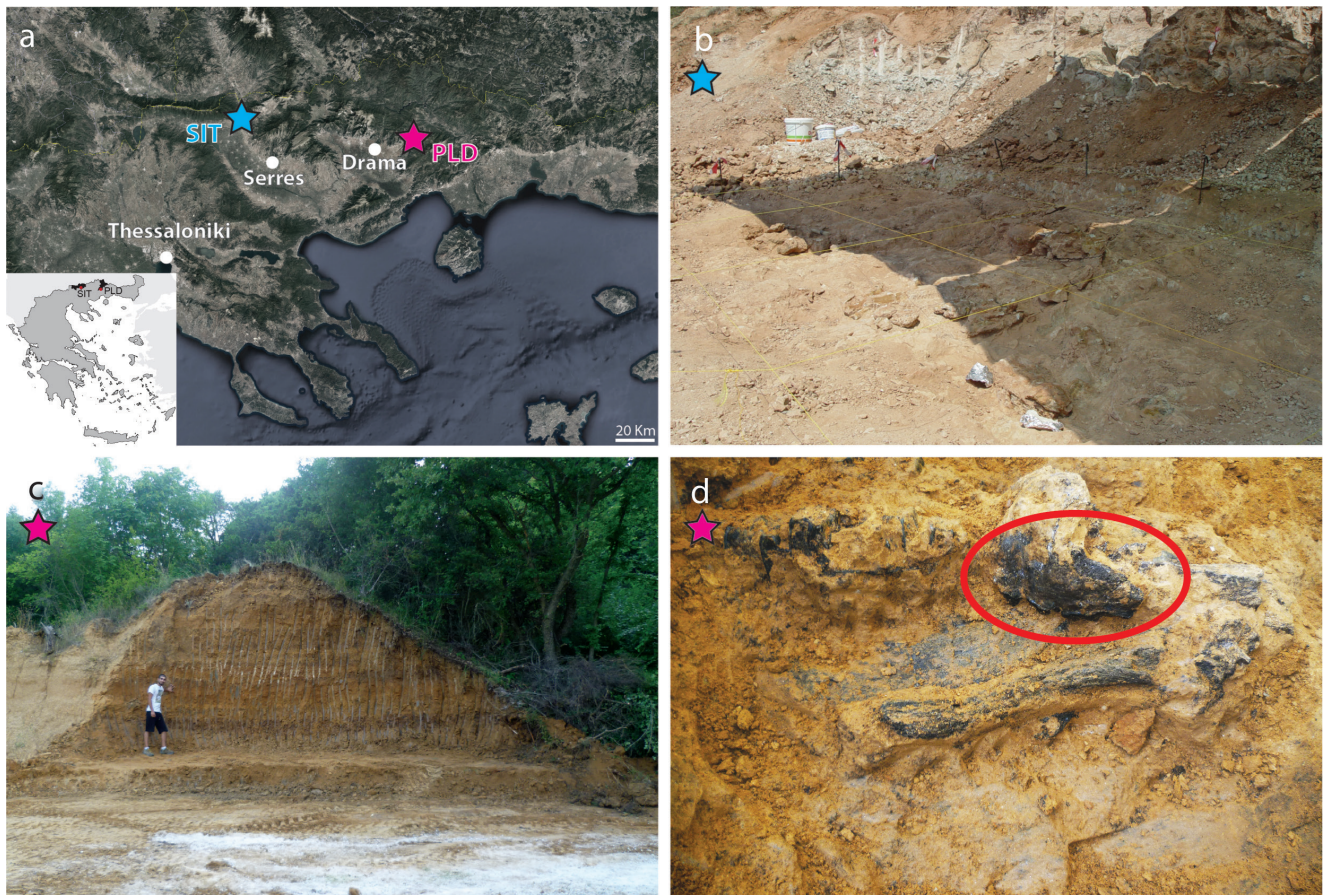
ant. – anterior; art. – articulation; B – breadth, width; bucc – buccal; d – lower deciduous premolar; dex – dextra, right; DAP – antero-posterior diameter; dia – diaphysis; dist., d. – distal; DT – transversal diameter; f. – facies; f. art. dist. ti – facies articularis distalis tibiae; f. art. mal. fib. – facies articularis malleoli fibulae; fib. – fibulae; f.s. – foram supracond – foramen supracondylicum; H – height; hy<sup>d</sup> – hypocond; I – Index; lab – labial; lat. – lateral; L – length; ling – lingual; M/m – upper/lower molars; max – maximal; md – mandible; med – medial; me<sup>d</sup> – metaconid; mid. – middle; min – minimal; mts – metastyle; mx – maxilla; P/p – upper/lower premolars; palat – palatal; pas – parastyle; post. – posterior; pr – protocone; prox. – proximal; s – sinistra, left; ti – tibiae; tl – talon; tl<sup>d</sup> – talonid.

## Fossil sites

### Thermopigi, Serres

The Miocene site of Thermopigi (SIT: Sidirokastro, Thermopigi; N 41.287778, E 23.364167, elevation 286 m a.s.l., Hellenic Grid, EGSA '87) is located in the Municipality of Sintiki (Serres province, Eastern Macedonia, Northern Greece), 4 km from the municipal center of Sidirokastro and 18 km from the Bulgarian border (Text-fig. 1a). Systematic paleontological excavations and research started at Thermopigi in 1998 by the Aristotle University of Thessaloniki, led by one of the authors (E.T.). Despite the great scientific interest and the abundant fossils, insufficient funding led to just seven excavation cycles by the AUTH. Collaboration with the Department of Paleontology of the University of Vienna, led by D.N., resulted in excavations in 2011, 2013, and 2015, with the participation of numerous Greek and Austrian students and collaborators (Text-fig. 1b). More than 2,100 mammal remains have been unearthed from reddish consolidated sandstones, indicative of a mainly browsing morphospace. The material is generally in good condition, but several bones exhibit a high degree of modification, as well as fracture distortions due to neotectonic activity in the area. The preliminary fauna list includes more than 20 different species. In addition to the carnivores studied in this article, proboscideans (*Deinotherium* sp., *Elephantimorpha* indet.), perissodactyls (hipparions, *Ancylotherium pentelicum* GAUDRY et LARTET, 1856, *Dihoplus pikermiensis* TOULA, 1906), and artiodactyls (*Microstonyx major* (GERVAIS, 1848), *Propotamochoerus* sp., *Samotherium major* BOHLIN, 1926, *Palaeotragus rouenii* GAUDRY, 1861, *Palaeotragus* sp., *Helladotherium duvernoyi* GAUDRY et LARTET, 1856, *Tragoportax cf. amalthea* (ROTH et WAGNER, 1854), *Palaeoreas lindermayeri* (WAGNER, 1848), *Gazella* sp., etc.) are represented (Geraads et al. 2007, Tsoukala 2018, Xafis et al. 2019, Konidaris and Tsoukala 2020). The preliminary faunal list suggests a Turolian age (Geraads et al. 2007). The co-occurrence of *Dihoplus pikermiensis* and *Ancylotherium pentelicum* most likely indicates a middle Turolian age (MN 12; Koufos et al. 2009), but these taxa co-occurred in Hadjidimovo, Bulgaria, which is placed in the second half/end of MN 11 (Li and Spassov 2017). A MN 12 age was also assessed from the coexistence of *Samotherium major* with *Palaeotragus rouenii* and a slightly larger *Palaeotragus* sp. (Xafis et al. 2019), even though the co-occurrence of the latter two palaeotragines may indicate an early Turolian age, MN 11 (Koufos et al. 2009). Regarding the Thermopigi hipparions, the cranium of *Cremohipparion* QIU et al., 1987 shows similarities with samples of *C. proboscideum* (STUDER, 1911) from RZO 5, as well as with some specimens of *C. mediterraneum* (ROTH et WAGNER, 1855), from Hadjidimovo and *C. cf. mediterraneum* from Perivolaki, whereas the *Hipparion* cranium is comparable to that of *H. philippus* KOUFOS et VLACHOU, 2016 [= *H. dietrichi* (WEHRLI, 1941) in previous publications] from Nikiti 2 and Perivolaki (L. Hristova, G. Lazaridis, pers. comm). In this way, hipparions indicate an age between MN 11 and the beginning of MN 12. A more definitive biochronological determination of the age of Thermopigi requires a more precise study of the remaining





**Text-fig. 1. a: Map of Greece with Miocene sites of Thermopigi (SIT), and Platania (PLD). b: SIT, excavation site with grid of squares. c: PLD, excavation site with (d) hyenid maxilla in situ.**

fauna of the site. However, for now it can be assessed as between MN 11 and pre-Pikermian beginning of MN 12 (Youlatos et al. in press).

### Platania, Drama

The Miocene site of Platania (PLD: Platania, Drama; N 41.196778, E 24.395000, elevation: 257 m a.s.l., Hellenic Grid, EGSA '87) is located in the Municipality of Paranesti (Drama district, Eastern Macedonia), 14 km from the municipal center of Paranesti. The research started in 2012, in the Aristotle University of Thessaloniki, led by E.T., and systematic excavations started from 2013 to 2016 (Text-fig. 1c). About 760 well-preserved fossils have been collected from yellow-brownish fine sandy mud, indicative of a more lacustrine environment. Several nearly complete skulls, mandibles, tooth-rows, antlers and post-cranial bones are blackish in color, like the hyena maxilla (Text-fig. 1d), due to geochemical processes during fossilization strongly related to manganese (Mn) content in the light-colored fossiliferous sediments, as the existing permanganate radical acts as a reagent in the fossilization process under redox conditions. The Mn-rich layer contains high levels of natural radionuclides, with the lowest sand fraction and the highest clay-cement associated with a high content of only the  $^{232}\text{Th}$  series, indicating a warm environment, as measured by the highest Th/K activity ratio (~1) (Zougrou et al. 2018). The preliminary fauna list includes more than 20 different species. In addition to the hyenid studied in

this article, the fauna includes antilopines (*Gazella* cf. *ancyrensis* TEKKAYA, 1973, *Gazella* sp., *Prostrepsiceros* aff. *syridisi* KOSTOPOULOS et KOUFOS, 1996, cf. *Palaeoreas*, *Palaeoryx minor* VASILEIADIS et al., 2019, *Tragoreas?* aff. *oryxoides* SCHLOSSER, 1904), bovinines (*Miotragoceros* sp.), perissodactyls (hipparions, *Ceratotherium neumayri* OSBORN, 1900), proboscideans (*Konobelodon* cf. *atticus* WAGNER, 1857), artiodactyls (giraffes, cervids, suids), and testudines (*Testudo* cf. *graeca* LINNAEUS, 1758) (Vlachos and Tsoukala 2014, Tsoukala 2018, Vasileiadis et al. 2019, Konidaris and Tsoukala 2020). The Platania fauna is a mix of both Vallesian and Turolian taxa, indicating a likely late Vallesian-early Turolian age.

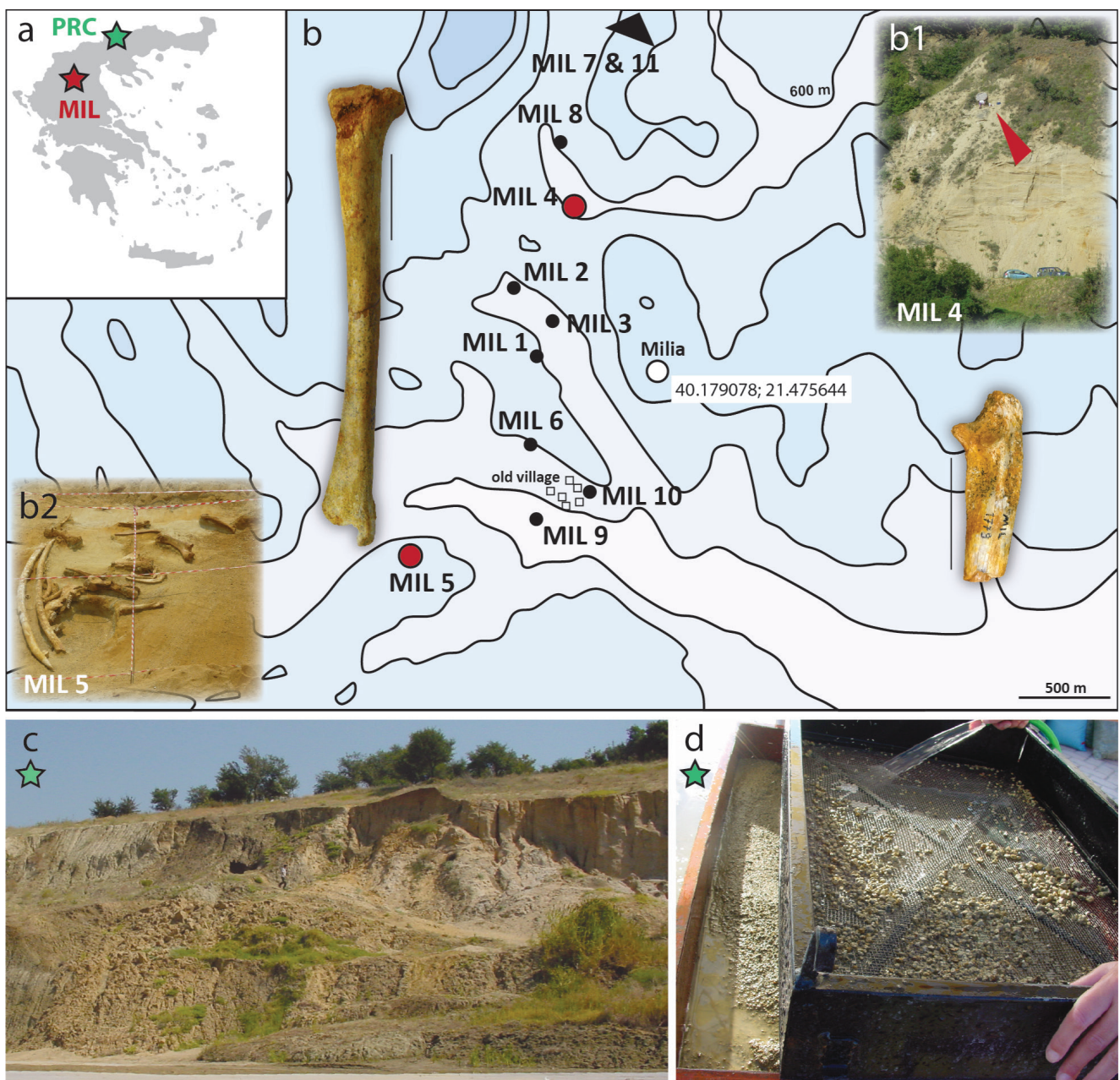
### Milia, Grevena

The Pliocene site of Milia (MIL, Grevena) includes 11 (MIL 1-11) localities, all situated west of the village of Milia (N 40.179562, E 21.474795, elevation: 552 m a.s.l. Hellenic grid, EGSA '87) of the Grevena Peripheral Unit of West Macedonia, 160 km west of Thessaloniki and 15 km northeast of the town of Grevena. The Milia fossils came to light after systematic paleontological excavations by the Aristotle University of Thessaloniki team, led by one of us (E.T.) since 1996, found in undifferentiated sand deposits. At the MIL 4 locality, the first primate specimen, an ulna, was discovered by a team member in 2011. Meanwhile, excavation works in the sandpit at MIL 5 locality under the supervision of the Ministry of Culture and the Milia Natural



History Museum provided more fossils to the collection. Among them, post cranial specimens of a primate and a felid are studied here (Text-fig. 2a, b). It comprises more than 1,800 specimens, of which more than 22 different species of vertebrates were identified: Proboscideans (*Mammuth borsoni* HAYS, 1834 and *Anancus arvernensis* CROIZET et JOBERT, 1828), perissodactyls (*Hipparion* sp. (*H. crassum* group), *Tapirus arvernensis* CROIZET et JOBERT, 1828, *Stephanorhinus jeanvireti* (FALCONER, 1859)), suids (*Sus arvernensis* DEPÉRET, 1885), bovids (*Grevenobos antiquus* CRÉGUT-BONNOURE et TSOUKALA, 2017, *Alephis* sp., Bovini indet., *Gazella borbonica* DEPÉRET, 1885, Antilopinae indet.), cervids (*Croizetoceros ramosus* (CROIZET et JOBERT, 1828), Cervidae indet., *Praeclaphus* cf. *lyra*, AZZAROLI, 1992), Ruminantia indet., felids (*Homotherium crenatidens* FABRINI,

1890), ursids (*Ursus etruscus* CUVIER, 1823, *Agriotherium* sp.), Aves indet. and testudines (*Mauremys* sp., *Titanochelon* sp., and *Testudo brevitesta* VLACHOS et TSOUKALA, 2015). The oldest presence of the Plio-Pleistocene porcupine species *Hystrix* cf. *refossa*, GERVAIS, 1852 in Europe is worth mentioning (Tsoukala 2000, Guérin and Tsoukala 2013, Tsoukala and Mol 2016, Vlachos and Tsoukala 2016, Crégut-Bonnoure and Tsoukala 2017, Vlachos et al. 2018, Lazaridis et al. 2019). Milia is a very important paleontological site in Greece, recently recognized as Large Mammal Faunal Unit, dated to 3 Ma and to the beginning of MN 16a (Konidaris and Kostopoulos 2024). A more precise chronology is under discussion. Although no micromammals other than *Hystrix* have been thus far identified, the composition of the faunal assemblage presents evidence of the transition between the



**Text-fig. 2.** a: Map of Greece showing Pliocene sites of Milia (MIL) and Promachonas (PRC). b: MIL, site with its eleven fossil localities; two of which, MIL 4 (b1) and MIL 5 (b2) provided ulna and tibia of a primate, respectively. c: New site PRC: greenish-gray argillaceous sediments on slopes of site. d: Isolated primate teeth found during sieving process in sieves of a 0.8 mm mesh (bottom sieve) and 5 mm (top sieve).





Text-fig. 3. *Mesopithecus delsoni*, Thermopigi. a: Humerus left SIT 986; a1: dorsal, a2: ventral, a3: medial view. b: Tibia right SIT 980; b1: anterior, b2: posterior, b3: lateral, b4: medial, b5: distal view. c: Calcaneus left SIT 1100; c1: anterior, c2: lateral, c3: medial, c4: posterior, c5: proximal, c6: distal view. Scale bars 30 mm.

**Table 1. *Mesopithecus delsoni*, Thermopigi (SIT). Measurements of humerus, tibia, calcaneus (in mm). (See abbreviations in text.)**

Humerus	SIT 986	Tibia	SIT 980	Calcaneus	SIT 1100
L dia	(114.86)	DT distal	18.06	Length maximum	35.38
DT prox. metaphysis	(18.73)	DAP distal	17.39	Length of manubrium	22.92
DAP prox. metaphysis	(14.09)	DT d. art.	13.89	Maximum width	19.35
DT dia middle	14.57	DAP d. art.	13.13	DAP tuber	18.24
DAP dia	10.58	DT dia at 40 mm from distal end	12.56	Diameter max. of art. for cuboideum	12.11
DT distal metaphysis	(19.28)	DAP dia (idem)	12.70	Width of sustentaculum tali	7.71
DAP distal metaphysis	(9.65)	DT f. art. dist. ti.	7.32	Maximum DAP	18.23
		DT f. art. mal. fib.	6.57	DT tuber	12.49

Ruscianian and early Villafranchian or early Villafranchian (Crégut-Bonnoure and Tsoukala 2017).

### Promachonas, Serres

The new Pliocene site of Promachonas (PRC: Serres; N 41.374444, E 23.369722, elevation: 113 m a.s.l. Hellenic grid, EGSA '87) reported here for the first time, is located close to Greek-Bulgarian borders. Geologically, the site is located in the southernmost part of the Sandanski basin. The latter is among the fault-bounded basins that developed along the NW-SE Strymon lineament, i.e., the lineament that fits the boundary between the Serbomacedonian and Rhodope massifs (Zagorchev 1992, Tranos et al. 2008). It is filled mainly with Neogene sediments. In the Promachonas site, the exposed gray-green argillaceous, fine-granulated sediments are stratigraphically of Pliocene age. The sediments were originally collected in a 2004 expedition by the Aristotle University team, led by E.T., and were washed for investigating micromammal remains on the sieves of a 0.8 mm mesh (the bottom sieve) and 5 mm (the above sieve). These resulted in seven primate teeth among gastropod opercula (Text-fig. 2c, d).

### Systematic paleontology

**Order Primates LINNAEUS, 1758**

**Suborder Haplorhini POCKOCK, 1918**

**Infraorder Anthroidea MIVART, 1864**

**Parvorder Catarrhini GEOFFROY SAINT-HILAIRE, 1812**

**Superfamily Cercopithecoidea GRAY, 1821**

**Family Cercopithecidae GRAY, 1821**

**Subfamily Colobinae BLYTH, 1863**

**Genus *Mesopithecus* WAGNER, 1839**

***Mesopithecus delsoni* BONIS, BOUVRAIN,**

**GERAADS et KOUFOS, 1990**

Text-fig. 3

Locality. Thermopigi.

Material. Humerus left SIT 986, tibia right SIT 980, calcaneus left SIT 1100.

Description. The humerus retains a curved diaphysis, with proximal and distal metaphyses (Text-fig. 3a, Tab. 1). It shows a high degree of modification or deformation due to neotectonic events, which is quite

common – it has been observed in several bones of large mammal remains from Thermopigi. Epiphyses are missing, likely due to the young juvenile (neonate?) age of the individual. The diaphysis shows a curvature in the middle and torsion of a relatively large cercopithecoid. The maximum height of the chord from the axis of the bone is 15.22 mm. The distal portion is slender, whereas the proximal portion, particularly the collum area, is robust.

The tibia retains the distal end, with a small part of diaphysis (Text-fig. 3b, Tab. 1). The epiphysis was not fused, and a suture is visible around the entire perimeter of the distal end. The part of the shaft appears relatively robust, is posteriorly rounded and anteriorly flat. The anterior surface is partly eroded. The malleolus tibiae is well developed with a sub-triangular facies articularis malleoli. The facies articularis distalis tibiae is sub-square but narrow, whereas the facies articularis malleoli fibulae is semicircular and wide. The cross-section of diaphysis at 40 mm from distal end is relatively rounded.

The calcaneus is complete, and well preserved (Text-fig. 3c, Tab. 1). It is robust, with a slightly concave squarish-shaped tuber below it, and laterally, a well-marked fossa. The lateral side of the calcaneal body is eroded, and the postero-medial and disto-medial edges of the sustentaculum tali are broken. From the lateral and posterior view, the sustentaculum tali curves anteriorly and medially respectively in relation to the manubrium. The articular surface for the cuboideum is broad and hollow. Detailed descriptions of the calcaneus can be found in Youlatos et al. (in press).

Discussion. The morphology of the humeral shaft implies a rather pronounced deltopectoral ridge, although it is difficult to judge, as it is rather incomplete. The shaft appears relatively robust and seems to be mediolaterally compressed. This morphology is reminiscent of more terrestrial *Macaca* LACÉPÈDE, 1799 species. All these characters suggest quadrupedal adaptations related to terrestrial activities (Harrison 1989).

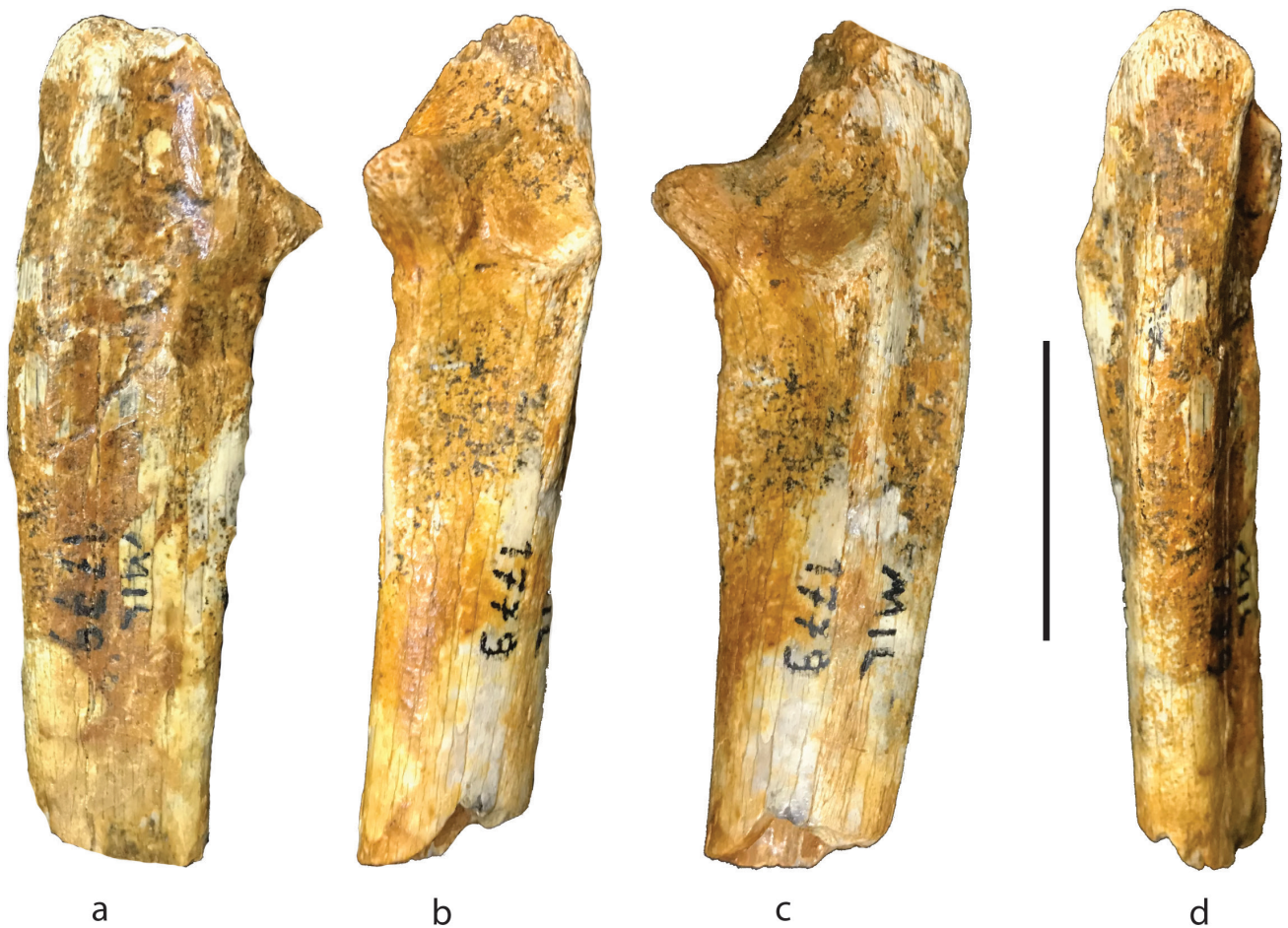
The tibial morphology is similar to most terrestrial cercopithecids (e.g., *Papio* DESMAREST, 1820), but different from the more medially expanded shafts of more arboreal colobines (DeSilva et al. 2010). The medial malleolus is moderately developed, triangular, and standing at an almost vertical angle to the trochlear facet. The overall morphology is similar to that of most terrestrial cercopithecids like *Papio* and differs substantially from the medio-laterally robust and protruding malleolus of hominoids (DeSilva et



al. 2010). The malleolus bears a slightly concave articular surface, ending distally at a pronounced ball-shaped area, a feature typical to cercopithecids, but absent in hominoids (Harrison 1989). Although the antero-distal part of this end is broken, the bulbous malleolar end is reminiscent of that of more terrestrial cercopithecines (e.g., *Papio*, *Theropithecus* I. GEOFFROY, 1843). This condition is different from that observed in the more arboreal colobines and from that in *Paradolichopithecus* NECRASOV et al., 1961 from Vatera (Sondaar et al. 2006). In distal view, the antero-posterior axis of the malleolus is set parasagittally, a condition observed in more semi-terrestrial and terrestrial cercopithecines (e.g., *Macaca*, *Theropithecus*), and is different from the medial tilt of most arboreal colobines (e.g., *Colobus* ILLIGER, 1811) (Youlatos 1994). The postero-distal part of the epiphysis and the malleolus are slightly damaged, and the groove that accommodates the tendons of the posterior tibialis and the long digital flexor is not visible (Ford 1986). In this character, SIT-980 is different from *Mesopithecus pentelicus*, where the groove is deep (Ingicco 2008), but is similar to most terrestrial cercopithecids. On the distal surface, the trochlear facet has a trapezoid shape, is smoothly concave, and mediolaterally narrow. The latter morphology is typical of cercopithecids (Harrison 1989), and more particularly that of more terrestrial forms (Laird et al. 2018). The facet bears an underdeveloped, relatively concave median antero-posterior ridge. The ridge is slightly perpendicular to the medio-lateral plane of the bone, is bordered by shallow medial and lateral depressions for articulation with the trochlear surface of the talus, and ends anteriorly to a V-shaped tubercle. The protuberance of the tubercle is reminiscent of that in *Macaca* and *Theropithecus*, and differs from that of more arboreal colobines (Youlatos 1994, Laird et al. 2018). The posterior border of the trochlear facet is smooth and relatively low. The anterior border appears sharper and relatively higher, and bears the anterior tubercle. On the lateral side of the bone and towards the anterior part of the trochlear facet lies the relatively shallow crescent of the fibular facet. This morphology is similar to that of cercopithecids. Overall, these characters of the distal tibia suggest terrestrial quadrupedal activities.

The calcaneal features indicate a typical cercopithecoid calcaneus, morphologically different from extant and fossil hominoids (Rose 1986, Strasser 1988). The proximal calcaneo-astragalar facet is relatively short, squared off, tightly curved, and tilts obliquely and faces more dorsally, whereas fossil and extant hominoids possess longer, gently curved, and acutely tilted facets (Langdon 1986, Rose 1986, Strasser 1988, Gebo 1989). Additionally, there is a distinct pressure facet for the fibula-calcaneal ligament on the lateral side of the proximal calcaneo-astragalar facet, a feature absent in hominoids (Strasser 1988). More distally, the middle and distal calcaneo-astragalar facets on the sustentaculum tali are discontinuous and acutely oriented relative to each other. This condition is different from the confluent facets of fossil and extant hominoids (Rose 1986, Strasser 1988). The middle facet is almost flat, with a disto-medial orientation, whereas the distal one is also flat and adjacent to the calcaneocuboid facet (Ford 1988). At the distal end, the calcaneocuboid joint is dorso-plantarly low and relatively flat, with a very shallow medial pit, but not

rounded and deeply concave, as in most hominoids (Rose 1986). These features support the attribution of SIT-1100 to cercopithecids. The overall size of the calcaneus appears larger than that of *M. pentelicus* from Pikerimi, and is more like that of large colobines, such as *Semnopithecus* DESMAREST, 1822 and *Pygathrix* LINNAEUS, 1771. However, as calcaneal features that distinguish between the two subfamilies demonstrate considerable variation, related to both phylogenetic and ecological constraints, it is difficult to classify this calcaneus at a subfamilial level. The calcaneal body is relatively robust and high, and is similar to that of extant colobines, and to a lesser extent to *Mesopithecus*. It is generally straight, a condition more reminiscent of terrestrial cercopithecines (Pina et al. 2011). On the dorsal surface of the calcaneal body lies the proximal calcaneo-astragalar facet. In SIT-1100, the facet is quite low, relatively narrow (like in *Erythrocebus* SCHREBER, 1775 and *Semnopithecus*), comparatively short, and tilts disto-medially, similar to that of *Papio* and *Erythrocebus*. It is generally reminiscent of the morphology of semi-terrestrial and terrestrial cercopithecines. Finally, on the dorso-lateral side of the facet, the pressure facet is smooth and short, but relatively wide. This condition is more similar to that of more terrestrial cercopithecids. The proximal region of the calcaneus is relatively high and curves medially, and its relative size seems intermediate between *Papio*, *Erythrocebus*, and *Semnopithecus* and the more arboreal colobines (e.g., *Colobus*) and cercopithecines (e.g., *Cercopithecus* LINNAEUS, 1758). On the lateral side near the proximal end of the calcaneus, SIT-1100 possesses a marked relatively deep fossa that accommodates the calcaneofibular ligament. This condition is similar to that of *Mesopithecus* and the terrestrial cercopithecines, and probably indicates a strong ligament that counteracts lateral tensions and transversely stabilizes the foot. At the proximal end of the calcaneus, the tuber calcanei, where mm. triceps surae insert, is very wide and relatively low. It ends dorsally on a rounded surface and proximally forms an extended, lightly concave surface. This morphology is similar to that of *Mesopithecus* from Pikerimi and that of more terrestrial (e.g., *Erythrocebus*) and semi-terrestrial (e.g., *Chlorocebus* J. E. GRAY, 1870, *Cercocebus* É. GEOFFROY, 1812) cercopithecines. Compared to *Mesopithecus pentelicus* from Kryopigi, the SIT-1100 calcaneus has a more squarish tuber than that of KRY, which is distinctly smaller in size and has an oval-shaped tuber, in proximal view. In SIT-1100, the distal region of the calcaneus appears relatively long and morphologically reminiscent of the calcanei of semi-terrestrial *Macaca*. On the distal and medial part of the calcaneus, the sustentaculum tali, which accommodates the middle and distal astragalo-calcaneal facets, is relatively short and narrow. The middle facet faces medio-plantarly and is relatively flat and relatively steeply inclined. The distal facet is also steeply set and is relatively flat. The overall morphology is similar to that of most terrestrial and semi-terrestrial cercopithecines (e.g., *Macaca*). The surface between the facets lacks the prominent fossa observed in some calcanei of *Mesopithecus*, indicating a weak astragalar neck ligament (Lewis 1989, Youlatos 1990). On the plantar side of the sustentaculum, the wide and very shallow groove that runs on the latero-plantar side of the calcaneal body suggests a less developed hallucal flexor. On the distal end



Text-fig. 4. *aff. Dolichopithecus sp.*, Milia. Proximal ulna left MIL 1779. a: medial, b: dorsal, c: lateral, d: palmar view. Scale bar 30 mm.

of the calcaneus, the calcaneocuboid facet of SIT-1100 is quite flat and relatively rounded, with a very shallow medial pit. This morphology is similar to that of *Mesopithecus* and terrestrial cercopithecines (e.g., *Papio*, *Theropithecus* I). The facet appears slightly symmetrical, similar to *Papio* and *Semnopithecus*, when compared to the highly asymmetrical facets of more arboreal colobines (e.g., *Pygathrix*). Moreover, on the plantar side of the calcaneocuboid facet, there is a quite well-developed plantar tubercle, similar to that observed in more terrestrial cercopithecines, such as *Papio* and *Theropithecus*. A well-developed tubercle indicates a strong calcaneocuboid ligament that stabilizes the joint (Langdon 1986). Overall, these characters most likely suggest quadrupedal adaptations on more stable, terrestrial substrates.

In Greece, *Mesopithecus delsoni* was established for the first time in Ravin des Zouaves 5, Axios Valley, Macedonia (type locality), of Late Miocene age and biozone MN 11 (Bonis et al. 1990). In addition, probable occurrences *M. cf. delsoni* are reported at Perivolaki (MN 12; Koufos 2006b) and Ravin-X in Axios Valley (MN 11; Koufos 2022d). In the revision, Koufos (2022d) referred to *Mesopithecus sp.* at Nikiti 2 in Chalkidiki (MN 11), and in Perivolaki and Vathylakkos (MN 12). On the other hand, *Mesopithecus pentelicus* is established at Pikermi in biozone MN 12, as well as at Chomateres (Attica), Dytiko 1, 3 (Axios Valley) and Kryopigi (Chalkidiki). Therefore, based on the presence

of this early form of *Mesopithecus* and the rest of the associated fauna, the stratigraphic age of the Thermopigi locality can be estimated between late MN 11 and pre-Pikermian MN 12 biozones.

**Genus *aff. Dolichopithecus* DEPÉRET, 1889**

***aff. Dolichopithecus sp.***

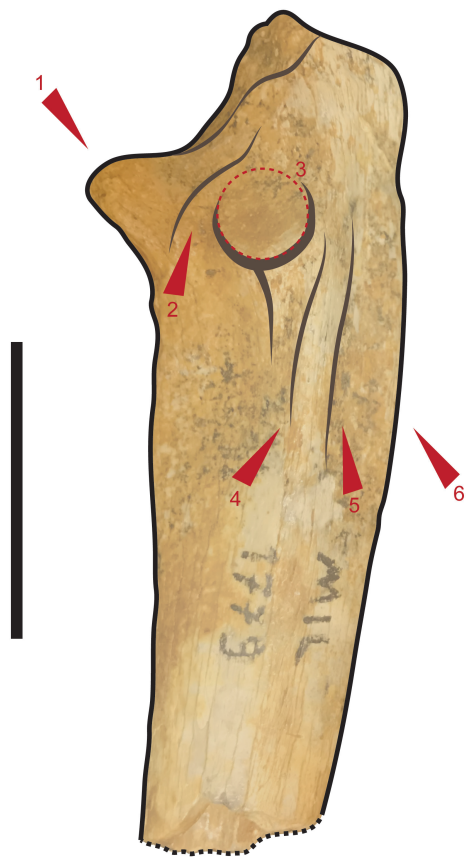
Text-figs 4–6

Locality. Milia.

Material. Ulna proximal left MIL 1779; tibia right MIL 530.

Description. The ulna retains only the proximal end and part of the diaphysis, slightly eroded, probably due to the action of water (Text-figs 4, 5). The olecranon process and about half of the sigmoid notch (*incisura semilunaris*) are missing. The specimen is preserved in good condition and bears well-defined morphological features. The *processus coronoideus* is well-developed and pointed, the radial notch (*incisura radialis*) is well-defined and laterally rounded, followed by intense *crista supinatoria*. The *tuberositas ulnae* is slender, followed by a rather sharp *margo volaris*, and a hollow impression is formed between it and the *crista supinatoria*. In addition, a *foramen nutricium* can be seen near the *margo volaris*, and approximately in the middle of the shaft. On the posterior, the *margo dorsalis* is relatively thick and has a curvature at a height below the sigmoid notch (Tab. 2).





**Text-fig. 5.** Ulna MIL 1779 with arrows 1–6 for comparison and discussion (see text for details). Scale bar 30 mm.

The tibia is almost complete and well preserved. Only the proximal part with the condylia, the eminentia intercondylica and the tuberositas tibiae are missing, whereas the margo infraarticularis is visible (Text-fig. 6e). The diaphysis is rather long and slender. The anterior crista is thick and rounded, whereas linea poplitea is well distinguished up to the foramen nutricium in the upper third of the diaphysis

(Text-fig. 6d, red arrow). The crista interossea is rounded. In the distal part, the sulcus malleoli tibiae is hollow, as well as the incisura fibularis. The malleolus tibiae is well developed with sub-triangular facies articularis malleoli. The facies articularis distalis tibiae is sub-square, whereas the facies articularis malleoli fibulae is semicircular and wide (Text-fig. 6, Tab. 2). Overall, the inferior view shows the articular surface relatively trapezoidal (Text-fig. 6f, red outline).

**Discussion.** The primate from Milia (MIL) is represented only by a few postcranial bones. A comparison of the ulna of Milia aff. *Dolichopithecus* sp. with that of Kryopigi *Mesopithecus*, apart from the dimensions, shows the following morphological characteristics: The coronoid process is more pointed (Text-fig. 5, arrow 1), in the radial notch there is a clear incisura (Text-fig. 5, arrow 2) between its medial and lateral circular-shaped articular facets (Text-fig. 5, arrow 3). The crista supinatoria is more pronounced (Text-fig. 5, arrow 4) and the impression deeper than that of the *Mesopithecus* (Text-fig. 5, arrow 5). The dorsal margin is relatively thick and less flat, bearing curvature (Text-fig. 5, arrow 6).

A specific feature of the ulna is the partial division of the radial incisure in two articular facets, one lateral (corresponding to some degree to the human radial notch) and one anterior, formed on the lateral surface of the coronoid process. The longitudinal ridge, which proximally reaches the lateral facet is strong, the depression posteriorly to it is shallower – not as deep and narrow as in *Paradolichopithecus*. At the same time the depression on the medial surface, posterior to the trochlear incisure is deep, similar to the condition in *Dolichopithecus* DEPÉRET, 1889 (see Delson 1973: fig. 59). The trochlear incisure (trochlear notch) is kidney-shaped, less broad than the one of *Paradolichopithecus*. Under the coronoid process the shaft expands proximally, though not as strongly as it does in *Paradolichopithecus*. The dimensions of the ulna MIL 1779 are relatively small in comparison with *Paradolichopithecus*, and also smaller than those of the known specimens of *Dolichopithecus ruscinensis* DEPÉRET, 1889 (see Szalay and Delson 1979: fig. 212).

**Table 2.** aff. *Dolichopithecus* sp., Milia (MIL). Measurements of ulna and tibia (in mm). (See abbreviations in text.)

Ulna	MIL 1779	<i>Pa. arvernensis</i> Vatera*	Tibia	MIL 530
L preserved	74.5		L preserved	>206.00
DT prox. art.	19.50	21.0/21.4 (prox)	DT prox. at metaphysis	34.47
DAP prox. preserved	27.43	23.1/22.2	DAP prox. at metaphysis	27.38
DT dia	10.10		DT dia	14.15
DAP dia	16.45		DAP dia	19.75
DT dia below art.	14.24		DT distal	25.86
DAP dia below art.	21.95		DAP distal	20.55
Diameter of circular art. for radius	9.30		DT d. art. (cochlea)	20.90
			DAP d. art.	14.05
			DT f. art. dist. ti.	12.32
			DT f. art. mal. fib.	8.58
			I DAP/DT distal	79.46

\*van der Geer and Sondaar 2002



Text-fig. 6. aff. *Dolichopithecus* sp., Milia. Tibia right MIL 530. a: cranial, b: medial, c: caudal, d: lateral, e: proximal, f: distal view. Scale bar 50 mm.





**Text-fig. 7.** *Dolichopithecus balcanicus*, Promachonas (PRC). Teeth. a: m2 left PRC 101. b: m2 right PRC 100. c: p4 PRC left 103. d: i2 right PRC 104. e: m1 frag, left PRC 102. f: m3 frag, left PRC 105. g: p4 frag, right PRC 106. a1, b1, c1, e, f, g – occlusal views; a2, b2, c2, d1 – lingual view; a3, b3, c3, d2 – labial view; d3 – right lateral view. Scale bar 5 mm.

Compared to male wild *Papio cynocephalus* (LINNAEUS, 1766) (RM753, col. National Museum of Natural History, Sofia), the tibia from Milia is visibly shorter, but more robust and with a larger surface of the articular distal end. The distal articular end is wider medio-laterally, displaying a more rectangular shape, but not squarish one, as in *Papio* (Text-fig. 6f). The shaft is slightly more curved in mediolateral view. The medial malleolus is shorter in comparison with *Papio*. In comparison with *Paradolichopithecus*, the lateral surface of the distal articular end in MIL 530 is less square, its malleolus is more ball-shaped, while in *Paradolichopithecus*, it bears a more flattened lateral surface. The bifurcated channel for the flexor muscle (see Sondaar et al. 2006) is barely noticeable,

which may not be solely due to the mentioned bone erosion. These features, apart from showing taxonomic differences with *Paradolichopithecus*, also suggest a weaker terrestriality of the Milia tibia in comparison with *Papio* and *Paradolichopithecus*. Considering the morphology, as well as the dimensions, the geological age and the geographical location, we can assume that both ulna and tibia from Milia may both belong to *Dolichopithecus balcanicus* SPASSOV et GERAADS, 2007, but this determination is for the moment only conjectural.

#### **Genus cf. *Dolichopithecus* DEPÉRET, 1889**

Type species. *Dolichopithecus ruscinensis* DEPÉRET, 1889.

cf. *Dolichopithecus balcanicus* SPASSOV et GERAADS, 2007  
Text-fig. 7

Locality. Promachonas.

Material. i2 right PRC 104, p4 left PRC 103, p4 frag. right PRC 106, m1 ant. frag. left PRC 102, m2 left PRC 101, m2 right PRC 100, m3 frag. left PRC 105. The tooth material is probably from one mandible.

Description. The lower second incisor is well-preserved (Text-fig. 7d, Tab. 3), slightly worn, with about half its single root length. The bicuspid fourth lower premolar PRC 103 (Text-fig. 7c) is complete with two roots: the mesial one is approximately 9 mm long, while the distal one is broken. The PRC 106 fragment (Text-fig. 7g) retains the anterior half of the tooth with the talonid missing. The metaconid and the protolophid are well developed in both teeth (Tab. 3). The lingual cuspid is larger than the labial. The trigonid basin is well distinct and relatively deep, whereas the talonid basin is broad. The first lower molar fragment PRC 102 (Text-fig. 7e) is slightly worn and preserves only the anterior lobe with well-developed metaconid (Tab. 3). The second lower molars PRC 101 (Text-fig. 7a) and PRC 100 (Text-fig. 7b) are bilophodont and slightly worn. The metaconid is distinctively higher than the hypoconid (Tab. 3). The hypo-, para- and metacristae are intense. There is an anterior cingulum. The former also preserves both roots, whereas the latter is about half length of the two roots. The transverse crests are well developed. The third lower molar fragment PRC 105 preserves only the talonid (Bm3 tl<sup>d</sup> = 4.83 mm) with the well-developed hypoconulid (H = 4.5 mm) (Text-fig. 7f), half hypoconid and the well-developed entoconid (H = 5.9 mm). According to the description above, the teeth could belong to the same individual, therefore the MNI seems to be 1.

Discussion. The primate material from Promachonas (PRC) consists of isolated, complete, or partial teeth. In the broader area of Serres, in Maramena of biozone MN 13/14, south of PRC, the cercopithecoid *Mesopithecus pentelicus* was initially identified through teeth (Küllmer and Doukas 1995), which was later attributed to *Mesopithecus* sp. (Koufos 2009b). There is a marked difference in the heights of the labial and lingual cuspids of the lower molars between *Mesopithecus* (KRY) and *Dolichopithecus* (Megalo Emvolo MEV and PRC), with the lingual being more pointed and higher than the buccal in the latter specimens. The most significant remains of the PRC monkey are the two second lower molars. Their proportions are typical of lower molars. They are slightly larger than those of *Mesopithecus delsoni* from Hadjidimovo (late MN 11), Bulgaria (Bogdanova et al. 2023); even one of the three male individuals from Hadjidimovo sample practically reaches their size (see Koufos et al. 2003). At the same time, the cuspids of the PRC specimen seem to be more similar to those of *Dolichopithecus*: more pointed (higher and mesio-distally narrower) than those of *Mesopithecus*, and their notches are deeper. In terms of size, they differ slightly from the m2 of the type specimen of *Dolichopithecus balcanicus* from Tenevo. The cuspids of the m2 from PRC do not appear to be as elongated as in the latter specimen, but this is possibly due to some extent to the greater individual age of the

Table 3. *Dolichopithecus balcanicus*, Promachonas (PRC). Measurements of teeth (in mm) (See abbreviations in text.) *Dolichopithecus* specimens used for comparison: PGU – Priozerne, Per – Perpignan, TEN/DOR – Tenevo/Dorkovo, MEV – Megalo Emvolo, D.r. – *D. rusciniensis*, D.b. – *D. balcanicus*.

Lower teeth	PRC 104		PRC 103		PRC 106		PRC 102		PRC 101		PRC 100		D. sp. PGU*		D. sp. PGU*	
	i2	i2	p4	p4	p4	p4	m1	m1	m1	m1	m2	m2	m1	m1	m2	m2
L	3.50	2.20	–	–	7.61	8.4	(9.20)	10.50	9.32	8.70	9.40	9.40	12.50	9.80	10.35	9.50
B	4.87	4.30	7.34	5.41	5.51	5.9		7.00/7.20	7.13	7.30	7.86	7.80	8.20/8.00	7.90	7.81	7.80
B ant							6.60		6.75	7.00	7.90	7.80			7.71	
B post									7.08	7.30/6.80	7.50	7.40		8.00	7.85	
H me <sup>d</sup>			5.15	5.14	5.83				5.85		6.39	5.93			6.96	
H hy <sup>d</sup>									5.60		5.61	5.33			7.08	
I B/L			73.00	–	72.40	70.00	71.00	68.00	76.50	84.00	84.00	86.00	64.00	81.00	74.50	

\*Mashchenko and Marareskul 2011, \*\*Koufos et al. 1991, \*\*\*Spassov and Geraads 2007



individual. The PRC teeth are slightly smaller and shorter than those of MEV, whose cuspids are also more pointed. Compared to the tooth dimensions of *Dolichopithecus* from the Pliocene of Pridnestrovie (Mashchenko and Marareskul 2011), Megalo Emvolo (Koufos et al. 1991) and Tenevo, as well as to the morphology of the Tenevo *Dolichopithecus* (Spassov and Geraads 2007), the PRC is tentatively attributed to *D. balcanicus* from the Latest Pliocene of Bulgaria, which is distinguished from the common European species, *D. ruscinensis* by its smaller size, much shallower mandibular corpus and marked congestion of the premolars (Spassov and Geraads 2007).

In Greece, Pliocene cercopithecids are mainly reported from cranial material of the middle Villafranchian, biozone MN 17, from Vatera, Lesvos Island [*Paradolichopithecus arvernensis* (DÉPÉRET, 1929)] (De Vos et al. 2002, van der Geer and Sondaar 2002, Lyras and van der Geer 2007), Karnezeika, Peloponnese (cf. *Paradolichopithecus* sp.) (Sianis et al. 2022), and Dafnero, Kozani (*P. aff. arvernensis*) (Kostopoulos et al. 2018). Earlier cercopithecids are reported from the Ruscinian biozone MN 14–15 in the Ptolemais basin (*Dolichopithecus ruscinensis*) (Doukas and De Bruijn 2002) and Megalo Emvolo (Koufos et al. 1991), the latter tentatively included in *D. balcanicus* (Spassov and Geraads 2007). The find from Promachonas represents possibly the same geologically younger Balkan *Dolichopithecus* species, which is distinguished from the common European species, *D. ruscinensis* by its smaller size, much shallower mandibular corpus and congestion of the premolars (Spassov and Geraads 2007).

**Order Carnivora BOWDICH, 1821**

**Suborder Feliformia KRETZOI, 1945**

**Family Hyaenidae GRAY, 1821**

**Subfamily Hyaeninae GRAY, 1821**

**Genus *Adcrocuta* KRETZOI, 1938**

***Adcrocuta eximia* (ROTH et WAGNER, 1854)**

Text-figs 8, 9

**Material. Thermopigi:** Skull with P2–M1 left SIT 1421; 2P2 right SIT 531 and left 940, P3 left SIT 1057, mandible with p2–m1 fr. left SIT 713+714; m1 right SIT 529, anterior pa<sup>d</sup>, d4 fr right SIT 1280, p3 right SIT 530; coprolite SIT 1359.

**Platania:** A maxilla with the right and left P2–P4, PLD 464.

**Description. Thermopigi:** The corroded skull SIT 1421 bears the very poorly preserved left tooth row P2–P4 and M1, nasals, nasal cavity, infra-orbital foramina, frontal with the orbital cavities and ecto-orbitals, post-orbital constriction to the parietals, most of the left zygomatic arch, and a palate showing a deep depression below the metastyle of the left P4, in front of the molar, followed by the choanae (Text-fig. 8a1–3). The toothrow is damaged (Text-fig. 8a4); only traces remain that allow us to make a few measurements (Tab. 4). There are traces of the mesial accessory cusp of the P2 and P3, and the metastyle of the upper carnassial. The worn and slender M1 rotates 90 degrees inwards; paracone, metacone and protocone are barely distinguishable. There is palatal asymmetry, on the right side of the maxilla, where

paleopathological evidence indicates a type of exostosis bearing the roots of P2 and P3.

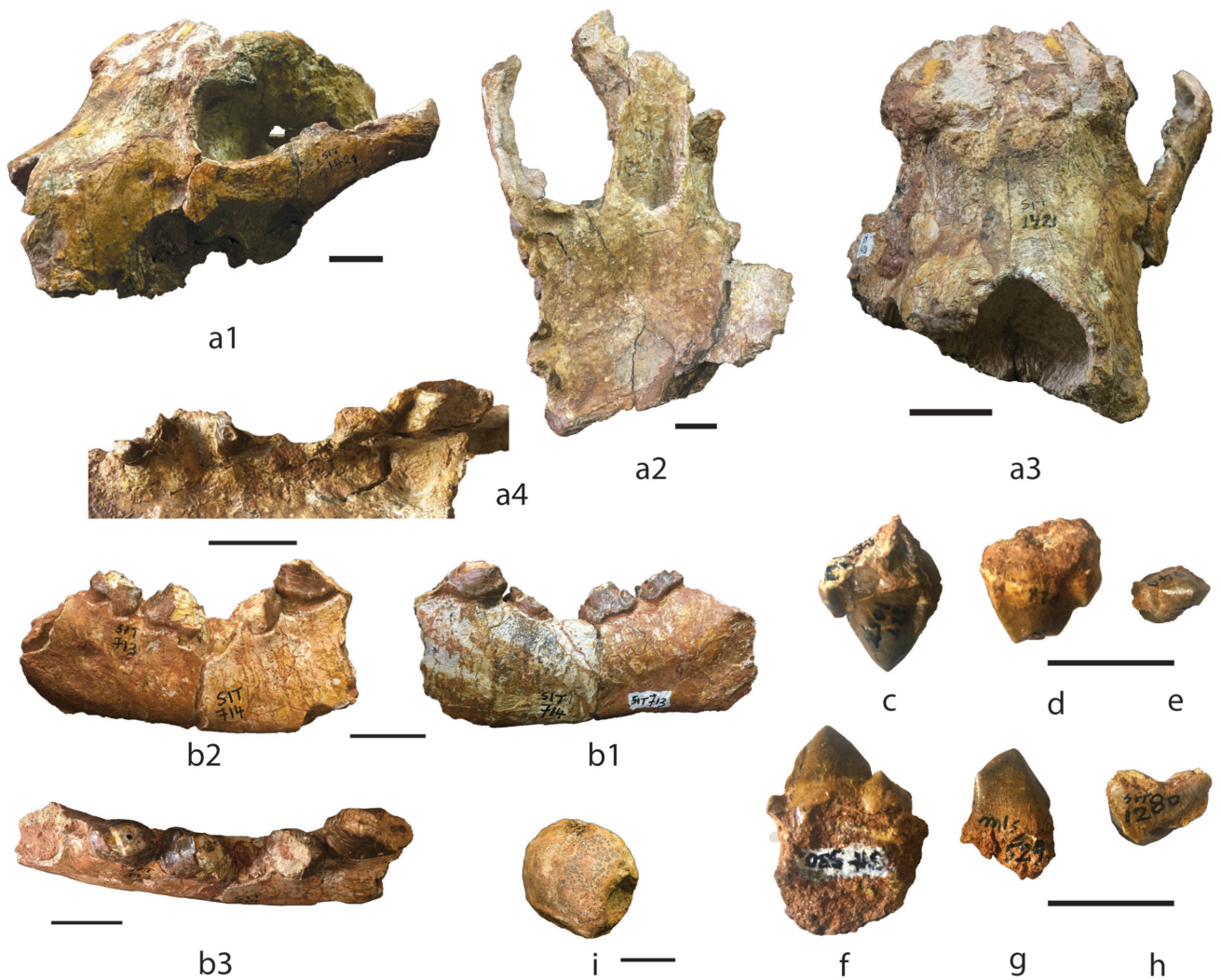
Of the two isolated P2s, SIT 940 retains only the upper part of the unworn crown, the pointed tip and the two well-defined crests (Text-fig. 8e). The preserved dimensions are: length 12 mm, breadth 8 mm. The P2 SIT 531 is almost complete and only a little worn (Text-fig. 8d). Two sharp anterior and posterior crests extend from the tip of the tooth, the latter meeting the well-distinct posterior accessory cusp (Tab. 4). The P3 SIT 1057 is almost complete, missing only the mesial part with the accessory cusp (Text-fig. 8c). The main cusp is unworn and strong with two sharp crests extending from the tip anterior and posterior of the tooth. The latter terminates in the well-developed posterior accessory cusp; dimensions in Tab. 4.

The left mandible SIT 713+714 preserves the corpus with p2–m1 (Text-fig. 8b1–3). The slightly worn tooth row consists of the complete p2, p3, the talonid of the damaged p4, and the mesial half of the lower carnassial. The alveolus of the single root p1 is also preserved (Depth = 4.45 mm), as well as parts of the symphysis. The corpus is relatively high and straight at its preserved inferior border. There are two mental foramina below p2: the larger below the middle and the smaller below the posterior border of the tooth. The p2 is short but robust, with a small anterior and a larger posterior accessory cuspid. There is a lingual cingulum. The larger p3 bears a strong anterior and a posterior accessory cuspids on the mesio- and distolingual sides of the tooth. There is a faint buccal cingulum. The p4 is damaged, and only the well-developed distal accessory cuspid is preserved on a large, raised base of the distal cingulum around the distal area of the tooth. The mesial part of the lower carnassial is preserved with a mesial cingulum at the crown base, whereas only the root of the distal part of the tooth remains. Dimensions of the mandible and teeth are in Table 4.

From the lower deciduous carnassial d4 SIT 1280, only part of the blade is preserved (Text-fig. 8h). It is slightly worn. The paraconid and protoconid form an angle of 115° at 13 mm between their peaks. The preserved dimensions are a length of 15.73 mm and breadth of 6.0 mm. The near-complete p3 SIT 530 is well-preserved and unworn. The protoconid is relatively high and the distal crest is sharp. The mesiolingual accessory cuspid is weak, while the distolingual one is larger (Text-fig. 8f). Dimensions are in Tab. 4. From the carnassial SIT 529, a half-fragment bears the unworn paraconid of a juvenile. The mesiolingual crest is strong. The preserved dimensions are a length of 13.10 mm and breadth of 10.05 mm (Text-fig. 8g).

The well-preserved coprolite SIT 1359 shows a typical constriction at one third of its total length and a shallow depression at one of its ends (Text-fig. 8i). Dimensions are length 47.31 mm, breadth 37.08 mm and height 24.49 mm.

**Platania:** Maxilla PLD 464 preserves both right and left tooth rows with P2–P4, nasal cavity and the left infraorbital foramen (ca. 6.5 mm) above and medial to the P3 roots (Text-fig. 9a–c). Both tooth rows are well-preserved; only the protocone of the right carnassial is missing. The high-crowned tooth rows are slightly worn and with lingual cingula. P2 is oval shaped with a palatal cingulum, with sharp anterior and posterior crests, a vestigial anterior and a small posterior accessory cusp. P3 is large, with sharp



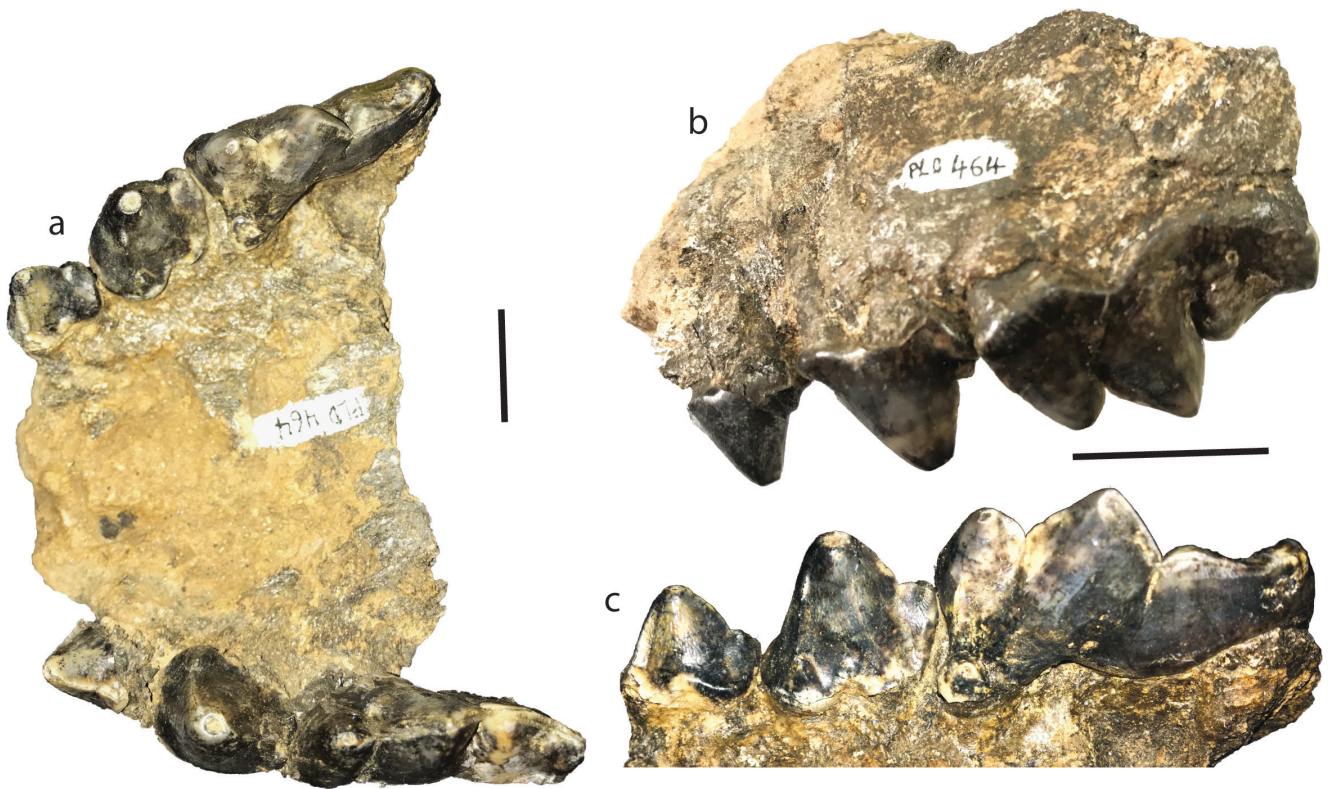
**Text-fig. 8.** *Adcrocuta eximia*, Thermopigi. a: Skull SIT 1421; a1: left lateral, a2: ventral, a3: frontal, a4: detail occlusal view. b: Left mandible with p2–m1 SIT 713+714; b1: lingual, b2: buccal, b3: occlusal. c–e: Upper teeth; c: P3 left SIT 1057, d: P2 right SIT 531, e: Tip 940 left. f–h: Lower teeth; f: p3 right SIT 530, g: m1 right SIT 529; anterior pa<sup>d</sup>, h: d4 frag. right SIT 1280; c–g – lingual, h – buccal view. i: coprolite SIT 1359. Scale bars 20 mm.

mesiopalatal and distal crests, a small anterior and a larger posterior accessory cusp. The anterior part of the tooth is broader than the posterior. The upper carnassial is large, long, and robust. The parastyle is well-developed, the paracone high and the metastyle forms a long blade. The protocone is relatively weak, confined to the base of the tooth, posteriorly to the anterior border of the parastyle, typical for *Adcrocuta* (dimensions in Tab. 4).

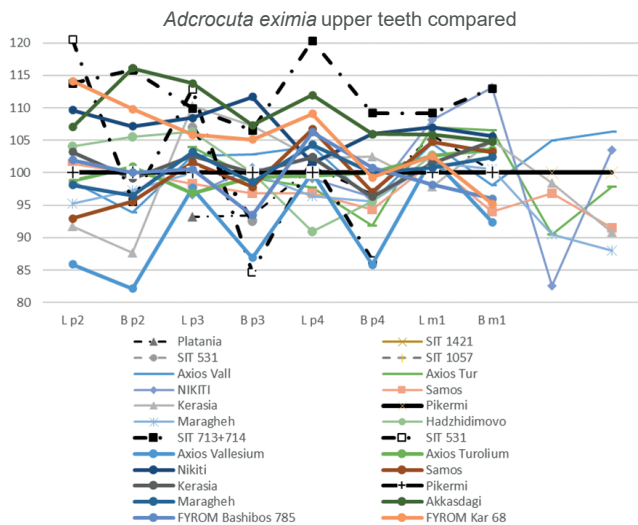
**Discussion.** The PLD maxilla is described and discussed here to compare the two richest Turolian mammal sites, located close to each other in eastern Macedonia: Thermopigi and Platania. Thermopigi *Adcrocuta* (SIT) appears less robust than Platania (PLD) hyena. They generally fall within the variation between Axios Vallesian and Axios Turolian (Text-figs 10, 11). When comparing SIT and PLD maxillae, it should be noted that (a) longer tooth row (even damaged) P2–P4 and carnassials in SIT than in PLD, (b) index B/LX100 for P2: SIT = 56.16, PLD = 71.10, (c) P3 higher but slenderer in SIT than in PLD and the B/HX100 index: SIT = 71.35, PLD = 84.53.

The morphology of the Platania P2–3 (relatively narrow, with a strong mesial additional cusp and a strong lingual cingulum) indicates an earlier geological age of the *Adcrocuta* from Platania, and places it apparently in the pre-middle Turolian stage of premolar evolution of this hyena, close to some other Balkan samples from the Vallesian/Turolian boundary (Spasov et al. 2018, 2019). This morphology seems to support the above-assumed biochronological position of the locality. Also, it is noteworthy to compare these two faunal associations of Thermopigi and Platania with *Adcrocuta*, as already discussed in earlier publications on rhinoceroses (Tsoukala 2018), proboscideans (Konidaris and Tsoukala 2020), bovids (Vasileiadis et al. 2019), turtles (Vlachos and Tsoukala 2014) and the paleoenvironment. The bite marks of *Adcrocuta* appear comparatively more often in the bone-remains of Platania than in those of Thermopigi. Especially in hipparions, young rhinos and bovids, there is a common presence of bitten and broken bones, presumably making it a feeding site for this top carnivorous scavenger.



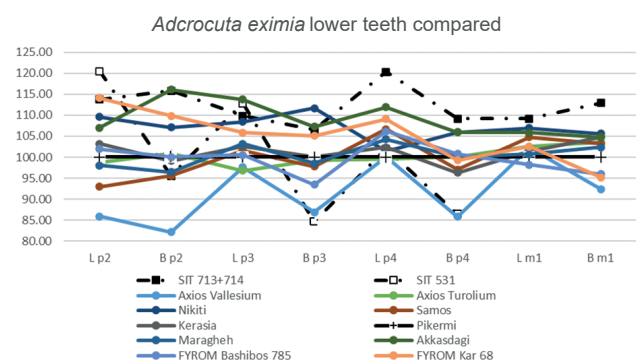


Text-fig. 9. *Adcrocuta eximia*, Platania. Maxilla PLD 464 with right and left tooth rows P2–P4. a: occlusal, b: left buccal, c: left palatal view. Scale bars 20 mm.



Text-fig. 10. *Adcrocuta eximia*: Comparative diagram of upper teeth from various sites in Greece and other well-known sites (Roussiakis 2002, Koufos 2016).

In Greece, *Adcrocuta eximia* is widespread and known from at least 20 sites dating from the late Vallesian to the late Turolian (Koufos 2022b). The dental dimensions are close to those of *Adcrocuta eximia* from sites of Northern Greece, such as Axios Valley (late Vallesian, MN 10), Nikiti (early Turolian, MN 11) (Koufos 2000, 2012, 2016) and Kryopigi Kassandra (MN 12/MN 13) (Lazaridis 2015). It must be noted that the upper carnassials are more robust in the SIT and PLD specimens than those of the other sites (Text-figs 10, 11).



Text-fig. 11. *Adcrocuta eximia*: Comparative diagram of lower teeth from various sites in Greece and other well-known sites (Roussiakis 2002, Koufos 2016).

Family Felidae FISCHER [DE WALDHEIM], 1817  
Subfamily Machairodontinae GILL, 1872

Genus *Paramachaerodus* PILGRIM, 1913

*Paramachaerodus* sp. (?*P. schlosseri* (WEITHOFER, 1888))

Text-figs 12a, b, 13

Locality. Thermopigi.

Material. Upper canine right SIT 712, humerus left SIT 711.

Description. The upper canine is almost complete and well preserved. Only the tip of the crown is missing. The canine is long and straight, generally flattened, and slender, with two sharp mesial and distal longitudinal crests,

**Table 4.** *Adcrocuta eximia*, Thermopigi (SIT), Platania (PLD). Measurements of cranium, maxilla, mandible and teeth. (See abbreviations in text.)

Cranium and teeth	SIT 1421	SIT 531	SIT 1057	PLD 464 sin	Mandible	SIT 713+714	SIT530
L P2–P4	85.80			75.18	L p2–m1	89.90	
L P2	18.00	17.93		16.30	L p2	17.75	
B P2	–	10.07		11.59	B p2	12.97	
H P2 lab	–			14.46	L p3	20.77	21.33
L P3	–		>19.00	22.20	B p3	14.59	11.59
B P3	–		13.70	15.47	L p4	25.00	
H P3 lab	–		19.20	18.30	B p4	14.63	
L P4	41.40			39.14	L m1	28.80	
B P4	–			18.37	B m1	14.12	
L P4 tr				23.94	H md p2 ant	44.85	
L P4 tl (mts)				15.48	H md p2/p3	42.44	
B P4 tl	–			11.94	H md at p3 mid.	35.66	
H P4 lab	–			22.98	H md at p4 mid.	38.43	
LM1	6.05			–	H md p3/p4	38.16	
BM1	15.40			–	H md p4/m1	43.87	
DT mx at P2-P2 lab				67.65	Thickness p2 ant	18.62	
DT mx at P2-P2 palat				44.11	Thickness p4 ant		
DT mx at P3-P3 lab				88.76		17.70	
DT mx at P3-P3 palat				56.36			
DT mx at P4-P4 lab pas	110.00			95.27			
DT mx at P4-P4 post palat				97.10			
L Nasion-Rhinion	64.00						
L Staphylion-Synsphenion	50.00						
DT between orbits min	75.30			–			
DT orbits lowermost	91.00			(72.27)			
DT Ecto-orbital-Ecto-orbital	91.42						
DT min cranium	56.49						
DT Zygion-Zygion	(174.00)						

and no sign of crenulation. The lingual side is flatter than the buccal side, which is more rounded. The root is well developed, almost half the height of the tooth (Text-fig. 12b); dimensions in Table 5.

The humerus retains the distal epiphysis, with the greater part of diaphysis slender and relatively straight; it is well preserved. The fossa olecrani is deep, with a heavy epicondylus medialis, weak epicondylus lateralis, rather short trochlea with a shallow fossa radialis and coronoidea, but a strong capitulum humeri. The foramen supracondylaris is large, with a high (proximal) position, and its external wall bends slightly forward; dimensions in Table 5.

**Discussion.** The dimensions of the upper canine SIT 712 fall well within the size range of *Paramachaerodus*

(Text-fig. 13), but the lack of serration makes it necessary to discuss this specimen further. There are several possible sabre-toothed cats to consider. Firstly, the genus *Yoshi* SPASSOV et GERAADS, 2014, then *Metailurus* ZDANSKY, 1924, *Paramachaerodus* PILGRIM, 1913 and *Pontosmilus* KRETZOI, 1929. Three of these four genera have canines without serration: *Yoshi*, *Paramachaerodus*, and *Metailurus*, so *Pontosmilus* can be excluded, according to Jiangzuo et al. (2022). These authors resurrect the species *Paramachaerodus schlosseri* (WEITHOFER, 1888), originally described from Pikermi, accept *Pa. ogygia* KAUP, 1833 and *Pa. transasiaticus* LI et SPASSOV, 2017 and added a new species, *Pa. yingliangi* JIANGZOU et al., 2022. They exclude the species *orientalis* KITTL, 1887 and *maximiliani* ZDANSKY,





**Text-fig. 12.** Felids, Thermopigi. a, b: *Paramachaerodus* sp. (?*P. schlosseri*). a: Humerus left SIT 711; a1 cranial, a2: palmar view. b: Upper canine right SIT 712; b1: buccal, b2: lingual view. c–e: *Pristifelis attica*. c. Radius distal right SIT 1492; c1: palmar, c2: dorsal, c3: lateral view. d. Ulna proximal right SIT 1493; d1: medial, d2: dorsal, d3: caudal view. e: Metapodial distal SIT 710, dorsal view. Scale bars 25 mm (a–d), 20 mm (e).

1924 from *Paramachaerodus*, and place them in the Asian genus *Pontosmilus*, as Kretzoi previously did. Jiangzuo et al. (2022) describe the main differences between the two genera as the presence of serrations on canines and cheek teeth, the distinct P4 preparastyle in *Pontosmilus* and the absence of these features in *Paramachaerodus*. They question the presence of *Metailurus* in Europe, and assume only an Asian distribution for this genus. We adopt the taxonomic decision

proposed by Jiangzuo et al. (2022), albeit with caution, and we believe that further studies are needed to clarify these taxonomic questions. Previously described early and middle Turolian *Paramachaerodus* material from Bulgaria and North Macedonia does not fit into this taxonomic scheme, as the canines and the cheek teeth are serrated and a minute preparastyle is observed in some of them (Kiro Kuchuk locality; Li and Spassov 2017, Spassov et al. 2018, 2019).

Table 5. Felids, Thermopigi (SIT). Comparative measurements of canines and humeri (in mm). (See abbreviations in text.)

Canine	<i>Paramachaerodus</i> sp. ( <i>?P. schlosseri</i> )		<i>Pa. orientalis</i>		<i>Yoshi cf. minor</i>		<i>Yoshi garevskii</i>		<i>Paramachaerodus</i> sp. ( <i>?P. schlosseri</i> )		<i>Pa. orientalis</i>	
	SIT 712	Puente Minero* MN 11 PM575	Maragheh* MN 12	Bataillones*	Kalimantani** Bulgaria	Karaslari** N. Macedonia	SIT 711	Pikermi*** NHML				
L C	15.44	16.71	17.00	15.20	10.40	13.20	59.34	59.10	DT distal			
B C	9.56	8.06	9.60	9.00	7.10	8.90	30.00		DAP distal			
H C	85.60						38.35		DT distal art.		39.80	
H crown	37.50				25.00	22.00	21.68		H trochlea lat			
I (B/L)*100	61.92				68.26	67.42	27.92		H trochlea med			
							18.48		H trochlea min			
							9.00		D max foram supracond.			
							8.67		DAP bone f.s.			
							20.38		DT fossa olecrani			
							18.33		DT dia			
							25.50		DAP dia			
							20.00		DAP dia min			

\*Salesa et al. 2010, \*\*Spassov and Geraads 2014, \*\*\*Roussiakis et al. 2006

Possessing only one upper canine from Thermopigi, it is difficult to judge whether the specimen belongs to *Pa. schlosseri* (if we accept the generic separation from *Po. orientalis*) or to *Pa. transasiaticus*, taking into account the aforementioned taxonomic issues: from a biochronological point of view, the assignment to *Pa. transasiaticus* seems logical. In this case, the “missing” serrations in SIT 712 could be due to a higher age of the individual or could be caused by mechanical abrasion in the taphonomic context. At this stage, we include the material from Thermopigi tentatively to *Paramachaerodus* sp. (*?P. schlosseri*), based on the lack of serration, albeit only provisionally. The size of the canine is too large to be attributed to *Yoshi* (Tab. 5).

In Greece, humeral dimensions match well with the Pikermi specimen (NHML M8960) attributed to *Paramachaerodus orientalis* PILGRIM, 1931 (MN 12) (Roussiakis et al. 2006) [= *P. schlosseri* sensu Jiangzuo et al. (2022)], also reported in Nea Silata in Chalkidiki (MN 13/ MN 14) (Koufos 2022a).

**C o m m e n t .** For explanation of the use of the spelling of the genus as *Paramachaerodus* rather than *Paramachairodus* (with an “i”) also used by Zdansky (1924), see Salesa et al. (2010).

#### Subfamily Felinae FISCHER [DE WALDHEIM], 1817

#### Genus *Pristifelis* SALESA, ANTÓN, MORALES et PEIGNÉ, 2012

#### *Pristifelis attica* (WAGNER, 1857)

Text-fig. 12c–e

**L o c a l i t y .** Thermopigi.

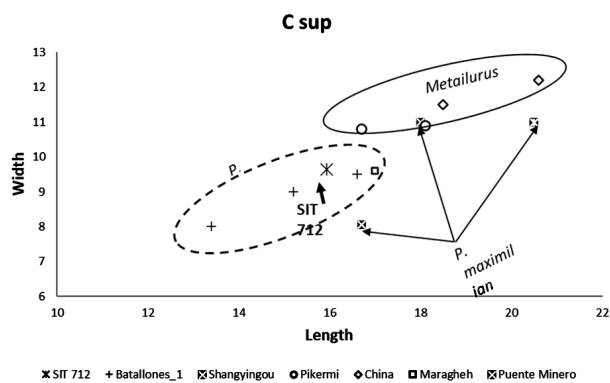
**M a t e r i a l .** Radius distal right SIT 1492; ulna proximal right SIT 1493, distal metapodial SIT 710.

**D e s c r i p t i o n .** The radius retains the distal epiphysis, with most of the diaphysis slender, dorso-palmarly compressed, with a gentle curvature (Text-fig. 12c1–3). The preserved length is 68 mm (dimensions in Tab. 6). The distal epiphysis is well-developed mediolaterally. The processus styloideus is intense, and the well-developed incisura ulnaris oval and prominent. The distal articular surface for the scapholunar is concave, with a latero-medially elongated oval shape.

The ulna preserves the proximal part, markedly latero-medially flattened, with most of the diaphysis being slender and almost straight, showing only a gentle curvature (Text-fig. 12d1–3). The preserved length is 87 mm (dimensions in Tab. 6). The olecranon is well-developed and high. Its proximal border is roughly horizontal, and continues medially to show a ridge along its caudal margin. The articulation for the radius is small and oval. The incisura semilunaris and the beak (processus anconaeus = foremost part of the olecranon) are well-developed. The dimensions, color and condition of the fossil indicate probably the right limb of the same individual.

The metapodial preserves the distal trochlea, with the medial crest running posteriorly (Text-fig. 12e). Dimensions are DT distal 9.20 mm, DT dist. art. 8.10 mm, DAP distal 8.20 mm. The diaphysis is rounded, with a diameter of 6.26 mm.





**Text-fig. 13.** Scatter diagram of upper canine of metailurine species from various sites: *Yoshi* (Spasov and Geraads 2014), *Paramachaerodus*: Batallones (Salesa et al. 2010), Maragheh, Puente Minero, Shangyingou (Salesa et al. 2010), *Metailurus* (Roussiakis 2002).

**D i s c u s s i o n .** Small felid postcranial remains are rarely described in contrast with cranial remains, so comparison and discussion are limited. Few dimensions show similarity with *P. attica* from Pikermi (Roussiakis 2002; Tab. 5). The type species of the genus *Pristifelis* is *Felis attica* WAGNER, 1857. The genus *Pristifelis*, termed “primitive *Felis*”, was established in by Salesa et al. (2012), with the oldest occurrence 11.6 Ma and the youngest 7.25 Ma, restricting the genus *Felis* to more recent taxa. In Greece, *Pristifelis attica* has been reported from Pikermi (MN 11/12, type locality of type species) (Roussiakis 2002), from locality A and some unknown locality(-ies) of Samos Island of MN 12–13 (Solounias 1981, Koufos 2022a). Arambourg and Piveteau (1929) initially reported *Felis* sp. from Vathylakkos 3, Axios Valley, of MN 11/12 (Koufos 2000), which was later determined as *Pristifelis attica* by Salesa et al. (2012).

**Subfamily indet.**

**Genus ?*Megantereon* CROIZET et JOBERT, 1828  
or *Puma* JARDINE, 1834**

Text-fig. 14

Locality. Milia.

Material. Tibia distal left MIL 974.

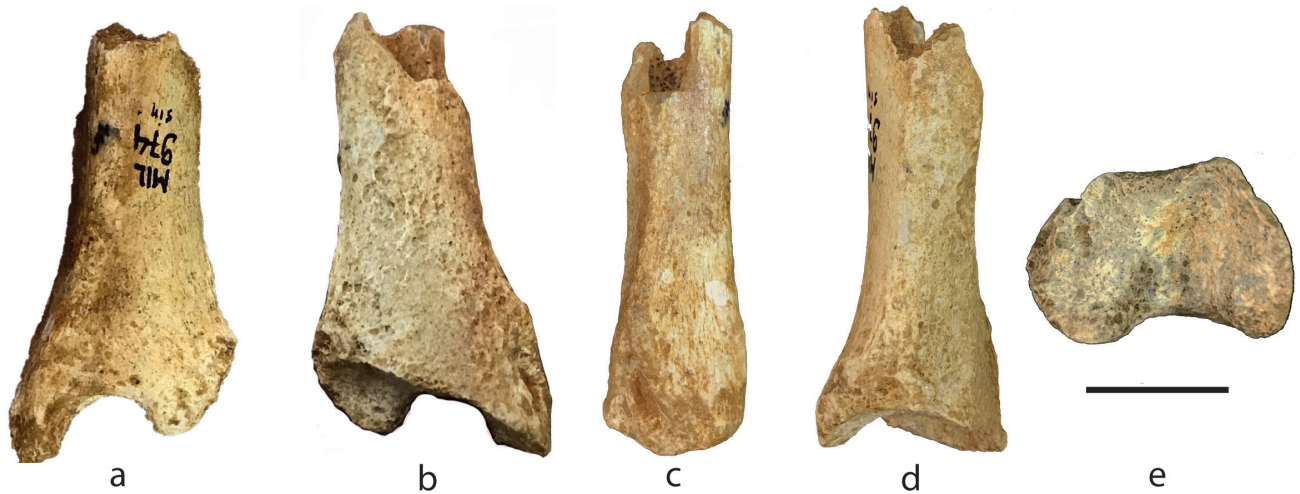
**D e s c r i p t i o n .** The distal part with the cochlea is well preserved, whereas stigmata on the bone are indicative of weathering, rolling or transport. The diaphysis appears to be straight and stout. The anterior crista is pronounced towards the tibial malleolus, while the sulcus malleoli tibiae and incisura fibularis are well marked. The malleolus tibiae is well developed and broad (Text-fig. 14, Tab. 7).

**D i s c u s s i o n .** This distal tibia represents a felid. This specimen is smaller than that of the scimitar-toothed cat *Homotherium* FABRINI, 1890, which is one of the three carnivores from the MN 16a mammalian assemblage of Milia (*H. crenatidens* (WEITHOFER, 1889), *Ursus etruscus* CUVIER, 1823, and *Agriotherium* sp.; Tsoukala et al. 2014). In addition, its intermalleolar notch is deeper than that of *Homotherium* (Ballesio 1963). The other scimitar-toothed cats, present during the Late Pliocene, are *Dinofelis* ZDANSKY, 1924 and *Megantereon*. In *Dinofelis*, the medial side is more concave than in the Milia tibia, because the medial malleolus is medially more prominent, and the line passing through the base of the medial malleolus and the lowest point of the central malleolus is less oblique (Werdelin and Lewis 2001: fig. 21). Concerning *Megantereon cultridens* (CUVIER, 1824), the distal articulation shows some similarities, but the distal width is greater than that in the Milia specimen (Christiansen and Adolfsen 2007). The Villafranchian *Acinonyx pardinensis* (CROIZET et JOBERT, 1828) has a shorter central malleolus and an intermalleolar notch less deep with, in cranial view, the inflection point of the notch’s curve in a more medial position (Hemmer 2001: pl. 137). The Milia tibia could belong to a felid with a size close to that of *Puma pardoides* (OWEN, 1846). This species could be a good candidate. The dimensions are of the same order as the individuals from La Puebla del Valverde (Madurell-Malapeira et al. 2010) and Untermassfeld (Hemmer et al. 2004), two localities that are more recent than Milia (Tab. 6). However, their morphology is not exactly the same: cranially, the inflection point of the intermalleolar notch’s curve has a rather more medial position than in Milia, and it is similar to the current *P. concolor* (LINNAEUS, 1771). The cochlear grooves of the Milia tibia are more asymmetric. Consequently, the attribution of the Milia tibia is under question. We are sure that it cannot belong to a *Homotherium*, *Dinofelis*, or a cheetah.

**Table 6.** *Pristifelis attica*, Thermopigi (SIT). Comparative measurements of postcranial bones (in mm). (See abbreviations in text.)

Radius	SIT 1492	Pikermi* AMPG PA 3551/91	Ulna	SIT 1493
DT distal	19.21	16.30	DT articulation	10.22
DAP distal	11.06	10.10	DAP proximal	16.53
DT dist. art.	14.56		H olecranon (beak-tuber olecrani)	20.20
DAP dist. art.	8.59		H incisura semilunaris (i.s.)	13.40
DT dia	11.82		DT dia below i.s.	8.13
DAP dia at DT	6.44		DAP dia at DT	15.48
			DT dia min	5.48
			DAP dia min	11.75

\*Roussiakis 2002



**Text-fig. 14.** Felid (?*Megantereon* or *Puma*), Milia. Distal tibia left MIL 974. a: cranial, b: caudal, c: medial, d: lateral, e: distal view. Scale bar 20 mm.

This single and incomplete specimen does not provide enough material to conclude with certainty that it belongs to a *Megantereon* female (the Senèze skeleton analysed by Christiansen and Adolfssen (2007) is undeniably a male) or a new species of *Puma*. In any case, regardless of the genus, this would most likely represent the oldest record in Eurasia: previously, the first appearance of *Megantereon* dated from the early Villafranchian (middle Pliocene; Berta and Galiano 1983) (first known in Europe probably in Les Étouaires; see Hemmer and Kahlke 2022), and that of *Puma* is at ca. 3.1 Ma in Asia (Mongolia) and around 2.8 Ma in Europe, i.e., MN 16b (also the French locality of Les Étouaires; Hemmer et al. 2004, Nomade et al. 2014). For the time being, it is more reasonable to leave the nomenclature open.

**Suborder Caniformia KRETZOI, 1943**

**Superfamily Musteloidea FISCHER [DE WALDHEIM], 1817**

**Family Mustelidae FISCHER [DE WALDHEIM], 1817**

**Subfamily Guloninae GRAY, 1825**

**Genus *Plesiogulo* ZDANSKY, 1934**

***Plesiogulo crassa* TEILHARD DE CHARDIN in TEILHARD**

**DE CHARDIN et LEROY, 1945**

Text-figs 15, 16

Locality. Thermopigi.

**Material.** Cranium with right I1–I3, C and left, P1, P2, P3, P4 SIT 1494.

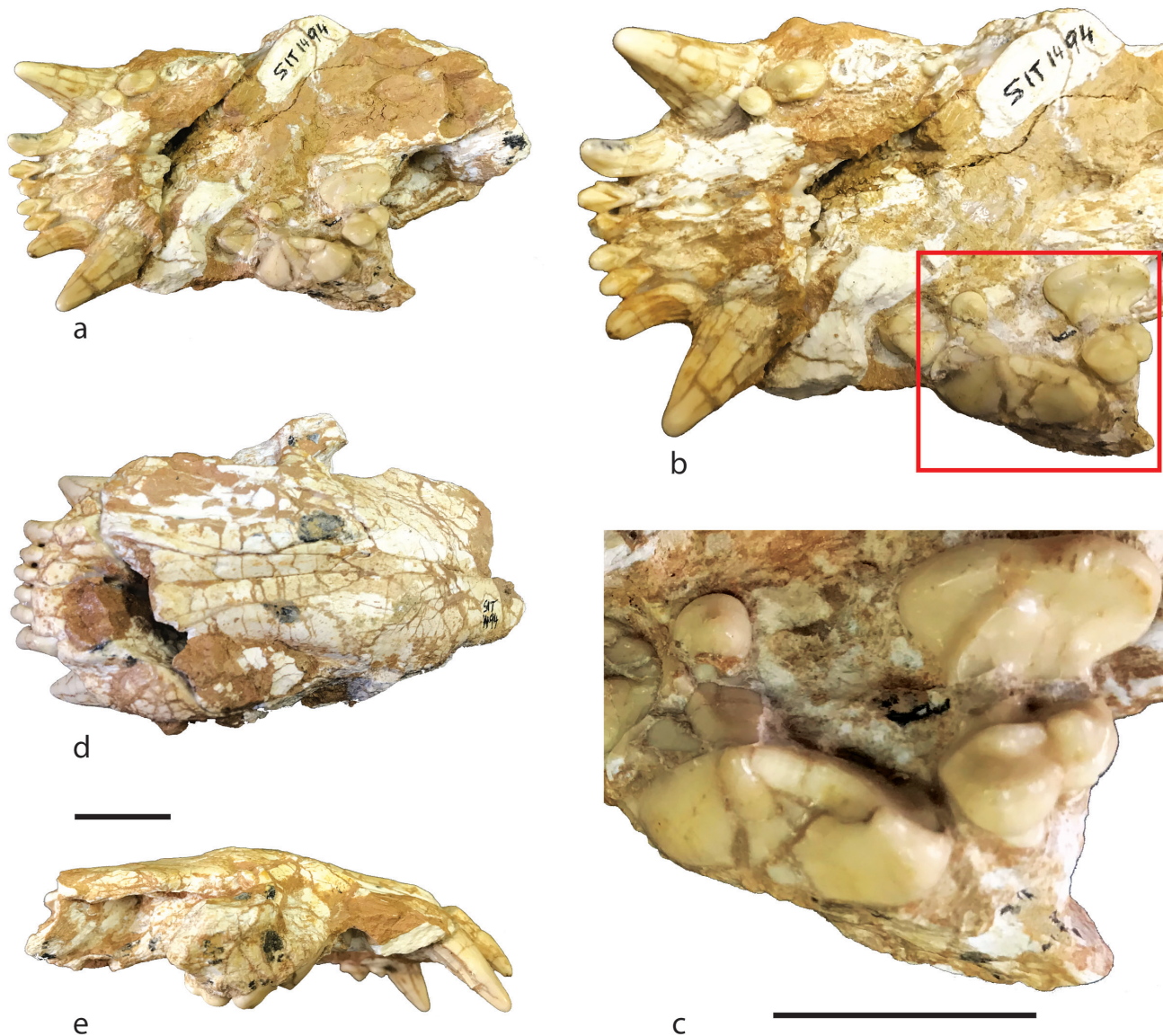
**Description.** The skull is deformed and compressed due to neotectonic activity in the area, but bears most of the teeth in good condition. It shows a short rostrum, and preserves the nasal and frontal bones, the anterior part of the zygomatic arch, the right orbit, and the small infraorbital foramen located above the anterior root of P4 and the protocone (Text-fig. 15a, d, e). There is a small diastema (ca. 3 mm) between I3 and C. The posterior part of the skull is missing, as well as the sagittal crest. The almost unworn dentition and the half-raised right P3 suggest a young individual. All incisors are well-preserved and show V-shaped palatal cingula. In addition, the much larger I3s exhibit slight torsion. The robust canines may indicate a male individual. They show wrinkled enamel at their base, and two well-defined anterior and posterior longitudinal crests. The P1 is a small, single-rooted tooth with the main cusp, and a distinct basal cingulum well-developed. The P2 is double-rooted, has a single main cusp and a crest extending along its midline, weaker anteriorly and more distinct posteriorly, terminating on a small tubercle on the posterior margin of the low, relatively distinct cingulum (Text-fig. 15b). The P3 is half-raised, with a strong main cusp and a basal cingulum. The upper carnassial, P4, is typically robust and three-

**Table 7.** Felid (?*Megantereon* or *Puma*), Milia (MIL). Comparative measurements of tibia (in mm). (See abbreviations in text.)

Tibia	MIL 974	<i>Puma pardoides</i> Untermassfeld*	<i>Puma pardoides</i> La Puebla del Valverde**
DT distal	35.54	34.50	37.3
DAP distal	22.92	21.50	24.3
DT distal articulation <sup>†</sup>	31.51		
DAP distal articulation	21.48		
DT dia. (~50 mm from the distal end)	20.23		22.70 (middle)
DAP dia. (idem)	16.89		22.10 (idem)

<sup>†</sup>including facies articularis: malleoli fibulae + distalis tibiae + malleoli, \*Hemmer et al. 2004, \*\*Madurell-Malapeira et al. 2010





**Text-fig. 15.** *Plesiogulo crassa*, Thermopigi. Cranium SIT 1494 with right and left I1–I3 and C, left P1, P2, right P3, P4, M1. a: palatal view, b: details of teeth – occlusal view, c: details of P4, M1, d: cranial view, e: right lateral view. Scale bars 20 mm.

rooted. The parastyle is weak but distinct, and includes a small, conical parastylar cusp. The paracone is broad and bears a pair of low crests along the anterior surface; the medial crest terminates just to the parastylar cusp, posterior to the parastyle. There is a relatively deep inflection of the anterior portion of the P4, located between the parastyle and protocone. The protocone is low and extends anteromedially from the base of the paracone, projecting nearly as far forward as the parastyle. The metastyle is mesially broad, but tapers distally. As regards the cingulum, the condition of the specimen does not allow any description. The paracone on the M1 is externally rounded, large (5.8 mm × 6.4 mm) and dominates over the metacone (3.8 mm × 4.3 mm). Both paracone and metacone are relatively short. The inner lobe is broad, expanding posterolingually to form a broad talon, with a slight constriction. Protocone and paraconule are joined by a pronounced crest. A cingulum surrounds the entire lingual part of the molar, and buccally there is a platform, more developed in the paracone area. It is further

bounded by a well-developed cingulum, which in its union with the paracone forms a rudimentary parastyle (Text-fig. 15c). Dimensions of skull are in Table 8.

**Discussion.** Many studies have described the expansion, evolution and extinction of *Plesiogulo*. The giant wolverine was the largest terrestrial mustelid, originating in Asia and migrating to North America between 7.0 and 6.5 Ma ago (Kurtén 1970, Hensley 1978, Harrison 1981, Alcalá et al. 1994, Haile-Selassie et al. 2004, Samuels et al. 2018 and references therein). It is known from several Middle to Late Miocene and Pliocene sites across Eurasia, North America, and Africa, and has long been discussed as a possible relative of *Gulo*. The earliest occurrence in Europe is from the Middle Miocene (MN 6, ca. 15.2–12.5 Ma) (Samuels et al. 2018). There is a question if *Plesiogulo crassa* was ecologically replaced in the Pliocene by the leopard-sized wolverine *Plesiogulo monspessulanus* VIRET, 1939 (Montpellier, MN 13), as some of its characters are intermediate between those of the Late Miocene form and

**Table 8. *Plesiogulo*, Thermopigi (SIT). Dental measurements (in mm). (See abbreviations in text.)**

Upper teeth	<i>P. crassa</i> SIT 1494	<i>P. crassa</i> Perivolaki*	Upper teeth	<i>P. crassa</i> SIT 1494	<i>P. crassa</i> Perivolaki*	<i>P. crassa</i> Paote**	<i>P. monspessulanus</i> Spain***
L C	13.80	14.50	L M1 palatal	14.60	15.00	13.22	15.40
B C	10.30	11.80	B M1	17.70	18.70	16.98	18.60
H C crown	21.70		L M1 buccal	10.00		8.40	
L I3	9.20	11.00	L P4	21.70	21.80	19.48	
B I3	8.30	10.20	B P4 pro	16.50	14.50	12.92	
L I2	6.60	9.10	B P4 met	9.50			
B I2	5.20	5.00	L P2	8.40	8.30	8.15	
L I1	6.00	7.00	B P2	5.50	6.40	5.90	
B I1	3.90	4.40	L P1	4.10			
			B P1	3.80			

\*Koufos 2006c, \*\*Kurtén 1970, Alcalá et al. 1994

modern *Gulo* (Kurtén 1970). *Gulo* has a distinct P4 parastyle. A weak parastyle appears in *Plesiogulo* SIT1494, contrary to the indication that the parastyle is absent in *Plesiogulo* (Harrison 1981, Samuels et al. 2018). The Thermopigi *Plesiogulo* displays robust anterior premolars with strong cingula, a P4 with a large protocone and relatively broad metastyle, and a large M1 with a posterolingually expanding inner lobe to form a broad talon. Ecologically, *Plesiogulo* as related to *Gulo* has traditionally been interpreted as a forest-dweller, and thus its presence may indicate a forest area near the deposition site. However considering its size and its abundance in faunas associated with hypsodont grazers and cursorial ungulates, it might have been a hunter in open grassland as well. Therefore, this genus was not a strictly woodland inhabitant. Harrison (1981) notes that most of the fossil localities with *Plesiogulo* have not produced a sample of significant statistical size, often no more than one individual, as is the case at Thermopigi.

As shown in Text-fig. 16 and in Table 7, the measurements of the SIT specimen are closer to *Plesiogulo crassa*. In Greece, *Plesiogulo crassa* is rather rare and besides Thermopigi, only a mandible fragment from Vathylakkos-3 (lower Axios valley, Northern Greece) (Koufos 1982), and an almost complete skull with mandible from Perivolaki (Thessaly) are reported. All are from the middle Turolian biozone MN 12, ~7.3 Ma (Koufos 2000, 2006b, c, 2022c). The southernmost occurrence of *Plesiogulo* in Europe, represented by humeral remains of *Plesiogulo* sp., is reported from Pikermi, Attika (Symeonidis 1975).

## Discussion

### Primates

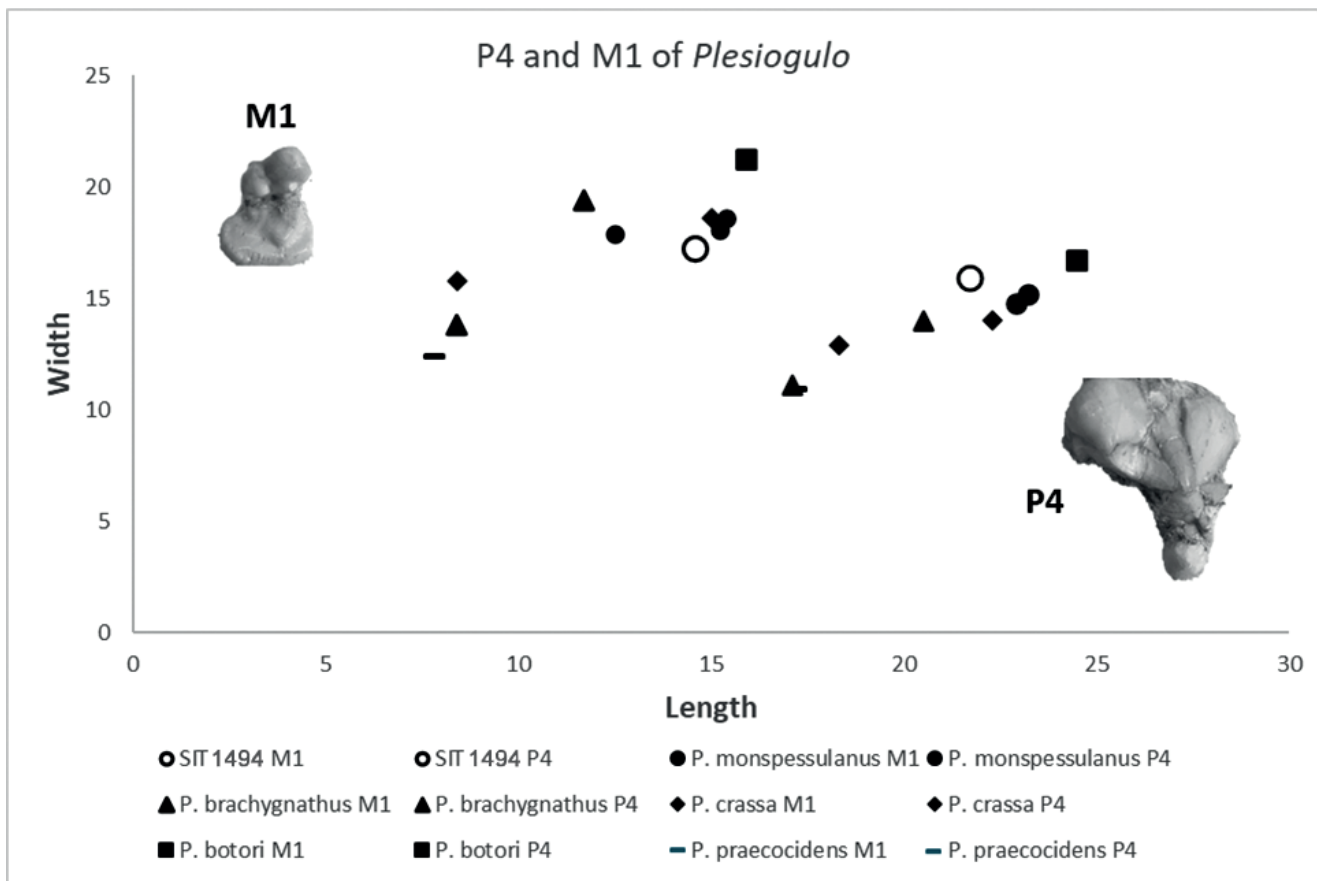
Primate fossils always attract special scientific interest, mainly due to their significance in understanding human evolution. As far as the Thermopigi (SIT) site is concerned, of the three fossil primate elements, humerus, distal tibia and complete calcaneus, the latter is of particular interest,

as its morphology provides important information about its kinship and allows conclusion about its locomotion and substrate preferences. Due to its direct contact with preferred substrates, the calcaneus is considered a relatively good indicator of the locomotion patterns. In this context, Youlatos et al. (in press) investigated the morphological and functional aspects of the SIT calcaneus using univariate and multivariate morphometric approaches that allow thorough discrimination of positional groups related to substrate preferences, with the aim of providing a qualitative and quantitative morphofunctional description. Ways in which these primates used and shared their paleoenvironment are assessed. Their results indicate clear terrestrial tendencies. Moreover, the morphology of the SIT distal tibia also corroborates the findings of the calcaneus, indicating strong similarities to more terrestrial *Macaca* spp., as well as *Papio* and *Theropithecus*. Considering the terrestrial lifestyle of both species and the terrestrial adaptations of the calcaneus, *Mesopithecus delsoni* from Thermopigi substantiates the terrestrial adaptations of this early colobine species (see also Bogdanova et al. 2023).

As far as Milia (MIL) is concerned, the two fossil primate elements, the proximal ulna and the tibia are of particular interest, as their morphology provides important morphofunctional information. Both elements provide evidence for increased terrestriality, although the tibia demonstrates a certain mobility of the hindlimb, suggesting a mixed habitus, with an emphasis on the use of the ground with occasional use of arboreal substrates. It should be noted that with the present study, the picture of the paleofauna of the area is completed, and we can now continue on to more certain results for the early Villafranchian (MN 16a) and the paleoenvironment, which is unique for Greece and rare in Europe.

Regarding the PRC site, an indicative collection of sediments from the new site was made during the micromammal survey. During the washing process, the teeth of primates emerged from among several opercula of gastropods. Primate teeth are of particular interest, as their morphology provides new data on the occurrence of the





Text-fig. 16. Scatter diagram of the upper carnassials and molars of various *Plesiogulo* species (Zdansky 1924, Kurtén 1970, Henedey 1978, Alcalá et al. 1994, Haile-Selassie et al. 2004, Koufos 2006c).

colobine genus *Dolichopithecus* in northern Greece and the Balkans in general.

### Carnivores

Fossils of carnivores are also important, due to their rarity and distribution in northern Greece. Regarding *Adcrocuta eximia*, the two Late Miocene sites of Thermopigi (SIT) and Platania, Drama (PLD) are of particular interest, as they represent the most dispersed and characteristic stratigraphic markers of the Late Miocene. It should be noted that the taphonomic observations of mammalian remains from both sites indicate the great importance of the presence of this hyper-carnivorous scavenger. On the other hand, the other primarily scavenger mustelid *Plesiogulo crassa*, described here from Thermopigi, is rarer, as it has been reported from only two sites in Greece so far.

The SIT felids are represented by *Paramachaerodus* sp. (?*P. schlosseri*) and *Pristifelis attica*. On the other hand, the new felid from Milia could be a female *Megantereon* or a new *Puma* species, but a certain amount of caution is needed, given the morphological differences observed in relation to *P. pardoides*. Further analysis is required to reach a definite conclusion. If the attribution to *Megantereon* or to *Puma* is confirmed, this would be its first occurrence in Greece, and the oldest record in Europe.

Milia has also yielded the oldest Plio-Pleistocene porcupine in Europe, *Hystrix refossa*, placed in the Late Pliocene biozone MN 16a. Thus far, the oldest known *Hystrix refossa* dates from MN 16b (Les Etouaires).

### Chronology of the sites

In Thermopigi (SIT), the co-occurrence of *Dihoplus pikermiensis* and *Ancylotherium pentelicum* most likely indicates a middle Turolian age (biozone MN 12; Geraads et al. 2007, Tsoukala 2018), but these taxa also co-occurred in Hadjidimovo, which is placed in the second half/end of MN 11. A similar conclusion was reached from the coexistence of *Samotherium major* with *Palaeotragus rouenii* and a slightly larger *Palaeotragus* sp. (Xafis et al. 2019), even though the co-occurrence of the two latter palaeotragines may point to an early Turolian age, biozone MN 11 (Koufos et al. 2009). Among the SIT hipparions, which are larger than those of Pikermi, the cranium of *Cremohipparion* shows similarities with specimens of *C. proboscideum* from RZO 5, as well as with some specimens of *C. mediterraneum* from Hadjidimovo and *C. cf. mediterraneum* from Perivolaki, while the *Hipparion* cranium is comparable with that of *H. philippus* (= *H. dietrichi* in previous publications) from Nikiti 2 and Perivolaki (Lazaridis G., Hristova L., pers. comm.). In this way, hipparions indicate an early Turolian age, mostly MN 11 or an age between MN 11 to beginning of MN 12. A more precise biochronological determination of the age of Thermopigi requires a more detailed study of the fauna of the site, as the study of the bovids and hipparions is still in progress. For the time being, Thermopigi could be assessed as dating between MN 11 and pre-Pikermi beginning of MN 12.

As far as the Platania (PLD) site is concerned, the fossil bovid assemblage of six Antilopinae and one Bovinae indicates a transition at the Vallesian/Turolian boundary

(MN 11/12; Vasileiadis et al. 2019). The PLD record may potentially document one of the earliest occurrences of these species. The evolutionary stage of *Adcrocuta eximia* confirms the biochronological position of this locality as indicated above.

The Milia (MIL) assemblage represents a unique earliest Villafranchian occurrence in Greece around the boundary between MN 15 and MN 16a, indicating an important Faunal Unit for Greece (Konidaris and Kostopoulos 2024).

Finally, the site of Promachonas (PRC) is, thus far, only represented by only a single primate taxon of the late Ruscinian (Late Pliocene), so further investigations are needed.

### Paleoenvironmental notes

Previous discussions and correlations between the two Late Miocene sites (SIT and PLD), based on either rhinoceroses or proboscideans, have been already published (Tsoukala 2018, Konidaris and Tsoukala 2020). For the former (SIT), the more conservative selective browser *Dihoplus pikermiensis* indicates the presence of some forested areas, which agrees with the presence of *Ancylotherium pentelicum*, also interpreted as a browser on arboreal vegetation (Geraads et al. 2007, Tsoukala 2018). In addition, four different species of giraffes at SIT, classified mostly as browsers or mixed feeders, indicate a browsing morphospace (Xafis et al. 2019). On the other hand, the fact that *Ceratotherium neumayri* in PLD is not a strict grazer and feeds on low-level vegetation indicates the existence of a more open and drier environment (Giaourtsakis et al. 2006, Tsoukala 2018). In SIT, the proboscidean postcranial material is attributed to *Deinotherium* sp. and *Elephantimorpha* indet., whereas the PLD proboscidean belongs to the tetralophodont amebelodontid *Konobelodon* cf. *atticus* (Konidaris and Tsoukala 2020). The carnivores from SIT include the *Adcrocuta*, a large hyenid that tended to hunt in open areas, as well as two scansorial feliforms (*Pristifelis* and *Paramachaerodus*) that occupied more closed environments. A mosaic of forested patches with open areas or a forest savannah most likely best describes the environment at both sites.

### Few taphonomical notes

Paleopathological evidence points to a type of exostosis on the right maxilla of the SIT *Adcrocuta* skull. Neotectonic events leading to a high degree of alteration and fracture deformations were noted on several large mammal remains from Thermopigi. Complete skulls, horn-cores, antlers, and tooth rows dominate the Platania assemblage, suggesting low energy transport, while the frequent presence of chewed and fragmented bones suggests a rather high impact of a hyper-carnivore scavenger, such as *Adcrocuta* especially on juveniles of large mammals, such as rhinoceroses. Finally, the felid tibia from Milia shows traces of weathering.

### Conclusions

The identification of postcranial bones of primates from among thousands of mammal remains from Thermopigi, Serres (SIT) and Milia, Grevena (MIL) sites, and teeth as single deposits from the new site of Promachonas (PRC)

contributes to our knowledge of the dispersal, evolutionary stage and the paleoenvironmental assemblage during the Late Miocene – Late Pliocene in northern Greece. The new primate remains presented here are attributed to *Mesopithecus delsoni* from the Late Miocene site of Thermopigi, cf. *Dolichopithecus balcanicus* from the Early Pliocene site of Promachonas in Serres and aff. *Dolichopithecus* sp. from the Late Pliocene site of Milia in Grevena. *Mesopithecus delsoni* was first recorded in Ravin des Zouaves 5, Axios Valley, of biozone MN 11, whereas in MN 12 *Mesopithecus pentelicus* was found in Pikermi. Therefore, the current age of the Thermopigi locality can be estimated to be between late MN 11 and pre-Pikermian MN 12, based on the evidence of the rest of the Thermopigi fauna. *Dolichopithecus balcanicus* from the late Ruscinian of the Balkans is distinguished from the common European species, *D. ruscinensis* by its smaller size, much shallower mandibular body and congestion of the premolars. *Dolichopithecus ruscinensis* of MN 14–15 from the Ptolemais basin and from Megalo Emvolo of the biozone MN 15 reveal a gap of occurrences in Greece between biozones MN 14–15 to MN 17, which is somehow filled with the Milia specimens (aff. *Dolichopithecus* sp.) of the earliest Villafranchian biozone MN 16a, more precisely around the boundary to MN 15 and MN 16a.

New carnivore material is attributed to the widespread hyenid *Adcrocuta eximia* (compared to the new *Adcrocuta* material from Platania), the felids *Paramachaerodus* sp. (?*P. schlosseri*) and *Pristifelis attica*, and the mustelid *Plesiogulo crassa* from Thermopigi, all from Late Miocene sites. *Plesiogulo crassa* is reported from Vathylakkos-3 and Perivolaki, both of middle Turolian age MN 12; *Plesiogulo* sp. are also reported from Pikermi. *Paramachaerodus orientalis* (which may actually represent *Pa. schlosseri*?) is rare and described from Pikermi in Attica (MN 12) and Nea Silata in Chalkidiki (MN 13/14). *Pristifelis attica* is reported from Pikermi (MN 11/12), and is the most widespread species among the Thermopigi felids.

Finally, additional carnivore material from Milia is attributed to a feline that could be either a female *Megantereon* or a *Puma*. In all cases, this would represent the oldest record of these genera in Europe and the first in Greece.

### Acknowledgements

E.T. and D.N. thank the members (Greek and Austrian students and collaborators) of the excavation periods in Thermopigi as well as for the preservation of the fossils and their display in the local museum of Thermopigi. Special thanks to our collaborators Vassileios Makridis (Kilkis) and Nikos Bacharidis, as well as Jordanis Poimenidis, Dr. Alex. Xafis and the preparators of the Vienna Department of Paleontology. E.T. thanks the Ioannidis family, †Eleftheriadis E., †Tomboulidis G., Maria Konstantinidou, Christina Suorts and Petros Stoikos. For the completion of the study, 3D scanning and printing of the primates used were done by Professor Vassilievos Tsioukas and Dr. Zoi Pantazopoulou of AUTH. Also deep thanks to Dick Mol and Wilrie van Logchem, collaborators and members of the Milia Research team, as well as the AUTH team. Special thanks to Dr. Asier Gomez, Prof. em. Antonis Bartsiakos,



Prof. George Lyras and, last but not least, Dr. Chatzopoulou Katerina, member of the AUTH excavation team, for her contribution, especially to the Serres (SIT and PRC) sites. Finally, our thanks also go to Prof. Serdar Mayda and Dr. Jan Wagner for their instructive suggestions that greatly improved this manuscript.

## References

- Alcalá, L., Montoya, P., Morales, J. (1994): New large mustelids from the Late Miocene of the Teruel Basin (Spain). – *Comptes Rendus de l'Académie des Sciences de Paris, Sér. II*, 319: 1093–1100.
- Arambourg, C., Piveteau, J. (1929): Les Vertébrés du Pontien de Salonique. – *Annales de Paléontologie*, 18: 59–138.
- Ballesio, R. (1963): Monographie d'un *Machairodus* du gisement Villafranchien de Senèze: *Homotherium crenatidens* FABRINI. – *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon, N. S.*, 9: 1–129.
- Berta, A., Galiano, H. (1983): *Megantereon hesperus* from the late Hemphillian of Florida with remarks on the phylogenetic relationships of machairodonts (Mammalia, Felidae, Machairodontinae). – *Journal of Paleontology*, 57(5): 892–899.
- Bogdanova, R., Youlatos, D., Spassov, N. (2003): Terrestriality as reflected in the humerus of *Mesopithecus delsoni* (Cercopithecidae, Colobinae) from Hadjidimovo, Bulgaria. – *Journal of Human Evolution*, 180: 103383 (18 pp.). <https://doi.org/10.1016/j.jhevol.2023.103383>
- Bonis, L. de, Bouvrain, G., Geraads, D., Koufos, G. D. (1990): New remains of *Mesopithecus* (Primates, Cercopithecidae) from the Late Miocene of Macedonia with the description of a new species. – *Journal of Vertebrate Paleontology*, 10: 473–483. <https://doi.org/10.1080/02724634.1990.10011830>
- Christiansen, P., Adolfssen, J. S. (2007): Osteology and ecology of *Megantereon cultridens* SE311 (Mammalia; Felidae; Machairodontinae), a sabrecat from the Late Pliocene – Early Pleistocene of Senèze, France. – *Zoological Journal of the Linnean Society*, 151: 833–884. <https://doi.org/10.1111/j.1096-3642.2007.00333.x>
- Crégut-Bonnoure, E., Tsoukala, E. (2017): The Late Pliocene Bovidae and Cervidae (Mammalia) of Milia (Grevena, Macedonia, Greece). – *Quaternary International*, 445: 215–249. <https://doi.org/10.1016/j.quaint.2016.10.043>
- De Vos, J., Van der Made, J., Athanassiou, A., Lyras, G., Sondaar, P. Y., Dermitzakis, M. D. (2002): Preliminary note on the Late Pliocene fauna from Vatera (Lesvos, Greece). – *Annales Géologiques des Pays Helléniques*, 39: 37–70.
- Delson, E. (1973): Fossil colobine monkeys of the circum-Mediterranean region and the evolutionary history of the Cercopithecidae (Primates, Mammalia); Ph.D. Dissertation. – MS, Columbia University, New York, USA, 856 pp. (copy in library of D.Y.)
- DeSilva, J. M., Morgan, M. E., Barry, J. C., Pilbeam, D. (2010): A hominoid distal tibia from the Miocene of Pakistan. – *Journal of Human Evolution*, 58: 147–154. <https://doi.org/10.1016/j.jhevol.2009.11.002>
- Doukas, C. S., De Bruijn, H. (2002): A new occurrence of *Dolichopithecus* (Mammalia, Primates) in N. Greece. – *Annales Géologiques des Pays Helléniques*, 39: 295–297.
- Ford, S. M. (1986): Subfossil platyrrhine tibia (Primates: Callitrichidae) from Hispaniola: A possible further example of island gigantism. – *American Journal of Physical Anthropology*, 70: 47–62. <https://doi.org/10.1002/ajpa.1330700110>
- Ford, S. M. (1988): Postcranial adaptations of the earliest platyrrhine. – *Journal of Human Evolution*, 17: 155–192. [https://doi.org/10.1016/0047-2484\(88\)90053-X](https://doi.org/10.1016/0047-2484(88)90053-X)
- Gebo, D. L. (1989): Locomotor and phylogenetic considerations in anthropoid evolution. – *Journal of Human Evolution*, 18: 201–233. [https://doi.org/10.1016/0047-2484\(89\)90050-X](https://doi.org/10.1016/0047-2484(89)90050-X)
- van der Geer, A. A. E., Sondaar, P. Y. (2002): The postcranial elements of *Paradolichopithecus arvernensis* (Primates, Cercopithecidae, Papionini) from Lesvos, Greece. – *Annales Géologiques des Pays Helléniques*, 39: 71–86.
- Geraads, D., Tsoukala, E., Spassov, N. (2007): A skull of *Ancylotherium* (Chalicotheriidae, Mammalia) from the Late Miocene of Thermopigi (Serres, N. Greece), and the relationships of the genus. – *Journal of Vertebrate Palaeontology*, 27(2): 461–466. [https://doi.org/10.1671/0272-4634\(2007\)27\[461:ASO-ACM\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27[461:ASO-ACM]2.0.CO;2)
- Giaourtsakis, I. X., Theodorou, G., Roussiakis, S., Athanassiou, A., Iliopoulos, G. (2006): Late Miocene horned rhinoceroses (Rhinocerotinae, Mammalia) from Kerassia (Euboea, Greece). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 239: 367–398. <https://doi.org/10.1127/njgpa/239/2006/367>
- Guérin, C., Tsoukala, E. (2013): The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the early Villafranchian site of Milia (Grevena, Macedonia, Greece). – *Geodiversitas*, 35(2): 447–489. <https://doi.org/10.5252/g2013n2a7>
- Haile-Selassie, Y., Hlusko, L. J., Howell, F. C. (2004): A new species of *Plesiogulo* (Mustelidae: Carnivora) from the Late Miocene of Africa. – *Palaeontologia africana*, 40: 85–88.
- Harrison, J. A. (1981): A Review of the Extinct Wolverine, *Plesiogulo* (Carnivora: Mustelidae), from North America. – *Smithsonian contributions to Paleobiology*, 46: 1–30. <https://doi.org/10.5479/si.00810266.46.1>
- Harrison, T. (1989): New postcranial remains of *Victoria-pithecus* from the Middle Miocene of Kenya. – *Journal of Human Evolution*, 18: 3–54. [https://doi.org/10.1016/0047-2484\(89\)90022-5](https://doi.org/10.1016/0047-2484(89)90022-5)
- Hemmer, H. (2001). Die Feliden aus dem Epivillafranchium von Untermaßfeld. – In: Kahlke, R.-D. (ed.), *Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen)*, Teil 3. Monographien, Römisch-Germanisches Zentralmuseums, 40(3): 699–782.
- Hemmer, H., Kahlke, R.-D. (2022): New results on felids from the Early Pleistocene site of Untermaßfeld. – In: Kahlke, R.-D. (ed.), *The Pleistocene of Untermaßfeld near Meiningen (Thüringen, Germany)*, part 5. Monographien des Römisch-Germanischen Zentralmuseums, 40(5): 1465–1566.

- Hemmer, H., Kahlke, R.-D., Vekua, A. K. (2004): The Old-World puma – *Puma pardoides* (Owen, 1846) (Carnivora: Felidae) – in the lower Villafranchian (upper Pliocene) of Kvabebi (East Georgia, Transcaucasia) and its evolutionary and biogeographical significance. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 233(2): 197–231.  
<https://doi.org/10.1127/njgpa/233/2004/197>
- Hendey, Q. B. (1978): Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. – *Annals of the South African Museum*, 76(10): 329–357.
- Ingicco, T. (2008): Analyse morphofonctionnelle des os longs de deux colobes fossiles: *Mesopithecus* et *Dolichopithecus*. – *Annali dell'Università di Ferrara, Museologia Scientifica e Naturalistica, Volume spécial 2008*: 91–97.
- Jiangzuo, Q., Nius, K., Li, S., Fu, J., Wang, S. (2022): A diverse Metailurine guild from the Latest Miocene Xingjiawan Fauna, Yongdeng, Northwestern China, and generic differentiation of Metailurine Felids. – *Journal of Mammalian Evolution*, 29: 845–862.  
<https://doi.org/10.1007/s10914-022-09622-8>
- Konidaris, G., Kostopoulos, D. (2024): The Late Pliocene–Middle Pleistocene Large Mammal Faunal Units of Greece. – *Quaternary*, 7(27): 1–15.  
<https://doi.org/10.3390/quat7020027>
- Konidaris, G., Tsoukala, E. (2020): Proboscideans from the upper Miocene localities of Thermopigi, Neokaisareia and Platania (Northern Greece). – *Annales de Paléontologie*, 106: 102380 (15 pp.).  
<https://doi.org/10.1016/j.anpal.2019.102380>
- Kostopoulos, D. S., Guy, F., Kynigopoulou, Z., Koufos, D. G., Valentin, X., Merceron, G. (2018): A 2Ma old baboon-like monkey from Northern Greece and new evidence to support the *Paradolichopithecus* – *Procy-nocephalus* synonymy (Primates: Cercopithecidae). – *Journal of Human Evolution*, 121: 178–192.  
<https://doi.org/10.1016/j.jhevol.2018.02.012>
- Koufos, G. D. (1982): *Plesiogulo crassa* from the upper Miocene (lower Turolian) of Northern Greece. – *Annales Zoologici Fennici*, 19: 193–197.
- Koufos, G. D. (2000): Revision of the Late Miocene carnivores from the Axios valley, Macedonia, Greece. – *Münchner Geowissenschaftliche Abhandlungen, A*, 39: 51–92.
- Koufos, G. D. (2006a): The Neogene mammal localities of Greece: Faunas, chronology, and biostratigraphy. – *Hellenic Journal of Geosciences*, 41: 183–214.
- Koufos, G. D. (2006b): The Late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece. 3. Primates. – *Palaeontographica, Abt. A*, 276: 23–37.  
<https://doi.org/10.1127/pala/276/2006/23>
- Koufos, G. D. (2006c): The Late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece. 4. Carnivora. – *Palaeontographica, Abt. A*, 276: 39–74.  
<https://doi.org/10.1127/pala/276/2006/39>
- Koufos, G. D. (2009a): The Neogene cercopithecids (Mammalia, Primates) of Greece. – *Geodiversitas*, 31: 817–850.  
<https://doi.org/10.5252/g2009n4a817>
- Koufos, G. D. (2009b): The genus *Mesopithecus* (Primates, Cercopithecidae) in the Late Miocene of Greece. – *Bollettino Società Paleontologia Italiana*, 48: 157–166.
- Koufos, G. D. (2011): The Miocene carnivore assemblage of Greece. – *Estudios Geológicos*, 67(2): 291–320.  
<https://doi.org/10.3989/egeol.40560.190>
- Koufos, G. D. (2012): New material of Carnivora (Mammalia) from the Late Miocene of Axios Valley, Macedonia, Greece. – *Comptes Rendus Palevol*, 11: 49–64.  
<https://doi.org/10.1016/j.crpv.2011.09.004>
- Koufos, G. D. (2013): Neogene mammal biostratigraphy and chronology of Greece. – In: Wang, X., Flynn, J. J., Fortelius, M. (eds), *Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp. 595–621.  
<https://doi.org/10.7312/columbia/9780231150125.003.0028>
- Koufos, G. D. (2016): Carnivora. – In: Koufos, D., Kostopoulos, D. (eds), *Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)*. *Geobios*, 49(1-2): 53–67.  
<https://doi.org/10.1016/j.geobios.2016.01.013>
- Koufos, G. D. (2022a): The fossil record of Felids (Mammalia: Carnivora, Felidae) in Greece. – In: Vlachos, E. (ed.), *Fossil Vertebrates of Greece, Vol. 2*. Springer, Cham, pp. 519–539.  
[https://doi.org/10.1007/978-3-030-68442-6\\_16](https://doi.org/10.1007/978-3-030-68442-6_16)
- Koufos, G. D. (2022b): The fossil record of Hyaenids (Mammalia: Carnivora, Felidae) in Greece. – In: Vlachos, E. (ed.), *Fossil Vertebrates of Greece, Vol. 2*. Springer, Cham, pp. 555–576.  
[https://doi.org/10.1007/978-3-030-68442-6\\_19](https://doi.org/10.1007/978-3-030-68442-6_19)
- Koufos, G. D. (2022c): The fossil record of Mustelids (Mammalia: Carnivora, Mustelidae) in Greece. – In: Vlachos, E. (ed.), *Fossil Vertebrates of Greece, Vol. 2*. Springer, Cham, pp. 641–659.  
[https://doi.org/10.1007/978-3-030-68442-6\\_24](https://doi.org/10.1007/978-3-030-68442-6_24)
- Koufos, G. D. (2022d): The fossil record of Old-World Monkeys (Mammalia: Primates: Cercopithecidae) in Greece. – In: Vlachos E. (ed.), *Fossil Vertebrates of Greece, Vol. 1*. Springer, Cham, pp. 639–655.  
[https://doi.org/10.1007/978-3-030-68398-6\\_17](https://doi.org/10.1007/978-3-030-68398-6_17)
- Koufos, G. D., Kostopoulos, D. S., Vlachou, T. D. (2009): The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 16. Chronology. – *Beiträge zur Paläontologie*, 31: 397–408.
- Koufos, G. D., Spassov, N., Kovatchev, D. (2003): Study of *Mesopithecus* from the Late Miocene of Bulgaria. – *Palaeontographica, Abt. A*, 269(1-3): 39–91.  
<https://doi.org/10.1127/pala/269/2003/39>
- Koufos, G. D., Syrides, G., Koliadimou, K. (1991): A Pliocene primate from Macedonia. – *Journal of Human Evolution*, 21: 283–294.  
[https://doi.org/10.1016/0047-2484\(91\)90109-9](https://doi.org/10.1016/0047-2484(91)90109-9)
- Küllmer, O., Doukas, C. (1995): The deciduous dentition of *Mesopithecus pentelicus* WAGNER (Primates, Mammalia). – In: Schmidt-Kittler, N. (ed.), *The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene)*. *Münchner Geowissenschaftliche Abhandlungen, A*, 28: 65–74.
- Kurtén, B. (1970): The Neogene wolverine *Plesiogulo* and the origin of *Gulo* (Carnivora, Mammalia). – *Acta Zoologica Fennica*, 131: 1–22.
- Laird, M. F., Kozma, E. E., Kwekason, A., Harrison, T. (2018): A new fossil cercopithecoid tibia from Laetoli and



- its implications for positional behavior and paleoecology. – *Journal of Human Evolution*, 118: 27–42.  
<https://doi.org/10.1016/j.jhevol.2018.02.005>
- Langdon, J. H. (1986): Functional morphology of the Miocene hominoid foot. – *Contributions to Primatology*, 22: 1–225.
- Lazaridis, G. (2015): Study of the Late Miocene vertebrate locality of Kryopigi and other localities of Kassandra Peninsula, Chalkidiki (Greece). Systematics, Taphonomy, Paleoecology, Biochronology. – *Scientific Annals, School of Geology, Aristotle University, Thessaloniki, Greece*, 174: 1–355.
- Lazaridis, G., Tsoukala, E., Maul, L. Ch. (2019): The earliest *Hystrix refossa*: A new early Villafranchian record from Milia (Grevena, Macedonia, Greece). – *Hystrix*, 30(1): 12–18.  
<https://doi.org/10.4404/hystrix-00140-2018>
- Lazaridis, G., Tsoukala, E., Rae, T. C., Gomez-Olivencia, A., Nagel, D., Bartsiakas, A. (2018): *Mesopithecus pentelicus* from the Turolian locality of Kryopigi (Kassandra, Chalkidiki, Greece). – *Journal of Human Evolution*, 121: 128–146.  
<https://doi.org/10.1016/j.jhevol.2018.04.003>
- Lewis, O. J. (1989): *Functional Anatomy of the Evolving Hand and Foot*. – Clarendon Press, Oxford, 359 pp.
- Li, Y., Spassov, N. (2017): A new species of *Paramachaerodus* (Mammalia, Carnivora, Felidae) from the Late Miocene of China and Bulgaria, and revision of *Promegantereon kretzoi*, 1938 and *Paramachaerodus* Pilgrim, 1913. – *Paläontologische Zeitschrift*, 91: 409–426.  
<https://doi.org/10.1007/s12542-017-0371-7>
- Lyras, G. A., van der Geer, A. A. E. (2007): The Late Pliocene vertebrate fauna of Vatera (Lesvos Island, Greece). – *Cranium*, 24: 11–24.
- Madurell-Malapeira, J., Alba, D. M., Moyà-Solà, S., Aurell-Garrido, J. (2010): The Iberian record of the puma-like cat *Puma pardoides* (Owen, 1846) (Carnivora, Felidae). – *Comptes Rendus Palevol*, 9(1-2): 55–62.  
<https://doi.org/10.1016/j.crpv.2009.12.002>
- Mashchenko, E. N., Marareskul, V. A. (2011): Ontogenetic Features of *Dolichopithecus* (Primates, Colobidae) from the Pliocene of Pridnestrovie. – *Paleontological Journal*, 45(6): 689–697.  
<https://doi.org/10.1134/S0031030111060104>
- McKenna, M. C., Bell, S. K. (1997): *Classification of Mammals above the Species Level*. – Columbia University Press, New York, 640 pp.
- Nomade, S., Pestre, J. F., Guillou, H., Faure, M., Guérin, C., Delson, E., Debard, E., Voinchet, P., Messenger, E. (2014): <sup>40</sup>Ar/<sup>39</sup>Ar constraints on some French landmark Late Pliocene to Early Pleistocene large mammalian paleofaunas: Paleoenvironmental and paleoecological implications. – *Quaternary Geochronology*, 21: 2–15.  
<https://doi.org/10.1016/j.quageo.2012.12.006>
- Pina, M., Salesa, M. J., Antón, M., Pastor, J. F. (2011): Functional anatomy of the calcaneum and talus in Cercopithecinae (Mammalia, Primates, Cercopithecinae). – *Estudios Geológicos*, 67(2): 385–394.  
<https://doi.org/10.3989/egool.40590.195>
- Rose, M. D. (1986): Further hominoid postcranial specimens from the late Miocene Nagri formation of Pakistan. – *Journal of Human Evolution*, 15: 333–367.  
[https://doi.org/10.1016/S0047-2484\(86\)80016-1](https://doi.org/10.1016/S0047-2484(86)80016-1)
- Roussiakis, S. J. (2002): Musteloids and feloids (Mammalia, Carnivora) from the Late Miocene locality of Pikermi (Attica, Greece). – *Geobios*, 35: 699–719.  
[https://doi.org/10.1016/S0016-6995\(02\)00083-9](https://doi.org/10.1016/S0016-6995(02)00083-9)
- Roussiakis, S. J., Theodorou, G. E., Iliopoulos, G. (2006): An almost complete skeleton of *Metailurus parvulus* (Carnivora, Felidae) from the Late Miocene of Kerassia (Northern Euboea, Greece). – *Geobios*, 39: 563–584.  
<https://doi.org/10.1016/j.geobios.2005.04.002>
- Salesa, M. J., Antón, M., Morales, J., Peigné, S. (2012): Systematics and phylogeny of the small felines (Carnivora, Felidae) from the Late Miocene of Europe: A new species of Felinae from the Vallesian of Batallones (MN 10, Madrid, Spain). – *Journal of Systematic Palaeontology*, 10(1): 87–102.  
<https://doi.org/10.1080/14772019.2011.566584>
- Salesa, M. J., Antón, M., Turner, A., Alcalá, L., Montoya, P., Morales, J. (2010): Systematic revision of the Late Miocene sabre-toothed felid *Paramachaerodus* in Spain. – *Palaeontology*, 53(6): 1369–1391.  
<https://doi.org/10.1111/j.1475-4983.2010.01013.x>
- Samuels, J. X., Bredehoeft, K. E., Wallace, S. C. (2018): A new species of *Gulo* from the Early Pliocene Gray Fossil Site (Eastern United States); rethinking the evolution of wolverines. – *PeerJ*, 6: e4648 (29 pp.).  
<https://doi.org/10.7717/peerj.4648>
- Sianis, P. D., Athanassiou, A., Kostopoulos, D. S., Roussiakis, S., Kargopoulos, N., Iliopoulos, G. (2022): The remains of a large cercopithecoid from the Lower Pleistocene locality of Karnezeika (southern Greece). – *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 114: 177–182.  
<https://doi.org/10.1017/S1755691022000226>
- Solounias, N. (1981): The Turolian fauna from the Island of Samos. – *Contributions to Vertebrate Evolution*, 6: 1–232.
- Sondaar, P. Y., van der Geer, A. A. E., Dermitzakis, M. D. (2006): The unique postcranial of the Old-World monkey *Paradolichopithecus*: more similar to *Australopithecus* than to baboons. – *Hellenic Journal of Geosciences*, 41: 19–28.
- Spassov, N., Geraads, D. (2007): *Dolichopithecus balcanicus* sp. nov., a new Colobinae (Primates, Cercopithecidae) from the Early Pliocene of southeastern Europe, with a discussion on the taxonomy of the genus. – *Journal of Human Evolution*, 52: 434–442.  
<https://doi.org/10.1016/j.jhevol.2006.11.002>
- Spassov, N., Geraads, D. (2014): A new Felid from the Late Miocene of the Balkans and the contents of the Genus *Metailurus* ZDANSKY, 1924 (Carnivora, Felidae). – *Journal of Mammalian Evolution*, 22: 45–56.  
<https://doi.org/10.1007/s10914-014-9266-5>
- Spassov, N., Geraads, D., Hristova, L., Markov, G. N. (2019): The Late Miocene mammal fauna from Gorna Sushitsa, Southwestern Bulgaria and the early/middle

- Turolian transition. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 291(3): 317–350.  
<https://doi.org/10.1127/njgpa/2019/0804>
- Spassov, N., Geraads, D., Hristova, L., Markov, G., Garevska, B., Garevski, R. (2018): The Late Miocene mammal faunas of the Republic of Macedonia (FYROM). – Palaeontographica, Abt. A, 311(1-6): 1–85.  
<https://doi.org/10.1127/pala/2018/0073>
- Strasser, E. (1988): Pedal evidence for the origin and diversification of cercopithecoïd clades. – Journal of Human Evolution, 17: 225–246.  
[https://doi.org/10.1016/0047-2484\(88\)90055-3](https://doi.org/10.1016/0047-2484(88)90055-3)
- Symeonidis, N. (1975): Ein grosser Mustelidae aus Pirkermi. – Annales Géologiques des Pays Helléniques, 26(1974): 314–319.
- Szalay, F., Delson, E. (1979): Evolutionary History of the Primates. – Academic Press, New York, 580 pp.
- Tranos, M. D., Kachev, V. N., Mountrakis, D. M. (2008): Transensional origin of the NE-SW Simitli basin along the Strouma (Strymon) Lineament, SW Bulgaria. – Journal of the Geological Society of London, 165: 499–510.  
<https://doi.org/10.1144/0016-76492007-089>
- Tsoukala, E. (2000): Remains of a Pliocene *Mammuth borsoni* (HAYS, 1834) (Proboscidea, Mammalia) from Milia (Grevena, W. Macedonia, Greece). – Annales de Paléontologie, 86: 165–191.  
[https://doi.org/10.1016/S0753-3969\(00\)80007-5](https://doi.org/10.1016/S0753-3969(00)80007-5)
- Tsoukala, E. (2018): Rhinocerotidae from the Late Miocene and Late Pliocene of Macedonia, Greece. A revision of the Neogene–Quaternary Rhinocerotidae of Greece. – Revue de Paléobiologie, 37(2): 609–630.
- Tsoukala, E., van Logchem, W., Lazaridis, G., Mol, D. (2014): Carnivores of the early Villafranchian site of Milia (Grevena, Macedonia, Greece). – In: Abstract Book, VI<sup>th</sup> International Conference on Mammoths and their Relatives, Grevena & Siatista, Greece, May 2014. Scientific Annals, School of Geology, Aristotle University, Thessaloniki, Greece, 102: 6–7.
- Tsoukala, E., Mol, D. (2016): The Proboscidea of the early Villafranchian site of Milia (Grevena, Macedonia, Greece). – Quaternary International, 406: 2–24.  
<https://doi.org/10.1016/j.quaint.2014.10.026>
- Vasileiadis, N., Tsoukala, E., Kostopoulos, D. (2019): The Late Miocene bovids from Platania (Drama, Greece), with description of a new species of *Paleoryx*. – Geobios, 55: 57–76.  
<https://doi.org/10.1016/j.geobios.2019.06.005>
- Vlachos, E., Tsoukala, E. (2014): *Testudo* cf. *graeca* from the new Late Miocene locality of Platania (Drama basin, N. Greece) and a reappraisal of previously published specimens. – Bulletin of the Geological Society of Greece, 48: 27–40.  
<https://doi.org/10.12681/bgsg.11046>
- Vlachos, E., Tsoukala, E. (2016): The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of *Testudo* LINNAEUS, 1758 (Testudines: Testudinidae). – Papers in Palaeontology, 2(1): 71–86.  
<https://doi.org/10.1002/spp2.1031>
- Vlachos, E., Tsoukala, E., Crégut-Bonnoure, E., Guérin, C., Mol, D. (2018): The Paradise Lost of Milia (Grevena, Greece; Late Pliocene, early Villafranchian, MN15/MN16a): faunal composition and diversity. – Quaternary 1(2): 13 (16 pp.).  
<https://doi.org/10.3390/quat1020013>
- Werdelin, L., Lewis, M. E. (2001): A revision of the genus *Dinofelis* (Mammalia, Felidae). – Zoological Journal of the Linnean Society, 132: 147–258.  
<https://doi.org/10.1111/j.1096-3642.2001.tb02465.x>
- Xafis, A., Tsoukala, E., Solounias, N., Mandic, O., Harzhauser, M., Grímsson, F., Nagel, D. (2019): Fossil Giraffidae (Mammalia, Artiodactyla) from the Late Miocene of Thermopigi (Macedonia, Greece). – Paleontologia Electronica, 22.3.67: 1–38.  
<https://doi.org/10.26879/889>
- Youlatos, D. (1990): Etude morphométrique du tarse (astragale et calcanéum) de *Mesopithecus pentelicus* WAGNER, 1839 (Cercopithecoïdeia, Primates). Comparaison avec les formes actuelles, interprétation fonctionnelle. – Mémoire DEA, Université Paris VII, Muséum National d'Histoire Naturelle, Paris, 102 pp. (copy in library of D.Y.)
- Youlatos, D. (1994): Maitrise de l'espace et accès aux ressources chez le singe hurleur roux (*Alouatta seniculus*) de la Guyane Française. Etude morpho-fonctionnelle; Thèse de doctorat. – MS, Muséum National d'Histoire Naturelle, Paris, France, 317 pp. (copy in library of D.Y.)
- Youlatos, D., Tsoukala, E., Nagel, D., N., Spassov, N. (in press): Functional morphology of a Late Miocene cercopithecoïd complete calcaneus from Thermopigi (Serres, Greece). – Geobios.
- Zagorchev, I. S. (1992): Neotectonic development of the Strouma (Kraistid) Lineament, southwest Bulgaria and northern Greece. – Geological Magazine, 129(2): 197–222.  
<https://doi.org/10.1017/S0016756800008281>
- Zdanksy, O. (1924): Jungtertiäre Carnivoren Chinas. – Palaeontologia Sinica, Ser. C, 2(1): 1–149.
- Zougrou, I. M., Stoulos, S., Kantiranis, N., Papadopoulou, L., Ioakeimidis, I., Katsikini, M., Paloura, E., Tsoukala, E. (2018): Natural radioactivity measurements in a paleontology site and paleoclimate interpretation of the last 8 Mya. – Journal of Environmental Radioactivity, 193-194: 1–14.  
<https://doi.org/10.1016/j.jenvrad.2018.08.012>