

The remains of a large cercopithecoid from the Lower Pleistocene locality of Karnezeika (southern Greece)

Panagiotis D. SIANIS^{1*} , Athanassios ATHANASSIOU²,
Dimitris S. KOSTOPOULOS³, Socrates ROUSSIAKIS⁴,
Nikolaos KARGOPOULOS⁵ and George ILIOPOULOS¹

¹ Department of Geology, University of Patras, 26504 Rio, Greece.

² Hellenic Ministry of Culture and Sports, Ephorate of Palaeoanthropology–Speleology, Ardittou 34B Athens, 11636, Greece.

³ Aristotle University of Thessaloniki, School of Geology, 54124 Thessaloniki, Greece.

⁴ Department of Geology and Geoenvironment, National and Kapodistrian University of Athens, 15784 Athens, Greece.

⁵ Department of Geoscience, Eberhard Karls University of Tübingen, Sigwartstrasse 10, 72076 Tübingen, Germany.

*Corresponding author. Email: pdsianis@gmail.com

ABSTRACT: The Lower Pleistocene Karnezeika locality, lies in the Peloponnese, southern Greece, and its fauna corresponds to the Middle Villafranchian biochronological unit (MN17). The recovered mammal assemblage includes, among others, a few remains of a large Cercopithecoid. Herein, we describe this material, including an upper second molar, a partially preserved proximal radius and, possibly, an upper first incisor. The teeth show advanced stages of wear but retain their typical papionin characters, such as a strong lingual cleft and four bilophodont cusps in the molar. The general morphology and wear pattern of the teeth rules out the possibility that the remains belong to the genus *Theropithecus*, while the general size of the corresponding material excludes the possibility of a *Macaca* representative as well. On the contrary, the studied material better fits the size range of *Paradolichopithecus*. Even though this genus is likely represented in the Villafranchian of Europe by a single species, *Par. arvernensis*, the scarcity of the studied material imposes reservations and thus the Karnezeika papionin is referred at the moment to *cf. Paradolichopithecus* sp. As in the rest of Europe, the *Paradolichopithecus* record is rare in Greece, having been found in only two localities, Vatera and Dafnero. Despite its scarcity, the new material from Karnezeika indicates a wide distribution of this important taxon in the Greek peninsula.



KEY WORDS: Papionini, *Paradolichopithecus*, Peloponnese, Primates, Villafranchian.

1. Introduction

Karnezeika in eastern Peloponnese, southern Greece, is a new Lower Pleistocene, fissure-filling locality yielding a mammal fauna that corresponds to the Middle Villafranchian biochronological unit (MN17) (Sianis *et al.* 2022). The fauna consists mainly of bovids, including *Gazella bouvrinae* Kostopoulos & Athanassiou 1997, *Gazellospira torticornis* (Aymard 1854), *Gallogoral meneghini* (Rüttimeyer 1878) and Caprini gen. et sp. indet (Sianis *et al.* 2022), but also other artiodactyl, perissodactyl and carnivoran taxa. Among the finds, there were also rare remains of a large cercopithecoid. The Cercopithecidae is a diverse family of Old-World monkeys (Catarrhini) with a former wide distribution across Africa, Asia and Europe. Taxonomically, it is divided in two subfamilies, Cercopithecinae and Colobinae, both of which are present in the fossil record of Europe (Eronen & Rook 2004), even though it is rather rare with respect to other families. In Europe, the cercopithecoids appear in the Late Miocene (MN11) with the colobine *Mesopithecus* Wagner 1839

and disappear in the Late Pleistocene. During the Pliocene and the Pleistocene, the family showed an increased taxonomic diversification in Europe, represented by the genera *Macaca* de la Lacépède 1799, *Dolichopithecus* Depéret 1889, *Theropithecus* Geoffroy Saint-Hilaire 1843 and *Paradolichopithecus* Necrasov *et al.* 1961 (Szalay & Delson 1979; Frost 2017).

In the Greek cercopithecoid fossil record, the colobine monkey *Mesopithecus* is the most frequent, known from several Upper Miocene localities of the central and northern parts of continental Greece (Koufos 2009), such as Pikermi near Athens (with *Mesopithecus pentelicus* Wagner 1839) and Axios Valley near Thessaloniki (with *Mesopithecus delsoni* de Bonis *et al.* 1990 and *Mesopithecus monspessulanus* Gervais 1848–1852). In addition, another colobine monkey, *Dolichopithecus*, is known from the Lower Pliocene locality Megalo Embolo near Thessaloniki (Koufos *et al.* 1991) and from a few isolated dental specimens found in the Ptolemais Basin (Doukas & de Bruijn 2002). Spassov & Geraads (2007) included the Megalo Embolo remains to a new species, *Dolichopithecus balcanicus* Spassov & Geraads

2007). However, this opinion was not followed by Koufos (2009, 2022), who continued to refer the Megalo Embolo sample to *Dolichopithecus cinensis* Depéret 1889. As far as the Cercopithecinae are concerned, the first finds include some isolated dental remains from the locality of Tourkovounia near Athens, which were ascribed by Symeonidis & Zapfe (1977) to *Macaca florentina* (Cocchi 1872). Very recently, new *Macaca* remains were unearthed from the locality of Marathousa-1 in the Megalopolis Basin, ascribed by Konidaris et al. (2022) to *Macaca sylvanus* cf. *pliocena* Owen 1846, as well as from the nearby locality of Kyparissia (*Macaca sylvanus* Linnaeus 1758; Konidaris et al. in press). Finally, the Villafranchian large cercopithecid *Paradolichopithecus* is currently known in Greece from two Lower Pleistocene localities: Vatera on Lesbos island; and Dafnero in north-wester Greece (de Vos et al. 2002; van der Geer & Sondaar 2002; Lyras & van der Geer 2007; Kostopoulos et al. 2018) – both ascribed to the Eurasian species *Par. arvernensis* (Depéret 1928). For a comprehensive and up-to-date review of the Greek fossil record of Cercopithecidae, see Koufos (2022).

The purpose of this article is to describe and provide possible taxonomic information for this new cercopithecid material. Moreover, the presence of a large cercopithecid provides additional information expanding our knowledge about the taxon's distribution and the understanding about the locality's palaeoenvironment.

2. Materials and methods

Details about the locality of Karnezeika and its geological and stratigraphic setting can be found in Kokotini et al. (2019) and Sianis et al. (2022). The studied cercopithecid material consists of possibly an upper incisor, an isolated upper second molar and the proximal part of a right radius. The dental specimens are curated in the Palaeontological Collection of the University of Patras (PCUP), while the radius is curated in the Athens Museum of Palaeontology and Geology (AMPG).

The dental terminology largely follows Swindler (2002). Linear measurements were taken with digital calipers at two decimals precision. All measurements are given in mm. Scatter plots were created with the use of LibreOffice Calc for Windows.

3. Systematic palaeontology

Order Primates Linnaeus 1758

Infraorder Catarrhini Geoffroy Saint-Hilaire 1812

Superfamily Cercopithecoidea Gray 1821

Family Cercopithecidae Gray 1821

Subfamily Cercopithecinae Gray 1821

Tribe Papionini Burnett 1828

Genus *Paradolichopithecus* Necrasov et al. 1961

Type species *Dolichopithecus arvernensis* Depéret 1928

Remark: traditionally, the authorship of *D. arvernensis* was attributed to Depéret (1929) where the species was fully described. However, recently, it has been shown (Delson E. pers. comm.) that the first (i.e. original) announcement of this taxon was actually provided a year earlier by Depéret (1928) himself. In this latter article, Depéret names his new species and provides a short but meaningful description of very basic features, that could satisfy the terms of name availability under Article 12 of the International Code of Zoological Nomenclature.

cf. *Paradolichopithecus* sp. (Fig. 1)

Locality: Karnezeika, Peloponnese, southern Greece.

Material: one upper incisor (PCUP KZ1400); one left upper second molar M2 (PCUP KZ1852); and one proximal part of a right radius (AMPG KRZ93).

Description: specimen KZ1852 is a well preserved isolated left upper molar, which retains all three of its roots (Figs 1a–d). The crown is almost square shaped (maximum mesiodistal diameter of M2 × 100/maximum buccolingual diameter of M2 = 96.5) and includes four low bilophodont cusps (two buccal and two lingual) following the typical bilophodont morphology for the molars of the Old-World monkeys (Swindler 2002). The tooth is in a very advanced stage of wear (stage F of Delson 1973), exposing the dentine over the entire occlusal surface and resulting in complete merging of the wear facets. The inner profile is also lost to wear, placing the individual in IDAS 4 (late adult) or IDAS 5 (senile) (*sensu* Anders et al. 2011). Enamel is only visible at the margins of the tooth. Due to the advanced wear, the occlusal surface is reduced to dentine and appears much lower than the enamel margins and almost completely smooth, lacking any morphological characteristics. Nevertheless, despite this advanced stage of wear, the tips of the buccal cusps remain relatively pointed. The lingual cones are much lower than the buccal cones. On the distal and mesial walls two contact facets can be clearly seen indicating that the tooth is a first or second molar and most likely the latter due to its dimensions (Table 1). Strong bulging appears on the buccal side of the paracone, as can be also observed in modern baboons and macaques. A well-developed cleft (*sensu* Delson 1975) is visible on the lingual side of the tooth. A weak flaring is detectable, more evident in the lingual side, which was calculated based on Benefit (1993) and Singleton (2003) and found to be equal to 0.3. Such a low value may be due to the advanced stage of wear.

The specimen KZ1400 is a right incisor, most likely an upper one (Figs 1e–g). The tooth is ascribed to the same taxon due to similarities with primate incisors, though with some reservation, because of its unusual wear pattern. The occlusal surface is oval shaped (elongated mesiodistally) and devoid of any morphological characteristics, as it is in advanced stage of wear. Almost all of the surface consists of exposed dentine. The centre of the surface is low while the mesial and distal enamel ridges are high, creating a valley-like structure. A longitudinal, mesiodistally oriented groove is present in the mesial side of the tooth, at the border of the crown and the cervix. This groove, as well as the tooth as a whole, is characterised by the presence of micro-cracks due to taphonomic modification, as well as black stains, most likely due to the presence of manganese oxides (Fernández-Jalvo & Andrews 2016). Labially, the crown appears wide and relatively short. The root is robust and curves laterally towards its apex. Its cross-section is elliptical, slightly compressed mesiodistally. No basal bulge nor any lingual cingulum is observed.

The radius (AMPG KRZ93) preserves only the proximal part of the bone, broken a few centimetres distally of the well-developed radial tuberosity (Figs 1h, i). The neck of the radius is short and slightly inclined in relation to the radial tuberosity. The head of the radius is sub-circular with a shallow articular surface.

4. Discussion and conclusion

Characters shown by the upper M2 specimen KZ1852, such as the low cusps, the lingual cleft, the flaring and the wear pattern are typical of Papionini (Delson 1973; Swindler 2002; Frost & Kullmer 2008). On the contrary, Colobinae are characterised by an increased crown relief and an asymmetrical curve of the distal margin of the upper teeth (Szalay & Delson 1979). *Dolichopithecus* can be excluded based on its smaller dimensions and the lack of strong crown relief, commonly found in Colobinae (Szalay & Delson 1979). Among known Plio-Pleistocene

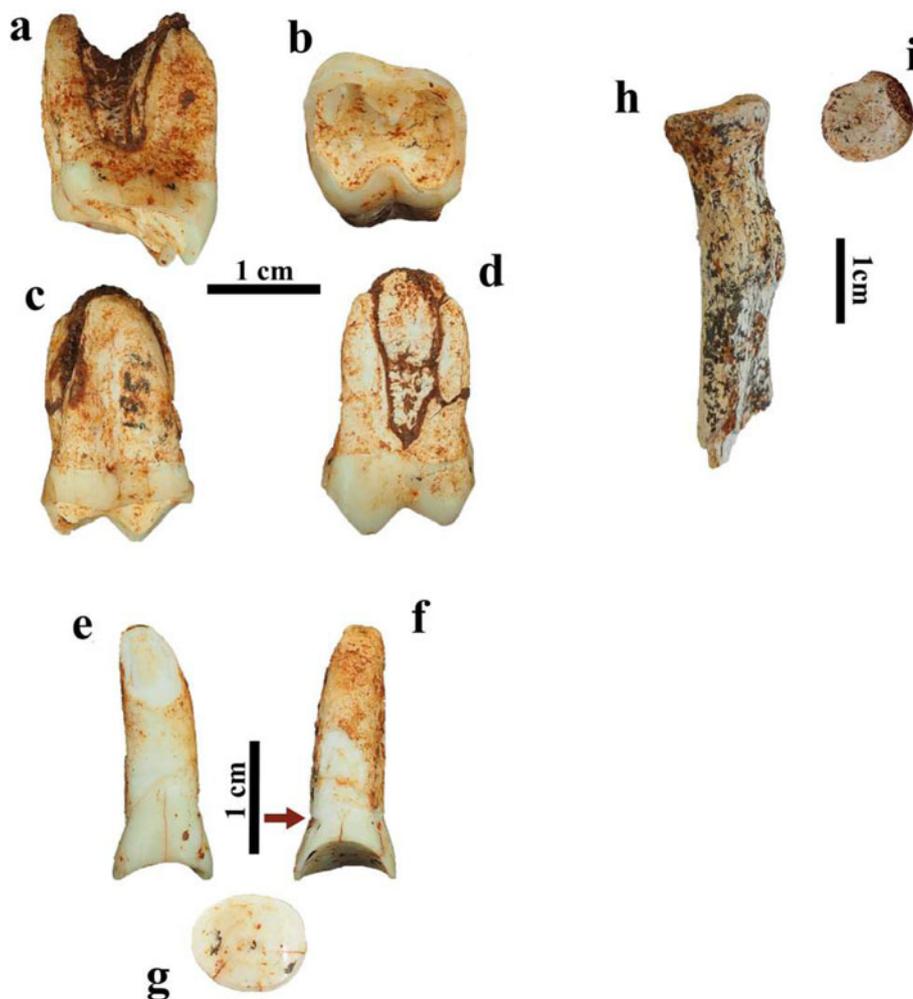


Figure 1 *cf. Paradolichopithecus* sp., Karnezeika: (a)–(d) left M2 (PCUP KZ1852), in mesial (a), occlusal (b), lingual (c) and buccal (d) view; (e)–(g) right I1 (PCUP KZ1400), in labial (e), lingual (f) and occlusal (g) view (the mesiodistal groove is indicated with an arrow); and proximal part of right radius (AMPG KZR93) in anterior (h) and proximal (i) view.

Eurasian Cercopithecidae, *Theropithecus* can easily be ruled out on the basis of its particular dental morphology with high crowns, columnar cusps and significantly developed enamel folding, as well as the characteristic double cross wear pattern (Jablonski 1993; Frost 2014). As far as the other three well-known genera are concerned, placing *Macaca* on the one side and the group *Paradolichopithecus–Procynocephalus* on the other, their molar morphology is quite similar but they differ

Table 1. Measurements of the teeth and radius of *cf. Paradolichopithecus* sp. from Karnezeika.

Measurement	<i>cf. Paradolichopithecus</i> sp.	
	<i>n</i>	Value (mm)
M2L	1	12.77
M2Wmes	1	13.07
M2Wdis	1	11.53
IL	1	8.68
IWmax	1	7.77
RaDmax	1	21.15
RaDmin	1	19.20

M2L = maximum mesiodistal diameter of M2; M2Wmes = mesial (first lobe) buccolingual diameter of M2; M2Wdis = distal (second lobe) buccolingual diameter of M2; IL = maximum mesiodistal diameter of I; IWmax = maximum labiolingual diameter of I; RaDmax = maximum head diameter of the radius; and RaDmin = minimum head diameter of the radius.

significantly in terms of size, as shown in Figure 2. The Karnezeika molar specimen seems to correspond metrically to the *Paradolichopithecus–Procynocephalus* group, while it appears consistently larger than all compared macaques. The occlusal surface dimensions can provide a safe criterion in distinguishing between *Macaca* and *Paradolichopithecus* dental remains (Alba *et al.* 2018), therefore attribution to the former can also be discounted.

Hence, based on the aforementioned morphological characters which are typical of the Papionini (excluding *Theropithecus*), and the tooth dimensions (much larger than *Macaca*), the specimen KZ1852 most likely belongs to the genus *Paradolichopithecus*. Dental remains of *Paradolichopithecus* are practically indistinguishable from *Procynocephalus* and their phylogenetic relationships along with the possibility of synonymy is still a matter of debate (see Simons 1970; Szalay & Delson 1979; Nishimura *et al.* 2010, 2014; Kostopoulos *et al.* 2018). Nevertheless, there is a consensus that the latter is an East Asian form. Moreover, in Greece the presence of *Par. arvernensis* has been documented already in two localities: Vatera (de Vos *et al.* 2002; van der Geer & Sondaar 2002; Lyras & van der Geer 2007); and Dafnero (Kostopoulos *et al.* 2018).

The incisor KZ1400 is quite problematic since it shows an unusual wear pattern. If its identification as a cercopithecoid upper incisor is valid, then it is very likely that it belongs to the same individual as the molar KZ1852, based on the similar degree of wear and the overall preservation. However, the wear

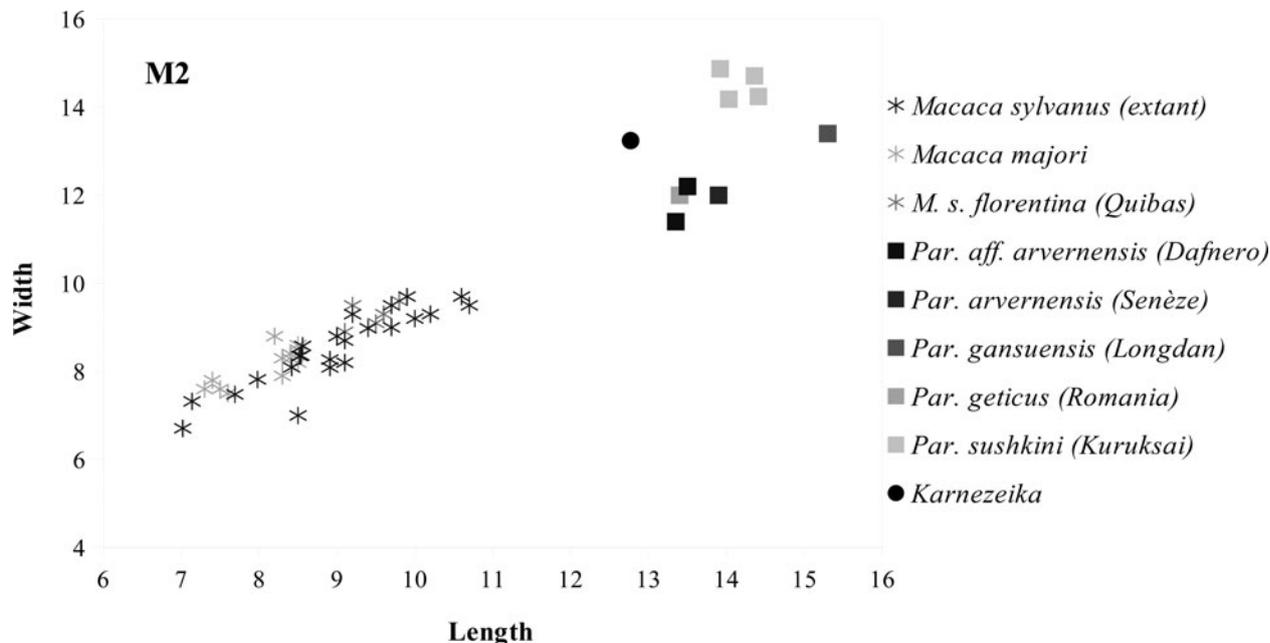


Figure 2 Bivariate plot of maximum length and width of the M2 of *cf. Paradolichopithecus* sp. from Karnezeika compared with other Papionini. Data from Takai *et al.* (2008) and references therein, Alba *et al.* (2011), Kostopoulos *et al.* (2018) and the PRIMO database (<http://primo.nycep.org>).

pattern does not correspond to the usual type found in Papionini and cercopithecine incisors, in which the labial surface appears significantly inclined, uniformly worn and the lingual side being more triangularly shaped (Shellis & Hiiemae 1986; Koufos & de Bonis 2017), and thus it could belong to a different mammal.

The articular surface of the proximal end of the radius exhibits a quite rounded shape (maximum head diameter of the radius (RaDmax) \times 100/minimum head diameter of the radius (RaDmin) = 110.15), which is similar to that of *Par. arvernensis* from Vatera (RaDmax \times 100/RaDmin = 111.28). *Macaca sylvanus florentina* is characterised by smaller dimensions and exhibits an even more rounded articular surface of the proximal end of the radius (RaDmax \times 100/RaDmin = 105.88 – see Figures 4 (c, d) in Alba *et al.* 2011). The studied radius from Karnezeika also differs from that of the modern baboon *Papio hamadryas* and the mandrill *Papio sphinx* as well. The two latter taxa have radii with an elliptical articular surface (see van der Geer & Sondaar 2002).

Whatever the case, the similarities with *Paradolichopithecus* cannot be dismissed based on the studied molar and radius; on the other hand, the two isolated dental elements and the partially preserved radius cannot be considered as conclusive and a comparison at the species level is not reliable at the moment. Therefore, due to this scarcity of material and for propriety reasons, it is considered best to ascribe the Karnezeika large-sized primate to *cf. Paradolichopithecus* sp.

The ecological profile of *Par. arvernensis* is yet poorly understood. However, postcranial evidence indicates a large-sized terrestrial (cursorial) monkey supposedly (see van der Geer & Sondaar 2002; Sondaar *et al.* 2006), while dental microwear analyses suggest a mixed/opportunistic and more abrasive diet with limited grass intake/consumption (see Williams & Holmes 2011; Plastiras 2021). This fits well with the Karnezeika palaeoenvironment of restricted open landscapes between rocky terrain (Sianis *et al.* 2022), which further implies the capability of this large cercopithecoid to occupy and exploit various habitats.

Biochronologically, the oldest *Paradolichopithecus* occurrence dates to around 3.2 Ma (Eronen & Rook 2004), while the most recent known record (Senèze, France) dates to around 2.1 Ma (Nomade *et al.* 2014; Delson *et al.* 2022). Sianis *et al.* (2022)

make some remarks concerning the similarity between the bovid mammal assemblage from the locality of Karnezeika and that of the well-known locality of Dafnero in north-western Greece (Koufos *et al.* 1991; Kostopoulos *et al.* 2019 and references therein). This may mean a similar age, possibly around 2.3 Ma (Benammi *et al.* 2020). Further biochronologic data that may become available in the future, will certainly result in a more reliable age estimation for the locality.

Paradolichopithecus remains a rare find in Greece (Koufos 2022) and in Europe as well, with only a few specimens referred to this genus. More specifically, in the Balkan area, apart from the Greek sites mentioned above (Vatera and Dafnero), the genus is also known from two Romanian localities: Valea Graunceanului (Necrasov *et al.* 1961; Terhune *et al.* 2020); and Malushteni (Delson 1973). Similar dental finds with the ones described herein, were recently described in the same manner from the locality of Ridjake in Serbia (Radović *et al.* 2019). Nevertheless, the few new finds described herein from Karnezeika indicate the possible presence of this important cercopithecoid taxon in Peloponnesus, widening further the distribution of *Paradolichopithecus* in Greece.

5. Acknowledgements

Some data for this work were acquired from PRIMO, the NYCEP PRIMate Morphology Online database (<http://primo.nycep.org>). Therefore, we thank Dr Eric Delson and his colleagues for allowing access to these data. Also, we thank the quarrying company Marmyk and its owner Thanasis Iliopoulos, firstly for extracting the fossiliferous block from the quarry and keeping it safely in the quarry facilities for years and secondly for providing their equipment to lift and carry the fossil-bearing blocks.

6. Financial support

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

7. Conflicts of interest

None.

8. References

- Alba, D. M., Carlos Calero, J. A., Mancheño, M. A., Montoya, P., Morales, J. & Rook, L. 2011. Fossil remains of *Macaca sylvanus florentina* (Cocchi, 1872) (Primates, Cercopithecoidea) from the Early Pleistocene of Quibas (Murcia, Spain). *Journal of Human Evolution* **61**, 703–18.
- Alba, D. M., Delson, E., Morales, J., Montoya, P. & Romero, G. 2018. Macaque remains from the early Pliocene of the Iberian Peninsula. *Journal of Human Evolution* **123**, 141–7.
- Anders, U., von Koenigswald, W., Ruf, I. & Smith, B. H. 2011. Generalized individual dental age stages for fossil and extant placental mammals. *Paläontologische Zeitschrift* **85**, 321–39.
- Aymard, M. 1854. Acquisitions d'ossements fossiles trouvés à Sainzelle, commune de Polignac; aperçu descriptif sur ce curieux gisement et détermination des espèces fossiles qu'il renferme [Acquisitions of fossil bones found in Sainzelle, commune of Polignac; descriptive overview of this curious deposit and determination of the fossil species it contains]. *Annales de la Société d'Agriculture, Sciences, Arts et Commerce du Puy* **18**, 51–4. [In French.]
- Benammi, M., Aidona, E., Merceron, G., Koufos, G. D. & Kostopoulos, D. S. 2020. Magnetostratigraphy and chronology of the Lower Pleistocene primate bearing Dafnero fossil site, N. Greece. *Quaternary* **3**, 22.
- Benefit, B. 1993. The permanent dentition and phylogenetic position of *Victoriapithecus* from Maboko Island, Kenya. *Journal of Human Evolution* **25**, 83–172.
- Burnett, C. T. 1828. Illustrations of the Manupeda or apes and their allies: being the arrangement of the Quadrumana or anthropomorphous beasts indicated in the outline. *The Quarterly Journal of Science, Literature and Art* **26**, 300–7.
- Cocchi, I. 1872. Su di due Scimmie fossili italiane [On two Italian fossil monkeys]. *Bollettino del R. Comitato Geologico d'Italia* **3**, 59–71. [In Italian.]
- de Bonis, L., Bouvrain, G., Geraads, D. & Koufos, G. 1990. New remains of *Mesopithecus* (Primates, Cercopithecoidea) from the Late Miocene of Macedonia (Greece), with the description of a new species. *Journal of Vertebrate Paleontology* **10**, 473–83.
- de la Lacépède, B. G. E. V. 1799. *Tableaux des divisions, sous-divisions, ordres et genres des mammifères. Discours d'Ouverture et de Clôture du Cours d'Histoire Naturelle, l'An VII de la République; et Tableaux Méthodiques des Mammifères et des Oiseaux* [ables of divisions, subdivisions, orders and genera of mammals. Opening and Closing Speeches of the Natural History Course, Year VII of the Republic; and Methodical Tables of Mammals and Birds]. Paris: Plassan. [In French.]
- Delson, E. 1973. *Fossil colobine monkeys of the circum-Mediterranean region and the evolutionary history of the Cercopithecoidea (Primates, Mammalia)*. PhD Thesis, Columbia University.
- Delson, E. 1975. Evolutionary history of the Cercopithecoidea. *Contributions to Primatology* **5**, 167–217.
- Delson, E., Baab, K. L., Capellini, T. D., Cooke, S., Freidline, S., Frost, S., Garrett, E. C., Harcourt-Smith, W. E. H., Hogg, R., McNulty, K., Pebun, T., Singleton, M., St. John, K., Steiper, M. & Van Couvering, J. A. 2022. Dating and site formation of the Late Villafranchian mammals from Senèze, France. Proceedings of 91st annual meeting of the American association of biological anthropologists, Denver March–April 2022. *American Journal of Biological Anthropology* **177**, 45.
- Depéret, C. 1889. Sur le *Dolichopithecus ruscinensis*, nouveau singe fossile du Pliocène du Roussillon [On *Dolichopithecus ruscinensis*, a new fossil monkey from the Pliocene of Roussillon]. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* **102**, 982–3. [In French.]
- Depéret, C. 1928. Les singes fossiles du Pliocène de France [Fossil monkeys from the Pliocene of France]. *Comptes-Rendus du XIV^e Congrès Géologique International, 1926*. Madrid. [In French.]
- Depéret, C. 1929. *Dolichopithecus arvernensis* Depéret: nouveau singe du Pliocène supérieur de Senèze (Haute-Loire) [*Dolichopithecus arvernensis* Depéret: new monkey from the Upper Pliocene of Senèze (Haute-Loire)]. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon* **15**, 5–12. [In French.]
- 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* **39A**, 37–70.
- 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.
- Eronen, J. T. & Rook, L. 2004. The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *Journal of Human Evolution* **47**, 323–41.
- Fernández-Jalvo, Y. & Andrews, P. 2016. *Atlas of taphonomic identifications. 1001 + images of fossil and recent mammal bone modification*. Dordrecht: Springer.
- Frost, S. 2014. Fossil Cercopithecoidea of the Konso Formation. In Suwa, G. (ed.) *Konso-Gardula research project, paleontological collections: background and fossil Aves, Cercopithecoidea, and Suidae*, 43–78. Bulletin: University Museum, University Tokyo **47**.
- Frost, S. R. 2017. Pleistocene primates. In Fuentes, A. (ed.) *The international encyclopedia of primatology*, 1–4. Chichester UK: John Wiley & Sons, **III**.
- Frost, S. R. & Kullmer, O. 2008. Cercopithecoidea from the Pliocene Chiwondo beds, Malawi-rift. *Geobios* **41**, 743–9.
- Geoffroy Saint-Hilaire, É. 1812. Tableau des Quadrumanes, 1. Ord. Quadrumanes [Table of Quadrumana, 1. Ord. Quadrumana]. *Annales du Muséum National d'Histoire Naturelle, Paris* 85–122. [In French.]
- Geoffroy Saint-Hilaire, É. 1843. Description des mammifères: nouveaux ou imparfaitement connus de la collection du Muséum d'histoire naturelle et remarques sur la classification et les caractères des mammifères [Description of mammals: new or imperfectly known from the collection of the Muséum d'histoire naturelle and remarks on the classification and characters of mammals]. *Archives du Muséum d'Histoire Naturelle, Paris*. [In French.]
- Gervais, P. 1848–1852. *Zoologie et paléontologie françaises (animaux vertébrés): ou nouvelles recherches sur les animaux vivants et fossiles de la France* [French zoology and palaeontology (vertebrate animals): or new research on the living and fossil animals of France]. Paris: Bertrand. [In French.]
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *The London Medical Repository Monthly Journal and Review* **15**, 296–310.
- Jablonski, N. G. 1993. *Theropithecus: the rise and fall of a primate genus*. Cambridge: Cambridge University Press.
- Kokotini, M., Kargopoulos, N., Iliopoulos, G., Roussiakis, S., Skandalos, P., Michailidis, D. & Svorligkou, G. 2019. Karnezeika (Argolis, Peloponnese): preliminary data concerning a new Villafranchian locality of Southern Greece. Proceedings of the 15th International Congress of the Geological Society of Greece. Bulletin of the Geological Society of Greece **Sp. Pub.** **7**, 104.
- Konidaris, G. E., Athanassiou, A., Panagopoulou, E. & Harvati, K. 2022. First record of *Macaca* (Cercopithecoidea, Primates) in the Middle Pleistocene of Greece. *Journal of Human Evolution* **162**, 103104.
- Konidaris, G. E., Athanassiou, A., Panagopoulou, E. & Harvati, K. in press. Fossil macaques (Cercopithecoidea, Primates) from the Middle Pleistocene of the Megalopolis basin, Greece. *Closing Symposium Human Evolution at the Crossroads, February 2022, Proceedings*.
- Kostopoulos, D. S., Aidona, E., Benammi, M., Gkeme, A., Grasset, L., Guy, F., Koufos, G., Kynigopoulou, Z., Le Maitre, A., Novello, A., Plastiras, C. & Merceron, G. 2019. The Lower Pleistocene primate-bearing fossil site of Dafnero (W. Macedonia, Greece): new data from classic and innovative approaches. *Proceedings of the 15th International Congress of the Geological Society of Greece, Bulletin of the Geological Society of Greece Sp. Pub.* **7**, 24.
- Kostopoulos, D. S. & Athanassiou, A. 1997. Les gazelles du Pliocène moyen-terminal de la Grèce continentale (Macédoine, Thessalie) [The gazelles of the middle-terminal Pliocene of mainland Greece (Macedonia, Thessaly)]. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **205**, 413–30. [In French.]
- Kostopoulos, D. S., Guy, F., Kynigopoulou, Z., Koufos, G. D., Valentin, X. & Merceron, G. 2018. A 2Ma old baboon-like monkey from Northern Greece and new evidence to support the *Paradolichopithecus-Procynocephalus* synonymy (Primates: Cercopithecoidea). *Journal of Human Evolution* **121**, 178–92.
- Koufos, G. D. 2009. The genus *Mesopithecus* (Primates, Cercopithecoidea) in the late Miocene of Greece. *Bollettino della Società Paleontologica Italiana* **48**, 157–66.
- Koufos, G. D. 2022. The fossil record of the Old-World monkeys (Mammalia: Primates: Cercopithecoidea) in Greece. In Vlachos, E. (ed.) *Fossil vertebrates of Greece, Vol. 1: basal vertebrates, amphibians, reptiles, Afrotherians, Glires, and primates*, 639–55. Cham: Springer.
- Koufos, G. D. & de Bonis, L. 2017. Upper incisor morphology of the Late Miocene hominoid *Ouranopithecus macedoniensis* from Axios Valley (Macedonia, Greece). *Anthropological Science* **125**, 141–51.
- Koufos, G., Kostopoulos, D. & Koliadimou, K. 1991. A new mammalian locality in the Villafranchian of Western Macedonia (Greece). *Comptes Rendus de l'Académie des Sciences (Série II)* **313**, 831–6.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis*,

- Synonymis, Locis [The System of Nature by the Three Kingdoms of Nature, according to Classes, Orders, Genera, Species, with Characters, Differences, Synonyms, Places]. In *Regnum Animale. Editio Decima, Reformata*, I. Stockholm: Laurentius Salvius. [In Latin.]
- Lyras, G. A. & van der Geer, A. A. E. 2007. The Late Pliocene vertebrate fauna of Vatera (Lesvos Island, Greece). *Cranium* **24**, 11–24.
- Necrasov, O., Samson, P. & Radulesco, C. 1961. Sur un nouveau singe catarrhinien fossile, découvert dans un nid fossilifère d'Olténie (R.P.R.) [On a new fossil catarrhine monkey, discovered in a fossiliferous nest of Oltenia (R.P.R.)]. *Analele științifice ale Universității "Al. I. Cuza" din Iasi* **7**, 401–16. [In French.]
- Nishimura, T. D., Ito, T., Yano, W., Ebbestad, J. O. R. & Takai, M. 2014. Nasal architecture in *Procyonocephalus wimani* (Early Pleistocene, China) and implications for its phyletic relationship with *Paradolichopithecus*. *Anthropological Science* **122**, 101–13.
- Nishimura, T. D., Zhang, Y. & Takai, M. 2010. Nasal anatomy of *Paradolichopithecus gansuensis* (early Pleistocene, Longdan, China) with comments on phyletic relationships among the species of this genus. *Folia Primatologica* **81**, 53–62.
- Nomade, S., Pastre, J. F., Guillou, H., Faure, M., Guérin, C., Delson, E., Debar, E., Voinchet, P. & Messager, E. 2014. 40Ar/39Ar Constraints on some French landmark Late Pliocene to Early Pleistocene large mammalian paleofaunas: Paleoenvironmental and paleoecological implications. *Quaternary Geochronology* **21**, 2–15.
- Plastiras, C. A. 2021. *Ecological diversity of Pliocene to Pleistocene Palaearctic cercopithecids (Primates, Mammalia); evidence from dental tissue*. PhD Thesis, School of Geology, Aristotle University of Thessaloniki, Annex Number of Scientific Annals of the School of Geology 221, 1–228.
- Radović, P., Lindal, J., Marković, Z., Alaburić, S. & Roksandić, M. 2019. First record of a fossil monkey (Primates, Cercopithecidae) from the Late Pliocene of Serbia. *Journal of Human Evolution* **137**, 102681.
- Rüttimeyer, L. 1878. Die Rinder der Tertiär-Epoche nebst Vorstudien zu einer Natürlichen Geschichte der Antilopen [The cattle of the tertiary epoch together with preliminary studies for a natural history of the antelopes]. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* **4–5**, 1–208. [In German.]
- Shellis, R. P. & Hiimae, K. M. 1986. Distribution of enamel on the incisors of Old-World monkeys. *American Journal of Physical Anthropology* **71**, 103–13.
- Sianis, P. D., Kostopoulos, D. S., Roussiakis, S., Athanassiou, A. & Iliopoulos, G. 2022. The Bovids (Artiodactyla) from the Lower Pleistocene Locality of Karnezeika (Southern Greece). *Historical Biology*. <https://doi.org/10.1080/08912963.2022.2060101>.
- Simons, E. L. 1970. The development and history of Old-World monkeys. In Napier, J. R. & Napier, P. H. (eds) *Old World monkeys*, 97–137. New York: Academic Press.
- Singleton, M. 2003. Functional and phylogenetic implications of molar flare variation in Miocene hominoids. *Journal of Human Evolution* **45**, 57–79.
- Sondaar, P., van der Geer, A. & Dermitzakis, M. 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**, 434–42.
- Swindler, D. R. 2002. *Primate dentition: an introduction to the teeth of non-human primates*. Cambridge: Cambridge University Press.
- Symeonidis, N. K. & Zapfe, N. 1977. Primatenzähne (Cercopithecidae) aus einer pliozänen Spaltenfüllung im Steinbruch Tourkobounia. Athen [Primate teeth (Cercopithecidae) from a Pleistocene fissure fill in the Tourkobounia quarry, Athens]. *Annales Géologiques des Pays Helléniques* **28**, 207–14. [In German.]
- Szalay, F. S. & Delson, E. 1979. *Evolutionary history of the primates*. New York: Academic Press.
- Takai, M., Maschenko, E. N., Nishimura, T. D., Anezaki, T. & Suzuki, T. 2008. Phylogenetic relationships and biogeographic history of *Paradolichopithecus sushkini* Trofimov 1977, a large-bodied cercopithecine monkey from the Pliocene of Eurasia. *Quaternary International* **179**, 108–19.
- Terhune, C., Curran, S., Croitor, R., Drăgușin, V., Gaudin, T., Petculescu, A., Robinson, C., Robu, M. & Werdelin, L. 2020. Early Pleistocene fauna of the Olteț River Valley of Romania: biochronological and biogeographic implications. *Quaternary International* **553**, 14–33.
- van der Geer, A. A. E. & Sondaar, P. Y. 2002. The postcranial elements of *Paradolichopithecus arvernensis* (Primates, Cercopithecidae, Papiionini) from Lesvos, Greece. *Annales Géologiques des Pays Helléniques* **39 A**, 71–86.
- Wagner, A. 1839. Fossile Ueberreste von einem Affenschädel und andern Säugthieren aus Griechenland [Fossil remains of a monkey skull and other mammals from Greece]. *Gelehrte Anzeigen. Königlich Bayerische Akademie der Wissenschaften* **38**, 305–11. [In German.]
- Williams, F. L. E. & Holmes, N. A. 2011. Evidence of terrestrial diets in Pliocene Eurasian papionins (Mammalia: Primates) inferred from low-magnification stereomicroscopy of molar enamel use-wear scars. *Palaios* **26**, 720–9.

MS received 22 March 2022. Accepted for publication 14 October 2022. First published online 7 November 2022