

24 FOSSIL MACAQUES (CERCOPITHECIDAE, PRIMATES) FROM THE MIDDLE PLEISTOCENE OF THE MEGALOPOLIS BASIN (GREECE) WITH DESCRIPTION OF A NEW SPECIMEN FROM KYPARISSIA 4

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24.1 INTRODUCTION

Recent fieldwork in the Megalopolis Basin (Greece) has mainly focused on two Middle Pleistocene sites, Marathousa 1 and Kyparissia 4, both of which yielded rich faunal assemblages (e.g., ostracods, molluscs, fishes, amphibians, reptiles, birds, mammals) in stratigraphic and spatial association with Lower Palaeolithic lithic artefacts, thus documenting hominin presence in the region (Harvati et al., 2018 and articles therein; Karkanas et al., this volume). Marathousa 1 (MAR-1), located in the Marathousa mine, was discovered during targeted fieldwork in 2013 and systematically excavated from 2014 to 2019 by a team from the University of Tübingen Paleoanthropology group

and the Ephorate of Paleoanthropology–Speleology (see Harvati et al., 2018 and articles therein). MAR-1 is dated to ca. 450 ka and is correlated to the Marine Isotope Stage 12 (Panagopoulou et al., 2018 and references therein). The site’s large mammal faunal assemblage includes (Konidaris et al., 2018): *Castor fiber* (beaver), *Mustela* sp. (weasel), *Lutra simplicidens* (otter), *Felis* sp. (wildcat), *Vulpes* sp. (fox), *Canis* sp. (medium-sized canid), *Palaeoloxodon antiquus* (straight-tusked elephant), *Hippopotamus antiquus* (hippopotamus), *Bison* sp. (bison), *Dama* sp. (fallow deer) and *Cervus elaphus* (red deer). Of particular interest are the skeletal remains of at least two elephant individuals, some of which preserve evidence of anthropogenic modifications. Kyparissia 4 (KYP-4), located in the Kypa-



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rissia mine, was discovered in 2007 (Athanassiou, 2018; Athanassiou et al., 2018) and was revisited during a targeted field survey by a joint team from the University of Tübingen Paleoanthropology group, the Ephorate of Palaeoanthropology–Speleology at Athens, and the American School of Classical Studies at Athens. Preliminary stratigraphic and biochronological data indicate that KYP-4 is older than MAR-1 and is dated to the lower part of the Middle Pleistocene (Karkanis et al., this volume; van Kolfschoten et al., this volume). The site's large mammal faunal assemblage includes (Athanassiou, 2018; Athanassiou et al., 2018, this volume): *Castor fiber*, *Vulpes* sp., *Palaeoloxodon antiquus*, *Stephanorhinus* sp. (rhinoceros), *Equus* sp. (horse), *Hippopotamus antiquus*, *Bison* sp., *Sus scrofa* (boar), *Dama* sp., *Cervus elaphus* and *Praemegaceros verticornis* (giant deer).

Until recently macaques were not known from the Megalopolis Basin. During the 2019 excavation at MAR-1, an almost complete mandible

(MAR-1B-9) was unearthed from the site's Area B and studied by Konidaris et al. (2022). More recently, during the 2021 field survey in the Kyparissia mine, an isolated upper first molar was found at KYP-4 (KYP4A-1075) in the sedimentary unit UA5 of Area A, which consists of dark grey sandy mud, very rich in organics and freshwater molluscs. This new macaque specimen is the primary focus of this study. Both specimens are housed at the Ephorate of Palaeoanthropology–Speleology (EPS) in Athens (Greece).

All European fossil macaque forms (except for the endemic insular *Macaca majori* Azzaroli, 1946 from Sardinia in Italy) are currently attributed to the Barbary macaque *Macaca sylvanus* (Linnaeus, 1758), a species that was geographically widely distributed in western Eurasia during the Plio-Pleistocene (Delson, 1975; Elton and O'Regan, 2014; Mecozzi et al., 2021). Three (chrono)subspecies are generally recognized (Szalay and Delson, 1979; Delson, 1980; Alba et al., 2011): *Macaca sylvanus*

TAXON	PROVENANCE	SOURCE
<i>Macaca sylvanus sylvanus</i>	extant	Alba et al. (2011), PRIMO (2021)
<i>Macaca majori</i>	Capo Figari (Italy)	PRIMO (2021)
<i>Macaca sylvanus prisca</i>	Balaruc (France)	PRIMO (2021)
	Cova Bonica (Spain)	Delson (1971)
	Gundersheim (Germany)	Rook et al. (2001)
	Montpellier (France)	PRIMO (2021)
	RDB quarry, Villafranca d'Asti (Italy)	Rook et al. (2001)
<i>Macaca sylvanus florentina</i> or <i>M. s. cf. florentina</i>	Cal Guardiola (Spain)	Alba et al. (2008)
	Estació de Vallparadís (Spain)	Alba et al. (2008)
	Monte Peglia (Italy)	PRIMO (2021)
	Quibas (Spain)	Alba et al. (2011)
	Tourkovounia-2 (Greece)	Symeonidis and Zapfe (1976)
	Upper Valdarno (Italy)	PRIMO (2021)
<i>Macaca sylvanus pliocena</i> or <i>M. s. cf. pliocena</i>	Gajtan (Albania)	PRIMO (2021)
	Heppenloch (Germany)	Adam (1975)
	Kudaro 1 (Caucasus)	PRIMO (2021)
	Quecchia Quarry (Italy)	Bona et al. (2016)

Table 1: Comparative dental sample (fossil and extant) used in the analyses of the Kyparissia 4 specimen.

prisca Gervais, 1859 from the Pliocene, *Macaca sylvanus florentina* (Cocchi, 1872) from the Early Pleistocene, and *Macaca sylvanus pliocena* Owen, 1846 from the Middle–early Late Pleistocene. The diagnosis of these subspecies relies mainly on differences in dental size and proportions; however, there is great overlap in almost all parameters among the fossil, as well as the extant, subspecies and therefore subspecific assignments are often based on (bio)chronological grounds rather than on diagnostic morphological features.

24.2 METHODS

Dental terminology follows Delson (1975). Standard dental measurements (following Alba et al., 2011) of maximum mesiodistal crown length (MD), and buccolingual crown breadth at the mesial [BLm=BL (maximum buccolingual crown breadth)] and distal (BLd) lobes, were taken with a digital caliper to the nearest 0.1 mm. A breadth/length index (BLI) was also calculated ($BLI = BL / MD \times 100$). Comparative dental measurements (Tables 1 and 2; following in some cases the taxonomic attributions of Alba et al., 2019) were obtained from the literature and from publicly available sources [PRIMO (the New York Consortium in Evolutionary Primatology PRimate Morphometrics Online) database, accessed November 2021; <http://primo.nycep.org>]. Box-and-whisker plots and statistical computations were performed with the software package PAST v. 4.09 (Hammer et al., 2001; <https://www.nhm.uio.no/english/research/resources/past/>).

24.3 THE MARATHOUSA 1 SPECIMEN

The mandible from Marathousa 1 (Fig. 1a–c) was studied in detail in Konidaris et al. (2022), and it

is only briefly presented here. The specimen originally consisted of two hemimandibles (deposited about 1.6 m apart) that fit together under the alveolus of the right P_3 . The refitted complete mandible (MAR-1B-9) bears the left canine and the left P_3 – M_2 , and the right P_4 – M_3 . The mandible belonged to a male individual of advanced ontogenetic age and of estimated body mass of ~13 kg. Mandibular and dental morphology, and dental size and proportions of MAR-1B-9 fit well within the range of extinct and extant *M. sylvanus*. The dental dimensions of the MAR-1 macaque fit better within the variation of *M. s. florentina* and *M. s. pliocena* rather than with the extant representative *M. s. sylvanus*. Moreover, a principal component analysis (combining M_1 MD, M_1 BL, M_2 MD, M_2 BL, M_3 MD, and M_3 BL of complete M_1 – M_3 tooth rows) shows that these two fossil subspecies differ from the modern representative in their longer and broader M_1 , and the longer M_3 . Although *M. s. florentina* and *M. s. pliocena* overlap greatly, the MAR-1B-9 macaque fits better with *M. s. pliocena* and does not fall within either the *M. s. florentina* or the extant *M. s. sylvanus* range (Fig. 1d).

24.4 THE KYPARISSIA 4 SPECIMEN

24.4.1. DESCRIPTION

The right M^1 KYP4A-1075 [MD = 8.3; BLm=7.9; BLd=7.2; crown height = 5.3 (at the paracone); all in mm; BLI=95] is almost unworn, and the crown is well-preserved; there is a mesial contact facet (Fig. 2a). It bears a single lingual root, a mesiobuccal one missing its tip, and a damaged distobuccal one. It displays a bilophodont occlusal pattern with a wider mesial lobe than the distal one. The lobes are separated by a relatively well-developed median lingual cleft and a less marked buccal one.

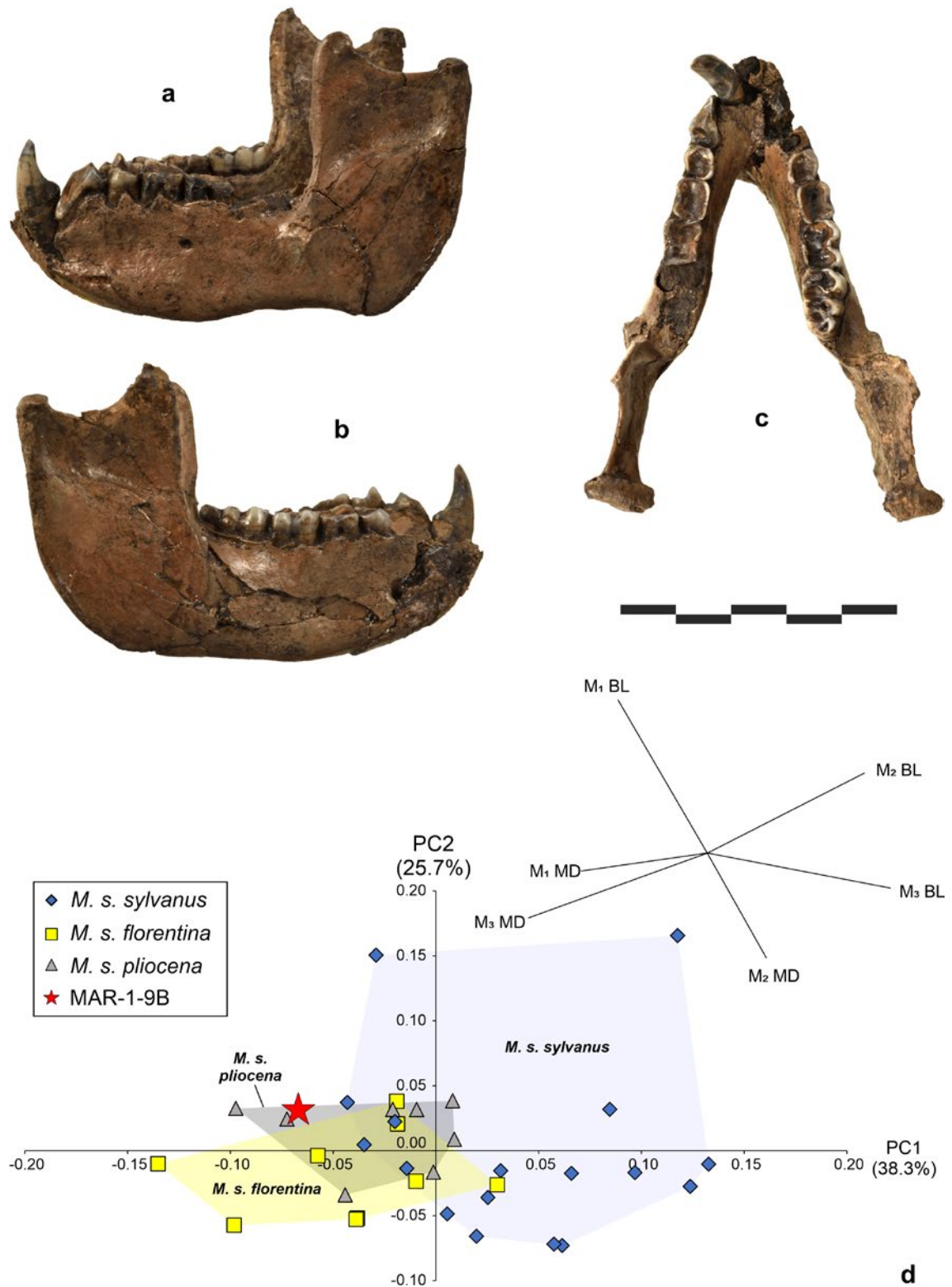


Figure 1: Mandible of *Macaca sylvanus* cf. *pliocena* (EPS-MAR-1B-9) from Marathousa 1, in a, left lateral; b, right lateral; and c, dorsal views; scale = 5 cm; d, principal component analysis of dental variables among *M. s. sylvanus* ($n = 17$), *M. s. florentina* ($n = 9$) and *M. s. pliocena* ($n = 8$) using Mosimann's Log-shape ratio transformation. Only complete M₁–M₃ tooth rows are included; for MAR-1B-9 the right tooth row is used. The principal component biplot depicting the projection of the original axes (variables) is also shown.

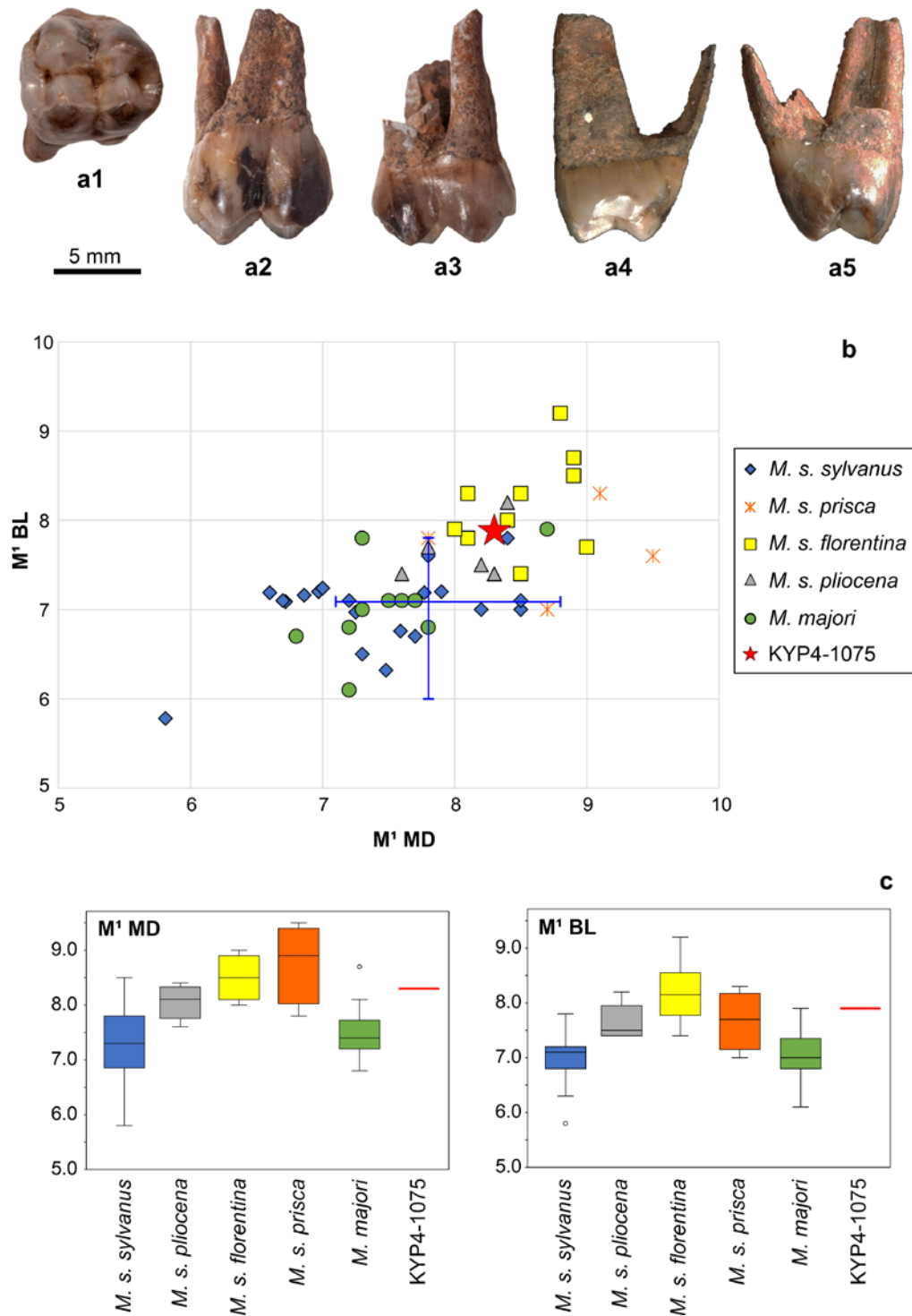


Figure 2: a, Right M¹ (EPS-KYP4A-1075) of *Macaca sylvanus* ssp. from Kyparissia 4; in a1, occlusal (mesial is to the left); a2, lingual; a3, buccal; a4, mesial; a5, distal views; b, Bivariate dental plot of BL vs. MD (in mm) for the macaque M¹ from Kyparissia 4, compared with those of modern and fossil *Macaca sylvanus* subspecies and *Macaca majori* from various localities (see Methods); the blue ranges in the plot correspond to the *M. s. sylvanus* sample ($n = 35$) of Alba et al. (2011); c, Box-and-Whisker plots of BL and MD (in mm) for the M¹ of extant and fossil macaques (colors correspond to those of 2b) compared with that from Kyparissia 4. Horizontal lines represent the median; boxes the 25 and 75 percentiles (interquartile range); whiskers the minimum-maximum values; circles the outliers. Comparative sample: *M. s. sylvanus* ($n = 21-25$), *M. s. pliocena* ($n = 5-6$), *M. s. florentina* ($n = 10$), *Macaca s. prisca* ($n = 4$), and *M. majori* ($n = 13-14$) from various localities (see Methods and Table 1).

The buccal notch is shallow relative to the height of the crown. Buccal (paracone and metacone) and lingual (protocone and hypocone) main cusps are almost aligned in each lobe. The paracone is slightly larger than the other main cusps. The mesial fovea, which is delimited by the preprotocrista, the preparacrista, and the rather strong and almost straight mesial marginal ridge, is relatively short but deep. The central fovea (trigon basin) is deeper and more expanded than the mesial and distal foveae. The distal fovea, which is delimited by the postmetacrista, the posthypocrista, and the rather strong and curved distal marginal ridge (formed by several tubercles in a row), is wide but rather shallow.

24.4.2. COMPARISONS

The generalized papionin occlusal pattern of KYP4A-1075 is compatible with an attribution to *Macaca* (e.g., Alba et al., 2008, 2011), while its dental size and proportions fit well within the

range of extinct and extant *Macaca sylvanus* (Fig. 2; Table 2). On the other hand, an assignment to *Paradolichopithecus*, the other extinct European papionin also present in the Pleistocene of Greece, can be safely excluded based on the larger dental dimensions of this genus (see e.g., Kostopoulos et al., 2018).

The crown measurements of KYP4A-1075 (MD=8.3 mm; BLm=7.9 mm) are below the known metrical variation of both M² and M³ of fossil *M. sylvanus* [M² MD=9.1–11 (*n*=26); M² BLm=8.0–10.9 (*n*=27); M³ MD=8.6–10.6 (*n*=17); M³ BLm=8.6–10.4 (*n*=17); from references cited in Table 1 plus Alba et al. (2016, 2018), Reumer et al. (2018) and van Kolfshoten (2020); see also the bivariate dental plots of M² and M³ in Alba et al. (2016: Fig. 4) and Alba et al. (2018: Fig. 3b), respectively], and fit well within the size range and proportions of M¹ (Fig. 2b, c). Furthermore, in contrast to the usually moderate and marked distal tapering of the crown in the M² and M³, respectively, in M¹ the tapering is rather weak (Alba et al., 2016, 2018), as it is in KYP4A-1075

		<i>n</i>	MEAN	SD	MINIMUM	MAXIMUM	Z-SCORE
M ¹ MD	KYP4A-1075	1	8.30	-	-	-	
	<i>M. s. sylvanus</i> *	25	7.33	0.69	5.80	8.50	1.40
	<i>M. s. sylvanus</i> **	35	7.81	0.41	7.10	8.80	1.20
	<i>M. s. pliocena</i>	6	8.05	0.31	7.60	8.40	0.81
	<i>M. s. florentina</i>	10	8.52	0.37	8.00	9.00	-0.59
	<i>M. s. prisca</i>	4	8.78	0.73	7.80	9.50	-0.65
M ¹ BL	KYP4A-1075	1	7.90	-	-	-	
	<i>M. s. sylvanus</i> *	21	7.00	0.43	5.80	7.80	2.12
	<i>M. s. sylvanus</i> **	35	7.09	0.41	6.00	7.80	1.98
	<i>M. s. pliocena</i>	5	7.64	0.34	7.40	8.20	0.77
	<i>M. s. florentina</i>	10	8.18	0.53	7.40	9.20	-0.53
	<i>M. s. prisca</i>	4	7.68	0.54	7.00	8.30	0.42

Table 2: Descriptive statistics and calculated z-scores for dental measurements of EPS-KYP4A-1075 compared with *Macaca sylvanus sylvanus* (*data from PRIMO, ** data from Alba et al., 2011), *Macaca sylvanus pliocena*, *Macaca sylvanus florentina* and *Macaca sylvanus prisca* (see Methods). When $z > |1.96|$, the null hypothesis that EPS-KYP4A-1075 fits within the variation of the comparative sample can be rejected at $p < 0.05$; in such cases, the z-score is typed in bold. SD = standard deviation.

(BLd=7.2 mm), while additionally the KYP-4 molar lacks any accessory cusp on the distal margin, which is frequently present in papionin last molars (Alba et al., 2018). Therefore, the KYP4A-1075 is recognized as M¹.

Morphologically, the molar does not show any substantial difference from those of extinct and extant *M. sylvanus*; therefore, we focus on dental crown dimensions. In the MD vs. BL biplot although some overlap exists, KYP4A-1075 is rather well-distinguished from *M. majori* and *M. s. sylvanus* and is comfortably placed with the fossil *M. sylvanus* subspecies (Fig. 2b). In the Box-and-Whisker plot, the MD dimension of the KYP-4 molar plots at the upper range of *M. s. sylvanus*, but outside its interquartile range; it is also distinguished from *M. majori* (Fig. 2c). The molar stands at the upper limit of the interquartile range of *M. s. pliocena*, and at the lower quartile of *M. s. florentina* and *M. s. prisca*. In terms of the BLm dimension, KYP4A-1075 is outside the range of *M. s. sylvanus* and plots at the maximum value of *M. majori*. It stands at the upper quartiles of *M. s. pliocena* and *M. s. prisca*, and at the lower quartile of *M. s. florentina*. Similar results are obtained by the statistical comparison using z-scores of KYP4A-1075 with the subspecies of *M. sylvanus* (Table 2). The analysis detects significant difference of KYP4A-1075 in terms of the M¹ BL with the extant *M. s. sylvanus*.

24.4.3. ONTOGENETIC AGE, SEX AND BODY MASS ESTIMATION

The ontogenetic age of the KYP-4 macaque individual can be estimated based on the sequence and timing of tooth eruption in primates, and on the degree of dental wear. The first permanent molar is particularly informative because it is the first of the permanent teeth to erupt in macaques and marks

the end of infancy (end of weaning) and the beginning of independence (Smith, 1994; Smith et al., 1994). The presence of a mesial contact facet in the KYP4A-1075 M¹ indicates that at the time of death the tooth had been already erupted and was functional, while the absence of a distal contact facet indicates that the M² was unerupted, at least not completely. Available dental eruption times for extant macaques show that the M¹ and the M² emerge at about 17–21 months and 39–45 months of postnatal life on average, respectively (Smith et al., 1994). Therefore, KYP4A-1075 would belong to an individual of a minimum age approximately between 1.5 and 2 years old, and considering the absence of a distal contact facet, of maximum age approximately between 4 and 4.5 years old. Taking into account the almost unworn state of the molar, an age at death closer to the minimum estimate, i.e., around 2 years is more plausible. Indeed, based on its minimal wear, the KYP-4 specimen can be placed towards the end of the individual dental age stage (IDAS) 1 (infant) and the beginning of IDAS 2 (juvenile) of Anders et al. (2011). KYP4A-1075 belonged to an individual of comparable age (perhaps only slightly younger) as that of the juvenile mandible of *Macaca sylvanus* cf. *pliocena* from Gruta da Aroeira (Spain), which preserves the fully erupted dP₃, dP₄ and M₁ (the latter only slightly worn), while the P₄ and M₂ are inside their alveoli; the age at death of this individual was estimated close to 2.5 years (Alba et al., 2019). Thus overall, the KYP-4 macaque can be regarded as a (subadult) juvenile individual.

To estimate the body mass of the KYP-4 macaque, we applied the allometric regressions of Delson et al. (2000: Table 7) for cercopithecines based on M¹ MD (8.3 mm), M¹ BLm (7.9 mm) and M¹ area [$MD \times 0.5(BLm + BLd)$]. The resulting body mass estimate was 10.6 kg. However, this value has to be regarded as corresponding to its adult stage (when the full permanent dentition would have

been erupted), and the expected body mass at the age of death of the KYP-4 macaque would be lower. Indeed, the body mass range of juveniles (with some of the permanent teeth erupted) of extant *M. s. sylvanus* is 6.2–8.6 kg ($n = 3$; Fooden, 2007: Table 2). Considering the larger dental dimensions of KYP4A-1075 than most of the comparative *M. s. sylvanus* sample (Fig. 2 b, c), a body mass at the age of death closer to the upper range (~8–9 kg) seems more plausible. On the other hand, the estimated body mass of 10.6 kg at the adult stage fits within the ranges of adult females and males, being however, very close to the mean values of females provided by Delson et al. (2000) and Fooden (2007).

24.5 DISCUSSION – CONCLUSIONS

24.5.1. TAXONOMIC ATTRIBUTION OF THE MEGALOPOLIS SPECIMENS

The metrical comparison of KYP4A-1075 separates it rather well from the extant *M. s. sylvanus* and reveals a better match with the fossil subspecies (*M. s. prisca*, *M. s. florentina* and *M. s. pliocena*); however, their great size overlap, the single specimen status, and the absence of clear-cut diagnostic criteria that may differentiate the European fossil subspecies, do not allow for a subspecific allocation at the moment. Therefore, KYP4A-1075 is attributed to a fossil European *Macaca sylvanus* ssp. Likewise, the study of the mandible MAR-1B-9 (Konidaris et al., 2022) showed that the dental dimensions fit better within the variation of *M. s. florentina* and *M. s. pliocena* rather than with the extant representative *M. s. sylvanus*, but additionally, the principal component analysis revealed a better match with *M. s. pliocena*; therefore, MAR-1B-9 was attributed to *M. s. cf. pliocena*, consistent also with the specimen's chronology.

24.5.2. IMPLICATIONS WITHIN THE REGIONAL AND EUROPEAN CONTEXT

The recent investigations in the Megalopolis Basin have enriched the *Macaca* record known from Greece, previously limited to the Early Pleistocene (Symeonidis and Zapfe, 1976), by adding material from secure stratigraphic, chronological and palaeoenvironmental contexts. Additionally, the Megalopolis specimens are important for several reasons:

- MAR-1B-9 represents the most complete fossil European macaque mandible known.
- The Megalopolis specimens constitute some of the very few known records of *Macaca* in the eastern sector of the peri-Mediterranean region and are among the southernmost European occurrences [see distribution maps of fossil macaques in Elton and O'Regan (2014) and Mezzozzi et al. (2021)].
- They mark the first known presence of macaques during the Middle Pleistocene of Greece.
- They extend the chronological range of cercopithecids (Late Miocene to Middle Pleistocene) in the country.
- They document for the first time the coexistence of macaques and hominins in Greece.
- The exquisitely preserved, rich and well-documented assemblages of both Megalopolis Basin sites allow not only their secure chronological placement, but also a detailed reconstruction of the environmental conditions under which these individuals lived, and of the prey-predator relationships among hominins, carnivores, and macaques (Konidaris et al., 2022).
- Marathousa 1 can be added to those European sites that document the coexistence of macaques and hominins, and it has yielded evidence of elephant butchering (Konidaris and Tzourloukis, 2021; Konidaris et al., 2022).
- The record of macaques in different stratigraphic levels within the Middle Pleistocene deposits of the Megalopolis Basin, including

periods of colder conditions during glacial or stadial stages (see Bludau et al., 2021; Boni et al., this volume; Butiseacă et al., this volume; Kyrikou et al., this volume; Papadopoulou et al., this volume), might point to a continuous presence in the region and suggests that this southern region could have acted as a refugium for European macaque populations. Recent palaeoenvironmental reconstruction indeed points to the presence of permanent freshwater bodies throughout the year even during glacial periods (Konidaris et al., 2018; Bludau et al., 2021)

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