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Macaca ulna from new excavations at the Notarchirico Acheulean site (Middle Pleistocene, Venosa, southern Italy)

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Introduction

The taxonomy of European macaques

The first records of macaque in Eurasia are from the latest Miocene fossiliferous sites of Almenara-Casablanca-M (Spain) (Köhler et al., 2000) and Moncucco Torinese (Italy) (Alba et al., 2014), yielding remains assigned to cf. *Macaca* sp. (Table SD1). These data suggest that macaques probably dispersed out of Africa between 5.9 and 5.3 Ma, when the sea level dropped during the Messinian Salinity Crisis (Agustí et al., 2006; Alba et al., 2014, 2015; Colombero et al., 2017). Although there is consensus to consider that the European fossil macaques belong to the *Macaca sylvanus* lineage, uncertainty persists regarding their specific taxonomic status. European fossil remains of macaques are usually grouped in chronologically successive subspecies of *Macaca sylvanus*: the Pliocene *M. sylvanus prisca* Gervais, 1859; the late Pliocene to Early Pleistocene *M. sylvanus florentina* Cocchi, 1872; and the Middle to Late Pleistocene *M. sylvanus pliocena* Owen, 1846 (Szalay and Delson, 1979; Delson, 1980; Alba et al., 2008, 2011, 2016; Marigó et al., 2014) (Table SD1). However, most of the taxonomic attributions are based on the chronology of the findings, with only subtle differences recognized between *M. sylvanus* subspecies (Szalay & Delson, 1979; Delson, 1980; Alba et al., 2019). Indeed, fossil remains of *M. s. florentina* are considered larger than those of *M. s. prisca*, but close to extant specimens of *M. s. sylvanus* (Rook et al., 2001); whereas specimens of *M. s. pliocena* are nearly identical to those of *M. s. florentina*,, except for slightly wider cheek teeth (Delson, 1980). Given the lack of adequate diagnostic characters, several attributions do not go beyond the species level (Montoya et al. 1999; Zapfe, 2001).

A second macaque lineage in Europe is represented by the extinct *Macaca majori*, an endemic primate from the Plio-Pleistocene of Sardinia (Italy) (Rook et al., 2001; Alba et al., 2014) (Table SD1). The rich sample collected from Capo Figari, Monte Tuttavista and Is Oreris (Rook &

O'Higgins, 2005; Rook, 2009; Alba et al., 2014; Zoboli et al. 2016) allows a clear diagnosis for this taxon (e.g., a short anteroposterior palatal length, reduced body size) (see Zoboli et al. 2016).

Fossil macaques from the Italian record

The majority of the Italian fossil primates was described from 1870s to the beginning of 1900s (Gervais, 1872; Cocchi, 1872; Forsyth Major, 1872a,b, 1875, 1914; Ottolenghi, 1898; Seguenza, 1902, 1907; Merciai, 1907; Portis, 1917). Nevertheless, this mammalian group was almost forgotten by Italian paleontologists during the last century, and as recently as in the last decades only a few studies were published (Rook & O'Higgins, 2005; Rook, 2009; Zoboli et al., 2016; Bona et al., 2017). However, one of the earliest occurrences of macaque in Europe is from Moncucco Torinese (dated approximately 5.41-5.33 Ma), where *Mesopithecus pentelicus pentelicus* is also documented (Alba et al., 2013; Colombero et al., 2017). Except for *M. majori*, the Italian Plio-Pleistocene record of macaque was poorly investigated (Gentili et al., 1998; Rook, 2009). The Pliocene macaque from Villafranca d'Asti is tentatively assigned to *M. s. prisca* (Rook et al., 2001), whereas the fossil remains from the Early Pleistocene are generally ascribed to *M. s. florentina* (Barberino del Mugello, Monte Peglia, Pietrafitta, Valdarno Superiore) (Rook, 1997; Gentili et al., 1998) (Table SD1). Many fossils recorded from the Middle Pleistocene sites of the Italian Peninsula are commonly referred to *Macaca sylvanus* ssp., but seldom described in detail (Table SD1). The latest occurrence of Barbary macaque from Italian Peninsula is currently attested by the early Late Pleistocene of Grotta degli Orsi Volanti (Mazza et al., 2005) (Table SD1).

Here the fossil macaque from recent fieldworks at Notarchirico (Venosa basin, southern Italy), which represents the southernmost and easternmost occurrence of *Macaca sylvanus* in the Italian fossil record, is described for the first time (Fig. 1a-c).

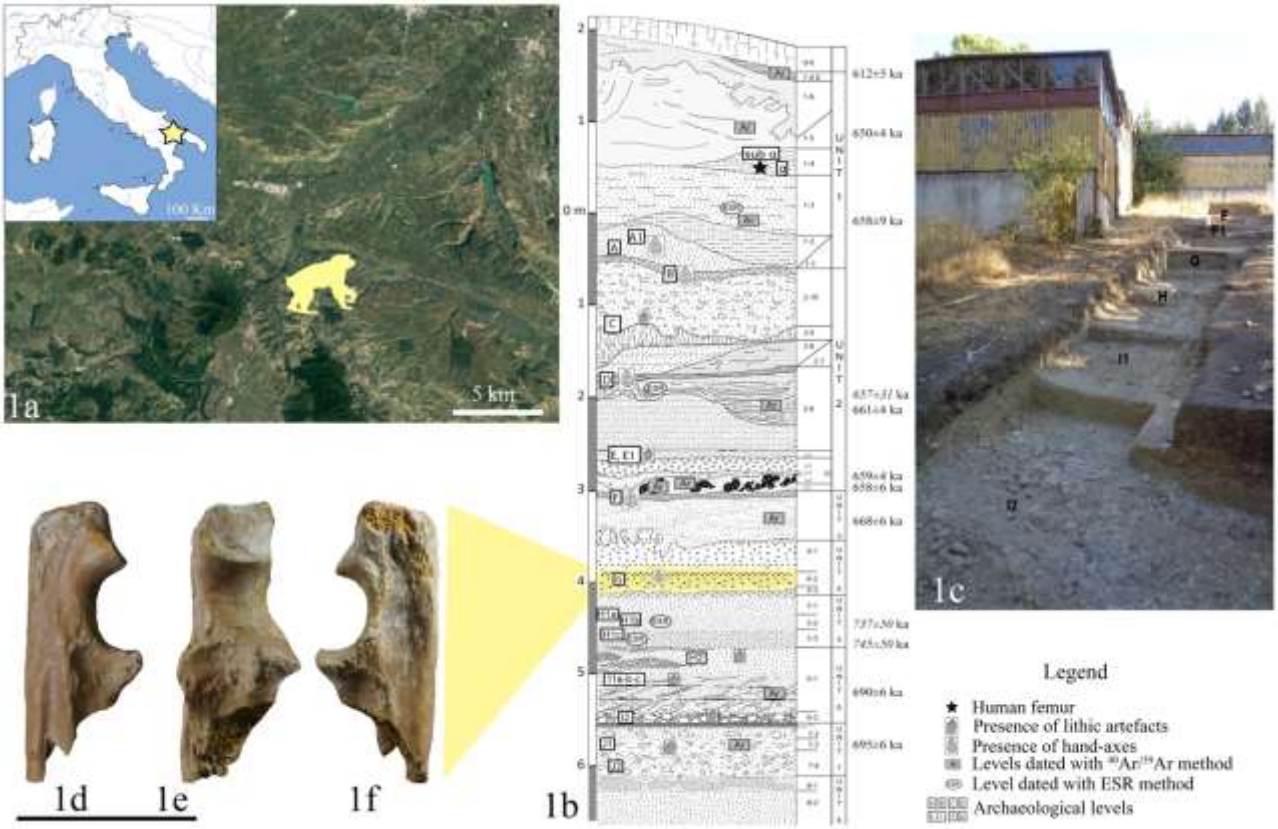

Fig. 1 – Location map (1a), view and description of the stratigraphic succession of Notarchirico (southern Italy) (1b-1c). Monkey outline in 1a indicates the geographic position of the site. B24GNC, fragmented right ulna from Notarchirico in medial (1d), anterior (1e) and lateral (1f) views. Scale bar for Figs. d-f 3 cm.

Geological and paleontological context

The Notarchirico site, discovered in 1979, has yielded a 7 m-thick sequence of fluvial sediments within eleven archaeological levels (Fig.1b-c). The old excavations found a rich fossil sample, including a hominin femur fragment found in the upper part of the sequence (level α, Belli et al., 1991). The faunal assemblage mainly collected from the upper part of the sedimentary succession was attributed to the Isernia faunal unit (Sala et al., 1999). $^{40}Ar/^{39}Ar$ ages and ESR dates have revised the chronology of the whole sedimentary sequence and constrained all archaeological levels between ca. 610 and 675 ka from the upper part of the sequence (level A to level F) excavated by M. Piperno in the 1980's (Pereira et al., 2015). Since 2016, new excavation campaigns started in the long archeological sequence of Notarchirico (Moncel et al., 2019). New fieldwork focusing on the unknown base of the sequence have permitted the team to recognize four additional units (G, H, I and J), all older than 668 ± 6 ka (Pereira et al., 2015, Moncel et al., 2019, 2020) (Fig. 1b-c). The $^{40}Ar/^{39}Ar$ ages calculated for levels I and J (695.2 ± 6.2 ka and 690.3 ± 5.8 ka) are undistinguishable, suggesting a rapid deposition of the mainly fluvial complex sediment during MIS 17 towards the MIS 16

transition (Moncel et al., 2020). Among large mammals, the main faunal association includes *Palaeoloxodon antiquus*, *Hippopotamus antiquus*, *Dama* cf. *clactoniana* and *Bison schoetensacki*, among others. Cervids are dominant among the large mammals, whereas equids, rhinocerotids and carnivorans are missing. The mammal association indicates the presence of humid zones in a varied landscape and a relatively warm climate. Biochronologically, it also permits to attribute the levels A and α, as well as the newly excavated levels G to I, to the Galerian period (Moncel et al., 2020), consistent with the recent chronometric dating (Moncel et al., 2020) and lithic artefacts (Moncel et al., 2020). Levels G, H and I yield evidence of hominin occupations with artefacts including bifaces in level G, pushing back the age of the biface production (and the Acheulean) in Southern Europe (Moncel et al., 2020).

Materials and methods

The macaque specimen from Notarchirico is a proximal fragment of a right ulna. The B24GNC specimen was recovered from the level G and is stored at "Museo Nazionale Archeologico di Venosa" (Potenza, Basilicata) (Fig.1b-c). To build our comparative dataset, we used the available literature on extant and Early – Late Pleistocene macaques, which include the fossil remains from Villafranca d'Asti (RDB quarry) and Pietrafitta, and extant specimens of *M. s. sylvanus* (Table 1) (Gentili et al., 1998; Rook et al., 2001). We also collected morphological data and measurements of Middle Pleistocene specimens of Barbary macaque from Fontana Ranuccio (FR; specimen 85; stored at Italian Institue of Human Paleontology) and Cava di Breccia di Casal Selce – upper level (CS; specimen 520; stored at PaleoFactory laboratory, Department of Earth Sciences, Sapienza University of Rome (PF)).

As comparative material, we included fossil specimen of *Mesopithecus pentelicus penticulus* from Moncucco Torinese (Alba et al., 2013) and Pikermi (Delson, 1973), and *Dolichopithecus ruscinensis* from Montpellier (=Perpignan) and Pestzentlorinc (Delson, 1973). We also used morphological and biometric data on extant specimens of *M. s. sylvanus* housed at Civic Zoology Museum of Rome and Royal Belgian Institute of Natural Sciences, Brussels.

Standard measurements of greatest breadth of olecranon (OB), greatest breadth across the anconeal process (APB), greatest breadth across the coronoid process (CPB), greatest height of olecranon fossa (HOF), greatest depth across the anconeal process (APD), were taken to the nearest 0.1mm (Table 1) (Fig. SD1). Boxplot of CPB and bivariate plot of HOF vs. CPB were realized to visually assess postcranial size and proportions.

Institutional abbreviations

CAM: Comparative Anatomy Museum, University of Modena; CZMR: Civic Zoology Museum of Rome; MGPT: Museum of Geology and Paleontology, Turin University; MHNG: Muséum d'Histoire Naturelle de Genève; MNAV: Museo Nazionale Archeologico di Venosa; NMB: Naturhistorisches Museum Basel; NHW: Naturhistorisches Museum Wien; PF: PaleoFactory laboratory, Department of Earth Sciences, Sapienza University of Rome; Italian Institute of Human Paleontology (IsIPU);

Description and comparison

The B24GNC is a proximal portion of the right ulna in a good state of preservation, which consists of about one-fourth of the shaft (Fig. 1d-f). Medially, the olecranon is relatively high, with the anterior border higher than the posterior one; its rough surface delineates the insertion area of the triceps brachii, brachialis and flexor carpis ulnaris muscles. In anterior view, the olecranon is mediolaterally compressed and its medial and lateral crests are similarly developed, and they are separated by a shallow groove. Laterally, the inner spongy bone of the olecranon is viewable due to the weathering, which obscures the attach area of the flexor carpis ulnaris muscles, in the proximal portion, and the epitrochleo-anconeus muscle, along the distal border. In medial view, at the level of the trochlear notch, the shaft surface is rough, which indicates the attach area of the flexor carpi ulnaris and extensor pollicis longus muscles. The anconeal process ends in a marked crest anteroposteriorly directed in medial view; its anterior border is disto-laterally inclined in anterior view; its process is robust and anteriorly projected in lateral view. The trochlear notch is quite reduced and its opening is semicircular in shape in medial and lateral views, whereas it is medio-laterally enlarged in anterior view, with a straight medial and a curved lateral outlines. The coronoid process is robust and anteriorly projected in medial and lateral views. The radial notch is well developed and its posterior border reaches the half of the shaft in medial view. Anteriorly, the radial notch is strongly concave, the border is inclined medially, and the facet is butterfly-shaped (according to Harrison, 1989). Despite the fragmentary nature of the specimen, its classification can be inferred since the morphology of the proximal epiphysis of the ulna is highly diagnostic. The overall morphology of the ulna from Notarchirico resembles the fossil remains of *M. s.* cf. *prisca* from Villanfranca d'Asti (V.J. 130) (Rook et al., 2001), *M. s. florentina* from Pietrafitta (IR-1703) (Gentili et al., 1998), *M. sylvanus* ssp. from Casal Selce (CS 520) and Fontana Ranuccio (FR 85), and extant specimens of *M. sylvanus* (Harrison, 1989) in several features: relatively long and straight olecranon with the anterior border higher than the posterior one in lateral and medial views; wide surface of articulation with the radius in lateral view; anteriorly-protruding anconeal process and coronoid process in lateral and medial views. The studied specimen differs from *Me. pentelicus* in the shape of the olecranon (e.g., a straight proximal outline in lateral and medial views), and in the profile of the trochlear and radial

notches (e.g., less anteriorly directed anconeal and coronoid process in lateral and medial views and less developed articular surface with the radius in lateral view) (Delson, 1973; Alba et al, 2013). Compared to *Dolichopithecus ruscinensis* from Montpellier (=Perpignan) and Pestzentlorinc (Delson, 1973), the studied ulna differs in the anteriorly-protruding coronoid process in lateral and medial views, the anterior border of the olecranon higher than the posterior one in lateral and medial views and a larger radial notch in lateral view. The ulnae of the extant colobines differ from that of Notarchirico since those possess an anterior concavity of the proximal shaft and a retroflected olecranon in lateral and medial views (Rose 1998; Egi et al., 2007). The ulnar morphology of *M. sylvanus* is strongly interrelated with that of the distal epiphysis of the humerus (with which forms the "humeroulnar joint"), and it is linked to its quadrupedal locomotion strategy, with the close-packing position of the elbow providing high stability during parasagittal movements (Rose, 1988).

The size of the macaque ulna from Notarchirico (Table 1) is compared with those of other extinct and extant macaques and *Me. penticulus* in Figure 2. The values of the CPB of the fossil specimens falls in the variation of the extant Barbary Macaque, with the exception of the studied fossil, which displays the largest size among the analyzed sample (Fig. 2a). In the figure 2b, the fossil specimens of *M. sylvanus* shows a relatively size variation, with the ulna from Notarchirico that occupies the extreme right of the plot. Furthermore, the fossil of *Me. pentelicus pentelicus* from Moncucco Torinese shows a different proportions of the ulna, with similar CPB value, but an higher trochlear notch compared with those of the fossil *M. sylvanus* (Fig. 2b). However, given the variation and the restricted sample available for extinct *M. sylvanus* and *Me. pentelicus pentelicus* , no taxonomic implication can be drawn from the ulna size.

Species	Catalogue number	Site	Age	Reference	OB	APB	CPB	HOF	APD
Macaca sylvanus cf. *prisca*	NMB VJ 130	RDB quarry	late Pliocene	Rook et al. (2001)			17.6	11.9*	8.3*
Macaca sylvanus	PF - CS520	Cava di Breccia di Casal Selce - upper level	Middle Pleistocene	This work			15.7	12.9	7.8
Macaca sylvanus	IsIPU - FR85	Fontana Ranuccio	Middle Pleistocene	This work	13.5	14.4	16.7	13.3	8.3
Macaca sylvanus	MNAV - B24GNC	Notarchirico	Middle Pleistocene	This work	14.1	18.0	20.7	13.1	9.3
Extant *Macaca sylvanus* sylvanus	CAM—1637			Rook et al. (2001)			15.0		
	CAM-283/4			Rook et al. (2001)			18.0		
	NHMW-34222			Rook et al. (2001)			14.0		
	NHMW-32990			Rook et al. (2001)			19.0		
	MHNG-3383			Rook et al. (2001)			20.0		
	MHNG—446·36			Rook et al. (2001)			18.0		
	CZMR - MP 128 - Dx			This work			16.3		
	CZMR - MP 128 - Sx			This work			15.5		
cf. *Mesopithecus pentelicus pentelicus*	MGPT-PU 130507	Moncucco Torinese	late Miocene	Alba et al. (2013)	14.1		16.0	14.4	

Table 1 - Measurements of ulna of extinct and extant specimens of Barbary macaque and extinct *Mesopithecus pentelicus pentelicus*. * estimated measurements from Rook et al. (2001).

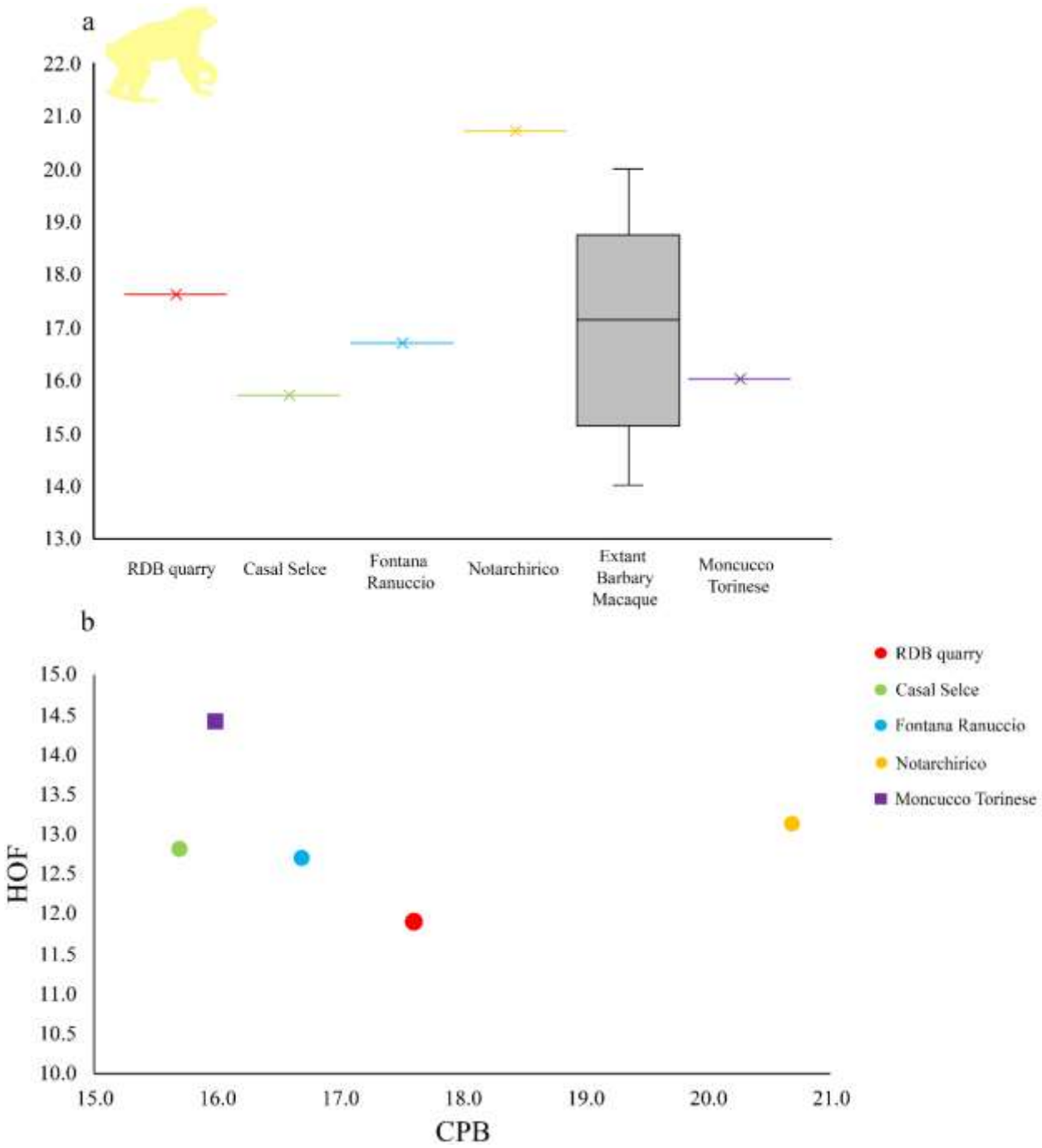

Fig. 2 - Proportions of the ulna of *Macaca sylvanus* from Notarchirico, compared to extinct and extant specimens of Barbary macaque and *Mesopithecus pentelicus pentelicus*. Specimens identified in more detail in Table 1. a – boxplot of the CBP measurements (CBP = greatest breadth across the coronoid process); b – plot of HOF (greatest height of olecranon fossa) vs. CBP (greatest breadth across the coronoid process).

Discussion and Conclusion

Taxonomy

In the last decades, new studies focused on the description of fossil macaques, involving both new finds and revisions of historical collections. Most of the available material of this primate consists of mandibular and maxillary remains, which are very similar to the extant North African subspecies. Following the proposal by Szalay and Delson (1979) and Delson (1980), fossil European macaques are often grouped in three temporal-geographic subspecies of *M. sylvanus,* but the reliability of this division is debated (e.g., Rook et al., 2001; Alba et al., 2008, 2018, 2019; Bona et al. 2016). Indeed, due to lacking clear-cut taxonomic criteria, classifications are often either chronologically-based (e.g., Alba et al., 2016, 2018, 2019), or limited to *M. sylvanus* ssp. (e.g., Montoya et al., 1999; Zapfe, 2001).

Moreover, this unresolved taxonomy is mainly established solely on craniodental remains. Indeed, postcranial ones are limited to a few findings across Europe, such as those from Untermassfeld (Zapfe, 1997), Deutsch-Altenburg (Fladerer, 1987) and Sierra de Quibas (Alba et al., 2011). Besides the Italian specimens, other ulnae of macaques were recorded from Swanscombe and Senèze (Singer et al., 1982), but the material was not described or figured. The morphological analysis conducted in this work reveals a strong affinity between the studied material and the fossil and extant specimens of *M. sylvanus* (Harrison, 1989; Gentili et al., 1998; Rook et al., 2001), and also stresses the differences with *Me. pentelicus pentelicus* (Delson, 1973; Alba et al, 2013), *Dolichopithecus ruscinensis* (Delson, 1973) and extant colobines (Rose, 1988). Biometrically, the specimens from the Middle Pleistocene sites of the Italian Peninsula fall within the range of variation of the extant Barbary macaque subspecies. The ulna from Notarchirico is slightly larger than the other analyzed specimens, but considering the restricted sample, these differences may not to be significative. Nevertheless, the only ulna known of *Me. pentelicus pentelicus* possesses different proportions, especially in the relatively higher trochlear notch if compared with that of extant and extinct Barbary Macaque. Thus, considering the lack of diagnostic features for Macaque subspecies, the ulna from Notarchirico is ascribed to *M. sylvanus*, avoiding the attribution to subspecies level based on chronological grounds.

According to recent literature (e.g., Bona et al., 2016; Alba et al., 2018, 2019), a more comprehensive analyses should clarify the alpha-taxonomy of extinct *M. sylvanus* subspecies.

Paleoenvironment

The Barbary macaque from Notarchirico was recovered from level G, associated with fossil remains of *Palaeoloxodon antiquus*, *Hippopotamus antiquus* and *Bison schoetensacki* (Moncel et al., 2020). Although only a few species were identified, these taxa indicate the presence of open-forest and

bodies of water, and warm climatic condition. As such, the level G of Notarchirico was accumulated during an interglacial. Considering the revised chronology of the site, this very likely indicates the end of MIS 17 (Moncel et al., 2019, 2020).

The extant Barbary macaque inhabits a variety of environments from shrublands to evergreen forests, and even herbaceous-dominated rocky ridges (Fooden, 2007, and references therein). The presence of arboreal vegetation is nonetheless a limiting factor, since the species requires trees for sleeping,, feeding, and escaping from predators (Delson, 2004; Fooden, 2007). In addition, it needs to be near water (Masseti and Bruner, 2009). Thereby, considering the ecological flexibile of the Barbary macaque, paleoecologically its presence at Notarchirico could suggests the presence of wooded and wet areas.

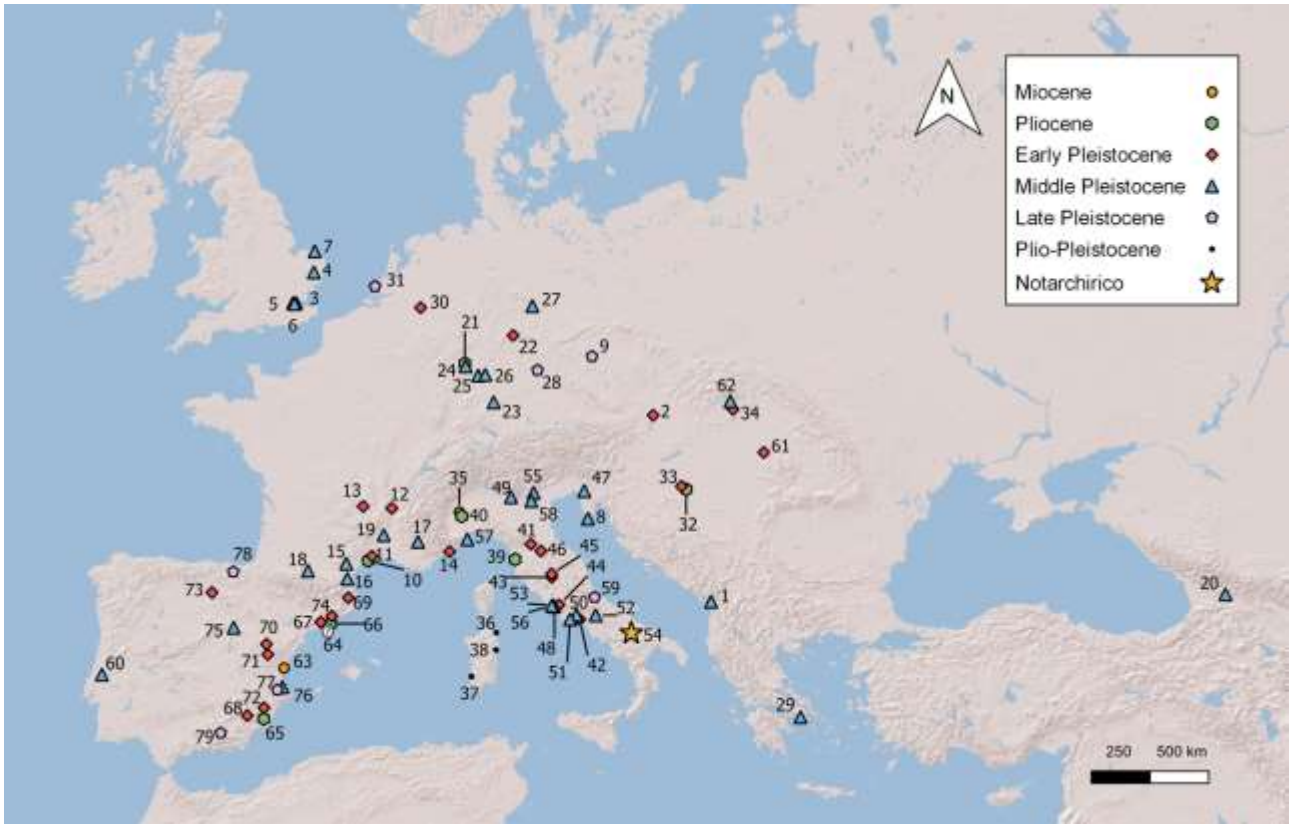

Fig. 3 - *Macaca* remains in the late Miocene to Late Pleistocene of Europe, details are provided in Table SD1. Question mark denotes uncertain age. Map produced with QGIS.

Paleobiogeographic and taphonomic implications

During the Pleistocene, European representatives of macaque subspecies mainly occurred in the Mediterranean area, being probably bound by both climatic and latitudinal factors (Ardito and Mottura, 1987; Elton and O'Regan, 2008) (Fig. 3). Indeed, a Mediterranean climate, with warm dry summers and relatively wet winters, also characterizes the current distribution range of the extant Barbary macaque populations, even though the species can tolerate winter snow at high elevations

(Delson, 2004; Fooden, 2007). Considering the known ecological tolerance, a strong relation between the areal expansion and Plio-Pleistocene climatic fluctuations for the extinct *M. sylvanus* subspecies has been hypothesized (Fooden, 2007; Elton and O'Regan, 2008). According to this idea, the European fossil macaques extended their geographical ranges to much higher latitudes during the interglacials, whereas they retreated into Mediterranean glacial refugia during cold episodes (Fooden, 2007; Elton and O'Regan, 2008). Its past distribution indicates that this primate was widespread along the Mediterranean coasts of Europe, especially in the Italian and Iberian peninsulas (Fig. 3). On the contrary, the presence of the species in central Europe, as well as in Britain, was only documented from deposit chronologically referred to an interglacial stage (Fig. 3). An exception is the Late Pleistocene site of Hunas (Germany) (Rosendahl et al., 2011), where the macaque remains were found in levels K-H, chronologically referred to MIS 4, therefore representing the only occurrence in central Europe during a glacial episode. As shown in Figure 3, the presence of the Barbary macaque at Notarchirico is the southernmost and easternmost known in Italy.

At Notarchirico, the co-occurrence of macaques and hominins is documented (Moncel et al., 2020), as in some other fossiliferous deposits (e.g., Gruta da Aroeira, Lezetxiki II and Grotta degli Orsi Volanti). Faunal remains coming from the levels F to I of the recent fieldworks are generally highly affected by abrasion (trampling and hydraulic transport) and bone surfaces are poorly preserved. Therefore, even though neither cut marks nor other anthropic percussion marks have been observed, this could be a mere lack of documentation. Likewise, despite a relatively good state of legibility (moderate abrasion), the macaque ulna shows no cut-marks. Similarly, the ulna from Fontana Ranuccio was found associated with lithic artefacts (Segre & Ascenzi, 1984; Strani et al., 2018), but there is no indication of human exploitation.

Despite the Barbary macaques being very widely distributed in Europe throughout the Pliocene and Pleistocene, the fossil record of this taxon is limited, and its presence in Europe was relatively rare. The majority of the documented specimens in Europe is isolated teeth and there are relatively few postcranial elements. Plio-Pleistocene *Macaca sylvanus* could probably have inhabited both deciduous and coniferous forest, but it could also be adapted to transitional environments.

The European macaque became locally extinct in the early Late Pleistocene. Elton & O'Regan (2014) pointed out that its extinction may be related to vegetation change, or increased predation from *Homo*, but also to stochastic factors occurring as a result of small population sizes. The early Late Pleistocene extinctions also included some megafauna (*Palaeoloxodon antiquus*, *Hippopotamus amphibius*, and *Stephanorhinus hemitoechus*), and it can be related to the lowering of global and regional temperatures in the Last Glacial period that caused reduction in forest cover. Another plausible factor is the influence of hominins. Definitely, the potential *Homo-Macaca* interactions during the

Pleistocene will deserve more emphasis from both paleoecological and archaeozoological viewpoints. During the Pleistocene in Europe *Macaca sylvanus* co-existed alongside earlier *Homo* species for over 1 million years, but the Barbary macaques became extinct before the earliest occurrence of *Homo sapiens* in Europe (Elton & O'Regan 2014). Modern *Macaca sylvanus* distribution is negatively affected by human occupation. In many Middle and Late Pleistocene sites hominins and macaques were found together and, especially in resource-limited environments. Although there is still no known evidence in paleontological literature, a possible scenario where *Homo* included primates in its diet cannot be ruled out (Meloro & Elton 2012). The environmental context given by this find of macaque provides informative data on the climatic conditions of the hominin occupations and the plant environments where hominins able to produce the earliest bifaces in southern Italy lived.

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Caption

Fig. 1 – Location map (1a), view and description of the stratigraphic succession of Notarchirico (southern Italy) (1b-1c). Monkey outline in 1a indicates the geographic position of the site. B24GNC, fragmented right ulna from Notarchirico in medial (1d), anterior (1e) and lateral (1f) views. Scale bar for Figs. d-f 3 cm.

Fig. 2 - Proportions of the ulna of *Macaca sylvanus* from Notarchirico, compared to extinct and extant specimens of Barbary macaque and *Mesopithecus pentelicus pentelicus*. Specimens identified in more detail in Table 1. a – boxplot of the CBP measurements (CBP = greatest breadth across the coronoid process); b – plot of HOF (greatest height of olecranon fossa) vs. CBP (greatest breadth across the coronoid process).

Fig. 3 - *Macaca* remains in the late Miocene to Late Pleistocene of Europe, details are provided in Table SD1. Question mark denotes uncertain age. Map produced with QGIS.

Table

Table 1 - Measurements of ulna of extinct and extant specimens of Barbary macaque and extinct *Mesopithecus pentelicus pentelicus*. * estimated measurements from Rook et al. (2001).

Supplementary

Tab.SD1 – Literature data on extinct of Barbary macaque from late Miocene to Late Pleistocene sites of Europe

Fig. SD1 – Standard measurements of ulna. Abbrevations: OB - greatest breadth of olecranon; APB - greatest breadth across the anconeal process; CPB - greatest breadth across the coronoid process; HOF - greatest height of olecranon fossa; APD - greatest depth across the anconeal process.

Number in figure 4	Country	Site	Species	Age	References
1	Albania	Gajtan 1	*Macaca* sp.	Middle Pleistocene	Fistani (1996)
2	Austria	Deutsch-Alternburg	*Macaca sylvanus* ssp.	Early Pleistocene	Fladerer (1987)
3	Britain	Grays Thurrock	*Macaca sylvanus pliocena*	Middle Pleistocene	Delson (1974); Szalay & Delson (1979); Singer et al. (1982);
4		Hoxne	*Macaca sylvanus* (=*Macaca sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Szalay & Delson (1979); Singer et al. (1982);
5		Purfleet	*Macaca sylvanus*	Middle Pleistocene	Schereve (2001); Schreve et al. (2002)
6		Swanscombe	*Macaca* sp.	Middle Pleistocene	Singer et al., (1982); Ardito & Mottura (1987)
7		West Runton	*Macaca sylvanus*	Middle Pleistocene	Delson (1974); Szalay & Delson (1979); Stuart (1992)
8	Croatia	Sandalja 1	*Macaca sylvanus pliocena* (*M. sylvanus florentina* in Szalay & Delson, 1979)	Middle Pleistocene	Szalay & Delson (1979): Fistani (1996)
9	Czech Republic	Zlaty Kun	*Macaca sylvanus pliocena*	Late Pleistocene	Delson (1974); Szalay & Delson (1979)
10	France	Balaruc 2	*Macaca* cf. *sylvanus* (*Macaca praeinutus* in Delson, 1974)	late Pliocene	Delson (1974); Delson (2004); Eronen & Rook (2004)
11		Montpellier	*Macaca* cf. *sylvanus* (*Macaca sylvanus prisca* in Delson, 1974 and Szalay & Delson, 1979)	Early Pleistocene	Delson (1974); Szalay & Delson (1979)
12		Saint Vailler	*Macaca* cf. *sylvanus* (*M. sylvanus florentina* in Szalay & Delson, 1979)	Early Pleistocene	Szalay & Delson (1979); Delson (2004); Eronen & Rook (2004)
13		Senéze	*Macaca* cf. *sylvanus* (*M. sylvanus florentina* in Szalay & Delson, 1979)	Early Pleistocene	Delson (1974); Szalay & Delson (1979); Ardito & Mottura (1987); Eronen & Rook (2004)
14		Vallonet	*Macaca sylvanus florentina* (=*M. sylvanus pliocena* in Szalay & Delson, 1979)	Early Pleistocene	Delson (1974); Szalay & Delson (1979)
15		Grotte d'Aldène	*Macaca* sp.	Middle Pleistocene	Ardito & Mottura (1987)
16		Caune de l'Arago	*Macaca sylvanus*	Middle Pleistocene	Moigne et al. (2006)
17		L'Escale	*Macaca* sp.	Middle Pleistocene	Delson (1974); Ardito & Mottura (1987)
18		Montsaunès	*Macaca* cf. sylvanus (=*M. sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Delson (1974); Szalay & Delson (1979); Ardito & Mottura (1987)
19		Orgnac 3	*Macaca* sp. (=*M. sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Szalay & Delson (1979); Ardito & Mottura (1987)
20	Georgia	Kudaro-1	*Macaca* sp. (=*M. sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Szalay & Delson (1979); Mashchenko (2005)
21	Germany	Gundersheim	*Macaca* cf. *sylvanus* (*Macaca sylvanus prisca* in Szalay & Delson, 1979)	late Pliocene	Delson (1974); Szalay & Delson (1979); Aridto & Mottura (1987); Eronen & Rook (2004)
22		Untermassfeld	*Macaca sylvanus* ssp.	Early Pleistocene	Zapfe (1997)
23		Heppenloch	*Macaca* cf. *sylvanus (=Macaca sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Delson (1974); Adam (1975); Szalay & Delson (1979)
24		Hohensülzen	*Macaca* cf. *sylvanus (=Macaca sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Delson (1974); Szalay & Delson (1979); Ardito & Mottura (1987); Kohler et al. (2000)
25		Mauer	*Macaca sylvanus*	Middle Pleistocene	Schreber & Loscher (2011)
26		Mosbach	*Macaca* sp. (=*Macaca sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Kalhke (1961); Delson (1974); Szalay & Delson (1979); Ardito & Mottura (1987)
27		Voigtsedt	*Macaca* cf. *sylvanus (=Macaca sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Delson (1974); Szalay & Delson (1979); Ardito & Mottura (1987)
28		Hunas	*Macaca sylvanus ssp.*	Late Pleistocene	Rosendahl et al. (2011)
29	Greece	Tourkobounja	*Macaca* sp.	Middle Pleistocene	Symeonidis & Zapfe (1977)
30	Hollande	Tegelen	*Macaca sylvanus florentina*	Early Pleistocene	Delson (1974); Szalay & Delson (1979); Eronen & Rook (2004)
31		Maasvlakte	*Macaca sylvanus*	Late Pleistocene	Reumer et al. (2017)
32	Hungary	Beremend 4	*Macaca* sp. *(Macaca Macaca sylvanus prisca* in Szalay & Delson, 1979)	late Pliocene	Delson (1974); Szalay & Delson (1979); Eronen & Rook (2004)
33		Csarnota 2	*Macaca* cf. *sylvanus (Macaca praeinutus* in Delson, 1974)	Early Pleistocene	Delson (1974)
34		Osztramos 1	*Macaca* sp.	Early Pleistocene	Eronen & Rook (2004)
35	Italy	Moncucco Torinese	*Macaca* sp.	late Miocene	Alba et al. (2013); Alba et al. (2014)
36		Capo Figari	*Macaca majori*	Plio-Pleistocene	Delson (1974); Szalay & Delson (1974); Eronen & Rook (2004); Rook & Higgins (2005)
37		Is Oreris	*Macaca majori*	Plio-Pleistocene	Eronen & Rook (2004); Zoboli et al. (2016)
38		Monte Tuttavista	*Macaca* cf. *majori*	Plio-Pleistocene	Abbazzi et al. (1994)
39		Orciano Pisano	*Macaca* cf. *sylvanus*	late Pliocene	Ristori (1890); Ardito & Mottura (1987)
40		Villafranca d'Asti	*Macaca sylvanus* cf. *prisca* (*M. sylvanus prisca* in Szalay & Delson, 1979)	late Pliocene	Delson (1974); Szalay & Delson (1979); Rook et al. (2001)
41		Barberino del Mugello	*Macaca sylvanus florentina*	Early Pleistocene	Delson (1974); Szalay & Delson (1979); Rook (1996); Eronen & Rook (2004)
42		Coste San Giacomo	*Macaca sylvanus*	Early Pleistocene	Bellucci et al. (2012)
43		Monte Peglia	*Macaca* cf. *sylvanus (=M. sylvanus pliocena* in Szalay & Delson, 1979)	Early Pleistocene	Szalay & Delson (1979); Ardito & Mottura (1987)
44		Monte Sacro	*Macaca* cf. *sylvanus*	Early Pleistocene	Portis (1917); Ardito & Mottura (1987)
45		Pietrafitta	*Macaca sylvanus florentina*	Early Pleistocene	Gentili et al. (1998)
46		Valdarno Superiore	*Macaca sylvanus florentina*	Early Pleistocene	Delson (1974); Azzaroli et al. (1982); Rook (1996)
47		Bristie II	*Macaca* sp.	Middle Pleistocene	Ardito & Mottura (1987); Bon et al. (1991)
48		Cava di Breccia di Casal Selce	*Macaca sylvanus*	Middle Pleistocene	This work
49		Cava di Quecchia	*Macaca sylvanus*	Middle Pleistocene	Bona et al. (2017)
50		Cava Pompi	*Macaca* cf. *sylvanus*	Middle Pleistocene	Ardito & Mottura (1987)
51		Fontana Ranuccio	*Macaca sylvanus*	Middle Pleistocene	Segre & Ascenzi (1984); Strani et al. (2018); this work
52		Isernia La Pineta	*Macaca sylvanus*	Middle Pleistocene	Di Nucci (2006)
53		La Polledrara di Cecanibbio	*Macaca sylvanus*	Middle Pleistocene	Anzidei et al. (2011)
54		Notarchirico	*Macaca sylvanus*	Middle Pleistocene	This work
55		San Vito Leguzzano	*Macaca* sp. (=*M. sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Delson (1974); Szalay & Delson (1979); Bon et al. (1991)
56		Torre del Pagliacetto (=Torre in Pietra)	*Macaca* cf. *sylvanus*	Middle Pleistocene	Ardito & Mottura (1987)
57		Valdemino	*Macaca sylvanus* (*Macaca sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Szalay & Delson (1979); Nocchi & Sala (1997)
58		Zoppega II	*Macaca* cf. *sylvanus*	Middle Pleistocene	Ardito & Mottura (1987); Bon et al. (1991)
59		Grotta degli Orsi Volanti	*Macaca* sp.	Late Pleistocene	Mazza et al. (2005)
60	Portugal	Gruta de Aroeira (=Galeria Pesada)	*Macaca sylvanus pliocena*	Middle Pleistocene	Marigó et al. (2014); Alba et al. (2019)
61	Romania	Betfia	*Macaca sylvanus pliocena*	Early Pleistocene	Delson (1974); Szalay & Delson (1979); Terzea (1984, 1996)
62	Slovakia	Gombasek	*Macaca sylvanus pliocena*	Middle Pleistocene	Delson (1974); Szalay & Delson (1979)
63	Spain	Almenara-Casablanca M	*Macaca* sp.	late Miocene	Kohler et al. (2000); Marigó et al. (2014)
64		Canal Negre I	*Macaca sylvanus* ssp. / *Macaca sylvanus* cf. *florentina*	Miocene - Pleistocene	Guillèn Castejòn (2010); Marigó et al. (2014)
65		Puerto de la Cadena	*Macaca sylvanus* cf. *prisca*	early Pliocene	Alba et al. (2018)
66		Cova Bonica	*Macaca sylvanus prisca*	late Pliocene	Delson (1971); Szalay &Delson (1979)
67		Cal Guardiola	*Macaca sylvanus* cf. *florentina*	Early Pleistocene	Marigó et al. (2014); Alba et al. (2008)
68		Cueva Negra del Estrecho del Quípar	*Macaca sylvanus* ssp.	Early Pleistocene	Marigó et al. (2014)
69		Incarcal	*Macaca sylvanus florentina*	Early Pleistocene	Alba et al. (2016)
70		Orrios 7	*Macaca* sp.	Early Pleistocene	Eronen & Rook (2004)
71		Puebla de Valverde	*Macaca sylvanus* cf. *florentina*	Early Pleistocene	Heinzt et al. (1971); Szalay & Delson (1979); Marigó et al. (2014)
72		Sierra de Quibas	*Macaca sylvanus*	Early Pleistocene	Montoya et al. (2001); Alba et al. (2011)
73		Sima de l'Elefante TE9	*Macaca* sp.	Early Pleistocene	Marigó et al. (2014)
74		Vallpardis Estaciò	*Macaca sylvanus* cf. *florentina*	Early Pleistocene	Alba et al. (2008); Marigó et al. (2014)
75		Ambrona	*Macaca* sp. (=*M. sylvanus pliocena* in Szalay & Delson, 1979)	Middle Pleistocene	Szalay & Delson (1979); Marigó et al. (2014)
76		Cova del Bolomor	*Macaca sylvanus*	MIddle Pleistocene	Blasco et al. (2008)
77		Cova Negra	*Macaca sylvanus* ssp.	Late Pleistocene	Marigó et al. (2014)
78		Lezetxiki II	*Macaca sylvanus* cf. *pliocena*	Late Pleistocene	Castaños et al. (2011)
79		Solana del Zamborino	*Macaca sylvanus* ssp.	Late Pleistocene	Martin Penela (1983); Marigó et al. (2014)

Tab. SD1

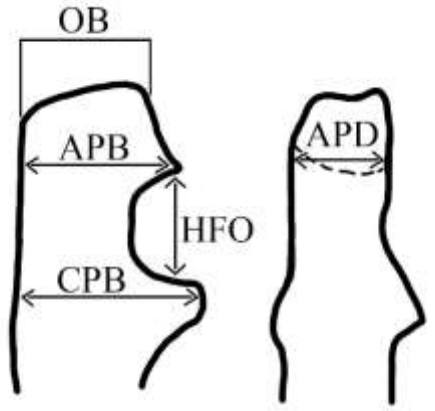

Fig. SD1