

The pioneering paleoprimatologist Charles Immanuel Forsyth Major (1843-1923), and a *Mesopithecus* tooth from an unrecorded locality of Italy (?Casino Basin) in the Basel Naturhistorisches Museum, Switzerland

Lorenzo ROOK & David M. ALBA

L. Rook, Dipartimento di Scienze della Terra, Università di Firenze, Italy; lorenzo.rook@unifi.it
D.M. Alba, Institut Català de Paleontologia Miquel Crusafont, Barcellona, Spain; david.alba@icp.cat

KEY WORDS - Forsyth Major Charles Immanuel, Fossil primate, *Mesopithecus*, Late Miocene, Early Pliocene, Casino Basin, Tuscany, Italy.

ABSTRACT - C.I. Forsyth Major was a pioneer of paleoprimatology as well as an extremely active field paleontologist. He collected a large quantity of fossil mammal remains of Neogene and Quaternary age during his fieldwork in Italy. A previously unpublished lower fourth premolar of *Mesopithecus* from the Forsyth Major collections housed in the Basel Naturhistorisches Museum is described and illustrated herein. Although the locality was not recorded, the specimen is considered as being from the Casino Basin (Tuscany, Italy). The specimen is attributed to the Late Miocene species *Mesopithecus pentelicus* on the basis of morphological characters such as dental size and proportions. Although significant statistical differences have been noted compared with the Pliocene species, *Mesopithecus monspessulanus*, based only on the single element presented here, a clear cut distinction between the two species is not observed.

RIASSUNTO - [Charles Immanuel Forsyth Major (1843-1923), pioniere della paleoprimatologia, e un dente di *Mesopithecus* proveniente da una località ignota (probabilmente il Bacino del Casino, Siena) nelle collezioni del Museo di Storia Naturale di Basilea] - C. I. Forsyth Major fu un pioniere della paleoprimatologia e un paleontologo di campagna molto attivo che, durante la sua permanenza in Italia, ha recuperato una grande quantità di resti mammiferi fossili in molte località italiane del Neogene e Quaternario. In questo lavoro si descrive e illustra un dente isolato (un quarto premolare inferiore) di *Mesopithecus* proveniente da una località italiana ignota (con tutta probabilità il Bacino del Casino, in provincia di Siena), conservato nella collezione Forsyth Major del Museo di Storia Naturale di Basilea. Il resto, sulla base di morfologia, dimensioni e proporzioni, è attribuito alla specie del Miocene Superiore *Mesopithecus pentelicus*. L'analisi statistica tuttavia rivela che, sebbene esistano differenze significative con la specie pliocenica *Mesopithecus monspessulanus*, sulla sola base di questo singolo elemento della dentatura non si possa osservare una separazione morfologica netta tra le due specie.

INTRODUCTION

Charles Immanuel Forsyth Major (1843-1923) was an eminent figure among mammal paleontologists, active across Europe from the 1870s to the beginning of the 1920s. A physician of Scottish origin who grew up in Switzerland, Forsyth Major graduated in Medicine in Basel in 1868 and started his professional practice in Florence (Italy), where he stayed for about a decade. Like many 19th-century medical doctors, however, he was fascinated by natural history and devoted much of his spare time to the study of fossil mammals. His interest in extinct vertebrates was distracting him from medicine, so that he finally decided to cease practising in the mid 1880s.

Forsyth Major's main interests were, generally speaking, Plio-Pleistocene mammals (Forsyth Major, 1872, 1875, 1877, 1879, 1880, 1890; Forsyth Major & Busatti, 1882). His entire scientific production clearly shows how deep his attention was for Tuscan vertebrate fossils, and while he was active in Florence, he systematically searched for new material, mainly in Tuscany but also in other Italian regions, supported by the recently established Italian government. His intensive field survey activity resulted in hundreds of specimens being deposited at the Florence Museum. At the same time, Forsyth Major had profuse relationships with colleagues and institutions across Europe, and especially in Basel, where he was based in the early 1900s. Among others,

Forsyth Major was a correspondent of Charles Darwin (Cioppi & Dominici, 2011; Dominici & Cioppi, 2012), who reported about their exchanges on different subjects in the (much improved) second edition of *The Descent of Man* published in 1874.

Forsyth Major's special interest was mostly focused on Primates. His first publication (Forsyth Major, 1872) was devoted to Italian fossil primates, and soon afterwards he reported about the mammal fauna associated with the fossil primate *Oreopithecus bambolii* (Forsyth Major, 1873). Later on (Forsyth Major, 1880) he expressed his opinion on the fossil hominoid status of the Late Miocene "enigmatic" *Oreopithecus bambolii* (albeit in a paper dealing with fossil horses). Between 1910 and 1914, Forsyth Major recovered abundant fossil collections in Sardinia and Corsica. Among these samples, the collection from the locality of Capo Figari (north-eastern Sardinia), which he sampled through systematic excavation, stands out. From this site comes an extraordinary rich collection of primate remains (mostly housed in the Basel Naturhistorisches Museum), which were classified as belonging to the genus *Macaca* by Forsyth Major (1913) himself, although he never described these fossils in detail. A small sample of *Macaca* from Capo Figari housed in Florence was described about 40 years later by Azzaroli (1946), who named the species *Macaca majori* after the family name of its discoverer (cfr. Rook & O'Higgins, 2005). After his Florentine experience, while working



Fig. 1 - This portrait of Charles Immanuel Forsyth Major may be found in the portrait gallery of eminent geologists and paleontologists in the Earth Sciences Department, University of Florence (Photo by Saulo Bambi, Florence Natural History Museum).

in London at the British Museum (Natural History) collections, the interest in fossil primates brought him to deal with material from Madagascar (Jenkins & Carleton, 2005). He studied both extant and extinct lemurs, which led to the erection of the new family Megaladapidae, the genus and species of extinct giant lemur *Megaladapis madagascariensis*, and some new species of the genera *Lepilemur* and *Cheirogaleus* (Forsyth Major, 1893, 1894a,b, 1896).

Samples collected during his Italian field surveys are now housed in several museums, amongst others the Natural History Museum in London (United Kingdom), the Collège Gaillard in Lausanne (Switzerland), and the Basel Naturhistorisches Museum (Switzerland). The present paper describes a previously unreported isolated tooth of *Mesopithecus* belonging to the Forsyth Major collection kept in the Basel Naturhistorisches Museum (NHMB).

THE GENUS *MESOPITHECUS*

Mesopithecus Wagner, 1839 is the oldest cercopithecoid genus from Europe. It is first recorded in a few putative Vallesian localities (albeit this dating has been

questioned; cfr. Andrews et al., 1996), and subsequently unambiguously recorded from the early Turolian (MN11) onwards (Szalay & Delson, 1979; Jablonski, 2002). The first appearance datum of *Mesopithecus* thus postdates the divergence time between African and Asian colobines, which is estimated on molecular grounds at around 10.8-9.5 Ma (Sterner et al., 2006; Ting, 2008). First tentatively considered to be more closely related to Asian colobines, mainly on biogeographic grounds (Szalay & Delson, 1979; Delson, 1994), most recently a closer relationship with the douc langurs from Southeast Asia (genus *Pygathrix*) has been favored by cladistic morphologic analyses (Jablonski, 1998, 2002). However, while extant colobines are restricted to Asia and Africa (Davies & Oates, 1994), *Mesopithecus* has been recovered from Western Europe to Central and South Asia during the Late Miocene (Szalay & Delson, 1979; Jablonski, 2002; Koufos, 2006, 2009a,b; Harrison & Delson, 2007; Jablonski et al., 2011) and appears to have survived in Europe until the Early Villafranchian (Late Pliocene; Pradella & Rook, 2007).

A distinction is currently drawn between two European *Mesopithecus* species, which differ in chronological range, overall size and dental proportions, and apparently the degree of terrestrial adaptation (Szalay & Delson, 1979; Jablonski, 2002): the Late Miocene *Mesopithecus pentelicus* Wagner, 1839, and the Pliocene *Mesopithecus monspessulanus* (Gervais, 1849). Both species might have briefly coexisted during the latest Turolian (MN13) (de Bonis et al., 1990, 1997; Koufos et al., 2004; Delson et al., 2005). A third European species, *Mesopithecus delsoni* de Bonis et al., 1990, has also been recognized based on some larger remains from Greece and Bulgaria (de Bonis et al., 1990, 1997; Koufos et al., 2003), although several authors have considered it a junior subjective synonym of *M. pentelicus* (Zapfe, 1991; Delson, 1994; Andrews et al., 1996). This taxonomic issue is further complicated by the recognition of numerous purported intermediate forms between *M. delsoni* and *M. pentelicus* (e.g., Koufos et al., 2004). Pending a thorough revision of the genus, the former taxon is provisionally considered here as a valid species, whereas the purported intermediate forms from Bulgaria and Greece - variously referred to as *M. cf. pentelicus*, *M. aff. pentelicus*, *M. cf. delsoni*, *M. aff. delsoni* and/or *M. delsoni/pentelicus* (see de Bonis et al., 1997; Koufos et al., 2003, 2004; Koufos, 2006, 2009a,b) - have been left unassigned as *Mesopithecus* sp.

MESOPITHECUS IN THE LATE TUROLIAN OF ITALY

Rook (1999) published a review of the *Mesopithecus* record in the Turolian of Italy, where the genus occurs in four localities: Brisighella (Faenza, Romagna), Baccinello V3 (Grosseto, Tuscany), Casino Basin (Siena, Tuscany) and Gravitelli (Messina, Sicily). Forsyth Major (1877) first reported the occurrence of "*Semnopithecus monspessulanus*" from Casino, and of the 9 specimens known from the locality, three are kept in the Natural History Museum (London) labelled as "From Dr. Major's room" (cfr. Rook, 1999).

The collections of the Basel Naturhistorisches Museum keeps, among the fossil collection from the Late Miocene

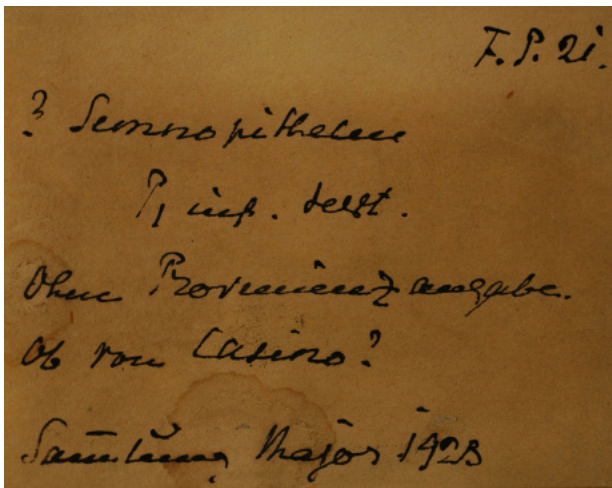


Fig. 2 - Basel Naturhistorisches Museum collections, label associated with the tooth described in this paper. The label (Hans Stehlin's writing) reports: "F.P. 21/? *Semnopithecus*/P1 inf. dext./ Ohne Provenienz Angabe/ob von Casino?/Sammlung Major 1923" [F.P. 21/?*Semnopithecus*/P1 inf. dext./without Provenance data/ maybe from Casino?/Collection Major 1923].

of Tuscany, an isolated *Mesopithecus* tooth associated with hand-written label (Fig. 2).

This specimen was actually registered within the NHMB collections in 1926 and the provenance was given by Stehlin as "unknown provenance, maybe from the lignite of Casino near Siena". Because 1923 corresponds to the year Forsyth Major passed away, the year notated on the labels may accord with the fact that just after his death, all Forsyth Major's collections left in his working space or office in Basel were included within the Museum collections. Stehlin's guess that the tooth could be from the Casino lignites is most probable, since this locality was well known to Forsyth Major (1875, 1877, 1879, 1899) and has produced other *Mesopithecus* specimens. As a matter of fact Forsyth Major described two "new species" from the Casino lignites (*Prolagus elsanus* and *Euprox elsanus*), but these taxa are not valid because their original description was not accompanied by a formal designation of the holotype, and furthermore the specimens are no longer available and probably lost (cf. Angelone & Rook, 2012).

Although originally described as Late Miocene in age, the Casino faunal assemblage has been subsequently considered Early Pliocene on the basis of the occurrence of *Tapirus* and *Sus* cf. *minor* (De Giuli et al., 1983; Azzaroli et al., 1986). However, the presence of *Tapirus* cf. *arvernensis* in the Messinian deposits of Baccinello V3 seems to indicate that this genus was already present in Italy at the end of the Turolian (Rook & Rustioni, 1991). Moreover, a recent revision of the suid material revealed that it is better attributable to the latest Turolian species *Propotamochoerus provincialis* (Gallai & Rook, 2011). Furthermore, a detailed geological, sedimentological and paleontological study of an exposed sedimentary succession in the north-western sector of the Casino/Val d'Elsa Basin (Abbazzi et al., 2008) allowed researchers to recognise a very complicated tectono-sedimentary history of the latest Miocene and Mio-Pliocene transition within

the Basin, with the continental fossil mammals belonging to units attributable to the latest Messinian.

SYSTEMATIC PALEONTOLOGY

Order PRIMATES Linnaeus, 1758
Suborder ANTHROPOIDEA Mivart, 1864
Infraorder CATARRHINI Geoffroy Saint-Hilaire, 1812
Superfamily CERCOPITHECOIDEA Gray, 1821
Family CERCOPITHECIDAE Gray, 1821
Subfamily COLOBINAE Blyth, 1875

Genus *Mesopithecus* Wagner, 1839

Mesopithecus pentelicus Wagner, 1839
(Fig. 3)

Description - The single tooth (NHMB F.P. 21) belonging to the Forsyth Major collection, and possibly from the Casino Basin, is an isolated right P₄ (Fig. 3). It is an almost unworn tooth with a sub-oval occlusal outline. The trigonid is much higher than the talonid. In the former, two distinct cusps (the protoconid and the metaconid) are clearly distinguishable, being joined to one another by a transverse crest (the protolophid), which separates the small and rounded mesial fovea (trigonid basin) from the more extensive and quadrangular talonid basin. The distal fovea is closed by a marked distal marginal ridge, with no secondary cuspulids at the distobuccal and distolingual corners of the crown.

Comparisons - From the same locality three other *Mesopithecus* P₄s are documented. The specimen NHMB F.P. 21 does not differ morphologically from the other specimens, kept in the Museo di Storia Naturale e del Territorio (Calci, Pisa) and attributed to *M. pentelicus* (Rook, 1999). In order to compare the size and proportions of the newly reported tooth with other *Mesopithecus* specimens, we relied on an analysis of variance (ANOVA) among *M. pentelicus* from Pikermi, *M. pentelicus* from other localities, and *M. monspessulanus* from Montpellier and other localities, for three standard variables of dental size and proportions. ANOVA results confirm the presence of statistically significant differences for length ($p < 0.001$; $F = 13.323$), breadth ($p < 0.01$; $F = 6.573$) and breadth/length index ($p < 0.05$; $F = 3.551$). Post-hoc pairwise

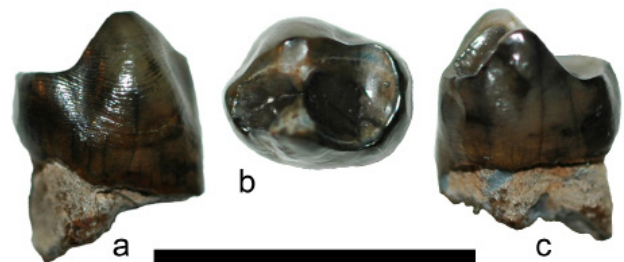


Fig. 3 - *Mesopithecus monspessulanus* (NHMB F.P. 21), right P₄ from ?Casino. a) labial, b) occlusal, c) lingual views. Scale bar represents 1 cm.

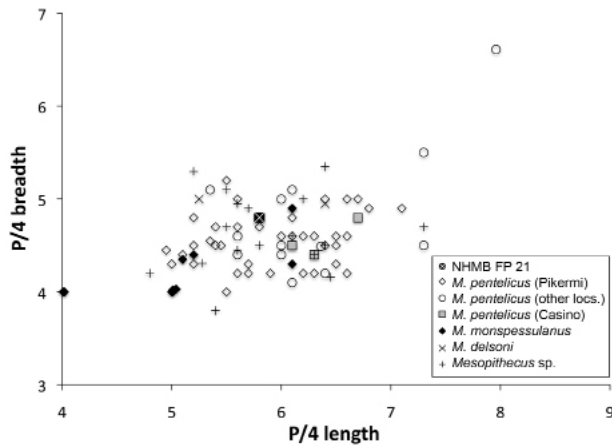


Fig. 4 - Scatter diagram showing the dental proportions of buccolingual breadth vs. mesiodistal length of the P₄ NHMB F.P. 21 from ?Casino compared to other *Mesopithecus* samples: *Mesopithecus pentelicus* from the type locality; *M. pentelicus* from Casino; *M. pentelicus* from other localities (Pikermi II, Kumanovo, Titov Veles, Maragheh, Maramena, Molayan and Kromidovo); *M. monspessulanus* from Montpellier (type locality); *M. monspessulanus* from other localities (RDB Quarry and Dorkovo); *M. delsoni* from Ravin des Zouaves 5 (type locality); and *Mesopithecus* sp. from several localities (Dytiko 1, Dytiko 2, Perivolaki, Vathylakkos 2, Vathylakkos 3, Ravin X, Kalimantsi and Hadjidimovo). Measurements were taken from the literature (de Bonis et al., 1990; Zapfe, 1991; Mottura & Ardito, 1992; Kullmer & Doukas, 1995; Rook, 1999; Koufos et al., 2003, 2004; Delson et al., 2005; Koufos, 2006; Pradella & Rook, 2007), measured by the authors, or kindly provided by Eric Delson and Nikolai Spassov.

comparisons (Bonferroni method) further indicate that the Pikermi sample does not significantly differ from the sample of *M. pentelicus* from other localities in any of the three investigated variables. On the contrary, the former sample displays significantly longer ($p < 0.001$) and broader ($p < 0.05$) P₄ than that of *M. monspessulanus*, in spite of not displaying significant differences regarding occlusal proportions ($p = 0.083$). Although a more detailed statistical analysis for the Casino sample is precluded by small sample size, the above-mentioned results suggest that size of the P₄ is a valid criterion for distinguishing between *M. pentelicus* and *M. monspessulanus*. Metrically (Table 1; Fig. 4), NHMB F.P. 21 is merely a little bit shorter (and hence relatively broader) than other specimens from Casino. However, when the variability displayed by *M. pentelicus* is taken into account, it can be concluded that the new specimen perfectly fits with this species, since all dental measurements fall within the maximum-minimum ranges for both the type locality (Pikermi) and other sites. On the contrary, the newly-reported specimen shows greater dimensions than the average values for *M. monspessulanus*, and in particular its buccolingual breadth is higher than the maximum values recorded for the topotypic population of the latter species and is exceeded by only one specimen from another locality. On this basis, a taxonomic attribution of NHMB F.P. 21 to *M. pentelicus* is favoured here, as previously achieved by Rook (1999) for the rest of the Casino sample, which further agrees with the late Turolian age estimated for the Casino locality. However, it should be taken into account

Length (mm)	N	Mean	SD	95% CI	Range
NHMB F.P. 21	1	5.8			
<i>M. pentelicus</i> (type locality)	42	5.9	0.56	5.7 6.1	5.0 7.1
<i>M. pentelicus</i> (other localities)	13	6.3	0.76	5.9 6.8	5.4 8.0
<i>M. pentelicus</i> (Casino)	3	6.4	0.31	5.6 7.1	6.1 6.7
<i>M. monspessulanus</i> (type locality)	7	4.9	0.71	4.2 5.5	4.0 6.1
<i>M. monspessulanus</i> (other localities)	3	5.5	0.55	4.1 6.8	5.1 6.1
<i>M. delsoni</i> (type locality)	2	5.8	0.81	-1.5 13.1	5.3 6.4
<i>Mesopithecus</i> sp.	21	5.8	0.61	5.5 6.1	4.8 7.3

Breadth (mm)	N	Mean	SD	95% CI	Range
NHMB F.P. 21	1	4.8			
<i>M. pentelicus</i> (type locality)	42	4.6	0.28	4.5 4.6	4.0 5.2
<i>M. pentelicus</i> (other localities)	13	4.8	0.68	4.4 5.2	4.1 6.6
<i>M. pentelicus</i> (Casino)	3	4.6	0.21	4.1 5.1	4.4 4.8
<i>M. monspessulanus</i> (type locality)	7	4.1	0.11	3.9 4.2	4.0 4.3
<i>M. monspessulanus</i> (other localities)	3	4.6	0.30	3.8 5.3	4.4 4.9
<i>M. delsoni</i> (type locality)	2	5.0	0.04	4.7 5.3	5.0 5.0
<i>Mesopithecus</i> sp.	17	4.6	0.42	4.4 4.9	3.8 5.4

Breadth/length index (%)	N	Mean	SD	95% CI	Range
NHMB F.P. 21	1	82.8			
<i>M. pentelicus</i> (type locality)	42	77.6	7.66	75.2 80.0	63.6 94.5
<i>M. pentelicus</i> (other localities)	13	76.5	9.15	71.0 82.0	61.6 95.3
<i>M. pentelicus</i> (Casino)	3	71.8	1.97	66.9 76.6	69.8 73.8
<i>M. monspessulanus</i> (type locality)	7	84.3	11.06	74.0 94.5	70.5 99.8
<i>M. monspessulanus</i> (other localities)	3	83.4	2.69	76.7 90.1	80.3 85.3
<i>M. delsoni</i> (type locality)	2	86.3	12.65	-27.4 200.0	77.3 95.2
<i>Mesopithecus</i> sp.	17	80.0	10.16	74.8 85.2	64.4 101.9

Table 1 - Descriptive statistics for three metrical variables (mesiodistal length, maximum buccolingual breadth and breadth/length index) of the *Mesopithecus* P₄, comparing the newly-reported tooth from ?Casino (NHMB F.P. 21) to the various species of this genus.

that the maximum-minimum ranges for both length and breadth of the P₄ largely overlap between the two species, so that a clearcut distinction between them on the basis of this single tooth is not possible.

SUMMARY AND CONCLUSIONS

Charles Immanuel Forsyth Major was a Scottish physician turned mammalian paleontologist of the late 1800's and early 1900's, with special interest in fossil primates. He collected mainly in the Italian later Cenozoic and gave his collections to museums in Florence, London and Basel. One specimen that he apparently collected, perhaps in the Casino Basin (Siena, Italy) is a previously unreported P₄ of the colobine monkey *Mesopithecus*, housed at the Basel Naturhistorisches Museum. It is described here. Like previously described remains of the same provenance (Rook, 1999), the newly reported tooth fits well with the sample from Pikermi (the type locality of *M. pentelicus*) as well as from other localities where this taxon has been reported. On this basis, and further taking into account the probably late Turolian age of the specimen, it is here attributed to *M. pentelicus*. It should be noted, however, that a clearcut distinction between the latter taxon and the Pliocene species *M. monspessulanus* is not possible on the basis of P₄ size and proportions alone. Thus, although we show here that the two species statistically differ in this regard, with *M. monspessulanus* distinguished by smaller dental dimensions, both species considerably overlap, thus precluding a conclusive assignment on the basis of a single, isolated lower fourth premolar.

ACKNOWLEDGEMENTS

We are deeply indebted to Dr. Loïc Costeur (Naturhistorisches Museum, Basel) for the access to the collection in his care, and for useful information from the NHMB archives. We also thank Eric Delson and Nikolai Spassov for sharing with us original unpublished measurements of *Mesopithecus* teeth; those provided by Delson are publicly available on the PRIMO database at <http://primo.nycep.org>. DMA is particularly grateful to Eric Delson for providing literature, access to casts and helpful discussion while making a short stay at the American Museum of Natural History and New York Consortium for Evolutionary Primatology. This work has been supported by the University of Florence (Fondi d'Ateneo), the Spanish Ministerio de Ciencia e Innovación (CGL2008-00325/BTE, CGL2011-28681, and RYC-2009-04533 to D.M.A.) and the Generalitat de Catalunya (2009 SGR 754 GRC).

REFERENCES

- Abbazzi L., Benvenuti M., Ceci M.E., Esu D., Faranda C., Rook L. & Tangocci F. (2008). The end of the Lago-Mare time in the SE Valdelsa Basin (Central Italy): interference between local tectonism and regional sea-level rise. *Geodiversitas*, 30: 611-639.
- Andrews P., Harrison T., Delson E., Bernor R.L. & Martin L. (1996). Distribution and biochronology of European and Southwest Asian Miocene Catarrhines. In Bernor R.L., Falhbusch V. & Mittman H.W. (eds), *The Evolution of Western Eurasian Mammal Faunas*, Columbia University Press, New York: 168-207.
- Angelone C. & Rook L. (2012). Neogene and Quaternary lagomorphs from Tuscany: a revision based on specimens in the Basel Naturhistorisches Museum and Florence University collections. *Swiss Journal of Paleontology*, 131(1): 127-145.
- Azzaroli A. (1946). La scimmia fossile della Sardegna. *Rivista di Scienze Preistoriche*, 1: 68-76.
- Azzaroli A., De Giuli C., Ficarelli G. & Torre D. (1986). Mammal succession of the Plio-Pleistocene of Italy. *Memorie della Società Geologica Italiana*, 31: 213-218.
- Blyth E. (1875). Catalogue of mammals and birds of Burma. *Journal of Asiatic Society Bengal*, 44 (part 2, extra number): 1-167.
- Cioppi E. & Dominici S. (2011). Origin and development of the geological and palaeontological collections. In Monechi S. & Rook L. (eds), *Il Museo di Storia Naturale dell'Università di Firenze. Volume 3° - Le collezioni geologiche e paleontologiche*, Florence University Press, Firenze: 19-55.
- Darwin C.I. (1874). *The descent of man, and selection in relation to sex*. John Murray, London (2nd edition), 688 pp.
- Davis A.G. & Oates J.F. (1994). *Colobine Monkeys: their Ecology, Behaviour and Evolution*. Cambridge University Press, Cambridge, 415 pp.
- de Bonis L., Bouvraïn 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: 473-483.
- de Bonis L., Bouvraïn G., Geraads D. & Koufos G. (1997). New material of *Mesopithecus* (Mammalia, Cercopithecoidea) from the late Miocene of Macedonia, Greece. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 1997(5): 255-265.
- De Giuli C., Ficarelli G., Mazza P. & Torre D. (1983). Confronto fra le successioni marine e continentali del Pliocene e Pleistocene inferiore in Italia e nell'area mediterranea. *Bollettino della Società Paleontologica Italiana*, 22: 323-328.
- Delson E. (1994). Evolutionary history of the colobine monkeys in paleoenvironmental perspective. In Davies A.G. & Oates J.F. (eds), *Colobine Monkeys: their Ecology, Behaviour and Evolution*, Cambridge University Press, Cambridge: 11-43.
- Delson E., Thomas H. & Spassov N. (2005). Fossil Old World monkeys (Primates, Cercopithecoidea) from the Pliocene of Dorkovo, Bulgaria. *Geodiversitas*, 27: 159-166.
- Dominici S. & Cioppi E. (2012). Evolutionary theory and the Florence Paleontological collection. *Evolution: Education and Outreach*, 5: 9-13.
- Forsyth Major C.I. (1872). Notes sur des singes fossiles trouvés en Italie, précédées d'un aperçu sur les quadrumanes fossiles en général. *Atti della Società Italiana di Scienze Naturali*, 15: 79-95.
- Forsyth Major C.I. (1873). La fauna des vertébrés de Monti Bamboli (Maremmes de la Toscana). *Atti della Società Italiana di Scienze Naturali*, 15: 290-303.
- Forsyth Major C.I. (1875). Considerazioni sulla fauna dei Mammiferi pliocenici e postpliocenici della Toscana. *Memorie della Società Toscana di Scienze Naturali*, 1: 7-40.
- Forsyth Major C.I. (1877). Considerazioni sulla fauna dei Mammiferi pliocenici e postpliocenici della Toscana. *Memorie della Società Toscana di Scienze Naturali*, 3: 202-227.
- Forsyth Major C.I. (1879). Cervi pliocenici del Val d'Arno superiore. *Atti della Società Toscana di Scienze Naturali, Processi verbali*, 1: 100-101.
- Forsyth Major C.I. (1880). Beiträge zur Geschichte der fossilen Pferde insbesondere Italiens. *Abhandlungen der Schweizerischen paläontologischen Gesellschaft*, 7: 1-154.
- Forsyth Major C.I. (1890). L'ossario di Olivola in Val di Magra. *Atti della Società Toscana di Scienze Naturali, Processi verbali*, 7: 57-76.
- Forsyth Major C.I. (1893). On *Megaladapis madagascariensis*, an extinct gigantic lemuroid from Madagascar. *Proceedings of the Royal Society*, 54: 176-179.
- Forsyth Major C.I. (1894a). On *Megaladapis madagascariensis*, an extinct gigantic lemuroid from Madagascar; with Remarks on

- the Associated Fauna, and on Its Geological Age. *Philosophical Transactions of the Royal Society of London, B*, 185: 15-38.
- Forsyth Major C.I. (1894b). Ueber die Malagassischen Lemuriden-Gattungen *Microcebus*, *Opolemur*, und *Chirogale*. *Novitates Zoologicae*, 1: 2-39.
- Forsyth Major C.I. (1896). Diagnoses of new mammals from Madagascar. *Annals and Magazine of Natural History*, 18: 318-325.
- Forsyth Major C.I. (1899). On fossil and recent Lagomorpha. *Transactions of the Linnean Society of London*, s. 2, 7: 433-520.
- Forsyth Major C.I. (1913). Observations sur la faune des Mammifères quaternaires de la Corse et de la Sardaigne. *Natura*, 4: 594.
- Forsyth Major C.I. & Busatti L. (1882). Di una breccia ossifera sul Monte Argentario. *Atti della Società Toscana di Scienze Naturali, Processi verbali*, 3: 45-48.
- Gallai G. & Rook L. (2011). *Propotamochoerus provincialis* (Gervais, 1859) (Suidae, Mammalia) from the latest Miocene (late Messinian; MN13) of Monticino Quarry (Brisighella, Emilia-Romagna, Italy). *Bollettino della Società Paleontologica Italiana*, 50: 29-34.
- Geoffroy Saint-Hilaire E. (1812). Tableau des quadrumanes, 1. Ord. Quadrumanes. *Annales du Museum d'Histoire Naturelle de Paris*, 19: 85-122.
- Gervais P. (1849). *Zoologie et Paleontologie Francaises*. Arthus Bertrand, Paris, 271 pp.
- Gray J.E. (1821). On the natural arrangement of vertebrate animals. *London Medical Repository*, 15: 296-310.
- Harrison T. & Delson E. (2007). *Mesopithecus sivalensis* from the Late Miocene of the Siwaliks [Abstract]. *American Journal of Physical Anthropology*, 132(S44): 126.
- Jablonski N.G. (1998). The evolution of the doucs and snub-nosed monkeys and the question of the phyletic unity of the odd-nosed colobines. In Jablonski N.G. (ed.), *The Natural History of the Doucs and Snub-nosed Monkeys*. World Scientific Publishing, Singapore: 13-52.
- Jablonski N.G. (2002). Fossil Old World monkeys: The late Neogene radiation. In Hartwig W.C. (ed.), *The Primate Fossil Record*, Cambridge University Press, Cambridge: 255-299.
- Jablonski N.G., Su D., Kelly J., Flynn L.J. & Ji X. (2011). The Mio-Pliocene colobine monkey, *Mesopithecus*, in China [Abstract]. *American Journal of Physical Anthropology*, 144(S52): 174.
- Jenkins P.D. & Carleton M.D. (2005). Charles Immanuel Forsyth Major's expedition to Madagascar, 1894 to 1896: beginnings of modern systematic study of the island's mammalian fauna. *Journal of Natural History*, 39: 1779-1818.
- Koufos G.D. (2006). The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 3. Primates. *Palaeontographica, A*, 276: 23-37.
- Koufos G.D. (2009a). The genus *Mesopithecus* (Primates, Cercopithecoidea) in the late Miocene of Greece. *Bollettino della Società Paleontologica Italiana*, 48: 157-166.
- Koufos G.D. (2009b). The Neogene cercopithecooids (Mammalia, Primates) of Greece. *Geodiversitas*, 31: 817-850.
- Koufos G.D., de Bonis L., Kostopoulos D.S., Viriot L. & Vlachou T.D. (2004). *Mesopithecus* (Primates, Cercopithecoidea) from the Turolian locality of Vathylakkos 2 (Macedonia, Greece). *Paläontologische Zeitschrift*, 78: 213-228.
- Koufos G.D., Spassov N. & Kovatchev D. (2003). Study of *Mesopithecus* (Primates, Cercopithecoidea) from the late Miocene of Bulgaria. *Palaeontographica, A*, 269: 39-91.
- Kullmer O. & Doukas C. (1995). The vertebrate locality of Maramena (Macedonia, Greece) at the Turolian-Ruscian Boundary (Neogene). 6 - The deciduous dentition of *Mesopithecus pentelicus* Wagner (Primates, Mammalia). *Münchner Geowissenschaftliche Abhandlungen*, 28: 65-74.
- Linnaeus C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines genera, species cum characteribus differentis, synonymis, locis*. Tomus 1: Regnum animale. Editio decima, reformata. Holmiae Impensis Direct. Laurentii Salvi, Stockholm, i-iv, 824 pp.
- Mivart St. G. (1864). Notes on the crania and dentition of the Lemuridae. *Proceedings of the Zoological Society, London*, 1864: 611-648.
- Mottura A. & Ardito G. (1992). Observations on the Turin specimen of *Mesopithecus pentelici* (Wagner, 1839). *Human Evolution*, 7: 67-73.
- Pradella C. & Rook L. (2007). *Mesopithecus* (Primates, Cercopithecoidea) from Villafranca d'Asti (Early Villafranchian, NW Italy) and palaeoecological context of its extinction. *Swiss Journal of Geosciences (Eclogae geologicae Helvetiae)*, 100: 145-152.
- Rook L. (1999). Late Turolian *Mesopithecus* (Mammalia, Primates, Colobinae) from Italy. *Journal of Human Evolution*, 36: 535-547.
- Rook L. & O'Higgins P. (2005). A comparative study of adult facial morphology and its ontogeny in the fossil macaque *Macaca majori* from Capo Figari, Sardinia, Italy. *Folia Primatologica*, 76: 151-171.
- Rook L. & Rustioni M. (1991). *Tapirus* cf. *arvernensis* from the Late Turolian Baccinello V3 Faunal Assemblage (Grosseto, Italy). *Bollettino della Società Paleontologica Italiana*, 30: 325-327.
- Sternner K.N., Raaum R.L., Zhang Y.-P., Stewart C.-B. & Disotell T.R. (2006). Mitochondrial data support an odd-nosed colobine clade. *Molecular Phylogenetics and Evolution*, 40: 1-7.
- Szalay F. & Delson E. (1979). *Evolutionary History of the Primates*. Academic Press, New York, 580 pp.
- Ting N. (2008). Mitochondrial relationships and divergence dates of the African colobines: evidence of Miocene origins for the living colobus monkeys. *Journal of Human Evolution*, 55: 312-325.
- Wagner A. (1839). Fossile Überreste von einem Affenschädel und anderen Säugethierreste aus Griechenland. *Gelehrte Anzeiger der Bayerischen Akademie der Wissenschaften*, 38: 301-312.
- Zapfe H. (1991). *Mesopithecus pentelicus* Wagner aus dem Turolien von Pikermi bei Athen, Odontologie und Osteologie. *Neue Denk-Schriften Naturhistorisches Museum Wien*, 5: 1-203.

Manuscript received 3 December 2011

Revised manuscript accepted 24 January 2012

Published online 27 June 2012

Editor Maria Rose Petrizzo