Bollettino della Società Paleontologica Italiana, 63 (2), 2024, 137-143. Modena

An *Oreopithecus bambolii* jaw in the Museum "Giorgio G. Gemmellaro" in Palermo

Luca Sineo*, Clément Zanolli, Roberto Maria Micciché, Giulia Santaluna, Gabriele Lauria, Gerlando Vita, Carolina Di Patti & Jacopo Moggi Cecchi

L. Sineo, Dipartimento di Scienze e Tecnologie Biologiche Chimiche e Farmaceutiche, Università di Palermo, Via Archirafi 18, I-90123 Palermo, Italy; luca.sineo@unipa.it **corresponding author*
C. Zanolli, Université de Bordeaux, CNRS, MCC, PACEA, UMR 5199, F-33600 Pessac, France; clement.zanolli@gmail.com
R.M. Micciché, Dipartimento di Scienze e Tecnologie Biologiche Chimiche e Farmaceutiche, Università di Palermo, Via Archirafi 18, I-90123 Palermo, Italy; robertomaria.micciche@unipa.it
G. Santaluna, Dipartimento di Scienze e Tecnologie Biologiche Chimiche e Farmaceutiche, Università di Palermo, Via Archirafi 18, I-90123 Palermo, Italy; giulia.santaluna@unipa.it
G. Lauria, Dipartimento di Scienze e Tecnologie Biologiche Chimiche e Farmaceutiche, Università di Palermo, Via Archirafi 18, I-90123 Palermo, Italy; gabriele.lauria03@unipa.it
G. Vita, Dipartimento di Scienze della Terra e del Mare, Università di Palermo, Via Archirafi 20, I-90123 Palermo, Italy; gerlando.vita03@unipa.it
C. Di Patti, Museo G.G. Gemmellaro, Università di Palermo, Corso Tukory 131, I-90133 Palermo, Italy; carolina.dipatti@unipa.it
J. Moggi Cecchi, Dipartimento di Biologia, Università di Firenze, Via del Proconsolo 12, I-50122 Firenze, Italy; iacopo.moggicecchi@unifi.it

KEY WORDS - Upper Miocene primate, morphology, microCT, museum specimen, historical notes.

ABSTRACT - In this contribution we describe a specimen attributed to Oreopithecus bambolii *Gervais, 1872 (Primates), preliminarily reported in the 1990's by E. Burgio, the then-curator of the Gemmellaro Museum in Palermo. It is a portion of a maxilla bearing the erupted right second molar, as well as the unerupted right canine and third molar, all excellently preserved. The fragment has been compared with specimens preserved in the Museum of Paleontology in Florence. It shows an overall appearance and taphonomic features that match those of the specimens from the lignite mines near Grosseto in Tuscany. Basic metric surveys and a microCT scan were carried out on the sample. The Museum's records do not allow us to define precisely how the specimen was acquired, but we report some research carried out in the archives at Palermo and Florence, in relation to a possible exchange that took place in the 1870's, between the then-directors G.G. Gemmellaro and I. Cocchi.*

INTRODUCTION

Oreopithecus bambolii Gervais, 1872 is a Late Miocene primate, with a chronological range that can be estimated between 9 and 6.7 million years ago (Rook et al., 2006). It inhabited the humid forests of the Tuscan-Sardinian paleobioprovince of present-day Italy in the central-northern Mediterranean. This peculiar species shows an unusual set of anatomical features, such as the tendency to verticalization of the muzzle (orthognathy), proportions of the upper limb and size of the hand with strong development in length of the metacarpals, and a pelvic girdle characterized by a triangular-shaped sacrum and iliac wing expanded in an anteroposterior direction, a series of features that can be interpreted as a decisive adaptation to brachiation (the movement in the three-dimensions of the forest through the preferential use of the upper limb). Nevertheless, it has been considered as having a possibly unique kind of bipedal locomotion (Harrison, 1991; Khoeler & Mojà-Solà, 1997, 2003).

This medium-large sized primate evolved in a condition of isolation, given that the Tuscan-Sardinian paleobioprovince at the end of the Miocene was in fact an island. This condition was presumably the driving force for a strong clustering of the characters which made *Oreopithecus* different and not easily correlated phylogenetically to the Eurasian hominoids which diversified in large numbers during the Middle and Late Miocene. Furthermore, perhaps in relation to this isolation, if *Oreopithecus* was a Miocene late onset species, it was also a late extinction species, having passed the Valaisian-Turolian climatic transition which instead caused the disappearance of hominoids in Europe (Agustí & Moyà-Solà, 1990).

The species was described by Paul Gervais in 1872, on the basis of a jawbone of an immature individual which Igino Cocchi, then Director of the Institute of Geology of the University of Florence, recovered in the Montebamboli locality (Grosseto province, southern Tuscany, Italy), in a lignite mine, ten years earlier, in 1862. However, this issue is unclear and perhaps the piece was purchased; in those years there was a flourishing trade in paleontological materials from the Grosseto mine area to museums and private collectors in Europe and one of the most active excavators and traders of fossils from the Tuscan lignite mines was Tito Nardi, an acquaintance of Cocchi and collectors such as Airoldi in Florence. The original piece, together with other faunal finds from Montebamboli, was immediately hosted at the Museum of Geology and Paleontology in Florence. From 1872 many finds from other lignite mines in the Grosseto area were described (Harrison, 1991). After World War II, the Swiss paleontologist Johannes Hürzeler began intense studies on *Oreopithecus*, resulting in descriptive publications (Hürzeler, 1949, 1958) and later in new excavations in mines which in 1958 brought to light a complete skeleton

ISSN 0375-7633 doi:10.4435/BSPI.2024.07

in Baccinello, with morphological characteristics not entirely matching those of the specimens of Montebamboli and of larger dimensions, as reconstructed several years later by Ronald J. Clarke. More recently, in 1994, remains attributed to *O. bambolii* were recovered in the locality of Fiume Santo, near Sassari (Sardinia, Italy; Abbazzi et al., 2008).

In 1994 Enzo Burgio (1946-2001), then curator of the Paleontological Museum of the University of Palermo (named after Gaetano Giorgio Gemmellaro, the founder of the institution in 1862), showed one of the authors (LS) a fragment of a jaw attributed to *O. bambolii*, discovered years earlier in the deposits of the Museum, unfortunately lacking documentation certifying its provenance. Burgio, who wrote his degree thesis on Italian fossil primates and in particular the primates of the Gravitelli fauna (Seguenza, 1907), was deeply interested in paleoprimatology. In the absence of more detailed information or adequate morphological analyses, Burgio suggested that the fragment could have come from Gravitelli or that it had in any case some relationship with the Sicilian Miocene horizons, that could have functioned as an interconnection of land bridges between different paleogeographic areas of North Africa and the Tuscan-Sardinian paleoprovince. Burgio misinterpreted the origin of this specimen, as the Messinian fauna of Gravitelli belongs to the Calabrian-Sicilian paleobioprovince, geographically isolated from the Tuscan-Sardinian paleobioprovince (Schmitt et al., 2021) and characterized by folivorous Cercopithecoidea (proto-Colobinae) of the genus *Mesopithecus*, which is also common in other European Messinian sites. Since then, the specimen has been never studied in detail except for an interesting scanning microscopy analysis on dental microwear (Carnieri & Mallegni, 2003).

In this brief note we want to describe the maxillary fragment from the Gemmellaro Museum, to disclose the main morphological characteristics of the teeth, and to provide some data about the internal dental structure after analysis performed with microCT. In addition to this, we present a brief historical examination of the biographies of Igino Cocchi and Gaetano Giorgio Gemmellaro, two important geologists of the newly unified Italian Kingdom, in the second half of the 19th century, whose personal and professional stories crossed several times, and on various occasions the two paleontologists could have interacted and speculated about *Oreopithecus*. In fact, our hypothesis is that Cocchi was able to favor the acquisition of the specimen by Gemmellaro, a find which, for a series of different reasons (among which the various and troubled transfers of headquarters endured by the Palermo collections, also due to the events of World War II) has lain unconsidered for decades with no accompanying documentation in the Museum.

MATERIALS AND METHODS

The *Oreopithecus* specimen at the Museum Gemmellaro in Palermo consists in a partial maxilla with parts of the dental arch and preserving the erupted right second molar (M^2), as well as the unerupted right canine and third molar, all perfectly preserved (Fig. 1). From a first investigation carried out in 2019 by LS and JMC with the help of Lorenzo Rook at the Department of Earth Sciences in Florence, the specimen, for its dimensions and taphonomic characteristics, among which is the typical dark grey-black color of the teeth, seems to come from the Baccinello area. The specimen is catalogued as MGUP TOS 001.

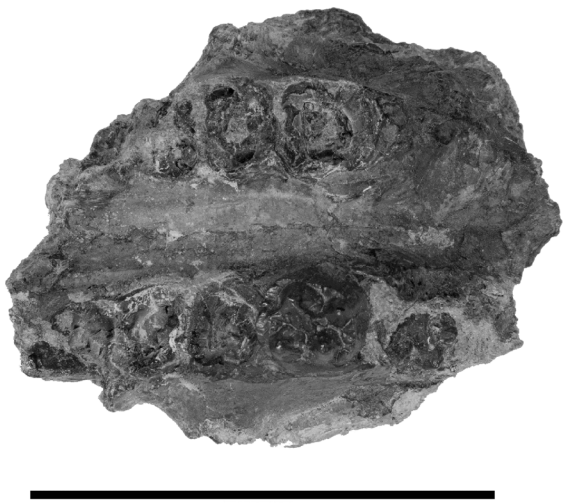


Fig. 1 - The *Oreopithecus bambolii* specimen MGUP TOS 001. Inferior view of the palatal region and alveolar arches. Note the taphonomically narrowed palatal region. On the right side of the maxilla (in anatomical position), the emerging C^1 and the M^2 and emerging M^3 are preserved. All other teeth appear damaged, and the crown is missing. Scale bar corresponds to 5 cm.

MicroCT analysis

The microCT analysis was carried out at the AtenCenter (Advanced Technologies Network Center) at the University of Palermo using a SkyScan 1272 compact scanner (SkyScan, Kontich, Belgium). The operational settings for the scans were: voltage of 100 kV, current of 100 μA, exposure time of 2400 ms, 180° rotations, and filtering with 0.11 mm copper filter, resulting in a scanning time of about three hours. The original scanning files (16-bit TIFF format) were reconstructed at a voxel size of 21.07 micrometers and saved as 8-bit bmp. To process and visualize the data, both the open-source software 3D Slicer (Fedorov et al., 2012) and Avizo v.7.1 (FEI Visualization Sciences Group Inc., Hillsboro) were used (Figs 1-3; Supplementary Online Material - SOM). Using Avizo v.7.1, a semi-automatic threshold-based segmentation was carried out to reconstruct the 3D volume of the M^2 dental tissues. Due to the high degree of X-ray absorption, contrasts are low and the segmentation had to be conducted in the three views of the dataset at the same time. The magic wand was used with manual corrections, and interpolations were applied in areas where contrasts were insufficient to reliably conduct the segmentation. Once the crown was segmented, the M^2 has been digitally reconstructed in 3D. This reconstruction allowed examining of the outer enamel surface (OES), as well as that of the enamel-dentine junction (EDJ), and quantifying tissue proportions of the enamel cap and underlying dentine (Fig. 4).

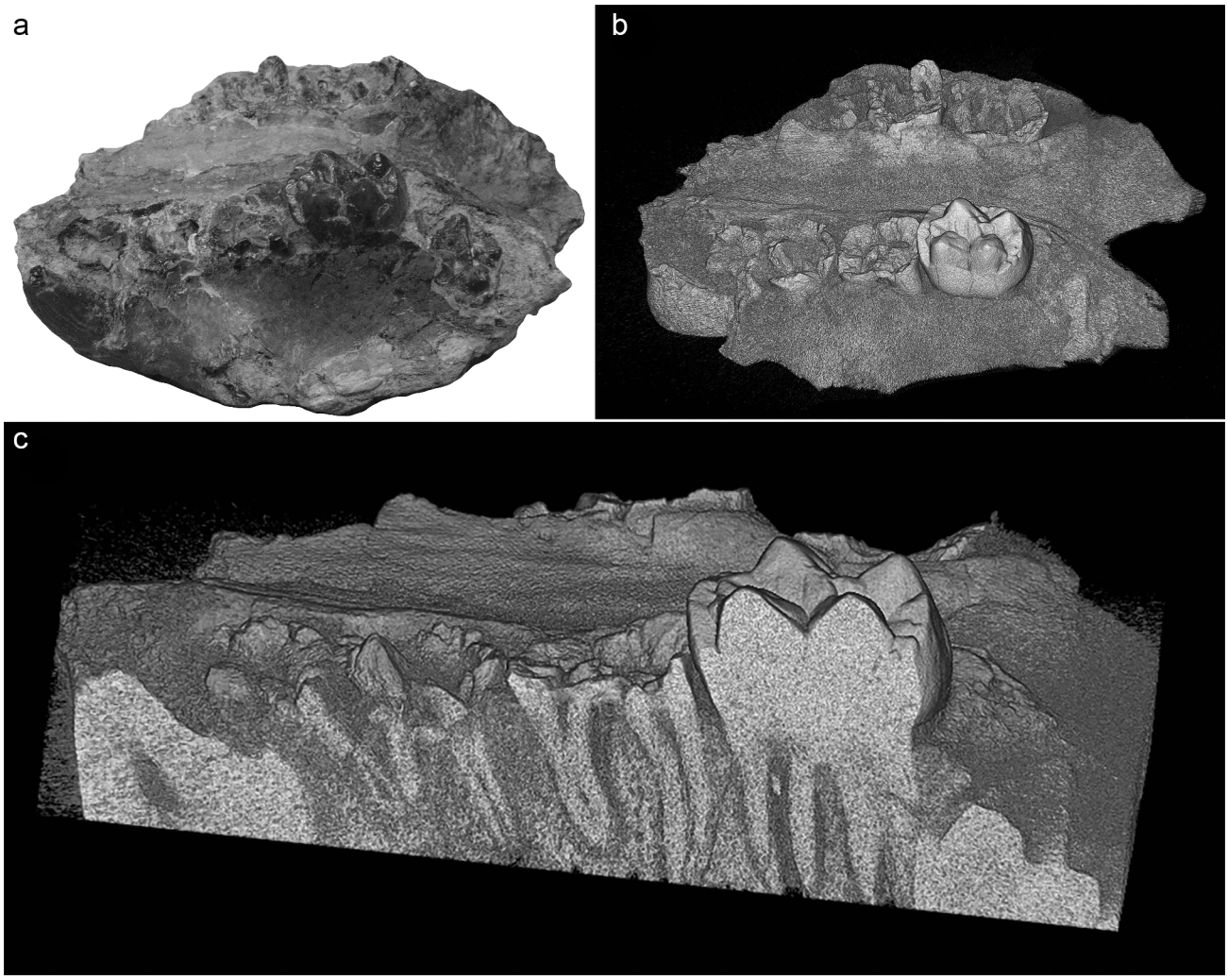


Fig. 2 - a) The *Oreopithecus bambolii* specimen MGUP TOS 001 in a non-conventional lateral view. b) MicroCT 3D reconstruction. c) CT section of the specimen with roots.

Relative enamel thickness (RET) was estimated in 2D, based on measurements taken on the virtual section perpendicular to the cervical plane and passing through the metacone and protocone (Zanolli et al., 2016; Fortuny et al., 2021). The 3D RET parameter was assessed following the method developed by Olejniczak et al. (2008) and used in other studies of Miocene hominoids (e.g., Macchiarelli et al., 2009; Zanolli et al., 2016; Fortuny et al., 2021).

RESULTS AND DISCUSSION

The specimen is an almost complete palatal portion of a maxilla, with the alveoli of the teeth fairly well preserved (Fig. 1). An MP4 video is available as SOM. The specimen suffered taphonomic deformation in a buccolingual direction, resulting in a reduced distance between the right and left dental arcades. On the left side the roots of the P^4, M^1, and M^2 are preserved (the crowns are missing and only the roots are present in the alveoli). The M^3 was still developing in the crypt, not visible externally (arrowed in the microCT image in Fig. 3). On the right side the erupting canine is present, its crown tip broken. Distal to it, the roots of the P^3, P^4, and M^1 are present, but none of them has the crown preserved. The M^2 is perfectly preserved with its crown intact. The right erupting M^3 is visible (Figs 1-3). Its crown is well preserved and its occlusal surface unbroken.

The crown of the M^2 shows high and well-defined cusps (Figs 2a-b and 5). Wear is minimal. The four main cusps are clearly delineated, deeply incised on the buccal and lingual surfaces. An incipient additional cuspule, the paraconule, is present on the mesial side between the protocone and the paracone, at the junction between the preparacrista and proparacrista, both at the OES and EDJ (Fig. 5). On the distal edge an incipient cuspule is also present, between the metacone and hypocone. A centroconule is visible at the center of the occlusal basin, at the junction of the postprotocrista, hypometacrista, and prehypocrista, both at the OES and EDJ (Fig. 5). On the OES, a well-developed cingulum is running along the mesial and lingual edges of the crown and, less so, on the distal and buccal faces. However, the EDJ only shows a shelf-like morphology on the lingual side and mesiolingual corner, and some fossae delimited by short and low crests on the buccal and distal aspects and mesiobuccal corner (Fig. 5). Basic measurements of the specimens have

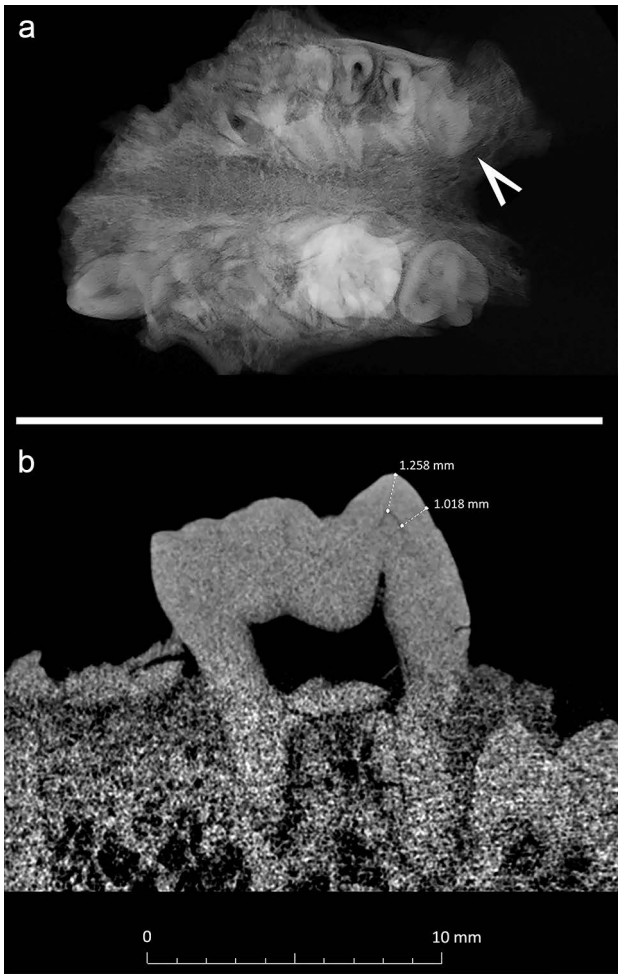


Fig. 3 - a) Digitally reconstructed radiography (DRR) of the specimen MGUP TOS 001 in inferior view; the white arrow points to the left M^3 still in its crypt. b) Enamel thickness in the right M^2.

been collected on the CT images (Tab. 1). The M^3 crown shows an incipient cuspule in the central fossa. Roots are preserved, even in tooth with missing crown (Fig. 2c). Enamel thickness of 1.255 mm has been evaluated at M^2 (Fig. 2d). The canine is still erupting; most of its crown is below the alveolar margin.

Results of the Relative enamel thickness (RET) evaluation and 3D RET of the M^2 of the *Oreopithecus* specimen MGUP TOS 001 are consistent with each other, showing values of 17.0 and 17.3, respectively (Tabs 2 and 3). Compared with extant and Miocene hominoids, MGUP TOS 001 displays higher values of RET and 3D RET than the average values of all dryopithecines and extant non-human great apes. Among the Miocene hominoids for which M^2 RET is available, only *Griphopithecus* exhibits thicker enamel than the *Oreopithecus* specimen (Tab. 2). Among the extant hominids, *Homo sapiens* is the only taxon showing thicker enamel than the *Oreopithecus* M^2.

A tentative hypothesis regarding the provenance of the sample

The specimen MGUP TOS 001 is part of the collections not on display of the Gemmellaro Geological Museum of Palermo, a museum that was founded in the second half of the 19th century.

In spite of accurate archival research (performed by LS and GS), no direct evidence of acquisition or exchanges of the material has been found. Considering that the fossil can be attributed to *Oreopithecus bambolii*, and given that the range of the species was limited to the Tuscan-Sardinian paleobiogeographic region, and that the holotype was stored in Florence since its discovery, and also evaluating the morphological similarity and the taphonomic appearance between the Palermo specimen and the fossils of the Florentine Museum of Paleontology, we hypothesize that the specimen derived from Florence and that it was acquired by the Palermo Museum a long

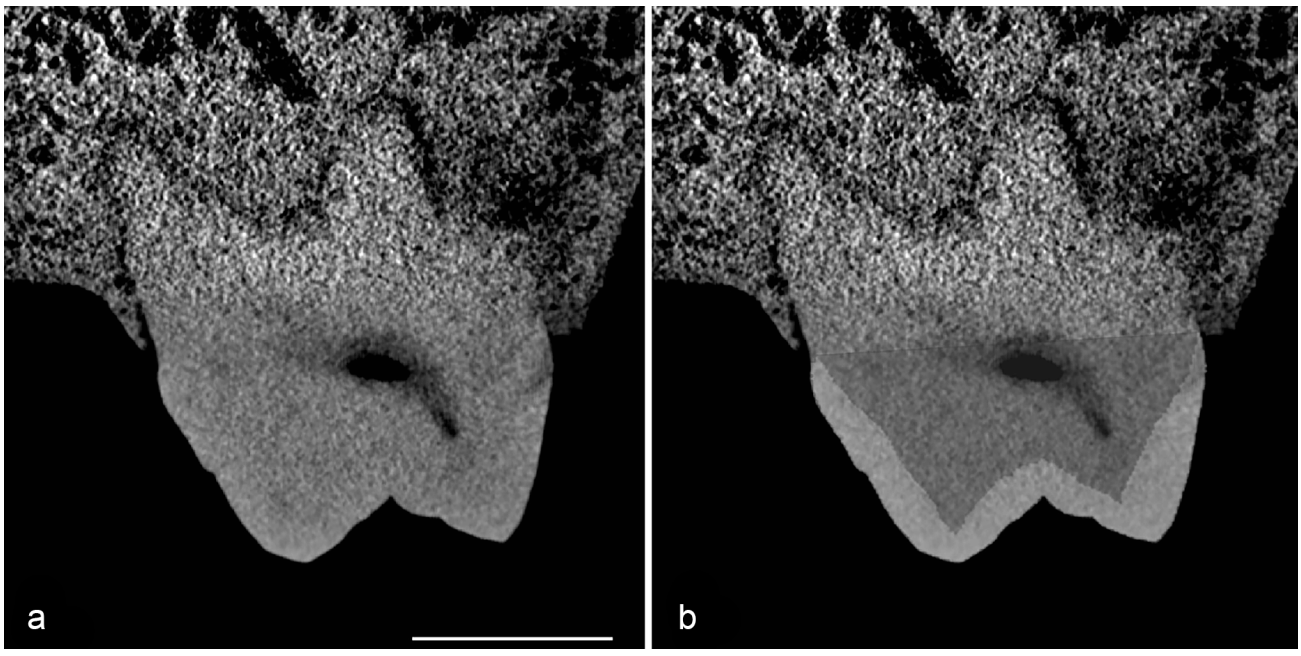


Fig. 4 - Microtomographic-based cross-section of the M^2 passing through the dentine horns of the mesial cusps (a) and the same image with the segmented crown tissues (b). Scale bar corresponds to 5 mm.

Variables	Measurements (mm)
Maximum length	57.80
M^2 mesiodistal diameter	10.84
M^2 buccolingual diameter	9.87
M^2 root length	6.86
C^1 crown height	4.86

Tab. 1 - MGUP TOS 001 specimen and dental linear measurements. The width has not been collected as the specimen is deformed.

time ago. Our reconstruction on the provenience of the specimen is therefore necessarily highly hypothetical.

Figure 6 shows a synoptic comparison of the parallel and crossed careers of the two paleontologists Gaetano G. Gemmellaro and Igino Cocchi, undoubtedly among the most prominent and influential geologists in the period following the birth of the Italian Kingdom (1861), the birth (or rebirth) of university institutions, and the drastic secularization of the Italian academic system.

Gaetano Giorgio Gemmellaro (1832-1904) was a physician, son of a well-known volcanologist from the University of Catania and therefore close to and interested in Geology, so much that he hosted Charles Lyell during his visits and geological explorations of Sicily. He certainly owes his political visibility to the fact that he demonstrated his distance from the Bourbon regime by participating in Garibaldi's expedition to Sicily and this, combined with the fact that he had a lay formation and a good culture, highlighted him as the creator and director of the Museum of Geology and Paleontology of the University of Palermo, in 1862. Entering the academic world, he necessarily met Igino Cocchi (1827-1913), a well-known and very active Florentine academic who boasts valuable collaborations with Roderick Impey Murchison in England and with various members of the Société géologique de France.

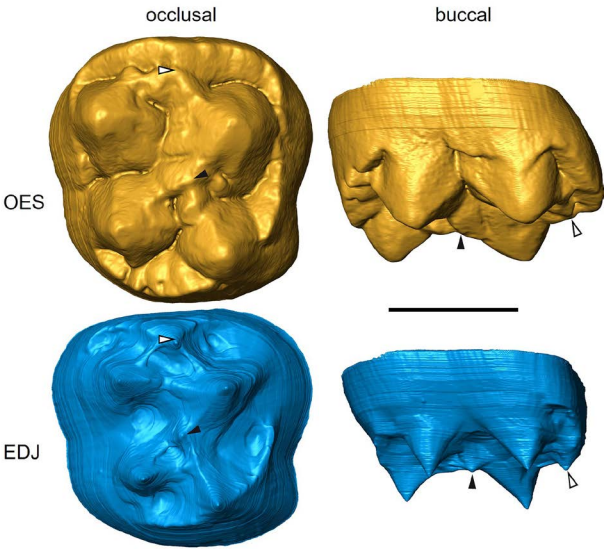


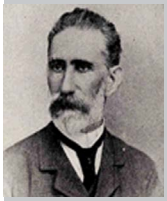
Fig. 5 - (color online) Virtual renderings of the M^2 crown showing the outer enamel surface (OES) and underlying enamel-dentine junction (EDJ) in occlusal (left) and buccal (right) views. The white arrows point to the paraconule and the black arrows indicate the centroconule. Scale bar corresponds to 5 mm.

Taxon		RET
Oreopithecus bambolii (1)[a]	value	17.0
Griphopithecus sp. (2)[b]	mean	19.0
	range	17.8-20.2
Anoiapithecus brevirostris (4)[c]	mean	15.2
	range	13.0-17.3
Pierolapithecus catalaunicus (2)[c]	mean	14.5
	range	14.4-14.6
Dryopithecus fontani (2)[c]	mean	12.0
	range	11.6-12.5
Hispanopithecus crusafonti (1)[c]	value	13.0
Hispanopithecus laietanus (1)[c]	value	13.1
Rudapithecus hungaricus (1)[d]	value	13.5
Pongo pygmaeus (12)[e]	mean	15.2
	range	10.8-18.2
Pongo abelii (7)[e]	mean	14.0
	range	11.2-19.3
Gorilla gorilla (2)[b]	mean	12.3
	range	11.6-13.0
Pan troglodytes (3)[b]	mean	11.4
	range	10.7-12.5
Homo sapiens (25)[b]	mean	21.6
	range	16.5-28.0

Tab. 2 - Bi-dimensional relative enamel thickness index (RET) in *Oreopithecus*, compared with extant and Miocene hominoid M2s (decreasing values). Sample size is reported in parentheses. [a]This study; [b]Smith et al. (2006); [c]Fortuny et al. (2021); [d]Smith et al. (2019); [e]Smith et al. (2012).

Taxon		3D RET
Oreopithecus bambolii (1)[a]	value	17.3
Anoiapithecus brevirostris (4)[b]	mean	13.3
	range	11.7-14.3
Pierolapithecus catalaunicus (2)[b]	mean	15.2
	range	14.9-15.5
Dryopithecus fontani (2)[b]	mean	11.4
	range	11.0-11.9
Hispanopithecus crusafonti (1)[b]	value	11.3
Hispanopithecus laietanus (1)[b]	value	12.2
Pongo pygmaeus (4)[c]	mean	15.6
	range	14.1-17.5
Pan troglodytes (1)[c]	value	12.7
Homo sapiens (5)[c]	mean	23.9
	range	20.5-31.6

Tab. 3 - Three-dimensional relative enamel thickness index (3D RET) in *Oreopithecus*, compared with extant and Miocene hominoid M2s (decreasing values). Sample size is reported in parentheses. [a]This study; [b]Fortuny et al. (2021); [c]Olejniczak et al. (2008).



Gaetano G. Gemmellaro (1832-1904)			Igino Cocchi (1827-1913)
Physician (son of C. Gemmellaro, volcanologist in Catania).			Zoologist and geologist.
Several incursions in Mineralogy and Geology.	1850-59	1850	Collaboration with Sir Roderick Impey Murchison.
Visiting Sicily with C. Lyell.	1857	1852-57	Collaboration with the Société géologique de France.
Participation in Garibaldi's campaign in Sicily.	1860	1852-73	Academic activity at the University of Florence.
Creator and Director of the (renewed) Museum of Geology and Paleontology in Palermo. First contacts with I. Cocchi for the Project Carta Geologica d'Italia.	1860 1861	1861	Advocate and supporter for the Project Carta Geologica d'Italia. First contacts with G.G. Gemmellaro.
Sponsorship (funds and specimens) from Count Airoldi Arrigoni in Florence. Participation to the Italian Geological Committee (CGI).	1860-67	1867	President of the Italian Geological Committee (CGI).
Director of the Project Carta Geologica d'Italia.	1861	1861	Still in the Project Carta Geologica d'Italia.
Exchanges and acquisition of fossils for the Museum, including specimens from L. Seguenza (Gravitelli) and natural casts.	1861-75	1872	Published a paper on O. bambolii (Gervais) from Montebamboli and Inuus ecaudatus (Macaca).
Rector of the University of Palermo. Il Naturalista Siciliano (1881).	1874-76 1881-86	1873	Abandoned the Presidency of the CGI and the University. Member of Lincei and Georgofili Academies.
Massive acquisition of specimens. Correspondence and international contacts. Member of the Italian Geological Society.	1881	1881	Among the proponents of the Italian Geological Society.
Further massive acquisitions of specimens. Epistolary exchanges and journal subscriptions with the Institute of Geology of Florence.	1887	1887	President of the Italian Geological Society.
President of the Italian Geological Society. Senator of the Italian Parliament.	1891 1892	1903	Scholar of Finnish literature and translator into Italian of the epic poem Kalevala.

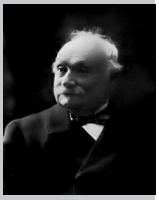


Fig. 6 - A synoptic comparison of the parallel and crossed careers of the two paleontologists Gaetano G. Gemmellaro and Igino Cocchi, in the course of Italian unification. The various occasions of personal and academic relationship may fuel speculations on the possible role of Cocchi in the acquisition of the specimen by Gemmellaro.

The contacts between the two scientists grew through time and, coincidentally, it is from Florence that Gemmellaro obtained the first direct support for his Museum. In fact, Count Airoldi Arrigoni donated part of his collections, but above all a substantial economic fund, to the Palermo Museum. The activity of collecting materials to expand the exhibitions of the Museum was continued by Gemmellaro for almost thirty years, a very intense period that also saw him as Rector and founder of the "Naturalista Siciliano" (1881), a still active journal. Gemmellaro and Cocchi exchanged editorial collections and articles and Gemmellaro carefully read the commentary that Cocchi wrote in 1872 in the "Bollettino del Comitato Geologico Italiano" on the subject of Gervais' description of *O. bambolii.*

Therefore, if we consider this series of contingencies and the repeated contacts between the two scientists, together with the fact that Gemmellaro was animated by a remarkable desire to rapidly acquire rare and representative specimens for his institution, we may hypothesize that the specimen was one of those traded through Cocchi. In fact, he had a certain control over a vast series of collectors and suppliers of original and significant materials, such as Nardi, for example, who became a wealthy collector and expert on the Tuscan Miocene fauna, starting as an explorer and collector in the abandoned lignite mines.

CONCLUSION

Given the evidences of its subadult status, the maxilla described (MGUP TOS 001) probably belonged to an individual of remarkable size, especially when compared with the Montebamboli type specimen. According to Harrison (1991), *O. bambolii* was a highly dimorphic species and the estimated weight of adults ranged from 40 kg for males to 25 kg for females.

The dental morphology of the M^2 is consistent with that of *O. bambolii*, that is characterized by very high pointed cusps that rise from a cingulum that surrounds the entire crown. The overall morphology of the maxilla

and teeth, including the presence of additional cuspules, like the paraconule and centroconule on the M^2, is typical of *Oreopithecus* (Harrison & Rook, 1997). Both RET and 3D RET values of the *Oreopithecus* M^2 are comparable with previously published data on lower molars (Zanolli et al., 2016).

Oreopithecus bambolii is one of the most intriguing Miocene primate species. It is a paradigmatic primate because it is presumably the first brachiating experiment recorded among the large hominoids and at the same time it has been investigated for its facultative bipedal capacity. The fossil remains ascribed to it, although not numerous, are significant and tell us about its paleobiogeographic distribution as well as its morphological variability. It therefore appears important that the scientific community is duly informed of specimens held in museums available for further investigations and insights.

SUPPLEMENTARY ONLINE MATERIAL

The supplementary Video in MP4 Format of the Volume rendering of the specimen deriving from Micro-CT is available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-632/

ACKNOWLEDGEMENTS

The authors thank Elisabetta Cioppi and all the organizers of the conference, as well as Lorenzo Rook for the possibility of comparing the sample with the *Oreopithecus* fossils hosted at the Museum of Paleontology of the University of Florence and for valuable comments. LS acknowledges Renzo Nelli (Biblioteca di Scienze, Geomineralogia, University of Florence) for his kind help in consulting the letters and notebooks of Igino Cocchi. The authors are grateful to the Editors and Marco Cherin for their useful comments, as well as to a second anonymous reviewer. The Aten Center MicroCT analysis has been funded by funds D8MASTS01-00B2 /D8MASTS01+00B2 (Università degli Studi di Palermo) to LS.

REFERENCES

Abbazzi L., Delfino M., Gallai G., Trebini L. & Rook L. (2008). New data on the vertebrate assemblage of Fiume Santo (Northwest Sardinia, Italy), and overview on the Late Miocene Tusco-Sardinian paleobioprovince. *Palaeontology*, 51: 425-451.

Agustí J. & Moyà-Solà S. (1990). Mammal extinctions in the Vallesian (Upper Miocene). *In* Kauffman E.G. & Walliser O.H. (ed.), Extinction Events in Earth History, Proceedings of the Project 216, Global Biological Events in Earth. *Lecture Notes in Earth Sciences*, 30: 425-432.

Carnieri E. & Mallegni F. (2003). A new specimen and dental microwear in *Oreopithecus bambolii*. *Homo*, 54: 29-35.

Fedorov A., Beichel R., Kalpathy-Cramer J., Finet J., Fillion-Robin J.C., Pujol S., Bauer C., Jennings D., Fennessy F., Sonka M., Buatti J., Aylward S.R., Miller J.V., Pieper S. & Kikinis R. (2012). 3D slicer as an image computing platform for the quantitative imaging network. *Magnetic Resonance Imaging*, 30: 1323-1341.

Fortuny J., Zanolli C., Bernardini F., Tuniz C. & Alba D.M. (2021). Dryopithecine palaeobiodiversity in the Iberian Miocene revisited on the basis of molar endostructural morphology. *Palaeontology*, 64: 531-554.

Gervais P. (1872). Sur un singe fossile, d'espèce non encore décrite, qui a été decouvert au Monte-Bamboli (Italie). *Comptes rendus de l'Académie des sciences*, 74: 1217-1223.

Harrison T. (1991). The implications of *Oreopithecus bambolii* for the origins of bipedalism. *In* Coppens Y. & Senut B. (eds), Origine(s) de la Bipédie chez les Hominidés, Éditions du Centre National de la Recherche Scientifique: 235-244.

Harrison T. & Rook L. (1997). Enigmatic anthropoid or misunderstood ape? The phylogenetic status of *Oreopithecus bambolii* reconsidered. *In* Begun D.R., Ward C.V. & Rose M.D. (eds), Function, Phylogeny, and Fossils; Miocene Hominoid Evolution and Adaptations. Plenum Press, New York: 327-362.

Hürzeler J. (1949). Neubeschreibung von *Oreopithecus bambolii* Gervais. *Schweizerische Paläontologische Abhandlungen*, 66: 1-20.

Hürzeler J. (1958). *Oreopithecus bambolii* Gervais, a preliminary report. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 69: 1-48.

Köhler M. & Moyà-Solà S. (1997). Ape-like or hominid-like? The positional behavior of *Oreopithecus bambolii* reconsidered. *Proceedings of the National Academy of Sciences USA*, 94: 11747-11750.

Köhler M. & Moyà-Solà S. (2003). Understanding the enigmatic ape *Oreopithecus bambolii*. *Courier Forschungsinstitut Senckenberg*, 243: 111-123.

Macchiarelli R., Mazurier A., Illerhaus B. & Zanolli C. (2009). *Ouranopithecus macedoniensis* (Mammalia, Primates, Hominoidea): virtual reconstruction and 3D analysis of a juvenile mandibular dentition (RPl-82 and RPl-83). *Geodiversitas*, 31: 851-863.

Olejniczak A.J., Tafforeau P., Feeney R.N.M. & Martin L.B. (2008). Three-dimensional primate molar enamel thickness. *Journal of Human Evolution*, 54: 187-195.

Rook L., Gallai G. & Torre D. (2006). Lands and endemic mammals in the Late Miocene of Italy: constraints for paleogeographic outlines of Tyrrhenian area. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238: 263-269.

Schmitt T., Fritz U., Delfino M., Ulrich W. & Habel J.C. (2021). Biogeography of Italy revisited: genetic lineages confirm major phylogeographic patterns and a pre-Pleistocene origin of its biota. *Frontiers in Zoology*, 18: 1-13.

Seguenza G. (1907). Nuovi resti di mammiferi pontici di Gravitelli presso Messina. *Bollettino della Società Geologica Italiana*, 26: 89-122.

Smith T.M., Olejniczak A.J., Reid D.J., Ferrell R.J. & Hublin J.J. (2006). Modern human molar enamel thickness and enamel-dentine junction shape. *Archive for Oral Biology*, 51: 974-995.

Smith T.M., Olejniczak A.J., Zermeno J.P., Tafforeau P., Skinner M.M., Hoffmann A., Radovčić J., Toussaint M., Kruszynski R., Menter C., Moggi-Cecchi J., Glasmacher U.A., Kullmer O., Schrenk F., Stringer C. & Hublin J.-J. (2012). Variation in enamel thickness within the genus *Homo*. *Journal of Human Evolution*, 62: 395-411.

Smith T.M., Tafforeau P., Pouech J. & Begun D.R. (2019). Enamel thickness and dental development in *Rudapithecus hungaricus*. *Journal of Human Evolution*, 136: 102649.

Zanolli C., Dean M.C., Rook L., Bondioli L., Mazurier A. & Macchiarelli R. (2016). Enamel thickness and enamel growth in *Oreopithecus*: combining microtomographic and histological evidence. *Comptes Rendus Palevol*, 15: 209-226.

Manuscript submitted 13 June 2023
Revised manuscript accepted 23 February 2024
Published online 4 June 2024
Guest-Editors Luca Bellucci, Fabio Di Vincenzo & Andrea Savorelli