

## In praise of *Oreopithecus*. A Miocene primate enshrouded in a 150-year-long mystery

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Significant events often have humble and seemingly negligible beginnings, the effects of which may be unforeseen to their protagonists. In 1872, the barely thirty-year-old Claude Monet painted a cold and foggy sunrise from the window of his hotel room overlooking the port of Le Havre. With swift brushstrokes and a personal sense of colour, he created a small painting, standing at less than half a meter in height, which he titled “Impression, soleil levant” (Impression, Sunrise). This work not only lent its name upon the burgeoning movement of Impressionism but also heralded the dawn of the modern conception of art, breaking with the academic tradition and influencing all that would ensue in figurative art, up to Picasso and even Banksy.

In the same year, also in France, another seemingly modest event would unfold, bearing unexpected consequences that continue to animate the contemporary scientific debate on the evolutionary history of humans and other primates. The naturalist Paul Gervais (1816-1879), then holder of the chair of Comparative Anatomy at the Muséum National d’Histoire Naturelle at the Jardin des Plantes, presented in the May 6<sup>th</sup>, 1872 session of the Académie des sciences in Paris the results of his research on a juvenile mandible of a fossil primate. The mandible was unearthed a decade earlier, in 1862, in a lignite quarry of Montebamboli in the Tuscan Maremma near the municipality of Massa Marittima. The account of the discovery was published in a note in the Comptes Rendus of the Academy (Gervais, 1872a), followed by a more extensive article on the Italian fossil mammals in the Journal de Zoologie (Gervais, 1872b).

Based on the unprecedented morphology of the tiny mandible, Gervais established a new genus and species of fossil primate which he named *Oreopithecus bambolii*, deriving the genus name from the Greek ὄρος, meaning “mountain” (Fig. 1). Note that the term refers to the elevated molar cusps rather than to the landscape context of the find site (Montebamboli) to which the species designation instead alludes. Gervais interpreted *Oreopithecus* as being related to apes, particularly to gorillas, albeit with a smaller dentition. Nevertheless, he also observed peculiar morphological features suggesting convergence with baboons and macaques, considering *Oreopithecus* as a kind of morphological intermediary between apes and monkeys. In the words of the French scholar, *Oreopithecus* “prendra rang à la fin de la série des Pithécins anthropomorphes après le Gorille, et avant

les Cynocéphales et les Macaques” (Gervais, 1872a, p. 1223) (“It will take its place at the end of the series of anthropomorphic Pithecines after the Gorilla, and before the Cynocephali and the Macaques”).

Gervais, however, could never have anticipated that this novel species, precisely due to its distinctive features, would unleash such extensive and enduring controversies among scholars, configuring *Oreopithecus* as a genuine paleontological enigma that continues to elude any definitive attribution, fuelling heated debates that persist to the present day. Indeed, few fossil vertebrates, and certainly no other primate species, have been the subject of so many diverse interpretations by scholars, contributing to a substantial and enduring uncertainty regarding its systematic position and adaptations.

A few years after Gervais’ initial description, and with the accumulation of new fossil remains attributed to *Oreopithecus bambolii* from the Upper Miocene layers not only of Montebamboli but also in other lignite quarries in the Tuscan Maremma, such as Montemassi, Casteani, and Ribolla (Forsyth Major, 1880; Ristori, 1890; Cioppi & Rook, 2010), systematic interpretations among scholars began to diverge significantly (Delson, 1986). These divergences centred around the dichotomy previously outlined by Gervais between Hominoidea and Cercopithecoidea, but also extended to consider *Oreopithecus* as a primate akin to *Apidium* (now considered a basal Simiiformes) and a possible evolutionary dead-end, or conversely, as a direct ancestor of humans within the hominin lineage (Hürzeler, 1954, 1958; Simons, 1960; Delson, 1986).

The phylogenetic classification of *Oreopithecus* varied significantly over time, ranging, as noted before, from cercopithecoids to basal hominoids and hominids, including hominins (e.g., Delson, 1986). Schwalbe (1915) even proposed a distinct family, Oreopithecidae, within hominoids, designating *Oreopithecus bambolii* Gervais, 1872 as its sole species. This taxonomic instability, involving prominent scholars in primate and evolutionary studies over the past century and a half, sharply contrasts with the uncertainty usually associated with vertebrate paleontology’s incertae sedis, which often involves scant and poorly preserved remains. In the case of *Oreopithecus*, however, the fossil material is notably rich and well-documented.

The extensive data on *Oreopithecus* arise not only from the Montebamboli type mandible but also from numerous

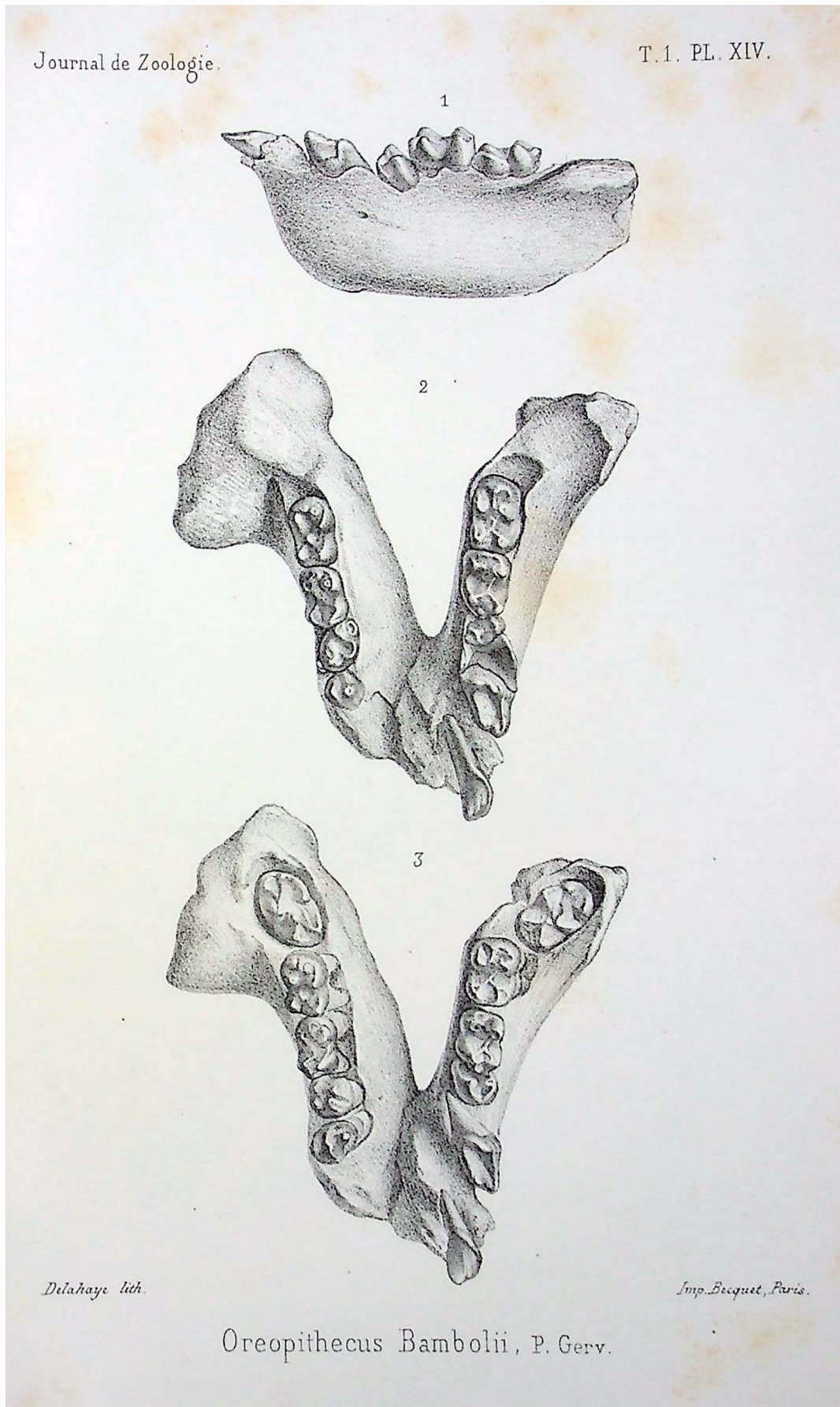


Fig. 1 - (color online) Original plate from the first volume of the *Journal de Zoologie* edited by Paul Gervais in 1872, which collects his two earlier articles on the *Oreopithecus*.

additional skeletal findings discovered through the years. These include craniodental elements mainly from Tuscan sites and, more recently, from an Upper Miocene site in Fiume Santo, Sardinia, near Porto Torres, where a mandibular fragment was discovered in 1994 (Cordy & Ginesu, 1994; Abbazzi et al., 2008). Notably, a nearly complete *Oreopithecus* skeleton was found in 1958 by the Swiss paleontologist Johannes Hürzeler in the Baccinello lignite mine in Maremma (Hürzeler, 1958; Cioppi & Rook, 2010). Consequently, *Oreopithecus* emerges as the most thoroughly documented Miocene primate among those uncovered to date (Harrison & Rook, 1997; Almécija et al., 2021).

Even more remarkable is the fact that the paradox concerning *Oreopithecus* extends not only to the debate about its phylogenetic position but also involves the nature and morpho-functional interpretation of its adaptations, particularly the postcranial ones (Sarmiento, 1983; Stern & Jungers, 1985; Susman, 1985, 2004, 2005; Szalay & Langdon, 1986; Moyà-Solà et al., 1999, 2005; Sarmiento & Marcus, 2000; Almécija et al., 2014). The analysis of the Baccinello skeleton, focused on the pelvis and trunk (Rook et al., 1999; Russo & Shapiro, 2013; Hammond et al., 2020) but also on the morphology of the semicircular canals of the inner ear (Rook et al., 2004), has led to divergent interpretations regarding

the locomotor behaviour of *Oreopithecus bambolii*. Indeed, the latter has been the subject of assessments ranging from some degree of orthogrady as an arboreal suspensory animal to fully embracing terrestrial bipedalism (Harrison, 1991; Köhler & Moyà-Solà, 1997; Rook et al., 1999; Wunderlich et al., 1999; Russo & Shapiro, 2013; Hammond et al., 2020).

To commemorate the 150<sup>th</sup> anniversary since Gervais described this iconic and enigmatic primate, and to provide an update on current knowledge regarding *Oreopithecus bambolii* and its environment, the Università di Firenze, under the auspices of Rector Alessandra Petrucci, hosted the International Conference “*Oreopithecus*150 a Miocene hominoid enshrouded in a 150-years-long mystery” on October 20<sup>th</sup>, 2022, at the Aula Magna of the University (Fig. 2). The conference was organized by the Sistema Museale di Ateneo in collaboration with the Dipartimento di Scienze della Terra of the same University.

Furthermore, a guided geological field trip to the localities of *Oreopithecus* and its associated fauna was arranged in southern Tuscany on October 21<sup>st</sup>, 2022 (Fig. 3). This field trip was organized in partnership with the Museo Archeologico of Massa Marittima (Grosseto), the Museo di Storia Naturale della Maremma (Grosseto) and the Parco Nazionale delle Colline Metallifere Grossetane/Tuscan Mining UNESCO Global Geopark.



Fig. 2 - (color online) Speakers and organizers of the “*Oreopithecus*150” Conference at the Aula Magna of the Università di Firenze. Top row from left: Saverio Bartolini Lucenti, Luca Pandolfi, Fabio Di Vincenzo, René Bobe, Lorenzo Rook, Marco Pierini, Daniel DeMiguel, Luca Bellucci, Marco Benvenuti, Alessandro Urcioli; Middle row from left: Andrea Savorelli, Adele Bertini, Andrea Faggi, Susana Carvalho, Luca Bondioli, Clément Zanolli, David M. Alba, Ashley S. Hammond, Roberta Pieraccioli, Alessandra Casini, Luca Sineo; first row from left: Weronika K. Cieszyńska, Luca Bindi, Elisabetta Cioppi, Stefano Dominicci, Barbara Montecchi (photo credit Sistema Museale di Ateneo, Università di Firenze).



Fig. 3 - (color online) A snapshot of the geological field trip at Rio Piastrello, near Montebamboli (photo credit Stefano Dominici).

The relationship linking *Oreopithecus* to the academic and scientific institutions of Florence in particular, spans entirely these 150 years of history and extends even further back to include the earliest reports of the discovery of pre-Messinian Late Miocene primate fossils in the lignite mines of Tuscany in the first half of the 1800s (Cioppi & Rook, 2010).

The type mandible of *Oreopithecus bambolii* is housed in the Museo di Geologia e Paleontologia of the Università di Firenze, belonging to the broader Museo di Storia Naturale. The latter traces its lineage back to the Regio Museo di Fisica e Storia Naturale di Firenze, recognized as Europe's oldest scientific museum open to the public, established on February 22<sup>nd</sup>, 1775 by Grand Duke of Tuscany Peter Leopold of Habsburg-Lorraine. Subsequently, the Museo di Storia Naturale merged into the Sistema Museale di Ateneo of the Università di Firenze. Alongside the mandible identified with catalogue number IGF 4335, the original data documenting the discovery are also preserved. This report represents the oldest record of the find, including information about its locality of origin, Montebamboli, and noting the name of Tito Nardi, who delivered the specimen to Igino Cocchi (1827-1913), then curator of the paleontological collections of the Regio Museo. In October 1871, Cocchi entrusted the small mandible from Montebamboli to

Gervais for a detailed study during the visit to Florence by the French scholar. Cocchi, who specialized in the study of fossil shells and marine invertebrates, had forged strong connections with prominent scholars thanks to his scientific visits to London and Paris. It seems likely that Cocchi, keen to acquire essential information about the somewhat enigmatic small fossil, sought out Gervais's expertise in comparative vertebrate anatomy. Conversely, Gervais, as reported by Cocchi in a note from 1872, showed eagerness to examine that intriguing specimen (Cocchi, 1872).

Additionally, within the Museo di Storia Naturale of Florence, the most spectacular specimen associated with *Oreopithecus* is also housed. This is the skeleton discovered by Hürzeler in 1958 and catalogued under the number IGF 11778. This specimen, discovered in anatomical connection and preserved within a lignite slab, albeit crushed, stands as the most complete and informative non-hominin hominoid known in the fossil record to date. Initially brought to Basel by Hürzeler, the skeleton returned to Florence in 1965 thanks to Augusto Azzaroli, the then director of the Museo di Geologia e Paleontologia in Florence. In the late 1990s, Ron J. Clarke restored the skull, which is now exhibited alongside the skeleton (Clarke, 1997, 2010). At the time of its discovery, the specimen sparked overwhelming media

interest worldwide (Hürzeler, 1958; Straus, 1958). The skeleton, nicknamed “Sandrone” after one of the two miners who first noticed its presence in the Baccinello coal quarry, has over the years become a true scientific icon and a natural treasure not only for the Museo di Geologia e Paleontologia of the Università di Firenze, but also for the city itself, and, in a broader sense, for Tuscany, which is usually associated with extraordinary artistic heritage stemming from human creativity. A big mural of “Sandrone” is displayed in the municipality of Baccinello to pay homage to the area mining tradition.

Although the mystery surrounding *Oreopithecus* persists, in recent years some light has been shed on fundamental aspects of its biology and the environment it inhabited. Many of its peculiar characteristics, seemingly evolved in convergence with other taxonomic groups, stem from being an endemism that evolved in partial or total isolation on what, during the Late Miocene, was an archipelago of islands with its own endemic fauna and few predators, constituting the Tusco-Sardinian insular paleobioprovince (Azzaroli et al., 1986; Rook et al., 1996; 1999; 2006; Moyà-Solà, 2010; Rook, 2016). *Oreopithecus* is one of the very few catarrhines that survived the Vallesian crisis in Europe, becoming extinct approximately 6.7 million years ago (Rook et al., 2011; Nelson & Rook, 2016). The causes of its disappearance are likely linked to the connection of the Tusco-Sardinian insular ecosystem with the mainland, leading to intense interaction with non-endemic invasive fauna (Azzaroli et al., 1986; Nelson & Rook, 2016; DeMiguel & Rook, 2018).

Taxonomically, its close relationship with hominins, as suggested by Hürzeler (1954, 1958), appears to be unlikely. *Oreopithecus* might belong to the group of nyanzapithecines that migrated from Africa, may have evolved locally from Eurasian dryopithecines, or even originated from Pliopithecoidea (von Koenigswald, 1969; Szalay & Berzi, 1973; Delson, 1979; Delson & Szalay, 1985; Harrison, 1986, 1987; Sarmiento, 1987; Alba et al., 2001; Köhler & Moyà-Solà, 2003; Zanolli et al., 2016, 2022). Although its locomotor adaptations are still under debate, and many of them result from parallel evolution, studying it remains crucial for understanding the evolutionary pathways, including bipedalism in hominins, among Miocene primates.

The present Thematic Issue “*Oreopithecus150*: A Miocene primate enshrouded in a 150-year-long mystery” gathers the contributions of participants in the International Conference “*Oreopithecus150*” providing a comprehensive overview—a “coup d’œil” as Gervais would say—of the biological, paleoenvironmental, stratigraphic, and paleogeographic aspects that have characterized research on *Oreopithecus bambolii* in these last 150 years.

This Issue starts with the paper by Cioppi et al. (2024) that offers to the readership a fundamental summary of research on this iconic primate from Gervais’ description. Moreover, the Authors pay tribute to Tito Nardi, the fossil collector who, in the second half of the 19<sup>th</sup> century, discovered the *Oreopithecus* mandible in a disused lignite mine of Montebamboli. Thanks to him, a great (never-ending) scientific history began.

The Issue continues with the work of Dominici & Benvenuti (2024) who challenge the traditional correlation between the Montebamboli lignite and the V2 interval of the Baccinello succession and provide a new and alternative paleobiogeographic scenario that hypothesizes a single phase of Tusco-Sardinian insularism bracketed between two intervals of faunal interchange when Tuscany and Sardinia came in contact with the continental mainland.

Sineo et al. (2024) present the results of a study on a fragmentary maxilla attributed to *Oreopithecus bambolii*, housed in the Museum “Giorgio G. Gemmellaro” in Palermo. The maxilla, unknown until now, was discovered among museum collections in the 1990s and appears to have been a gift from Iginio Cocchi to his Sicilian colleague Giorgio G. Gemmellaro, the founder of the museum in Palermo bearing his name.

Cieszynska (2024) deals with the odontometric traits of *Oreopithecus bambolii* specimens from Tuscany and Sardinia. Its primitive teeth, adapted for a folivorous diet, did not reveal significant differences in the length of the molars among populations from various paleontological sites.

Alba et al. (2024) discuss the state-of-the-art of one of the most debated research questions on *Oreopithecus*, i.e., its phylogenetic position within “still largely unresolved puzzle of Miocene ape phylogeny”. The Authors present a novel perspective that fundamentally shifts the way we understand the distinctive characteristics of *Oreopithecus* morphology in order to interpret its phylogenetic position. Rather than regarding *Oreopithecus* as an anomaly that disrupts our understanding of Miocene primate evolution, the Authors argue from the premise that current phylogenetic theories concerning non-cercopithecoid Miocene primates are largely unresolved and problematic. From this vantage point, the morphology of *Oreopithecus*, with its numerous potential homoplasies compared to other taxonomic groups, emerges as the key for interpreting and comprehending the intricate complexities of primate phylogeny during the Miocene. In summary, the Authors’ aim, as expressed in their own words, is to assert “Maybe the time has come to stop considering that *Oreopithecus* is an oddball Miocene ape or an enigma that must be solved within the current framework of Miocene ape phylogeny”.

DeMiguel & Rook (2024) review the main hypotheses that have been proposed to determine *Oreopithecus*’ extinction and, in the light of recent data, to reevaluate the most viable explanation for its disappearance. They confirm that faunal interaction (both competition and predation) with invading species can be considered as the most feasible explanation for the decline and disappearance of *O. bambolii* and associated fauna.

This Thematic Issue ends with the work of Martinetto et al. (2024) that revises for the first time the whole macroflora from Montebamboli including remains of the palm tree now attributed to *Sabal rhapifolia*, thus providing new data to reconstruct the paleoclimate of the area as warm temperate and humid.

To conclude, the scientific significance and interest in *Oreopithecus* have remained steadfast throughout the years. As stated by the former curator of the fossil vertebrate collection of the Museo di Geologia e Paleontologia

of the Università di Firenze, Elisabetta Cioppi: “this Miocene hominoid has been called enigmatic, intriguing, mysterious, anomalous, controversial, or problematic by the many who have studied it and, for these reasons, it has been on the crest of the wave for at least 150 years”.

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