



## 150 years of discoveries, research, and debates on *Oreopithecus bambolii* Gervais, 1872

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**KEY WORDS** - Montebamboli, lignite mines, hominoids, Tito Nardi, Miocene ape.

**ABSTRACT** - A brief review of the studies and historical context of the Miocene ape *Oreopithecus bambolii* Gervais, 1872 is undertaken to celebrate the 150<sup>th</sup> anniversary of the establishment of the species by Gervais in 1872, in the frame of the conference held on 20-21 October 2022 at the Università degli Studi di Firenze, where the holotype is preserved. The discovery of the jaw type in the Montebamboli lignite mine (Massa Marittima, Tuscany) by Tito Nardi marked an epoch-making turning point for the study of primate origins. From its first appearance to the present day, this Miocene ape has been the subject of great debate, triggered by its unique endemic features.

### INTRODUCTION

Solid fossil fuel mining activities gained momentum in the second half of the 1800s, and as early as 1839, the Montebamboli (Massa Marittima, Grosseto, Tuscany, Italy) lignite mine was opened. It remained open until 1873, when it was abandoned. Many local geologists and researchers such as Leopoldo Pilla, Paolo Savi and Giuseppe Meneghini argued for the convenience of reactivating ancient mining activities in Maremma. The Tuscan Maremma picea lignite was excellent in quality, and difficult to distinguish from valuable English coal, like that from Newcastle (Savi, 1843; Le Neve Foster, 1874). The mines were worked by shafts, dug with the help of donkeys that allowed drilling and that were also used for carrying the material to the coast. In 1849 a railway of about 20 km was built to bring the lignite to the coast, near Torre Mozza, Follonica, and Grosseto, and the movement of the convoys took place partly by gravity and partly by animal traction (Casini & Pagani, 2022). In addition to Montebamboli, mining activity was also conducted in sites nearby, such as Casteani, Ribolla, Tatti, Cana and Montemassi. Numerous Miocene vertebrate remains have been found during those years in the Maremma lignite mines, e.g., artiodactyls (bovids, giraffids, suids), carnivores (ursids, mustelids) and abundant herpetofauna (turtles and crocodiles), many of which are now hosted in the Museo di Geologia e Paleontologia of the Università degli Studi di Firenze (Cioppi & Rook, 2010).

The first record of *Oreopithecus bambolii* Gervais, 1872 (established in Gervais, 1872a) dates back to 1862 –as stated in the Florentine Museum tag still preserved today (Fig. 1)– when a juvenile primate mandible from Montebamboli was sold by Tito Nardi, local researcher and fossil collector, to Iginio Cocchi, Professor at the Istituto di Studi Superiori di Perfezionamento di Firenze,

and Curator of the Paleontological Collection of the Regio Museo di Fisica e Storia Naturale di Firenze, the present Museo di Geologia e Paleontologia of the Università degli Studi di Firenze (Sozzi & Pieraccioli, 2022). The mandible remained in the Florentine collection until October 1871, when it was entrusted to the study of Paul Gervais, holder of the chair of Comparative Anatomy at the Muséum national d'Histoire naturelle in Paris, who was visiting Florence at the time.

The study of this specimen led to the establishment of a new genus and species, the renowned *Oreopithecus bambolii*, presented by Gervais during the May 6, 1872 session at the Académie des sciences in Paris, with these words: “In summary, the fossil ape of the Monte Bamboli lignites seems to constitute a separate genus, which will rank at the end of the series of anthropomorphic Pithecines after the Gorilla, and before the Cynocephalus and the Macaques. I will give this genus the name *Oreopithecus*, alluding to the prominent shape of the tubercles of its molar teeth, and the species which serves as its type will be *Oreopithecus bambolii*, a name taken from the locality where it was discovered” (Gervais, 1872a, p. 1223). Gervais also reiterated the news of the discovery of an anthropomorphic ape similar to the gorilla but smaller in size in a note on Italian fossil mammals (Gervais, 1872b).

This mandible is the holotype of the species; it is preserved and exhibited at the Museo di Geologia e Paleontologia of the Università degli Studi di Firenze (IGF 4335), along with the Miocene fauna of Maremma, and has undergone many interpretations in the last 150 years (Fig. 2). Over time other cranial and postcranial remains have been found in the lignite mines of the Maremma, and many scholars have tackled this species, perhaps generating more controversial interpretations than consensus, finding the presence of anatomical characters that have thrown uncertainty on its phylogeny.

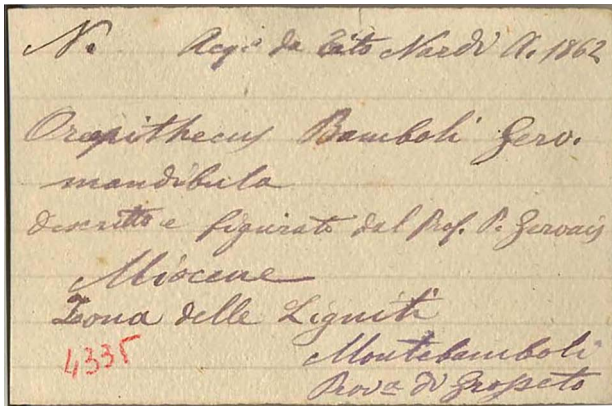


Fig. 1 - (color online) The first entry tag of *Oreopithecus bambolii* Gervais, 1872 in the collection of the Museo di Geologia e Paleontologia, Università degli Studi di Firenze.

#### TITO NARDI: FOSSIL RESEARCHER AND COLLECTOR

Scholars who have dealt with this small Miocene anthropomorphic ape have so far neglected or underappreciated the figure and importance of Tito Nardi, the man that in the second half of the 19<sup>th</sup> century found the *Oreopithecus* mandible in the disused lignite mine of Montebamboli.

We report what appears in the introduction of Cocchi's note entitled "Su di due Scimmie fossili italiane" ("On

two Italian fossil monkeys"), published in 1872 in the "Bollettino del Regio Comitato Geologico d'Italia" (Cocchi, 1872, p. 59): "In the Italian Central Collection of Paleontology existing in this city [Florence], the lower jaws of two distinct types of Monkeys are preserved. The first of these fossils I had a few years ago from Mr. Tito Nardi, who collected it in the ceased lignite mine of Monte Bamboli in Maremma, famous for the beautiful fossils provided especially to the collections of Florence, Pisa and Paris. Last year, in October, I was pleased to entrust this fossil to the illustrious Prof. P. Gervais, who was eager to study it".

Concerning the collector of *Oreopithecus*, in a note of 1854, Giuseppe Meneghini, Director of the Museo di Storia Naturale dell'Università di Pisa, wrote (Meneghini, 1854, p. 58): "... we owe these new and precious materials to the active and diligent research of Mr. Tito Nardi, who, for the exact topographical knowledge, for the natural aptitude for observation and for the rare ability to search for fossils and to cut rocks in regular and instructive samples, has already bought a well-deserved celebrity among the Tuscan and foreign naturalists collectors. As well as in the vicinity of Campiglia, so both on the Suvereto and Sassetta sides, he also found some fossils in the white dolomitic limestone below the red ammonitic limestone in the Cornate di Gerfalco. Among these fossils there are two species of Pectinids, at least one of which looks new and was therefore named *Pecten Nardii* Mgh. [...] In the red ammonite limestone of the Cornate di Gerfalco several species of Ammonites had already been collected in the past, but much



Fig. 2 - (color online) *Oreopithecus bambolii* Gervais, 1872, holotype. Mandible found by Tito Nardi in Montebamboli (IGF 4335; length: 7 cm; width: 5.5 cm; height: 4.5 cm).



Fig. 3 - (color online) Commemorative plaque on Monte Calvi, Livorno.

more has been found by Nardi, and thanks to the numerous specimens that he found, the previous determinations were confirmed or corrected, and other species could be added to eight already known [...] In the red limestone of Monte Calvi, only fragments of *Pentacrines* had been found so far, and it was highly desirable to find there also some Ammonites to confirm the stratigraphic deductions. Thanks to the work of Nardi two hundred and fifty specimens of Ammonites were discovered, many of them gigantic in size, and numerous specimens of Belemnites also collected on Monte Calvi and near Sassetta”.

In particular, the discovery of fossils on Monte Calvi allowed Meneghini to classify and define, in 1853, the geological age of what was called the “Nardi layer”. In memory of this, in February 2017, on the Cima Nardi of Monte Calvi, named after him, an inscription was placed by the Associazione Culturale Parchi GeoStorici of Castagneto Carducci (Fig. 3).

In the “Rapporto dei prodotti del regno inorganico” (“Report on the products of the inorganic kingdom”), Ubaldino Peruzzi (1854, p. 13) reports a paragraph entitled “Signor Tito Nardi di Campiglia”, which explains: “Mr. Tito Nardi di Campiglia, who collects the rocks, fossils and minerals to sell them to natural science scholars, public museums and shopkeepers who come from abroad to buy them to fuel their extensive trade in these objects, appeared worthy of encouragement for the intelligence and expertise shown in the very advantageous discovery of new fossil deposits, in the choice of essays he exhibited and for the size and shape of the same. Indeed, it is most comforting to see among us a trade managed by an intelligent man, a trade too often abandoned to ignorant men; where for the increase of the same one and for the profit of the science and the country it agrees that it is founded on the trust in the honesty and skill of the collector”.

In later publications, dating back to the second half of the 19<sup>th</sup> century, Nardi is indicated as the owner of a farm near Gabbro, in the Livorno Mountains (De Bosniaski, 1878), where he had meanwhile moved (Malfatti, 1881) and where he acquired an important fossiliferous deposit (Capellini, 1878).

In summary, Tito Nardi was born in Livorno in 1818 and later moved to Campiglia Marittima; he was a skilled researcher and a collector of fossils, rocks, and minerals, which he sold or donated to Tuscan and foreign scientific institutions (Sozzi, 2021). His fame grew over time to such an extent that he probably led a comfortable life thanks to the sale of these “natural products”. In 1860, he married Adelaide Ferrari in Campiglia and later moved to Castelnuovo di Misericordia, near Gabbro (Rosignano Marittimo, Livorno), where he bought a farm and a fossil deposit. He died in 1881 in Villa Nardi.

#### HISTORICAL BACKGROUND AND STUDIES - PART I (1872-1957)

In the years around the discovery and the subsequent formalization of the species *Oreopithecus bambolii*, there was a great debate on human evolution, triggered largely by the publication of Charles Darwin’s “On the Origin of Species” (1859) and “Human Descent and Selection in Relation to Sex” (1871), and Thomas Huxley’s “Man’s Place in Nature” (1863). Darwinian theories triggered a strong, destabilizing revolution in which philosophy, religion and science came into conflict. Furthermore, these were politically lively years in Italy; on March 17, 1861, the unification of Italy was proclaimed with Vittorio Emanuele I as King of Italy; the capital was initially settled in Turin, then moved to Florence in 1865,

where it remained for five years. Iginio Cocchi, a student of Leopoldo Pilla and Paolo Savi, graduated from Pisa, furthered his studies in Paris and London, held the chair of Mineralogy, Geology and Paleontology in Florence from 1860 to 1873 and established there the “Collezione Paleontologica Centrale Italiana” (Cioppi & Dominici, 2010). We can attribute to Iginio Cocchi the decision not to study that mandible, which had remained unpublished in the Florentine collections for ten years, to this phase of delicate scientific debate and to the academic relationships he established in Europe (Corsi, 2009), even though he was obviously interested in this find. Instead, Cocchi delegated this task to a great French academic, Gervais. On February 27, 1872 Cocchi sent a note to the “La Nazione di Firenze”, which kicked off a long series of newspaper articles related to the species *Oreopithecus bambolii*, a sort of local preview before the publication by Gervais on May 6. Then Cocchi (1872) published his article “Su di due Scimmie fossili italiane” in which he reported the translation of the work of the “famous Parisian professor”.

From this time onward, until today, this Miocene primate has certainly been one of the most closely studied in the field of primate evolution, presenting specialized adaptations and morphological features catalyzing scientific debate on its phylogenetic relationship.

After Gervais’s description, studies on *Oreopithecus bambolii* multiplied with conflicting attributions to different families. Ludwig Rüttimeyer (1875), Professor of Zoology and Comparative Anatomy at the Universität Basel, regarded it closer to gibbons, by starting the Swiss connection with Tuscan institutions and fossiliferous localities, that has persisted until more recent years (Rook, 2012). Charles Immanuel Forsyth Major, a physician of Scottish origin who grew up in Switzerland, student of fossils and a correspondent of Charles Darwin, came to the Museum of Florence in the 1870’s for studying new material and mostly for new excavations in Tuscany (Montopoli and Olivola), and he noted some resemblance to humans (Forsyth Major, 1872, 1879).

Montebamboli’s specimen could not fail to end up in the European capitals most involved in the evolutionary debate. So, in Paris, Jean Albert Gaudry, Professor of Paleontology at the Muséum National d’Histoire Naturelle, in his monograph on the classification of the Animal World (Gaudry, 1878) in the chapter on “quadrumanes” observes some curious similarities between the teeth of *Oreopithecus bambolii* and those of some bunodont “pachyderm” (= artiodactyl) like *Choeropotamus*, while admitting that the similarities may be simple adaptations to similar diets, found even in animals far apart. The “Catalogue of the specimen illustrating the Osteology and Dentition of Vertebrated animals, recent and extinct” of the Museum of the Royal College of Surgeons of England in London indicates that there was a cast of the *Oreopithecus bambolii* mandible exposed (Flower, 1884). Later, according to the guidebook “A guide to the fossil remains of man in the Department of Geology and Palaeontology in the British Museum (Natural History)” with a short preface by A. Smith Woodward dated to 1915, prepared for an exhibition after the “Pitdown case”, casts of the original mandible of *Oreopithecus* were also present.

But the most widely accepted view in the early studies was that of the German paleontologist Max Schlosser, who called *Oreopithecus bambolii* a cercopithecoid (Schlosser, 1887), a view confirmed by Weithofer (1888).

In Italy, besides Cocchi, *Oreopithecus* is mentioned also in the works by Carlo De Stefani (1876, 1881) and Dante Pantanelli (1886), but only Ristori (1890a) undertook a thorough revision. Ristori, including new specimens from the Casteani lignite, analyzed the features of “lower ape” and “higher”, the latter proving to be more numerous and important, and considered *Oreopithecus* a progenitor of the anthropomorphs, openly contrasting Schlosser’s assertion regarding its affinity with the cercopithecoids and with *Theropithecus*. Ristori (1890a, p. 102-103) stated: “From direct comparison of these characters and consideration of their relative importance, it seems reasonable to me, following in part the opinion of Schlosser, that *Oreopithecus* could be among the lower apes, but just after the anthropomorphs or at the end of these, because if on the one hand, we cannot discern in this fossil ape characters of inferiority, especially in the mandibular dentition, it cannot be denied that in the upper teeth and some bones [...], there exist numerous and important characters relating *Oreopithecus* to the higher apes [Hominoidea]. Following on, it is, in my opinion, more accurate to consider *Oreopithecus* as the ancestor of anthropomorphs rather than, as Schlosser argued, that of the [papionins], especially *Theropithecus*. In this case, to retain Schlosser’s opinion would imply in *Oreopithecus* the presence of organic regression, inconsistent with present theories of evolution”.

Other studies focused on new *Oreopithecus* remains discovered in the mines of the Tuscan Maremma, such as that of Ottolenghi (1898), who described a left mandibular branch from Montemassi and Merciai (1907), who focused on remains from Ribolla housed in Pisa.

Later, careful analysis by the German anthropologist Gustav Schwalbe ruled out altogether the attribution of *Oreopithecus* to the Cercopithecidae, suggesting a position in the new family Oreopithecidae within the Hominoidea (Schwalbe, 1915).

Interest in this species, of which no new remains emerged, waned dramatically up to the end of World War II, when George Gaylord Simpson, Curator of the fossil mammals and birds at the American Museum of Natural History of New York (AMNH), interpreted the taxa as a cercopithecoid primate but in an uncertain subfamily (Simpson, 1945).

In 1949 Johannes Hürzeler, from the Naturhistorisches Museum Basel that hosted some remains including an ancient plaster cast of the type specimen of *Oreopithecus bambolii*, asked Giovanni Merla, Director of the Istituto di Geologia in Florence which then kept the paleontological collections, through the intercession of Augusto Azzaroli, permission for a study visit to examine the original type and the other specimens preserved in Florence. After some days spent examining and drawing the specimens in the Florentine collection, Hürzeler (1949) redescribed *Oreopithecus bambolii*, observing characters found only in hominids. From here on, Hürzeler devoted himself to the study of *Oreopithecus bambolii* (Hürzeler, 1952, 1954, 1956), which could find confirmation in new remains from the still open lignite mines in the Maremma. This

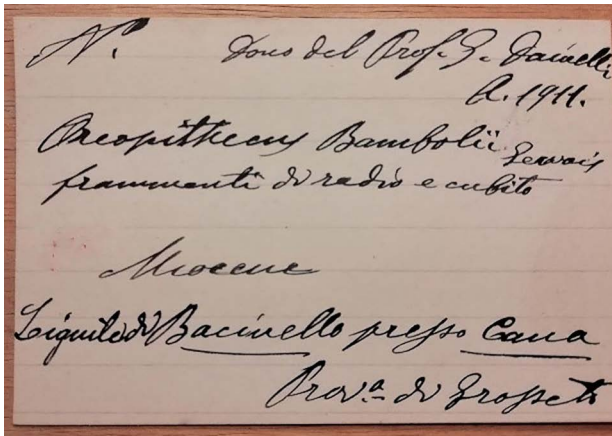


Fig. 4 - (color online) Entry tag in the Museo di Geologia e Paleontologia di Firenze of *Oreopithecus* specimens recovered in 1911 by Giotto Dainelli near Baccinello.

required a great deal of financial commitment, which was met by funds from the Wenner Gren Foundation, which financed his excavation campaigns. Fragments of radius and ulna of *Oreopithecus* were donated to the Museum of Florence in 1911 by Giotto Dainelli (Fig. 4), a renowned geologist and geographer, who was the Mayor of Florence during the Second World War and Director of the Museo di Geologia e Paleontologia dell'Università degli Studi di Firenze. Hürzeler needed new remains of *Oreopithecus* to advance his hypotheses, and to obtain them he had to find the funds essential for a long series of searches in mining areas. Thus, he started a media campaign that animated the scientific world. Contributions from the Wenner Gren Foundation enabled him to travel to New York and Harvard University, armed with suitcases containing fossil specimens, to illustrate his ideas, and newspapers around the world covered it, rekindling the controversy between creationists and evolutionists. Media coverage of *Oreopithecus* was extensive and involved the international press, such as the New York Times, which headlined "Fossil research questions Darwin evolution theory" (Fig. 5) and Le Figaro, "Darwin s'est trompé" ("Darwin was wrong"). The German geologist and anthropologist Helmut de Terra, convinced of the rightness of Hürzeler (de Terra, 1956), volunteered to help him in his research in Tuscany. The hoped-for result came and with the funds obtained, and the collaboration of de Terra, Hürzeler settled for many months in 1956 and the following years in the small village of Baccinello, sharing with the miners his fervent hope of finding significant hominid remains. Investigations returned many fossils brought to the Basel Museum, where they are kept today.

#### HISTORICAL BACKGROUND AND STUDIES - PART II (1958-2022)

The mine's operation was in crisis, perhaps more risky than profitable, and in late summer 1958 it was scheduled to close for good. In the last season of lignite mining, almost miraculously, there was a collapse in a tunnel that caused an almost complete skeleton of *Oreopithecus bambolii* to be exposed on the vault of the mine. Thus,

the two miners Enzo Boccalini e Azelio Giustarini immediately called Hürzeler, on his very last evening of stay at Baccinello, who descended directly into the mine and made an initial sketch of the skeleton's location, fearing for more collapses in the tunnel. The debate about this species was further ignited with this new discovery of the almost complete skeleton, nicknamed "Sandrone".

The news immediately circulated in the press all over the world, starting with articles by Andrea Barbato in "Il Messaggero" (August 2, 1958: "A man who lived twelve million years ago returned to light in a Tuscan village"), "La Vanguardia Española", "Le Monde", and other international newspapers, followed by a renewed contrast between creationists and evolutionists. Several scientists followed Hürzeler's thinking by seeing in the origin so dated for hominids an evolutionary line unique to humankind, separate from that of apes, whereas others found many shared characters with apes. The Catholic Church also became interested in the *Oreopithecus* discovery: on February 1959, Cardinal Eugène Tisserant, head of the College of Cardinals, attended a Hürzeler lecture at the University of Rome (now Sapienza Università di Roma), and the following day the Swiss paleontologist was received by Pope John XXIII. Among scientists, this was understood as an implicit acceptance by the Church of the theory of evolution (Florensa, 2016). The skeleton was at that time in Basel, and in December 1958 Hürzeler was allowed to take "Sandrone" to Switzerland, only after pledging its return to Italy. In Basel some bones were roughly isolated and cleaned from the original slab of lignite, and the skeleton was studied by Hürzeler (1958, 1960). It came back to Italy in 1963, when Augusto Azzaroli, Director of the Museo di Geologia e Paleontologia dell'Università degli Studi di Firenze, with Annalisa Berzi, Curator of the Museum, went to Basel to pick up the skeleton to bring it to Florence, where it received further cleaning from the lignitic matrix and detailed preparation in the Museum's restoration laboratory. Restoration of the skeleton IGF 11778 in the Florence laboratory by Fabio Cozzini, Silvano Migliorini and Vittorio Borselli led to increasing research and it was for the first time exhibited to the public in the Museo di Geologia e Paleontologia dell'Università degli Studi di Firenze, in a specially dedicated mirrored display case (Fig. 6), enriched by the two reproductions of the original lignite plates, impression and counter impression (Berzi, 1973). However, the skull had not yet undergone any restoration work and was badly flattened laterally, especially the braincase. The dentition of *Oreopithecus* was described in detail relying on many other specimens brought to Basel and was also studied by Butler & Mills (1959). Straus (1963) stated that "the supposed dental resemblance of *Oreopithecus* to cercopithecoids will not hold water. It is true that in a few characters the lower molars of *Oreopithecus* approximate those of cercopithecoids, but their overall pattern is strikingly non-cercopithecoid. In its relative length, the neck of the *Oreopithecus* femur most closely resembles those of hominoids, especially those of the great apes and man". Also, Simpson (1963) confirmed Straus's conclusions. In 1973, Szalay and Berzi made a thorough study of the flattened skull, highlighting its sagittal crest and other unique characteristics (Szalay & Berzi,

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## Fossil Research Questions Darwin Evolution Theory

**Bones Found in 1872 Now Listed as Those of Man 10 Million Years Old**

By ROBERT K. PLUMB

American anthropologists for a week have been quietly pondering what appears to be one of the most astonishing fossil discoveries ever made.

The find suggests that man was well along the process of evolution some 10,000,000 years ago. It suggests there is no connection between ape and man, ancient or modern. The discovery challenges the Darwinian dogma, in the opinion of Dr. Helmut de Terra, research associate in the Columbia University Department of Geology.

The new theory is that a double handful of fossil fragments found in northern Italy in 1872 are the bones of a human-like creature about 10,000,000 years old. The fragments include a lower jawbone complete with teeth.

A full account of the fossils and the theory they suggest was presented last Saturday by Dr.



Dr. Johannes Hürzeler

Johannes Hürzeler, curator of vertebrate paleontology of the Basle (Switzerland) Natural History Museum. He presented his report at a special meeting of

Continued on Page 7, Column 2

## EISENHOWER WINS IN NEW FARM TEST; NIXON BREAKS TIE

**Casts Deciding Vote to Block High Supports on Wheat—'Deals' Again Charged**

By WILLIAM M. HARRIS

WASHINGTON, March 9—Vice President Richard M. Nixon cast a disputed deciding vote in the Senate tonight to give the Administration another victory on its farm policy. The vote was 46 to 45.

The Vice President's vote, knocked from the Senate farm bill a restoration of rigid price supports on wheat. The vote supported the Senate's rejection yesterday of rigid supports on other crops.

Senator Albert Gore, Democrat of Tennessee, threw the Senate into a wrangle over the validity of Mr. Nixon's vote.

He contended that the Vice President had no right to vote in the situation, caused by a



**TURBULENCE IN MEDITERRANEAN AREA:** Frenchmen ransacked Tunis (1) while mobs clamoring for independence in Algeria (2) rioted in French Morocco (3) marked its approach to independence. The British Archbishop Makarios from Cyprus (4) set off protests in Greece (5). Jordan (7) from Britain and ally her with Egypt, Syria and Saudi Ara

## TUNIS MOB SACKS TWO U. S. OFFICES

## Algerian Marchers Police and Army

By HENRY GINGER

Fig. 5 - New York Times, March 10, 1956: *Oreopithecus*, a man 10 million years old.

1973), as pointed out to one of the authors (Berzi) by Augusto Azzaroli. In 1983 it was Azzaroli who entrusted the skull to Eric Delson by sending it to the AMNH for restoration, there made by Otto Simonis. The face and the mandible were disassembled, while no intervention was made on the braincase (Delson, 1986). Only ten years later the braincase was restored by Ron J. Clarke of the Palaeoanthropology Research Group at the University of the Witwatersrand in Johannesburg, invited to Florence by Azzaroli. Starting from the original part still badly crushed, Clarke (1997) made a complete reconstruction of the skull through a very difficult and detailed restoration work, also noticing the absence of some fragments visible in the model made before the partial reconstruction performed at the AMNH of New York. Once requested they were found and returned to Florence by Delson himself. Clarke's complete reconstructed skull of the 1958 skeleton (IGF 11778), facial and neural parts are now on exhibit in the Museo di Geologia e Paleontologia dell'Università degli Studi di Firenze (Fig. 7). Whereas *Oreopithecus bambolii* had already been in the limelight for decades, anatomical studies of the skull and postcranial skeletal parts multiplied from August 1958 onwards, leading to even more heated debates among scholars worldwide. As has been pointed out (Harrison, 1986), it is almost paradoxical that despite the great knowledge of its anatomy, an ongoing debate about its phylogenetic

position remains active. Paleoenvironmental studies also became increasingly refined, focusing on the Miocene fauna and flora of the area.

A study of the geology of the Baccinello area was undertaken by Louis Vonderschmitt, Director of the Institute of Geology at the Universität Basel and President of the Geological Commission of Switzerland, and his assistant Lukas Hottinger (de Terra, 1956), whose name appears on a map of the geological survey of the area in the archives of the Museum of Florence. Later, Lorenz, Hürzeler's collaborator, defined the stratigraphy of the area, and three vertebrate beds (V1, V2, V3) were identified, from the Late Miocene to the Early Pliocene (Lorenz, 1968). *Oreopithecus* and the associated fauna (V1) are unique to the sites in Maremma (Tuscany), demonstrating a high level of endemism. The species recovered suggest an insular environment, a swampy mesophytic forest (Azzaroli et al., 1986; Harrison & Harrison, 1989), with dense vegetation interspersed with marshes and brackish lagoons, as evidenced by the presence of crocodiles (*Crocodylus bambolii* Ristori, 1890b), aquatic chelonids (*Trionyx bambolii* Ristori, 1891; *Mauremys campanii* [Ristori, 1891]), otters (*Paludolutra campanii* [Meneghini, 1863]) and even a recently documented dugongid (*Metaxytherium* sp.) (Meneghini, 1863; Ristori, 1890b, 1891; Pandolfi et al., 2022). The same paleoenvironmental context of lowland mixed



Fig. 6 - Old showcase of the first public display of the skeleton (IGF 11778) from Baccinello isolated from lignite, Museo di Geologia e Paleontologia, Firenze.

mesophytic forest results from chemical analyses carried out on lignite from Montebamboli and Ribolla (Staccioli et al., 2001). In the Museo di Geologia e Paleontologia dell'Università degli Studi di Firenze a rich paleobotanical collection from the Maremma *Oreopithecus*-bearing sites is housed, belonging to the private collection of Marquis Carlo Strozzi, donated by his grandson to the Università degli Studi di Firenze in 1910, with several species described in a monograph (Gaudin & Strozzi, 1859, 1862), currently catalogued and under revision.

A review of the historical collections of natural history museums, preserving all documentation associated with the specimens, such as “museum excavations”, is increasingly important. For example, a molar of *Oreopithecus bambolii* and some cranial fragments of the alcelaphine bovid *Maremmia haupti* from the lignite mine at Serrazzano (Val di Cecina, Tuscany) remained unnoticed in a drawer since 1916-1918, when they were donated by Eng. Trabucco to the Museo di Geologia e Paleontologia dell'Università degli Studi di Firenze, extending the geographical range of *Oreopithecus* (Rook & Cioppi, 1997). Outside Tuscany, *Oreopithecus* was found in Sardinia in 1994 in the locality of Fiume Santo, near Porto Torres (Cordy & Ginesu, 1994). Fragments of a mandible of *Oreopithecus* were recovered by Rook in 1992 along the Trasubbie River, near Baccinello, in V2, 100 m above the V1 lignite horizon (Rook et al., 1996).

Since the Tuscan-Sardinian bioprovince in the Late Miocene was insular, the species shows unique adaptations and morphology. Many studies on *Oreopithecus* in the last decades have addressed various morpho-functional characters of the cranial and postcranial skeleton. Just to mention a few: some papers concentrated on the hand (Moyà-Solà et al., 1999; Almécija et al., 2014), others on the hip bone (Rook et al., 1999), lower torso (Hammond et al., 2020), dentition (L'Engle Williams, 2013), ear (Rook et al., 2004; Urcioli et al., 2020), with implications on diet, manipulative precision ability, adaptations to tree climbing as well as bipedal locomotion. A complex mixture of primitive and specialized features has made it difficult to place *Oreopithecus* phylogenetically but has fueled scientific debate, making this species still alive and fascinating, 150 years after its description, with a promising future of research on it.

## CONCLUSIONS

The value of the Florentine paleontological collections is very high and renowned. It is not only its numerical richness, of course, that constitutes the significance, but all the information surrounding each specimen, from the descriptions in historical catalogues, to the tags associated with the finds, to the various archival



Fig. 7 - (color online) Clarke complete reconstructed skull of the skeleton (IGF 11778) (length: 19 cm; width: 13.3 cm; height: 14 cm) in the Museo di Geologia e Paleontologia, Firenze.

materials that are here carefully preserved in a museum history of over four centuries. In particular, specimens of Tuscan provenance have always been the natural port of call in Florentine naturalistic collections. Moreover, it is precisely on several of these specimens that scientific debates have been based. The mandible type specimen of *Oreopithecus bambolii* within the Florentine Museum's collection of Miocene vertebrates (Cioppi & Rook, 2010) certainly represents one of the most fitting examples of all these aspects. Multifaceted aspects of complex interpretation have emerged on this Miocene ape since its first discovery in the Montebamboli lignite mine.

Scholars from all over the world have come to Florence to study the specimens of *Oreopithecus* preserved here, and they all agree on one thing: the difficulty of placing the species in a precise phylogenetic context given its uniqueness, with endemic traits related to its island ecosystem. Surely many studies, new research and discoveries will still concern this enigmatic Miocene ape and enable us to better understand its complexity. Above all, historical studies in paleontology, especially when referring to unique specimens as in this case, enrich the value of the find itself and the Museum collections to which it belongs.

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