

An updated overview on the extinction of *Oreopithecus bambolii*

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ABSTRACT - *Oreopithecus bambolii*, the large-bodied endemic ape that lived in the Tusco-Sardinian bioprovince during the Late Miocene (ca. 8.2-6.7 Ma; Turolian), has been for more than half a century, and despite being one of the most complete hominoids in the fossil record, the focus of great controversy over its phylogenetic status, postural/locomotor behaviour, and extinction in an insular context. In reference to the latter issue, *O. bambolii* went extinct at ca. 6.7 Ma, being the last hominoid to survive in Europe, but it has remained unresolved—primarily because its environmental context and ecological needs have not been until recently clearly investigated—as to whether its extinction was due to a marked shift in climate and environments or, instead, to intensive interaction with an invading faunal complex from mainland Italy. The present work seeks to review the main hypotheses that there have been proposed to determine *Oreopithecus*' extinction and, in the light of recent data, to reevaluate the most viable explanation for its disappearance. Multiple lines of evidence have reported the existence of a shift in climate throughout the Baccinello-Cinigiano sequence. However, recent views showed that although environmental shifts did indeed take place, the floral composition spanning the extinction event (level V3; 6.7-6.4 Ma) was similar to that of previous ecosystems (level V1; 8.3-8.1 Ma) inhabited by *Oreopithecus*. Moreover, its dietary versatility—wider than previously thought—was very likely an integral part of adaptations of *Oreopithecus* to cope with changes in the habitats under which it lived. Collectively, this suggests that the environmental change, even though it did indeed take place, was not significant enough to deeply affect *Oreopithecus*' lifestyle. Hence, 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.

INTRODUCTION

Oreopithecus bambolii Gervais, 1872 is a large-bodied Late Miocene ape endemic to the Tusco-Sardinian archipelago, which existed during Turolian (late Tortonian) times in the North Tyrrhenian area. *Oreopithecus* lived and evolved under conditions of extreme insularity (Rook et al., 2000, 2006; Bernor et al., 2001) between ca. 8.2 Ma and 6.7 Ma (Rook, 2016) and, as a result, it is one of the few apes known to have evolved a suite of primitive and derived anatomical features that successive authors have qualified as unique—and in some regards as “bizarre” (Moyà-Solà & Köhler, 1997)—which makes it strikingly different from other Miocene apes.

The first known *O. bambolii* specimen (the type mandible) from the site of Montebamboli was donated by Mr. Tito Nardi to Prof. I. Cocchi in 1862 and first described by Gervais in 1872 (Cioppi & Rook, 2010). Since then, in the late 1800s and earliest 1900s, other *Oreopithecus* fossils have been recovered from lignite mines in southern Tuscany (the sites of Casteani, Montebamboli, Ribolla, Acquanera and Montemassi) (Weithofer, 1888; Ristori, 1890; Hürzeler, 1949; Benvenuti et al., 2001); however, most of what is known about *O. bambolii* is documented basically by the partial and taphonomically flattened skeleton IGF 11778 found in 1958 by Hürzeler (Straus, 1958) in the lignite mine of Baccinello (Tuscany, Italy) (Fig. 1). More recently, the discovery of *Oreopithecus* dental remains and associated fauna in Sardinia (in the fluvial sediments at the site of Fiume Santo) expanded the known geographical range of this faunal complex

across the Tyrrhenian area (Cordy & Ginesu, 1994; Abbazzi et al., 2008a) (Fig. 1). Over the years, numerous studies have been aiming to investigate *Oreopithecus*—and its notably endemic accompanying faunas (the “Maremma fauna”) which has proven to be very different from contemporaneous Turolian vertebrates of elsewhere in Eurasia—which have increased largely our knowledge of this emblematic ape and the palaeontology, geology and sedimentology of the Baccinello-Cinigiano Basin (e.g., Gervais, 1872; Hürzeler, 1949, 1951, 1954, 1958, 1982, 1983, 1987; Berzi, 1973; Hürzeler & Engesser, 1976; Thomas, 1984; Azzaroli et al., 1986; Delson, 1986; Engesser, 1989; Harrison & Harrison, 1989; Rook, 1993, 2016, 2017; Rook et al., 1996, 1999a, b, 2000, 2004, 2006, 2011; Harrison & Rook, 1997; Köhler & Moyà-Solà, 1997, 2003; Moyà-Solà & Köhler, 1997; Moyà-Solà et al., 1999, 2005; Alba et al., 2001a, b; Benvenuti et al., 2001, 2015; Abbazzi et al., 2008a; Delfino & Rook, 2008; Chesi et al., 2009; Casanovas-Vilar et al., 2011a, b; Matson et al., 2012; Russo & Shapiro, 2013; Alméjida et al., 2014; Cirilli et al., 2016; Nelson & Rook, 2016; Zanolli et al., 2016, 2017; Angelone et al., 2017, 2022; DeMiguel & Rook, 2018; Hammond et al., 2020; Pandolfi & Rook, 2023).

Despite these efforts, and although *O. bambolii* is dentally and skeletally well represented, it deserves the honour of being the fossil ape for which the greatest number of different phylogenetic (see Delson, 1986 and Alba et al., 2024; this issue) and postural/locomotion interpretations (see Alba et al., 2024; this issue) have been presented. This is primarily due to the peculiar combination of anatomical features observed in the fossil



Fig. 1 - (color online) Italian Peninsula (center) showing the regions of Tuscany (right) and Sardinia Island (left). The dots indicate the geographical position of fossiliferous localities with record of *Oreopithecus* mentioned in the text. F: Fiume Santo; S: Serrazzano; M: Montebamboli; Ca: Casteani, R: Ribolla; Ci: Cinigiano; B: Baccinello.

material of *Oreopithecus bambolii*. Hence, it has been variously reconstructed as a cercopithecoid relative or a separate anthropoid lineage (perhaps belonging to its own family [Oreopithecidae]) (Schlosser, 1887; Delson, 1979; Szalay & Delson, 1979), a distinctive hominoid (Schwalbe, 1915; Straus, 1963; Harrison, 1986; Sarmiento, 1987), or an early hominin (Hürzeler, 1954; Straus, 1957); whereas the main views from its postcranial anatomy are that it was a slow-moving (Schultz, 1960), an agile suspensory/climber (Szalay & Delson, 1979; Jungers, 1984, 1987; Harrison, 1986; Sarmiento, 1987; Harrison, 1991; Wunderlich et al., 1999), or even a bipedal ape (Straus, 1963; Köhler & Moyà-Solà, 1997; Rook et al., 1999a). At present, no conclusive evidence has yet been provided to confidently address some of the above interpretations.

Discussions concerning the extinction of *Oreopithecus* have been particularly contentious as well, primarily because its palaeoenvironmental context and habitat requirements have received until recently relatively little attention. The most controversial claims are that *Oreopithecus* went extinct due to a marked shift in climate or to the connection of its insular ecosystem to the mainland. Its last occurrence is recorded at ca. 6.7 Ma (Rook et al., 2011), being the latest known Miocene ape to survive in Europe (Casanovas-Vilar et al., 2011a). This extinction event is associated with regional tectonism and palaeogeographical changes (Rook et al., 1999b; Sartori, 2001; Nelson & Rook, 2016), that ultimately led to a non-endemic faunal turnover dated 6.7-6.4 Ma (Bernor et al., 2001, 2011; Chesi et al., 2009; Rook et al., 2011). *Oreopithecus*' extinction therefore contrasts strongly with that of some of the diverse Eurasian kenyanthropines (*Griphopithecus*) and dryopithecines (*Pierolapithecus*, *Anoiapithecus*, *Dryopithecus*, *Hispanopithecus* and *Ouranopithecus*), ultimately driven by an increase in environmental uniformity and the resulting loss of habitat suitability (van Dam, 2006; Agustí et al., 2013; DeMiguel et al., 2014).

The present work presents an historical synthesis of the main works that focused on the Baccinello-

Cinigiano Basin and succinctly summarises the major hypotheses proposed in the last decades to determine *Oreopithecus*' extinction, with works being contextualised and discussed. In the light of the most recent arguments, we further reevaluate the most viable explanation for the disappearance of *Oreopithecus*.

A SYNTHESIS ON THE BACCINELLO-CINIGIANO SUCCESSION

The occurrence of continental vertebrate faunas in the fluvio-lacustrine basins of southern Tuscany has been known since the mid-1800s thanks to findings connected with the activities of coal mining which exploited the lignite deposits of Upper Miocene successions in various basins in the northern area of the Maremma region in Tuscany (Montebamboli, Montemassi, Casteani, Ribolla, Serrazzano, Baccinello). The singular uniqueness of these faunas, together with the occurrence of the peculiar ape *O. bambolii* (Gervais, 1872; Rook, 2016), is a high degree of endemism (such as markedly hypsodont cheek teeth and continuously growing incisors; see also the section below “the *Oreopithecus* Zone Faunas”), low taxonomic diversity, and absence of carnivores other than otters (*Tyrrhenolutra*, *Paludolutra*).

In the area of the Baccinello-Cinigiano Basin, although the first investigations concerning the exploitation of lignite-bearing successions date back to the end of the 19th century (Stoppani, 1880), the first report of the occurrence of continental fossil vertebrates dates back to the mid-1900s (de Terra, 1956). The geology and palaeontology of the Baccinello-Cinigiano area was intensely studied at the time thanks to research carried out by Basel Naturhistorisches Museum researchers (de Terra, 1956; Hürzeler, 1958; Gillet et al., 1965; Lorenz, 1968) in the context of the stratigraphic and faunal placement of the *Oreopithecus* remains recovered in the Baccinello mine (the latter was opened in 1918 and remained active, between alternating openings and closures, until 1958,

when the mining activities definitively ended). The first studies of the 1950s were followed by the publication of sheet 128 “Grosseto” of the Geological Map of Italy at 1:100,000 (Motta, 1969) in which the complex lithostratigraphy described by Lorenz (1968) was simplified by including all the continental succession of the basin in a single formation extensively outcropping throughout the Baccinello-Cinigiano area.

Since the 1990s, research conducted by the Vertebrate Palaeontology Research Group of the University of Florence has increased the knowledge of the palaeontology, geology, and sedimentology of the area (Benvenuti et al., 1995, 1999, 2001, 2015; Rook et al., 2000, 2011; Ligios et al., 2008), allowing a better understanding of the sedimentary and environmental evolution of basin.

The Late Miocene Baccinello-Cinigiano succession (Fig. 2), although it includes four successive local biochronologic units (detailed below), has long been lacking a reliable chronological calibration, being described only in informal lithostratigraphic terms (Fig. 2; and see Rook, 2016 for a detailed stratigraphic description of the sequence). The occurrence of volcanic activity in the Baccinello-Cinigiano Basin succession was first reported by Lorenz (1968). Doubts were cast by the possibility that this deposit was reworked, even though a K-Ar date of 8.4 Ma (J. Hunziker, personal communication in Hürzeler & Engesser, 1976) was approximately in agreement with the existing local and regional geochronologic constraints. In the late 1990's, extensive field surveys along the eastern margin of the Baccinello-Cinigiano basin allowed the discovery of a thin tephra at a site known as “Passonaio” (Rook et al., 2000). The Passonaio ash was geochronologically dated ($^{40}\text{Ar}/^{39}\text{Ar}$) at 7.55 ± 0.03 Ma. The Passonaio tephra, being located stratigraphically within the Baccinello-Cinigiano Basin sedimentary succession between the units (see description below and Fig. 2b) that have yielded *Oreopithecus* samples, provided a good constraint on the age of the *Oreopithecus* faunas (Rook et al., 2000; Rook, 2016).

In early 2000's, different data suitable for a firmer chronological calibration and for the Baccinello-Cinigiano Basin stratigraphic correlation have been provided by a sampling for a magnetostratigraphic study (Rook et al., 2011; Benvenuti et al., 2015). The correlation of the investigated sedimentary sections of the basin succession with the standard polarity scale has been carried out by integration of the basin analysis (Benvenuti et al., 1995, 1999, 2001), radiometric dating (Rook et al., 2000), and biostratigraphy (Rook et al., 1999b). The magnetostratigraphic correlation allowed framing of the entire set of evidence derived in previous studies within a coherent chronological framework (Rook et al., 2011; Benvenuti et al., 2015), with fossil mammal remains grouped into distinct vertebrate assemblages (named as vertebrate-rich horizon V0, V1, V2 and V3) (Fig. 2b): 1) the oldest assemblage (V0) includes a murid, *Huerzelerimys vireti* (Schaub, 1938), whose occurrence allows a correlation with European sites assigned to MN11 unit (8.7-7.5 Ma) (Engesser, 1989; Casanovas-Vilar et al., 2011b); 2) the oldest *Oreopithecus* bearing sediments in the Baccinello-Cinigiano Basin (V1) are found in upper C4r, and so are likely to have an age between 8.3 and 8.1 Ma; 3) the youngest *Oreopithecus* remains are from sediments attributed to C3Ar, with an age between 7.1 and 6.7 Ma; 4)

the *Oreopithecus* maximum chronologic range within the Baccinello-Cinigiano Basin is about 1.5 Ma long, bracketed between 8.2 and 6.7 Ma; and 5) the V3-bearing deposits, with an age between 6.7 and, probably, 6.4 Ma (C3An.2n), belong to the early Messinian (very early MN13).

Two contributions (Harrison & Harrison, 1989; Benvenuti et al., 1995) published in the early 1990s treated the Baccinello-Cinigiano Basin palaeovegetational characterisation by means of pollen analysis. Harrison & Harrison (1989) limited their study to samples of the lignites that yielded the *Oreopithecus* specimens, while Benvenuti et al. (1995) studied several samples that covered the entire succession. The early Baccinello-Cinigiano Basin filling was characterised by a period with a subtropical climate and high precipitation throughout the year, favouring lacustrine flooding. The evidence from palynological sampling along the Baccinello-Cinigiano Basin succession seems to indicate that a climatic signature on the deposition produced a distinct trend during deposition of the entire succession, from warm and humid conditions to an inconsistent regime with irregularly alternating dry and moist phases (Benvenuti et al., 1995). A similar trend was identified by a palaeoecological analysis of fossil ostracods from the Baccinello-Cinigiano Basin deposits (Ligios et al., 2008). The analysis of fossil ostracod communities carried out by Ligios et al. (2008) identified several physicochemical variations in the water body of the basin providing a detailed description of the palaeoenvironment and basin evolution, from humid and warm climatic conditions to a more irregular climatic regime with alternations of arid and more humid phases, consistent either with sedimentological data as well as with pollen analyses along the succession.

THE “*OREOPITHECUS* ZONE FAUNAS”

The use of continental biochronology and an accurate attention to the distribution along the sedimentary succession of the fossil vertebrate documentation has allowed to enhance the stratigraphic and chronologic significance of the faunal associations identified in different stratigraphic levels within the Baccinello-Cinigiano succession (Hürzeler & Engesser, 1976; Rook, 2016). The Baccinello-Cinigiano Basin records a succession of four consecutive associations with fossil mammals, which cover a time ranging from the late Tortonian to the Messinian (Fig. 2e). The faunal assemblages known as “V1” through “V3” were established by Lorenz (1968), who united different mammal localities with similar faunas into distinct assemblage zones (Fig. 2b). A small mammal fauna discovered some twenty years later in a gray marl underlying the V1 lignite was later described as “V0” (Engesser, 1989; Cirilli et al., 2016). The first three successive Baccinello-Cinigiano faunal assemblages (V0 to V2) all belong to an endemic faunal complex (the so called “*Oreopithecus* Zone Faunas” sensu Bernor et al., 2001), while the V3 assemblage includes continental taxa with European affinities (Hürzeler & Engesser, 1976; Rook et al., 2000, 2011; Rook, 2016; Angelone et al., 2017; Pandolfi & Rook, 2017, 2023; DeMiguel & Rook, 2018).

The high level of endemism of the V1 fauna (8.3-8.1 Ma), in conjunction with the low taxonomic diversity, the

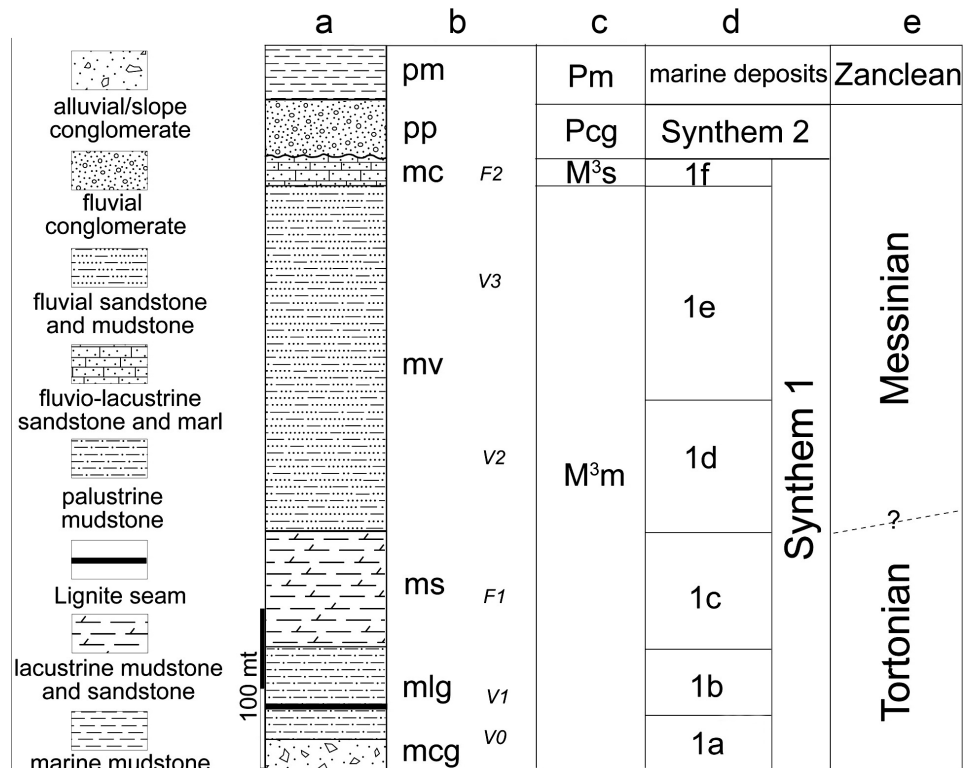


Fig. 2 - Lithostratigraphic column of the Baccinello-Cinigliano Basin (a), with a synopsis of informal stratigraphic units recognised by Lorenz (1968) (b), Motta (1969) (c), Benvenuti et al. (2001) (d), and chronostratigraphy (e). Column b also reports the position of vertebrate-rich horizons (V0-V3) and mollusk-rich horizons (F1-F2). Figure modified from Rook (2016). Abbreviations: column b - mcg: Formation "mcg" described as "Konglomerat in vorwiegend rotem, meistens sandigem, mergelig-tonigem Bindemittel, vorwiegend aus sandigen Komponenten von Macigno-Typus bestehend" in Lorenz (1968); mlg: Formation "mlg" described as "Wechsellagerung von mehr oder weniger mergeligen Tonen, Silten und Sanden, an deren Basis ein durch das Vorkommen von Lignitflöz auftritt" in Lorenz (1968); ms: Formation "ms" described as "Wechsellagerung von feinen Konglomeraten, Sanden, Silten und Mergeln, welche häufig feinstes ligistisches Material enthalten. Durch eine an Individuen sehr reiche Brack- und Süßwasserfauna charakterisiert, in welcher in überwiegender Anzahl Cardien auftreten" in Lorenz (1968); mv: Formation "mv" described as "Alternanz von Sanden mit feinkonglomeratischen Einschlüssen, Silten, Mergeln und Tonen mit verhältnismässig häufigen Resten von Wirbeltieren" in Lorenz (1968); mc: Formation "mc" described as "Düngebankte Süßwasserkalke, dicht und vielfach sandig in den höheren Lagen, kreidig und mergelig in unteren Teil. Meistens ein geringmächtiges Lignitflöz einschliessend Zum Teil stark fossilführenden (Melanopsis, Dreissensia)" in Lorenz (1968); pp: Formation "pp", described as "Polimiktes Konglomerat, aus grobe Komponenten führend mit linsenförmigen Einlagerungen von fast durchweg sandigen Tonen und Mergeln, sowie von grobkörnigen Sandsteinbänken" in Lorenz (1968); pm: Formation "pm", described as "Mehr oder weniger sandige marine Tone und Mergel mit einer reichen Micro- und Macrofauna. Linsenförmige Zwischenlagen von extrem feinkörnigen, sterilen Dolomitbänken" in Lorenz (1968); F1: Mollusk-rich fossiliferous horizon described as "Alternance de lits de sables jaune-vert, de silt et de marnes bleues. Fréquents lits de limonite, pellicules de lignite et fréquents petit cristaux de gypse. Cet horizon se distingue par une riche faune dulçaquicole" in Gillet et al. (1965), and "Unteres Mollusken-führendes" in Lorenz (1968); F2: Mollusk-rich fossiliferous horizon described as "Calcaires crayeux légèrement marneux avec un riche faune bien conservé" in Gillet et al. (1965), and "Oberes Mollusken-führendes" in Lorenz (1968); V0: Vertebrate-rich level described as "V-0 horizon" in Engesser (1989); V1: Vertebrate-rich level described as "Unteres Vertebraten-führenden" in Lorenz (1968); V2: Vertebrate-rich level described as "Mittleres Vertebraten-führenden" in Lorenz (1968); V3: Vertebrate-rich level described as "Oberes Vertebraten-führenden" in Lorenz (1968). Column c - Pm: Formation Pm described as "Marne e argille grigio azzurre, con lenti sabbiose ed elementi sciolti di puddinga" in Motta (1969); Pcg: Formation Pcg described as "Conglomerati poligenici" in Motta (1969); M3s: Formation M3s described as "Sabbie ed arenarie, più o meno compatte, ben stratificate; calcari fetidi soletiformi chiari, ricchi di gasteropodi palustri, a luoghi con sottili livelli di lignite" in Motta (1969); M3m: Formation M3m described as "Marne e argille lacustri, grigio azzurre più o meno sabbiose e talora gessose con lenti ciottolose, frequentemente fossilifere, con banchi di lignite nella zona basale" in Motta (1969). Column d - 1f: deltaic-lacustrine unit 1f in Benvenuti et al. (2001); 1e: Alluvial plain unit 1e in Benvenuti et al. (2001); 1d: Alluvial plain unit 1d in Benvenuti et al. (2001); 1c: Shallow lakes unit 1c in Benvenuti et al. (2001); 1b: Peat bogs unit 1b in Benvenuti et al. (2001); 1a: Slope-palustrine unit 1a in Benvenuti et al. (2001).

predominance of specialised bovids, the tendency for the development of hypsodonty, the large body size in some of the small mammals, and the absence of non-lutrine carnivores, are all indicative of an endemic (insular) environment (Hürzeler & Engesser, 1976; Sondaar, 1977; Engesser, 1989; Casanovas-Vilar et al., 2011a, b; Angelone et al., 2022). The V2 fauna again represents an insular community, similar to that of the earlier V1 fauna. However, it is quite different, as its detailed composition

is quite dissimilar. Although both share a few species, such as *Tyrrhenotragus gracillimus* (Weithofer, 1888), *Anthracoglis marinoi* Engesser, 1983, and *O. bambolii* (Rook et al., 1996, 2011; Benvenuti et al., 2001), key differences are evident between the V1 and V2 faunas due to the arrival of new immigrants into the region (i.e., *Parapodemus* sp. II and *Eumaiocoerus etruscus* [Michelotti, 1861]), as well as, most probably, *Indarctos anthracitis* (Weithofer, 1888). These differences hint at

a temporary reconnection with Europe (Benvenuti et al., 2001) and also suggest the appearance of new species resulting from the in situ evolutionary transformation of locally endemic forms (i.e., *Anthracomys majori* Schaub, 1938 from *Huerzelerimys oreopitheci* Engesser, 1989, *Paludolutra campanii* [Meneghini, 1863] from *Tyrrhenolutra helbingi* [Hürzeler, 1987], *Maremmia lorenzi* [Hürzeler, 1983] from *Maremmia haupti* [Weithofer, 1888], and *Paludotona minor* Angelone et al., 2017 from *P. aff. minor*).

The V3 mammal assemblage (6.7-6.4 Ma) represents the major reorganisation in the palaeobiogeography of the Tyrrhenian area that occurred during the Messinian. From a faunistic (land mammal) viewpoint, this time interval is characterised by a dramatic change that points to a renewed and definitive palaeobiogeographical connection with Europe. This change marks the moment when the Corso-Sardinian massif was definitively isolated from southern Tuscany by the opening of the Tyrrhenian Sea, and southern Tuscany became fully connected with the newly formed Apennine chain. The dispersal of European land mammal fauna throughout the newly emerged lands of this early Italian Peninsula, towards the present-day southern Tuscany, is testified by findings from several localities along the slopes of the newly emerged Apennines (Rook et al., 2006; Abbazzi et al., 2008b; Angelone et al., 2011; Colombero et al., 2014), that constituted a wide pathway for the dispersal of mammal communities along this early Italian Peninsula.

AN OVERVIEW ON THE HYPOTHESES ON THE EXTINCTION OF *OREOPITHECUS*

Over the years, there have been two main alternative views about the factors underpinning the disappearance of *O. bambolii*: one abiotic (i.e., climate change) and the other biotic (i.e., species interaction).

The consensus among palynological, palaeontological and sedimentological studies is that changes in climate and/or habitat may have occurred at the time of *Oreopithecus*' extinction. Some of the works described above based on pollen assemblages (Benvenuti et al., 1995), faunal body size and hypsodonty (Bernor et al., 2001), and fossil ostracods (Ligios et al., 2008) from Baccinello have suggested increasing environmental variability over time, from warm and humid conditions to an inconsistent regime with irregularly alternating dry and moist phases, leading to the view that forest loss and fragmentation, in conjunction with aridification (as revealed by a strong increase in xerophilous herbaceous plants; Benvenuti et al., 1995), was a likely cause of the disappearance of *O. bambolii*. In this case, the cause surrounding the extinction might have been somewhat similar to that of the Miocene hominoid *Sivapithecus* (ca. 13-8.4 Ma), from the Siwalik Group of Pakistan, for which a reduction in habitat diversity (i.e., decrease in forest and increase in open areas) has been reported (Nelson, 2007).

Alternatively, not all researchers interpret a change in climate as the reason for *Oreopithecus* extinction. For example, Matson et al. (2012) reported stable carbon and oxygen isotope values of organic matter in

palaeosols at Baccinello, and found very low differences in carbon isotope composition between *Oreopithecus*-levels and the time period subsequent to its extinction. This was interpreted by these authors as indicative of environmental uniformity through time, with no (or no significant) changes being detected. Additionally, a more recent research by DeMiguel and Rook (2018) is in favour of the alternative hypothesis that local changes in climate did indeed take place but did not lead to the extinction of *Oreopithecus*. Based on ungulate hypsodonty and tooth wear (which are informative for both palaeodiet and palaeohabitat reconstruction), DeMiguel & Rook (2018) found fluctuation in diet composition for the species and hence an environmental diversity throughout the Baccinello-Cinigiano succession (from *Oreopithecus*-levels [V1 and V2] to the post-extinction level [V3]) more heterogeneous than that proposed by Matson et al. (2012). However, the overall picture of this work (DeMiguel & Rook, 2018) maintains that these changes were not drastic enough to substantially alter the conditions under which *Oreopithecus* lived, since the type of environments in both V1 and V3 would correspond to forests with a relatively open canopy, whereas V2 experienced a pulse of increased humidity that resulted in more forested habitats. The faunal assemblage (e.g., *Hippotherium*, *Dicerorhinus*, *Propotamochoerus*, *Machairodus*, *Mesopithecus*) found shortly after *Oreopithecus* became extinct has proven to record a time of tectonic collision of the Tusco-Sardinian province. This implied the establishment of extensive land bridges with neighbouring palaeoprovinces and the creation of inland seas (which were periodically desiccated) that facilitated the connection of the insular ecosystem of *Oreopithecus* to the mainland Italy and intermittent faunal interchanges (Rook, 2016). As such, the interpretation by several authors (Agustí, 2007; Abbazzi et al., 2008a; Chesi et al., 2009; Rook et al., 2011; Matson et al., 2012; Nelson & Rook, 2016; DeMiguel & Rook, 2018) is that the disappearance of *Oreopithecus* was driven largely by intensive interaction with invading species ca. 6.7-6.4 Ma rather than by environmental change.

DIETARY AND BEHAVIOURAL VERSATILITY AS A KEY TO *OREOPITHECUS* SURVIVAL

Food and ecological requirements of *Oreopithecus* are pivotal to understand why the environmental change that took place at the extinction interval (V3) did not affect *Oreopithecus*' lifestyle (although it probably influenced its behaviour in some way) in the various habitats in which it lived, especially if considering the special conditions of island ecosystems and insular faunas. There have been some attempts recently to clarify this.

Though Ungar & Kay (1995) and Carnieri & Mallegni (2003) interpreted the derived pattern of crest and cusp morphology as evidence that *Oreopithecus* was a highly folivorous ape that concentrated on leaves, preserved microscopic patterns of tooth wear (Galbany et al., 2005; DeMiguel et al., 2014) and enamel texture (Williams, 2013) in *Oreopithecus* are clearly like those of modern primates with more eclectic diets (e.g., *Cebus nigrivittatus* Wagner, 1846; see DeMiguel et al., 2014).



Fig. 3 - (color online) Illustration depicting the possible cause of extinction of *Oreopithecus babolii* as a result of predation by the large saber-toothed cat *Machairodus* (artwork by Flavia Strani).

Therefore, *Oreopithecus* probably adopted a much broader versatility in terms of exploitation of nutrients and resources than traditionally thought in the various habitats of the Tusco-Sardinian palaeobioprovince, preferentially relying on soft fruits, but also on a wide range of mechanically resistant foods (or foods found near ground level) (DeMiguel & Rook, 2018). This versatile diet also fits with post-canine teeth of *Oreopithecus* which exhibit adaptations (e.g., high, voluminous bunodont cusps linked together by a number of crests and some accessory cusps; development of cingula; pronounced dental relief; and intermediate-thick enamel; Martin, 1985; Zanolli et al., 2016, 2017) for omnivory rather than for folivory (Alba et al., 2001b). This is noteworthy because the potential to adapt to any (subtle or not) environmental change in eclectic taxa is higher than in specialised ones (DeMiguel et al., 2014; DeMiguel, 2016). Moreover, some postcranial features (such as short broad pelvis and femur with significant bicondylar angles or tucked-in knees) and hands and feet with human-like precision grip capability seen in *Oreopithecus* are understood to be adaptations to efficient bipedal posture and locomotion (Straus, 1963; Jungers, 1987; Moyà-Solà & Köhler, 1997; Moyà-Solà et al., 1999, 2005; Rook et al., 1999a; but see Harrison, 1986, 1991). This might have favoured more efficient terrestrial foraging, which might provide a pathway for *Oreopithecus* to interact with a greater range of habitats (DeMiguel & Rook, 2018).

Taken together, these observations suggest that dietary versatility (probably including arboreal soft-fruits and leaves, C₃ grasses, herbs close to ground, hard objects, etc.) in conjunction with behavioural and ecological flexibility in *Oreopithecus* were very likely an integral part of its adaptations to cope with the underlying change in plant composition and food supply that occurred in the island ecosystems of the Baccinello-Cinigiano Basin.

FAUNAL INTERACTION AS THE UNDERLYING CAUSE FOR THE EXTINCTION OF *OREOPITHECUS*

All the above can be interpreted to mean that a change in plant composition of the landscapes was not an important factor is driving the disappearance of the insular, endemic faunal complex of the Baccinello-Cinigiano Basin, including the ape *Oreopithecus*. However, the fact that they finally became extinct convincingly demonstrates that things other than an environmental change occurred in this region during the latest Miocene.

Abundant literature has reported that a major reorganisation in the palaeobiogeography of the Tyrrhenian area occurred during the Messinian, and hence many authors (Hürzeler & Engesser, 1976; Abbazzi, 2001; Bernor et al., 2001; Agustí, 2007; Abbazzi et al., 2008a, b; Rook, 2009, 2016; Rook et al., 2011; DeMiguel & Rook, 2018) have argued in an extensive way that the setting of a new, continental, European vertebrate assemblage (especially mammals and chelonians) is the most feasible explanation for the extinction of *Oreopithecus* (Fig. 3). That is, all the taxa belonging to the endemic faunal complex in the Baccinello-Cinigiano Basin disappeared and were replaced by a new faunal assemblage (V3), including continental taxa with clear European affinities (among which three-toed equids *Hippotherium*, deer and carnivores). The renewed mammal assemblage V3 is most comparable to typical late Turolian (6.8-5.6 Ma; Messinian) European faunas of MN13 (Hürzeler & Engesser, 1976; Engesser, 1989; Rook et al., 1991; Rook, 1999, 2016; Abbazzi, 2001; Bernor et al., 2011). It is therefore probable that some of the large predators and potential competitors found in level V3 encountered the endemic faunal complex of the Baccinello-Cinigiano on a short (non-geological) timescale. At this point, two

(not necessarily exclusive) hypotheses can explain the extinction of *O. bambolii*. First, the arrival of the colobine monkey *Mesopithecus* at ca.7 Ma (Rook, 2009; Alba et al., 2015) likely led to a reduction in niche breadth of *Oreopithecus* due to competition, as *Mesopithecus* has been reported as a widespread, opportunistic feeder (Merceron et al., 2009), and the existence of two ecologically similar species in the same spatiotemporal range results in strong and continuous competition (DeMiguel et al., 2012; Strani et al., 2018; Strani & DeMiguel, 2023). Second, *Oreopithecus* might have been subject to predation by *Machairodus* (Rook et al., 1999b), as carnivorans are usually at the top of the food chain and felids are among the most prominent predators of modern primates across the world (Hart, 2007; Meloro & Elton, 2012). In this case, it is therefore very likely that, if the opportunity arose, this large carnivore would prey on *Oreopithecus*.

CONCLUSIONS

Oreopithecus bambolii is a Late Miocene ape that lived and evolved under insular conditions in Tuscany and Sardinia ca. 8.2–6.7 Ma. As a result of a high level of endemism, a number of different interpretations over its taxonomical status, type of locomotion, and extinction have been offered over the years.

This work summarises several decades of research regarding *Oreopithecus*, especially in reference to the causes of its extinction. The interpretation of the disappearance of *Oreopithecus* has been controversial primarily because its environmental context and ecological requirements have not been until recently deeply explored. On the one hand, some authors have proposed that *Oreopithecus* went extinct as a result of a marked shift in climate; on the other hand, others have considered that *Oreopithecus* disappeared when a connection with the mainland was established, due to intense interaction with non-endemic invading fauna.

An alternative view, proposed by DeMiguel & Rook (2018) in their study of the ungulate fauna (prior to, during, and roughly after the extinction of *Oreopithecus*) of the Baccinello-Cinigiano sequence, maintains that an environmental shift did indeed take place at the extinction interval (indeed there were two; a first between ca. 8.1–7.1 Ma [V1 to V2] and other ca. 6.7 Ma [V3]), as other authors found before. Paradoxically, this study is contrary to the role of environmental change as a contributing factor in the extinction of *Oreopithecus* for two reasons. First, the floral composition after the extinction event (i.e., V3) was quite similar to that of the ecosystems of V1 under which *Oreopithecus* successfully evolved. Second, *Oreopithecus* likely had a dietary versatility wider than previously thought, which may have been an integral part of its adaptations to cope with climatic and vegetation changes in the habitats.

Clearly, this suggests that, albeit abiotic as well as biotic changes indeed took place, the role of faunal interaction through invading species from mainland Italy was more important than the abiotic cause per se, and therefore the most feasible interpretation for the disappearance of *O. bambolii* and associated fauna.

AUTHORS' CONTRIBUTIONS

D.D.M. conceived the study. D.D.M. wrote the final version of the manuscript with input from L.R. The two authors contributed equally to develop the ideas, discussed the results, and reviewed the final version of the manuscript.

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