



ELSEVIER

Contents lists available at ScienceDirect

## Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution

## Geopalaeontological setting, chronology and palaeoenvironmental evolution of the Baccinello-Cinigiano Basin continental successions (Late Miocene, Italy)



*Cadre géo-paléontologique, chronologie et évolution des paléoenvironnements dans la succession continentale du bassin de Baccinello-Cinigiano (Miocène supérieur, Italie)*

Lorenzo Rook

Dipartimento di Scienze della Terra, Università di Firenze, Firenze, Italy

## ARTICLE INFO

## Article history:

Received 12 March 2015

Accepted after revision 22 July 2015

Available online 9 October 2015

Handled by Lars vanden Hoek Ostende

## Keywords:

Geological setting

Chronology

Palaeoenvironmental evolution

*Oreopithecus* faunas

Long continental succession

Late Miocene

Italyur

Italie

## ABSTRACT

The Latest Miocene succession of the Baccinello-Cinigiano Basin in southern Tuscany (Italy) recorded a faunal turnover documenting the extinction of an older, insular, endemic faunal complex characterised by the extinct ape *Oreopithecus bambolii* and the setting of a new, continental, European faunal complex including the colobine monkey *Mesopithecus*. A similar turnover pattern (Late Miocene ape/Latest Miocene Cercopithecidae) is generally observed in Late Miocene continental successions of Eurasia, from Spain to central Europe, Southwest Europe, the near East, and Southwest Asia. Abundant literature reports that the Late Miocene Eurasian hominoid primate distribution closely tracks the climatic/environmental changes occurring during the 12–9 Ma interval, until their extinction in western Europe. In the primate record, the dispersion of Cercopithecidae and the contraction of hominids is interpreted as an event depicting a pattern of “continentalisation” in the Old World. The sedimentary succession of the Baccinello–Cinigiano basin, one of the longest continuous vertebrate-bearing continental successions in the Neogene Italian record, contributes to the debate on this hypothesis. This paper provides an overview of the main characteristics of the sedimentary succession, the chronological constraints (biochronology, radiometric datings, magnetostratigraphy), and the palaeoenvironmental evolution as derived from palaeobiological approaches and from the study of stable carbon and oxygen isotope contents along the entire sedimentary succession. The 2 myr geological history of the Baccinello Cinigiano Basin, which documents the evolutionary history of *Oreopithecus* and associated faunas, does not have a direct relation with the event of the Messinian Salinity Crisis. The evolutionary history of Baccinello–Cinigiano Basin and its palaeontological record have been mainly driven by the regional tectonism and palaeogeographic changes that affected the northern Tyrrhenian regions in Late Miocene (Latest Tortonian–Messinian) times.

© 2015 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

E-mail address: [lorenzo.rook@unifi.it](mailto:lorenzo.rook@unifi.it)<http://dx.doi.org/10.1016/j.crpv.2015.07.002>

1631-0683/© 2015 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

## R É S U M É

*Mots clés :*

Mise en place géologique  
 Chronologie  
 Évolution paléoenvironnementale  
 Faunes à *Oreopithecus*  
 Longue succession continentale  
 Miocène supérieur  
 Italie

La succession du Miocène terminal du bassin Baccinello-Cinigiano dans le Sud de la Toscane (Italie) a enregistré un *turnover* faunique documentant un complexe faunique endémique insulaire antérieur, caractérisé par le grand singe éteint *Oreopithecus bambolii* et l'établissement d'un nouveau complexe faunique européen continental, incluant le singe colobine *Mesopithecus*. Un schéma similaire de *turnover* (grand singe du Miocène supérieur/Cercopithecidae du Miocène terminal) est généralement observé dans les successions continentales du Miocène supérieur, depuis l'Espagne jusqu'à l'Europe centrale, l'Europe du Sud-Ouest, le Proche-Orient et l'Asie du Sud-Ouest. Une abondante littérature rapporte que la répartition des primates hominoïdes eurasiens du Miocène supérieur suit les changements environnementaux et climatiques de l'intervalle 12–9 Ma, jusqu'à leur extinction en Europe de l'Ouest. Dans l'enregistrement des primates, la dispersion des Cercopithecidae et la contraction des hominidés constituent un événement typique d'une continentalisation dans l'Ancien Monde. La succession sédimentaire du bassin de Baccinello-Cinigiano, l'une des plus longues successions continentales continues renfermant des vertébrés dans le registre néogène italien, contribue au débat à propos de cette hypothèse. L'article présente une vue d'ensemble sur les principales caractéristiques de la succession sédimentaire étudiée, les contraintes chronologiques (biochronologie, datations radiométriques, magnétostratigraphie) et l'évolution paléoenvironnementale d'après des approches paléobiologiques et l'étude des teneurs en isotopes stables du carbone et de l'oxygène le long de l'entière succession sédimentaire. L'histoire géologique du bassin Baccinello-Cinigiano sur 2 Ma, qui documente l'histoire évolutive d'*Oreopithecus* et des faunes associées, n'a pas de relation directe avec la crise de salinité messinienne. L'histoire évolutive du bassin et son registre paléontologique ont été principalement régis par la tectonique régionale et les changements paléogéographiques qui ont affecté les régions nord-tyrrhéniennes au cours du Miocène supérieur (Tortonien terminal et Messinien).

© 2015 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

The Latest Miocene continental record of the Italian peri-Tyrrhenian regions (Tuscany and Sardinia) documents the existence of a peculiar bioprovince characterised by the occurrence of vertebrate faunas with manifestly endemic features that differ from coeval mammal faunas, either from Europe or Africa: the so-called Tusco-Sardinian palaeobioprovince (“*Oreopithecus* Zone Faunas”, or OZF in Bernor et al., 2001). The Latest Miocene faunal succession of the Tusco-Sardinian area has been known for a long time in the literature, and the geological setting, the evolutionary patterns of vertebrate records and their biogeographic significance have been exhaustively reported in a number of papers (e.g., Abbazzi et al., 2008b; Azzaroli et al., 1986; Benvenuti et al., 2001; Chesi et al., 2009; Delfino and Rook, 2008; Hürzeler and Engesser, 1976; Rook et al., 2011).

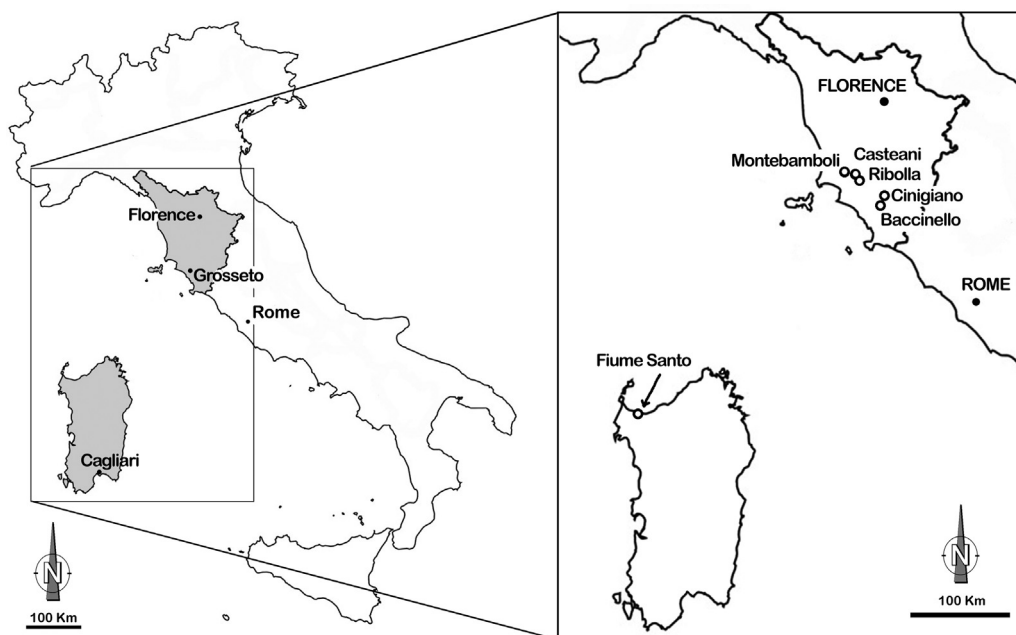
A celebrated taxon within these endemic faunal complexes is the endemic ape *Oreopithecus bambolii* (Gervais, 1872; Harrison and Rook, 1997; Hürzeler, 1951, 1958; Moyà-Solà and Köhler, 1997), whose fossils have been recovered since the nineteenth century from several mines exploiting lignite deposits in southern Tuscany (Fig. 1). Among these localities (Casteani, Montebamboli, Ribolla, etc.), the geology and palaeontology of the Baccinello area are the best known, thanks to the early research led by J. Hürzeler from the Basel Naturhistorisches Museum (De Terra, 1956; Gillet et al., 1965; Lorenz, 1968; Rook, 2012), who recovered abundant faunal remains from different stratigraphic levels. Since the 1990s, research conducted by the Vertebrate Palaeontology Research Group of the University of Florence (Fig. 2) has increased our knowledge of

the palaeontology, geology and sedimentology of the area (Benvenuti et al., 1999a,b, 2001, 2015; Rook et al., 2000, 2011), allowing a better understanding of the sedimentary/environmental evolution of the Baccinello-Cinigiano Basin (henceforth referred to as the BC Basin).

## 2. Geological setting of the Baccinello-Cinigiano Basin

During the Late Miocene (Tortonian-Messinian), the topography of the Maremma region was influenced by concurrent regional tectonic processes: orogenic activity in the axial portion of the uplifting northern Apennines and the opening of the Tyrrhenian Sea (Boccaletti et al., 1990; Martini and Sagri, 1993; Martini et al., 2001). As a consequence, shallow basins, characterised by the deposition of fluviolacustrine sediments, started to form on the western side of the northern Apennine chain. The Late Serravallian-Early Tortonian Arenarie di Ponsano Formation, characterised by shallow marine sandstones deposited in small basins (Foresi et al., 1997), constrained the onset of emerged landscapes in the Tusco-Sardinian area to the mid-Late Tortonian. This terrestrial setting caused mammal immigrants from Europe to undergo progressive morphological change due to persisting interruption of the connections with the European mainland (Rook et al., 2006).

The BC Basin, a Late Neogene basin located 25 km east of Grosseto in southern Tuscany (Fig. 1), is one of the largest continental sedimentary basins of the region (Martini and Sagri, 1993; Marroni et al., 2015). It is filled with a minimum



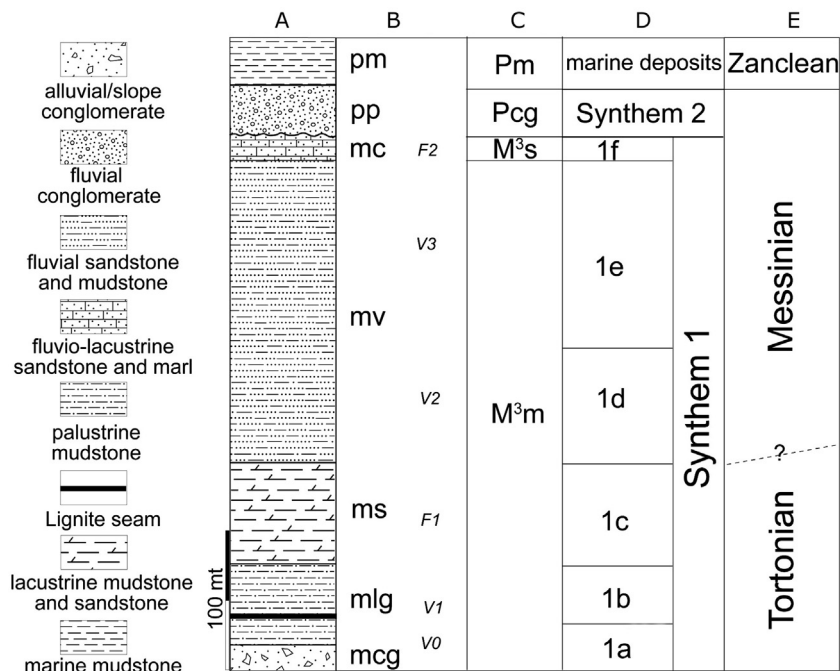
**Fig. 1.** Outline of Italy (left) showing (enhanced in grey) the regions of Tuscany (with the cities of Florence and Grosseto) and Sardinia Island (with the city of Cagliari). The inset on the right shows an enlargement of the northern Tyrrhenian area, with the geographical position of Baccinello and Cinigiano (the two hamlets from which the name of the sedimentary basin discussed in this paper is derived), as well as of other fossiliferous localities mentioned in the text.

**Fig. 1.** Carte schématique de l'Italie (à gauche), montrant (teintées en gris) la Toscane (avec les villes de Florence et Grosseto) et la Sardaigne (avec la ville de Cagliari). L'encart sur la droite montre un agrandissement de la zone nord-tyrrhénienne, avec la localisation géographique de Baccinello et Cinigiano (les deux hameaux dont est tiré le nom du bassin sédimentaire dont il est question dans l'article), ainsi que les autres localités fossilifères mentionnées dans le texte.



**Fig. 2.** (Color online.) Author's first excursion at Baccinello in 1987. Johannes Hürzeler (1908-1995) stands in the center, surrounded by (from left) Lorenzo Rook, Johannes Lorenz, Terry Harrison, Burkart Engesser, and Claudio de Giulli (1938-1988).

**Fig. 2.** (Couleur en ligne.) Première excursion des auteurs à Baccinello en 1987. Johannes Hürzeler (1908-1995) est au centre de la photo, entouré de gauche à droite par Lorenzo Rook, Johannes Lorenz, Terry Harrison, Burkart Engesser et Claudio de Giulli (1938-1988).



**Fig. 3.** Lithostratigraphic column of the Baccinello-Cinigiano Basin (A) with a synopsis of informal stratigraphic units recognised by (B) Lorenz (1968), (C) Motta (1969), (D) Benvenuti et al. (2001). Column B reports the position of vertebrate-rich horizons (V0–V3) and mollusc-rich horizons (F1–F2). Modified from Rook et al. (2011).

**Fig. 3.** Colonne lithostratigraphique du Bassin Baccinello-Cingiano (A), avec un résumé des unités stratigraphiques reconnues par (B) Lorenz (1988), (C) Motta (1969), Benvenuti et al. (2001). La colonne B indique la position des horizons riches en vertébrés (V0–V3) et les horizons riches en mollusques (F1–F2). Modifié d'après Rook et al. (2011).

of 250 m of Upper Miocene continental conglomerates, sands, silty clays bearing lignite seams, and freshwater carbonates (Benvenuti et al., 1999a, b, 2001; Lorenz, 1968), making up a succession that has been described only in informal lithostratigraphic terms (Fig. 3). Before the publication of the official Geological Map of Italy, only scattered areas of the BC Basin were the object of research, mainly related to lignite exploitation (e.g. Stoppani, 1880).

The first stratigraphic investigations in the basin began in the late 1950s (De Terra, 1956; Lorenz, 1968). The official Geological Map of Italy, scale 1:100,000, sheet 128 “Grosseto” (Motta, 1969) reduces the complex lithostratigraphy described by Lorenz (1968) to two main informal formations. The Tortonian–Messinian “M3m” formation, widely exposed in the basin, is represented by lacustrine marls, mudstones with lignite seams, and subordinate sandstones and conglomerates. The Messinian “M3s” formation includes sandstones rich in palustrine shell remains, representing the top of the succession. The same map shows the Late Miocene deposits as capped by the “Pcg” formation made of alluvial conglomerates referred to the Early Pliocene. Successive studies on the Pliocene exposed on the western side of the basin (Bossio et al., 1991) have demonstrated a Late Messinian age of these conglomerates.

In recent times, this Upper Miocene succession has been referred to as two unconformity-bounded stratigraphic units (Synthems 1–2; Benvenuti et al., 2001). Synthem 1, the Upper Tortonian–Lower Messinian, rests unconformably on the pre-Tortonian substratum made of

limestone, claystone and sandstone. Synthem 1 is further subdivided into six main units, in some cases with subunits, deposited within different palaeoenvironments, ranging from slope-palustrine settings (unit 1a) to peat bogs (unit 1b) to shallow lakes (unit 1c), alluvial plains (units 1d, 1e; Figs. 4, 5) and deltaic-lacustrine settings (unit 1f) (Benvenuti et al., 2001). Fine-grained deposits in the different units bear relatively abundant fossil mammal remains, which are grouped into distinct vertebrate assemblages (named as V0, V1, V2 and V3; Lorenz, 1968; Rook et al., 1996, 1999a) mostly characterised by endemic taxa. Specific lacustrine mudstone (unit 1c) and limestone (units 1b and 1f) are characterised by mollusc-rich levels known in the literature as F1 and F2 (Esu and Girotti, 1989; Gillet et al., 1965; Ligios et al., 2008). Synthem 2 rests unconformably on the deposits of Synthem 1 and is referred to as Late Messinian, overlain by Early Pliocene marine deposits ascribed to the *Sphaeroidinellopsis* Zone (Benvenuti et al., 2001, 2015; Bossio et al., 1991). This second Synthem, constituted primarily of conglomerate and sandstone, records the development of alluvial systems, which mark the definitive end of lacustrine conditions in the basin.

Benvenuti et al. (1999a,b, 2001), summarise the BC Basin palaeoenvironmental evolution as driven both by tectono-sedimentary and climatic changes. The former mainly controlled the first and last phases of the basin evolution [activation (unit 1a), basin subsidence (units 1b–1c) and closure (Synthem 2)], while the latter affected the





**Fig. 4.** (Color online.) Sediments of unit 1e (V2) outcropping along the Trasubbie river. This exposure is known as GTO (Great Trasubbie Outcrop).

**Fig. 4.** (Couleur en ligne.) Sédiments de l'unité 1e (V2) affleurant le long de la rivière Trasubbie. La coupe est connue sous le sigle GTO (Great Trasubbie Outcrop).

lake-level fluctuations (unit 1c) and the environmental changes from a lacustrine to a fluvial floodplain and palustrine environment (units 1d–1f).

### 3. Baccinello-Cinigiano Basin chronological constraints: biochronology, radiometric dating and magnetostratigraphy

#### 3.1. Biochronology

The peculiar Late Miocene palaeogeographic configuration of emerged lands in the central Mediterranean area

gave rise to a specific continental vertebrate palaeobio-province (Abbazzi et al., 2008b; Rook et al., 1996), whose more complete faunal succession is provided by the geologic record of the BC Basin. Four vertebrate-bearing faunal assemblages have been distinguished in Synthem 1 of the BC Basin, referred to as V0, V1, V2 and V3. The faunal assemblages V1 through V3 were established by Lorenz (1968), who united different mammal localities with similar faunas into distinct assemblage zones. An older small mammal fauna was discovered some twenty years later, in a grey marl underlying the V1 sediments, and was described as V0 by Engesser (1989).



**Fig. 5.** (Color online.) Sediments of unit 1d (V3) outcropping along the Melacce river. This section is known as “Ribaldella”, from the name of a nearby farm (“Podere”).

**Fig. 5.** (Couleur en ligne.) Sédiments de l'unité 1d (V3) affleurant le long de la rivière Melacce. La coupe est connue sous le nom de « Ribaldella », du nom d'une ferme voisine (« Podere »).

### 3.1.1. The V0–V2 mammal assemblages

The first three successive BC Basin faunal assemblages (V0 to V2) all belong to an endemic faunal complex (the “*Oreopithecus* Zone Faunas [OZF]”, sensu [Bernor et al., 2001](#)) that differs from coeval mammal faunas either from European or African continental realms. The phylogenetic affinities of these mammals are predominantly with species from the European continent, but connection with the African biome cannot be ruled out for the ancestry of some taxa, namely some of the artiodactyls, such as the alcelaphine *Maremmia* or the small neotragine *Tyrrhenotragus* ([Abbazzi, 2008](#); [Hürzeler, 1983](#); [Thomas, 1984](#)).

The oldest faunal assemblage, V0, includes a murid, *Huerzelerimys vireti*, whose occurrence allows a correlation with European sites assigned to MN11 unit (8.7–7.5 Ma; Early Turolian) in the European Neogene biochronological scale ([Casanovas-Vilar et al., 2011b](#); [Engesser, 1989](#)).

The BC Basin V1 fauna occurs in a lignite layer and is considered equivalent to the faunas recovered in coal mines of southern Tuscany (Casteani, Montebamboli and Ribolla; [Hürzeler and Engesser, 1976](#); [Cirilli et al., in press](#)). The high level of endemism of the fauna—in conjunction with the low taxonomic diversity, the predominance of specialised bovids, the tendency for development of hypsodonty, the large body size in some of the rodents, and the absence of non-lutrine carnivores—are all indicative of an endemic (insular) environment ([Engesser, 1989](#); [Hürzeler and Engesser, 1976](#)). The remains of *Oreopithecus bambolii* are extremely abundant in V1 ([Fig. 6](#)), and the species represents one of the commonest mammals from these sites ([Moyà-Solà and Köhler, 1997](#); [Moyà-Solà et al., 1999, 2005](#); [Rook et al., 1999b, 2004](#)).

The BC Basin V2 faunal assemblage occurs in fluvial sediments located several tens of meters above the V1 lignite ([Benvenuti et al., 2001](#); [Lorenz, 1968](#)). This fauna, like that of V1, exhibits a high level of endemism. The V2 fauna represents an insular community, similar to that of the earlier V1 fauna; however, it is quite different in its detailed composition. Relatively few species are found in common: *Tyrrhenotragus gracillimus*, *Anthracoqlis marinoi*, *Paludotona etruria*, *Oreopithecus bambolii*, and an unidentified species of soricid ([Benvenuti et al., 2001](#); [Rook et al., 1996](#)). The key differences between the V1 and V2 faunas arise due to the arrival of new immigrants into the region (i.e., *Parapodemus* sp. II and *Eumaichoerus etruscus*, as well as, most probably, *Indarctos anthracitis*; [Fig. 7](#)), hinting at temporary reconnection with Europe ([Benvenuti et al., 2001](#)), and to the appearance of new species resulting from in situ evolutionary transformation of locally endemic forms (i.e. *Anthracomys majori* from *Huerzelerimys oreopithecii*, *Paludolutra campanii* from *Tyrrhenolutra helbingi*, and *Maremmia lorenzi* from *Maremmia haupti*). A quite rich “OZF” assemblage, correlated with the V2 fauna, is recorded in the Latest Miocene sediments in northern Sardinia, at Fiume Santo ([Abbazzi et al., 2008b](#); [Casanovas-Vilar et al., 2011a,b](#); [Rook et al., 2006](#)).

### 3.1.2. The V3 mammal assemblage

A major reorganisation in the palaeobiogeography of the Tyrrhenian area occurred during the Messinian. From a faunistic (land mammal) point of view, this time



**Fig. 6.** (Color online.) The *Oreopithecus bambolii* skeleton (IGF11778) recovered by J. Hürzeler from the Baccinello lignite mine (V1) in 1958 (photo credits: S. Bambi, Museo di Storia Naturale, Università di Firenze). **Fig. 6.** (Couleur en ligne.) Squelette d'*Oreopithecus bambolii* (IGF11778), récolté par J. Hürzeler à la mine de Baccinello en 1958 (photo S. Bambi, Museo di Storia Naturale, Université de Florence).



**Fig. 7.** (Color online.) The type specimen of *Indarctos anthracitis* (IGF718 V), right mandible (buccal view) from Montebamboli. This “coal bear” is one of the taxa that characterise the renewed “OZF” V2 assemblage (photo credits: S. Bambi, Museo di Storia Naturale, Università di Firenze). **Fig. 7.** (Couleur en ligne.) Spécimen type d'*Indarctos anthracitis* (IGF718 V) mandibule droite (vue buccale) de Montebamboli. Cet « ours du charbon » est l'un des taxons qui caractérisent l'assemblage renouvelé « OZF » V2 (photo S. Bambi, Museo di Storia Naturale, Université de Florence).

interval is characterised by a dramatic change that points to a renewed and definitive palaeobiogeographical connection with Europe. All the taxa belonging to the endemic faunal complex in the BC Basin disappeared, and were replaced by a new faunal assemblage (V3), including continental taxa with clear European affinities ([Fig. 8](#)). The





**Fig. 8.** (Color online.) The type specimen of *Hippotherium malpassii* (IGF9400V), left P<sup>2</sup>-M<sup>3</sup> in labial (a), and occlusal (b) views, from Podere Firenze badlands, where sediments belonging to unit 1d outcrop along the Melacce river. The tridactyl horse *Hippotherium malpassii* is one of the typical European taxa characterising the V3 faunal assemblage (the scale bar represents 5 cm).

**Fig. 8.** (Couleur en ligne.) Spécimen type d'*Hippotherium malpassii* (IGF9400V), P<sup>2</sup>-M<sup>3</sup> gauches en vues labiale (a) et occlusale (b), en provenance des badlands près de Podere Firenze, où les sédiments appartenant à l'unité 1d affleurent le long de la rivière Melacce. Le cheval tridactyle *Hippotherium malpassii* est l'un des taxons européens typiques qui caractérisent l'assemblage faunique V3 (la barre d'échelle représente 5 cm).

renewed mammal assemblage V3 is most comparable to typical Late Turolian (6.8–5.6 Ma; Messinian) European faunas of MN13 (Abbazzi, 2001; Bernor et al., 2011; Engesser, 1989; Hürzeler and Engesser, 1976; Rook, 1999; Rook et al., 1991). A peculiar characteristic of this turnover is seen in the different pattern shown by mammals and herpetofauna (e.g., endemic chelonians such as *Mauremys campanii*). The latter, in fact, does not show the same turnover pattern of mammalian genera, but persists across the faunal assemblages (Chesi et al., 2009).

This faunal 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 (Abbazzi et al., 2008a; Angelone et al., 2011; Colombero et al., 2014; Rook et al., 2006). The latter constituted a wide pathway for the dispersal of mammal communities, although westward, to the structural high point known as the “Mid-Tuscan Ridge”, other sedimentary basins still existed, occupied by shallow marine areas with evaporitic deposition (Martini and Sagri, 1993).

### 3.2. Radiometric dating

The Late Miocene Synthem 1 of the BC Basin succession, although it includes four successive local biochronologic units spanning from the very base of the Synthem (unit 1a; V0) to the top (unit 1e; V3), has long been lacking a reliable chronological calibration. Faunal assemblages

V1 and V2 (the best known since the early investigation in the basin) both exhibit a high level of endemism, which has made biostratigraphic correlations with other European sites extremely difficult (Engesser, 1989; Rook et al., 1999a). The occurrence of the non-endemic murid *Huerzelerimys vireti* in the V0 assemblage (associated with endemic taxa) allowed a tentative correlation of this fauna with the MN11 unit of the Neogene European biochronologic scale, while the youngest faunal unit (V3) is comparable with European localities correlated with MN13 (Bernor et al., 2011; Engesser, 1989; Rook et al., 1996).

The occurrence of volcanics in the BC 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 and Engesser, 1976) was approximately in agreement with the existing local and regional geochronologic constraints.

Extensive field surveys, carried out in the late 1990s on good exposures of the lacustrine deposits of Synthem 1 along the eastern margin of the BC basin, allowed the discovery of a thin tephra within a section outcropping at the “Podere Passonaio” site (Rook et al., 2000). The Passonaio ash was sampled and prepared for geochronological determination (Ar<sup>40</sup>/Ar<sup>39</sup> dating) at the Berkeley Geochronology Center. The result for the age of the ash layer was 7.55 ± 0.03 Ma, furnishing a good constraint on the age of *Oreopithecus* faunas (Rook et al., 2000). This new Ar<sup>40</sup>/Ar<sup>39</sup> determined age is younger than the previous K–Ar result, possibly due to reworked older biotites in the K–Ar sample. The Passonaio tephra, being located stratigraphically within the BC Basin sedimentary succession between the units that have yielded *Oreopithecus* samples

(unit 1c), provided an opportunity to improve the chronology of the *Oreopithecus bambolii*-bearing sediments.

### 3.3. Magnetostratigraphy

Data suitable for a firmer chronological calibration and for the basin stratigraphic correlation have been provided by a sampling for a magnetostratigraphic study within the BC Basin stratigraphic succession and analysis of its magnetostratigraphic signature (Benvenuti et al., 2015; Rook et al., 2011). The correlation of the investigated sedimentary sections of the BC Basin succession with the standard polarity scale (Lourens et al., 2004; updated as by Hilgen et al., 2012) has been carried out by integration of the basin analysis (Benvenuti et al., 1999a,b, 2001), radiometric datings (Rook et al., 2000), and biostratigraphy (Rook et al., 1999a). A clear magnetostratigraphy is achieved for the stratigraphic units established in both Synthem 1 and Synthem 2.

The magnetostratigraphic correlation allowed framing of the entire set of evidence derived in previous studies within a coherent chronological framework (Benvenuti et al., 2015; Rook et al., 2011): i) the oldest *Oreopithecus* bearing sediments in the BC Basin (V1) are found in upper C4r, and so are likely to have an age between 8.3 and 8.1 Ma; ii) the youngest *Oreopithecus* remains (from the so-called V2 assemblages) are from sediments attributed to C3Ar, and have an age between 7.1 and 6.7 Ma; iii) the *Oreopithecus* maximum chronologic range within the BC Basin is about 1.5 Ma long, bracketed between 8.2 and 6.7 Ma; iv) 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); v) the F2 mollusc rich level (post V3) in the BC Basin refers to the latest Early Messinian, being represented by C3An.1r (6.4–6.3 Ma); vi) the normal C3An-1n subchron is missing in the BC Basin, possibly because of the hiatus separating Synthems 1 and 2; vii) the lower portion of BC Basin Synthem 2, a palaeovalley fill, records a reverse polarity that may be reasonably correlated to the Late Messinian C3r chron (6.0–5.4 Ma); viii) the final filling of the BC Basin Synthem 2 palaeovalley, and its subsequent marine flooding, occurred in the the Earliest Zanclean C3n chron (post 5.3 Ma).

## 4. Baccinello-Cinigiano Basin palaeoecology and environmental evolution: pollens, fresh water ostracods, mammals and stable isotope analyses

### 4.1. Palynology

Two contributions published in the early 1990s (Benvenuti et al., 1999a; Harrison and Harrison, 1989) treated the BC Basin palaeovegetational characterisation by means of pollen analysis. Harrison and Harrison (1989) limited their study to samples (historical collections at Basel Naturhistorisches Museum) of the V1 coals that yielded *Oreopithecus* specimens, while Adele Bertini (in Benvenuti et al., 1999a) studied a number of samples that covered the entire BC Basin succession.

Based on their pollen analyses of V1 coals, Harrison and Harrison (1989) hypothesised that *Oreopithecus* habitats

resembled forests characterised by subtropical evergreen broadleaf trees and subtropical monsoon forests similar to those growing in the Yangtze River valley of east central China today.

The BC Basin succession pollen flora identified by A. Bertini (in Benvenuti et al., 1999a) includes arboreal and non-arboreal taxa that presently live in climatically different regions: western Europe (*Carpinus*, *Quercus*, *Ulmus*), Asia, and/or America (*Tsuga*, Taxodiaceae). Taxa with a southern Mediterranean distribution are absent. Tropical-subtropical elements (represented principally by *Engelhardtia*) and subtropical and warm-temperate elements, which also live under year-long humid and warm conditions but are especially related to local edaphic or/and microclimatic conditions (*Taxodium*, *Myrica*, etc.), are well represented, principally in the basal samples (units 1a, 1b). The deciduous-forest elements characteristic of warm-temperate and temperate climates (*Quercus*, *Carpinus*, *Tilia*, *Carya*, *Pterocarya*, etc.) and other arboreal elements that are not climatically significant but are indicative of local edaphic conditions (principally *Alnus*), are similarly represented. Mediterranean evergreen elements are very rare. In most samples, *Pinus* and other Pinaceae are generally overestimated, probably due to a dispersal bias; they are very abundant, especially in units 1b–1c. Here, an increase is observed in temperate, cold-temperate and mountain elements that require year-long humid conditions (*Picea*, *Abies*). The herbaceous plants (Chenopodiaceae, Compositae Tubuliflorae and Liguliflorae, Dipsacaceae, etc.) are scantily represented in the basal samples, and better represented in the samples of unit 1d.

The early BC Basin filling was characterised by a period with a subtropical climate and high precipitation throughout the year, favouring lacustrine flooding (in agreement with Harrison & Harrison, 1989). The evidence from palynological sampling along the BC Basin succession seems to indicate that a climatic signature on the deposition produced a distinct trend during deposition of the entire Synthem 1, from warm and humid conditions (unit 1b) to an inconsistent regime with irregularly alternating dry and moist phases (units 1e and 1f) (Benvenuti et al., 1999a).

### 4.2. Freshwater ostracods

A palaeoecological analysis of fossil ostracods from the BC Basin deposits was recently performed by Ligios et al. (2008). The analysis of fossil ostracod communities in this study identified several physicochemical variations in the water body of the basin, providing a detailed description of the palaeoenvironment and basin evolution well in agreement with sedimentological data.

The early infilling stage of the basin (unit 1a) was characterised by a subaerial deposition, whereas the fine-grained sediments of the subsequent units show that the environmental conditions in the basin gradually shifted to flooded or poorly drained plains or palustrine–lacustrine conditions (unit 1b, biochronological levels V0–V1).

The subsequent depositional stage of the BC Basin, bracketed between the V1–F1 biochronological intervals and characterised by clayey and silty deposits of unit 1c, is distinguished by the enlargement of the V0–V1 lake to the



south. On the whole, the wide lake of the F1 biochronological interval from unit 1c seems to be represented by a more proximal facies to the east, subject to terrigenous inputs by inflowing streams, and by a more distal facies to the south. This wide lake was most likely rather homogeneous, not very deep and characterised by oligo-mesohaline waters. The uppermost sediments and fossils point to a progressive lowering of the lake level, which precludes the increasing filling of the lake by coarse-grained fluvial sediments (unit 1d) in an alluvial fan-floodplain setting during the biochronological interval V2 (Benvenuti et al., 2001). The alluvial plain environment persisted through time, including the biochronological level V3. Unit 1e still mirrors a flood plain, which was interrupted occasionally by coarse-grained deposition related to small channels.

Meteoric and superficial waters most likely supplied the water body, although a slight salinity increase was recorded from time to time. This environment of shallow water bodies was rather unstable and disturbed by inflowing streams, which increased the water turbulence and supplied coarse- to medium-grained sands to the basin. The unstable environmental conditions recorded for the formation of the biochronological interval V3 are in contrast to the uniform conditions detected in the deeper V1–F1 lake. The change from humid and warm climatic conditions to a more irregular climatic regime with alternations of arid and more humid phases is consistent with data from pollen analyses along the BC Basin succession (Benvenuti et al., 1999a).

#### 4.3. Mammal palaeoecology

The palaeoenvironment associated with *Oreopithecus*, as derived from mammal faunas, has been the subject of some debate. Palaeobotanical data (Benvenuti et al., 1999a; Harrison and Harrison, 1989) indicate that small swamps interrupted mixed mesophytic forests, whereas the study of the herbivorous mammals points to a markedly different direction. Specifically, the high diversity and abundance of hypsodont bovids have been related to the occurrence of dry and open environments (Abbazzi et al., 2008b; Bernor et al., 2001, 2011; Hürzeler, 1983).

A recent paper (Casanovas-Vilar et al., 2011a) focused on the functional morphology of the murid (rats and mice) molars from the *Oreopithecus* faunas. This is the only mammal family of the OZF assemblages for which phylogenetic relationships are well resolved (Casanovas-Vilar et al., 2011b; Engesser, 1989).

Casanovas-Vilar et al. (2011a) examined the possibility that the changes in molar morphology seen in these endemic murids were related to a dietary adaptation with a grass component, with the aim of supporting or challenging previous mammal-based reconstructions of the environment of *Oreopithecus* as a dry and open landscape. Results from this study showed that the successive species of endemic insular murids (*Huerzelerimys* and *Anthracomys*) evolved a number of adaptations observed only in extant family members that include significant proportions of grass in their diet. This fits the pattern exhibited by large mammals, but it contrasts with the available palaeobotanical information, which indicates that grasses were minor

components of the vegetation (at least in the earliest phases of the basin infill). This contradiction may be explained because these endemic murids may have been adapted to the consumption of particular food items, such as the hard parts of aquatic plants (as shown by some extant murid species). However, because it is unlikely that the remaining herbivore mammals were adapted to this diet as well, an alternative hypothesis is favoured that takes into account the peculiar ecological conditions of insular ecosystems, which lead to a density-dependent selective regime with strong competition (Köhler & Moyà-Solà, 2009; Yoder et al., 2010). This type of regime would promote the selection of dental adaptations that would increase feeding efficiency and durability of the dentition (such as hypsodonty), as seen in some fossil insular ruminants.

In addition, other evidence may explain that the increase of hypsodonty seen in the OZF murids is not incompatible with the scarcity of grasses. It has been proved in fact that the development of hypsodonty in fossil herbivorous species does not show a clear correspondence with the acquisition of a grazing habit, and that the increase of wear in tooth and of hypsodonty is driven by elements such as i) the presence of extraneous particles (grit, soil and dust) attached to the foods in dry environments, and ii) high masticatory efforts as a result of low-nutritional, mechanically resistant foods, more than the grass component in diet (Damuth & Janis, 2011; DeMiguel et al., 2008; Mendoza & Palmqvist, 2007).

#### 4.4. Stable isotope analyses

The palaeoenvironmental evolution along the entire BC Basin succession (and the potential role of environmental change as a contributing factor in the extinction of *Oreopithecus* and associated fauna) was investigated by two different studies dealing with carbon and oxygen stable isotope analyses. Matson et al. (2012) analysed the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  stable isotope record from organic matter in palaeosols from the BC Basin, while Nelson & Rook (in press) focused on the study of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  stable isotopes from inorganic carbonate in tooth enamel.

The data provided by Matson et al. (2012) on the  $\delta^{13}\text{C}$  stable isotope record from organic matter in palaeosols throughout the BC Basin succession have very low variability relative to the range for modern plants, implying plant ecosystem stability through time. These isotopic data provide no evidence for an ecologically significant difference in vegetation between the ecosystems inhabited by endemic OZF assemblages and those from after their extinction. This result suggests that environmental change was not an important factor in the disappearance of *Oreopithecus* and associated fauna, and indirectly supports the interpretation by previous workers (Abbazzi et al., 2008a; Rook, 2009; DeMiguel et al., 2014) that the extinction was driven largely by interaction with species from mainland Europe.

However, the low variability of  $\delta^{13}\text{C}$  values from organic matter throughout the BC Basin succession stands in contrast to palynological, palaeontological and sedimentological studies, which indicate a trend toward irregularly

alternating dry and moist phases during the Latest Miocene in the BC Basin.

More recently (Nelson & Rook, in press), a study of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  from inorganic carbonate in tooth enamel has been carried out (on total sample of 92 individuals from 22 taxa spanning the entire BC Basin succession) with the purpose of reconstructing OZF and post-OZF habitat, and habitat changes. The dietary  $\delta^{13}\text{C}$  values from faunal specimens from OZF localities were compared to botanical isotope samples to test the hypothesis, based on pollen analyses (Harrison and Harrison, 1989), that *Oreopithecus* inhabited habitats resembling subtropical evergreen broadleaf trees/subtropical monsoon forests (like the Yangtze River valley of eastern central China today). With respect to this hypothesis, Nelson & Rook (in press) demonstrate that significantly higher  $\delta^{13}\text{C}$  values are obtained for vegetation from OZF localities than from monsoon forest  $\text{C}_3$  plants, suggesting that *Oreopithecus* inhabited forests with greater evaporative stresses due to less canopy coverage, warmer temperatures and/or lower annual rainfall. When the isotopic comparison is extended to a wider range of habitats, isotopic values suggest that *Oreopithecus* and associated OZF faunas inhabited forests with greater evaporative stresses than are seen in modern European temperate forests, perhaps due to higher temperatures, but lower evaporative stresses than are encountered in African woodlands and savannahs, due either to cooler temperatures or greater humidity.

A second question addressed by the analysis by Nelson & Rook (in press) relates to whether *Oreopithecus* and associated faunas inhabited a forest similar to those inhabited by other great apes (both modern and fossil, including early hominins). Compared to other ape habitats, both modern and fossil, *Oreopithecus* faunas yield significantly higher  $\delta^{13}\text{C}$  values, suggesting that this taxon inhabited a forest experiencing greater evaporative effects. Given the geological and palynological evidence for lacustrine/swamp-like conditions, *Oreopithecus* forests likely experienced higher light stress, rather than water stress, due to less-continuous canopies. Furthermore, *Oreopithecus* habitats lack the open grasslands of early hominin habitats and yield some  $\delta^{13}\text{C}$  values lower than those of the early hominin localities, suggesting forests with denser canopies.

Finally, a further point addressed by the analysis by Nelson & Rook (in press) relates to the determination of whether the extinction of *Oreopithecus* and its contemporaneous endemic fauna was associated with changes in their environment. Interestingly (and in contrast to the results presented by Matson et al., 2012), the tooth enamel isotopic evidence shows that the time periods after the OZF assemblage went extinct isotopically resemble either modern or fossil ape habitats, while the period in which *Oreopithecus* lived does not resemble the habitat of any other rainforest ape reconstructed from isotopes. Apparently, extinctions of *Oreopithecus* and its contemporaneous endemic fauna were associated with a change in environment, but, unlike other Miocene ape extinctions, the former were not associated with loss of forest (Casanovas-Vilar et al., 2011a; DeMiguel et al., 2014; Nelson, 2007).

The changes in faunal isotope values surrounding the extinction of *Oreopithecus* (Nelson and Rook, in press) are apparently not in agreement with the study of BC Basin palaeosols (Matson et al., 2012). In fact, while Matson et al. (2012) found no significant differences in  $\delta^{13}\text{C}$  values between palaeosols from *Oreopithecus* levels and post-extinction V3 fauna, the changes recorded by tooth enamel suggest a conversion from warm humid conditions to an inconsistent climate regime (the latter is consistent with evidence from sedimentology, and different palaeontological data). Nelson & Rook (in press) provide a possible explanation for this inconsistency in the evidence. In fact, whereas palaeosols reflect a broad-scale record of vegetation across the ecosystem, tooth enamel records a fine-scale record, as seen by the herbivorous mammals that can move about the landscape and feed from specific patches. Given these different views of the palaeoenvironment, isotopic discrepancies between palaeosols and tooth enamel are to be expected. Surprisingly, though, rather than capture the average values of the fauna, palaeosols captured the wettest parts of the habitat used by the fauna from OZF localities, whereas they captured the drier parts in the V3 assemblage. By capturing the different extremes, palaeosols do not show the shifts in  $\delta^{13}\text{C}$  values that fauna do. Differences between fauna and soils for OZF levels may simply reflect a small sample size for soil organic matter, whereas differences in the V3 assemblage may reflect soils too wet to preserve organic matter or to form carbonate nodules.

## 5. Conclusions

This paper summarises several decades of fieldwork regarding the Late Miocene stratigraphy and palaeontology of the Baccinello Cinigiano continental basin in southern Tuscany. Data from different research disciplines provide constraints for the age of the BC Basin continental sedimentary succession and the palaeoenvironmental reconstruction of the lacustrine system and of the emerged surrounding lands, and they provide information on the palaeogeography of the central sector of the Mediterranean area during the Latest Miocene times.

The integration of radiometric datings, magnetostratigraphy and the biochronologic constraints provided by terrestrial and aquatic taxa (mammals, ostracods, pollen assemblages) suggests that the BC Basin Synthem 1 records a 2 myr history of geologic time, bracketed from the sediments of Unit 1a dating back to an age between 8.3 and 8.1 Ma (upper C4r chron; Late Tortonian) and the Unit 1f referring to an age of 6.4–6.3 Ma (C3An.1r chron; latest Early Messinian). The 2 myr geological history of the BC Basin, which documents the evolutionary history of *Oreopithecus* and associated fauna, dispersal events and turnovers of OZF and post-OZF mammal assemblages, does not have direct relation with the event of the Messinian Salinity Crisis.

The evolutionary history of BC Basin and its palaeontological record have been mainly driven by the regional tectonism and palaeogeographic changes that affected the northern Tyrrhenian regions in Late Miocene (latest Tortonian–Messinian) times.

## Acknowledgements

This paper summarizes almost three decades of researches coordinated by the author and it would be impossible to mention all the people who, over such a long time span, have been of help in different ways (from working together in the field, to granting access to collections for comparative studies, to fruitful discussions, and much more). However, I cannot omit to mention here the late Professors Johannes Hürzeler and Claudio De Giuli (Fig. 2) for their outstanding guidance, not limited to Baccinello studies. This contribution is based upon background work supported by grants—among others—from the The Leakey Foundation (1998), the National Geographic Society (7484-03), the National Science Foundation under NSF Award #BCS-0321893 (RHOI; University of California, Berkeley), and the University of Florence (Fondi di Ateneo).

## References

- Abbazzi, L., 2001. Cervidae and Moschidae (Mammalia, Artiodactyla) from the Baccinello V3 faunal assemblage (Late Miocene, Late Turolian, Grosseto, central Italy). *Riv. It. Paleont. Strat.* 107, 107–123.
- Abbazzi, L., 2008. Late Miocene endemic bovids in the Tyrrhenian Palaeobioprovince: from Africa or Europe? In: Salem, M.J., El-Arnauti, A., El Sogher Saleh, A. (Eds.), *The Geology of East Libya*, Vol. 3, pp. 297–302.
- Abbazzi, L., Benvenuti, M., Ceci, M.E., Esu, D., Faranda, C., Rook, L., Tangocci, F., 2008a. The end of the Lago-Mare time in the SE Valdelsa Basin (central Italy): interference between local tectonism and regional sea-level rise. *Geodiversitas* 30, 611–639.
- Abbazzi, L., Delfino, M., Gallai, G., Trebbini, L., Rook, L., 2008b. New data on the vertebrate assemblage of Fiume Santo (North-West Sardinia, Italy), and overview on the Late Miocene Tusco-Sardinian palaeobioprovince. *Palaeontology* 51, 425–451.
- Angelone, C., Colombero, S., Esu, D., Giuntelli, P., Marcolini, F., Pavia, M., Trenkwalder, S., van den Hoek Ostende, L.W., Zunino, M., Pavia, M., 2011. Moncucco Torinese, a new post-evaporitic Messinian fossiliferous site from Piedmont (NW Italy). *N. Jahrb. Geol. Paläont. Abh.* 259, 89–104.
- Azzaroli, A., Delson, E., Moratti, G., Torre, D., 1986. Chronological and paleogeographical background to the study of *Oreopithecus bambolii*. *J. Hum. Evol.* 15, 533–540.
- Benvenuti, M., Bertini, A., Rook, L., 1999a. Facies analysis, vertebrate paleontology and palynology in the Late Miocene Baccinello-Cinigiano basin (southern Tuscany). *Mem. Soc. Geol. It.* 48 (1994), 415–423.
- Benvenuti, M., Papini, M., Testa, G., 1999b. Sedimentary facies analysis in paleoclimatic reconstructions. Examples from the Upper Miocene–Pliocene successions of south-central Tuscany (Italy). In: Agustí, J., Rook, L., Andrews, P. (Eds.), *The Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge, pp. 355–377.
- Benvenuti, M., Papini, M., Rook, L., 2001. Mammal biochronology, UBSU and paleoenvironment evolution in a post-collisional basin: evidence from the Late Miocene Baccinello-Cinigiano basin in southern Tuscany, Italy. *Boll. Soc. Geol. It.* 120 (1995), 97–118.
- Benvenuti, M., Moratti, G., Sani, F., Bonini, M., Oms, O., Papini, M., Rook, L., Cavallina, C., Cavini, L., 2015. Messinian–Earliest Zanclean tectonic-depositional dynamics of the Cinigiano-Baccinello and Velona basins (Tuscany, Italy). *It. J. Geosci.* 134, 237–254.
- Bernor, R.L., Fortelius, M., Rook, L., 2001. Evolutionary biogeography and paleoecology of the “*Oreopithecus bambolii* Faunal Zone” (Late Miocene, Tusco-Sardinian Province). *Boll. Soc. Paleont. It.* 40, 139–148.
- Bernor, R.L., Kaiser, T., Nelson, S., Rook, L., 2011. Systematics and Paleobiology of *Hippotherium malpassii* n. sp. (Equidae, Mammalia) from the Latest Miocene of Baccinello V3 (Tuscany, Italy). *Boll. Soc. Paleont. It.* 50, 175–208.
- Boccalletti, M., Ciaranfi, N., Cosentino, D., Deiana, G., Gelati, R., Lentini, F., Massari, F., Moratti, G., Pescatore, T., Ricci Lucchi, F., Tortorici, L., 1990. Palinspastic restoration and paleogeographic reconstruction of the peri-Tyrrhenian area during the Neogene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 77, 41–50.
- Bossio, A., Costantini, A., Foresi, L., Mazzei, R., Monterforti, B., Salvatorini, G., Sandrelli, F., 1991. Notizie preliminari sul Pliocene del bacino del medio Ombrone e della zona di Roccastrada. *Atti Soc. Tosc. Sci. Nat. A* 98, 259–269.
- Casanovas-Vilar, I., Van Dam, J., Moyà-Solà, S., Rook, L., 2011a. Late Miocene insular mice from the Tusco-Sardinian paleobioprovince provide new insights on the paleoecology of the *Oreopithecus* faunas. *J. Hum. Evol.* 61, 42–49.
- Casanovas-Vilar, I., Van Dam, J.A., Trebbini, L., Rook, L., 2011b. The rodents from the *Oreopithecus*-bearing site of Fiume Santo (Sardinia, Italy): systematic palaeontology, palaeoecology and biostratigraphy. *Geobios* 44, 173–187.
- Chesi, F., Delfino, M., Rook, L., 2009. Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): evidence of terrapin persistence after a mammal turnover. *J. Paleontol.* 83, 379–388.
- Cirilli, O., Benvenuti, M.G., Carnevale, G., Casanovas-Vilar, I., Delfino, M., Furió, M., Papini, M., Villa, A., Rook, L., in press. Fosso della Fittaita: the oldest Tusco-Sardinian late Miocene endemic vertebrate assemblages (Baccinello-Cinigiano Basin, Tuscany, Italy). *Riv. It. Paleont. Strat.*
- Colombero, S., Angelone, C., Bonelli, E., Carnevale, G., Cavallo, O., Delfino, M., Giuntelli, P., Mazza, P., Pavia, G., Pavia, M., Repetto, G., 2014. The Messinian vertebrate assemblages of Verduno (NW Italy): another brick for a Latest Miocene bridge across the Mediterranean. *N. Jahrb. Geol. Paläont. Abh.* 272, 234–287.
- Damuth, J., Janis, C.M., 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biol. Rev.* 86, 733–758.
- Delfino, M., Rook, L., 2008. African crocodylians in the Late Neogene of Europe: a revision of *Crocodylus bambolii* Ristori, 1890. *J. Paleontol.* 82, 336–343.
- DeMiguel, D., Alba, D.M., Moyà-Solà, S., 2014. Dietary Specialization during the Evolution of western Eurasian Hominoids and the Extinction of European Great Apes. *PLoS ONE* 9 (5), e97442.
- DeMiguel, D., Fortelius, M., Azanza, B., Morales, J., 2008. Ancestral feeding state of ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae. *BMC Evol. Biol.* 8, 1–13.
- De Terra, H., 1956. New approaches to the problem of man's origin. *Science* 124, 1282–1285.
- Engesser, B., 1989. The Late Tertiary small mammals of the Maremma region (Tuscany, Italy): II Part. Muridae and Cricetidae (Rodentia, Mammalia). *Boll. Soc. Paleont. It.* 29, 227–252.
- Esu, D., Girotti, O., 1989. Late Miocene and Early Pliocene continental and oligohaline molluscan faunas of Italy. *Boll. Soc. Paleont. It.* 28, 253–263.
- Foresi, L., Pasqucci, V., Sandrelli, F., 1997. Sedimentary and ichnofacies analysis of the epiligurian Ponsano Sandstone (northern Apennines, Tuscany, Italy). *Giorn. Geol.* 59, 301–314.
- Gervais, P., 1872. Sur un singe fossile d'un espèce non encore décrite, qui a été découverte au Monte Bamboli. *C. R. Hebd. Acad. Sci. Paris* 74, 1217–1223.
- Gillet, S., Lorenz, H.G., Woltersdorf, F., 1965. Introduction à l'étude du Miocène supérieur de Baccinello (environs de Grosseto, Italie). *Bull. Serv. Carte Géol. Als. Lorr.* 18, 31–42.
- Harrison, T., Harrison, T., 1989. Palynology of the Late Miocene *Oreopithecus*-bearing lignite from Baccinello, Italy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 76, 45–65.
- Harrison, T., Rook, L., 1997. Enigmatic anthropoid or misunderstood ape: the phylogenetic status of *Oreopithecus bambolii* reconsidered. In: Begun, D.R., Ward, C.W., Rose, M.D. (Eds.), *Function, Phylogeny and Fossils: Miocene Hominoid Origins and Adaptations*. Plenum Press, New York, pp. 327–362.
- Hilgen, F.J., Lourens, L., van Dam, J., 2012. The Neogene period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), *The Geologic Time Scale 2012, Volume 2*. Elsevier, Amsterdam, pp. 923–978.
- Hürzeler, J., 1951. Contribution à l'étude de la dentition de lait d'*Oreopithecus bambolii* Gervais, 1872. *Ecl. Geol. Helv.* 44, 404–411.
- Hürzeler, J., 1958. *Oreopithecus bambolii* Gervais: a preliminary report. *Verh. Naturf. Gesell. Basel* 69, 1–47.
- Hürzeler, J., 1983. Un alcéaphiné aberrant (Bovidé, Mammalia) des lignites de Grosseto en Toscane. *C. R. Acad. Sci. Paris, Ser. II* 296, 497–503.
- Hürzeler, J., Engesser, B., 1976. Les faunes des mammifères néogènes du Bassin de Baccinello (Grosseto, Italie). *C. R. Acad. Sci. Paris, Ser. D* 283, 333–336.
- Köhler, M., Moyà-Solà, S., 2009. Physiological and life history strategies of a fossil large mammal in a resource limited environment. *Proc. Natl. Acad. Sci. USA* 106, 20354–20358.
- Ligios, S., Benvenuti, M., Gliozzi, E., Papini, M., Rook, L., 2008. Late Miocene palaeoenvironmental evolution of the Baccinello-Cinigiano Basin (Tuscany, central Italy) and new autoecological data on rare fossil fresh- to brackish-water ostracods. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 264, 277–287.



- Lorenz, H.G., 1968. Stratigraphisches und mikropaläontologisches Untersuchungen des Braunkohlengebietes von Baccinello (Grosseto, Italien). Riv. It. Paleont. Strat. 74, 147–270.
- Lourens, L., Hilgen, F., Shackleton, N.J., Laskar, J., Wilson, J., 2004. Orbital tuning calibrations and conversions for the Neogene Period. In: Gradstein, F., Ogg, J., Smith, A. (Eds.), A Geologic Time Scale. Cambridge, pp. 469–471.
- Marroni, M., Moratti, G., Costantini, A., Conticelli, S., Benvenuti, M.G., Pandolfi, L., Bonini, M., Cornamusini, G., Laurenzi, M.A., 2015. Geology of the Monte Amiata region, Southern Tuscany, Central Italy. It. J. Geosci. 134, 171–199.
- Martini, P.I., Sagri, M., 1993. Tectono-sedimentary characteristic of Late Miocene–Quaternary extensional basins of the northern Apennines, Italy. Earth Sci. Rev. 34, 197–233.
- Martini, P.I., Sagri, M., Colella, A., 2001. Neogene–Quaternary basins of the inner Apennines and Calabrian arc. In: Vai, G.B., Martini, I.P. (Eds.), Anatomy of an Orogen: the Apennines and adjacent Mediterranean basin. Kluwer Academic Publishers, Dordrecht, pp. 375–400.
- Matson, S., Rook, L., Oms, O., Fox, D., 2012. Carbon isotopic record of terrestrial ecosystems spanning the Late Miocene extinction of *Oreopithecus bambolii*, Baccinello Basin (Tuscany, Italy). J. Hum. Evol. 63, 127–139.
- Mendoza, M., Palmqvist, P., 2007. Hipsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? J. Zool. 274, 134–142.
- Motta, S., 1969. Note Illustrative della Carta Geologica d'Italia alla scala 1:100.000, foglio 128, Grosseto. Servizio Geologico d'Italia, Roma, pp. 1–78.
- Moyà-Solà, S., Köhler, M., 1997. The phylogenetic relationships of *Oreopithecus bambolii* Gervais, 1872. C. R. Acad. Sci. Paris, Ser. Ila 324, 141–148.
- Moyà-Solà, S., Köhler, M., Rook, L., 1999. Evidence of hominid-like precision grip capabilities in the hand of the European Miocene ape *Oreopithecus*. Proc. Natl. Acad. Sci. USA 96, 313–317.
- Moyà-Solà, S., Köhler, M., Rook, L., 2005. The *Oreopithecus*' thumb: a strange case in hominoid evolution. J. Hum. Evol. 49, 395–404.
- Nelson, S., 2007. Isotopic reconstructions of habitat change surrounding the extinction of *Sivapithecus*, a Miocene hominoid, in the Siwalik Group of Pakistan. Palaeogeogr. Palaeoclimatol. Palaeoecol. 243, 204–222.
- Nelson S., Rook L., in press. Isotopic reconstructions of habitat change surrounding the extinction of *Oreopithecus*, the last European ape. Am. J. Phys. Anthropol.
- Rook, L., 1999. Late Turolian *Mesopithecus* (Mammalia, Primates, Colobinae) from Italy. J. Hum. Evol. 36, 535–547.
- Rook, L., 2009. The Italian fossil primate record: an update and perspective for future research. Boll. Soc. Paleont. It. 48, 67–77.
- Rook, L., 2012. Basel–Tuscany, a long lasting link. Swiss J. Palaeont. 131, 7–9.
- Rook, L., Abbazzi, L., Engesser, B., 1999a. An overview on the Italian Miocene land mammal faunas. In: Agustí, J., Rook, L., Andrews, P. (Eds.), The evolution of Neogene terrestrial ecosystems in Europe. Cambridge University Press, Cambridge, pp. 191–204.
- Rook, L., Bondioli, L., Casali, F., Rossi, M., Köhler, M., Moyà-Solà, S., Macchiarelli, R., 2004. The bony labyrinth of *Oreopithecus bambolii*. J. Hum. Evol. 46, 347–354.
- Rook, L., Bondioli, L., Köhler, M., Moyà-Solà, S., Macchiarelli, R., 1999b. *Oreopithecus* was a bipedal ape after all: evidence from the iliac cancellous architecture. Proc. Natl. Acad. Sci. USA 96, 8795–8799.
- Rook, L., Ficarelli, G., Torre, D., 1991. Messinian carnivores from Italy. Boll. Soc. Paleont. It. 30, 7–22.
- Rook, L., Gallai, G., Torre, D., 2006. Lands and endemic mammals in the Late Miocene of Italy: constraints for paleogeographic outlines of Tyrrhenian area. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238, 263–269.
- Rook, L., Harrison, T., Engesser, B., 1996. The taxonomic status and biochronological implications of new finds of *Oreopithecus* from Baccinello (Tuscany, Italy). J. Hum. Evol. 30, 3–27.
- Rook, L., Renne, P., Benvenuti, M., Papini, M., 2000. Geochronology of *Oreopithecus*-bearing succession at Baccinello (Italy) and the extinction pattern of European Miocene hominoids. J. Hum. Evol. 39, 577–582.
- Rook, L., Oms, O., Benvenuti, M., Papini, M., 2011. Magnetostratigraphy of the Late Miocene Baccinello–Cinigiano basin (Tuscany, Italy) and the age of *Oreopithecus bambolii* faunal assemblages. Palaeogeogr. Palaeoclimatol. Palaeoecol. 305, 286–294.
- Stoppani, A., 1880. Cenni sulle nuove miniere di lignite in territorio di Cana (Toscana). Tipografia degli Ingegneri, Milano, 1–8.
- Thomas, H., 1984. Les origines africaines des Bovidae (Artiodactyla, Mammalia) miocènes des lignites de Grosseto (Toscane, Italie). Bull. Mus. nat. Hist. Nat. Paris, Sér. 4, C 6, 81–101.
- Yoder, J.B., Clancey, E., Des Roches, S., Eastman, J.M., Gentry, L., Godsoe, W., Hagey, T.J., Jochimsen, D., Oswald, B.P., Robertson, J., Sarver, B.A.J., Schenk, J.J., Spear, S.F., Harmon, L.J., 2010. Ecological opportunity and the origin of adaptive radiations. J. Evol. Biol. 23, 1581–1596.