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Received 25 September 1986
Revision received 4 March 1987
and accepted 15 April 1987

Publication date August 1987

Keywords: *Oreopithecus*, Miocene, Maremma, Baccinello, fauna, paleogeography, land-bridge, Africa, Europe.

Chronological and Paleogeographical Background to the Study of *Oreopithecus bambolii*

Oreopithecus bambolii belongs to a unique faunal assemblage found only in Tuscany. Six localities have yielded specimens of this Maremma Local Fauna, which at Baccinello can be seen to occur in two horizons: V2, dated to about 8·5 Ma, and the older V1. The Casteani faunule corresponds to the latter, while Monte Bamboli (type locality of *O. bambolii*) is similar to V2. Updated faunal lists for the two horizons are provided. Several rodents and a charophyte indicate European affinities for part of the assemblage, while two bovids and *Oreopithecus* are of African origin. Although the paucity of species (especially carnivores) and the presence of "giant" rodents suggested an insular environment to Hürzeler and Engesser, the lack of any concomitant reduction in size of the large mammals does not support this view. Faunal and floral considerations indicate that although open country may have occurred nearby, *Oreopithecus* probably inhabited a swampy forest. Analysis of the regional paleogeography suggests that a tectonically folded passageway may have permitted the one-way "filter-bridge" migration of terrestrial mammals from northern Africa and from continental Europe into Tuscany, but probably at different times.

Journal of Human Evolution (1986) **15,** 533–540

Introduction

This paper is designed to serve as background to the renewed studies of *Oreopithecus* presented in this issue and currently in progress (Harrison, 1987; Szalay & Langdon, 1987; Delson, in prep.; Rosenberger & Delson, in prep.; Delson & Szalay, in prep.; Jungers, in prep.; Grine, Martin & Kraus, in prep.). Not only is *Oreopithecus* interesting in terms of its paleobiology and phylogenetic placement, but the fauna which accompanies it also raises the problem of regional paleogeography: the mammals document an association of taxa with European and African affinity otherwise unknown in the Late Miocene of western Europe. In this paper, we attempt to place these Maremma faunas in their correct geochronological and paleogeographical settings. Traditional biostratigraphic dating proved difficult and unreliable, because of the highly endemic character of the assemblage, but a single radiometric date provided invaluable corroboration of one alternative. The paleogeographic reconstruction is derived from a more comprehensive work (Boccaletti *et al.*, in press) on the Tertiary evolution of the Tyrrhenian area, in which is presented the full evidence for the results summarized here. That study was based mainly on data from the marine realm and utilized the terminology of marine biostratigraphy, which is employed here in summarizing it, although mammalian biochronological terms are adopted in discussion of the Maremma fauna. Such terminological duality is a reflection of the problems (and benefits) involved in this investigation.

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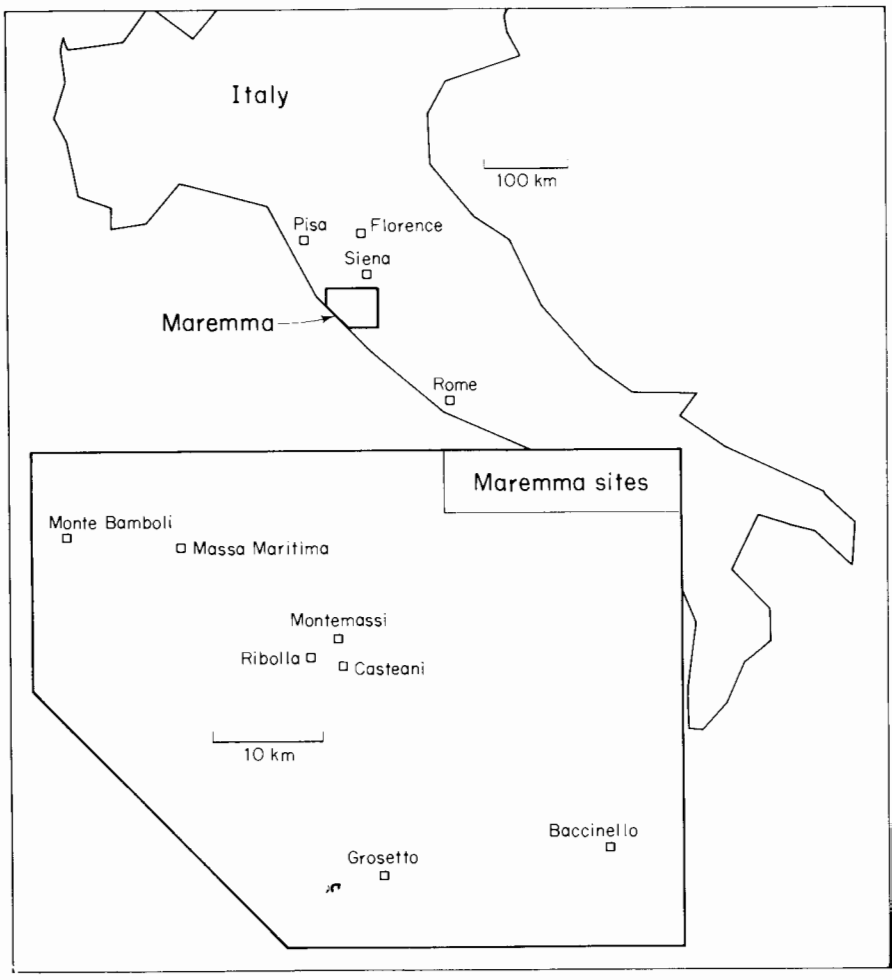
The Maremma Local Fauna: Composition, Chronology and Paleoenvironment

Oreopithecus bambolii is one element of a distinctive, endemic fauna known only from the Maremma district of southwest Tuscany, central Italy (Figure 1). The peculiar character of this Late Miocene local fauna has been pointed out repeatedly (most recently by Hürzeler, 1975, 1982, 1983; Hürzeler & Engesser, 1976; Thomas, 1984). Following Lorenz (1968), the faunal assemblages are localized in two horizons, most clearly distinguished in the Baccinello area, where they are termed V1 and V2 and overlain by the Early Pliocene V3 fauna. The V1 assemblage occurs in a lignite facies, as do its apparent faunal

Figure 1. Location of the major localities yielding the Maremma local fauna: Italy, with major cities and box around Maremma region; (inset) the Maremma region, with two major towns (Massa Maritima and Grosetto) and the five localities ("field" in the case of Baccinello) yielding *Oreopithecus bambolii*.



equivalents at Casteani, Montemassi, Ribolla and Acquanera; V2 occurs at the base of a 50 m thick layer of alternating silt and marl, while its (time?) equivalent is the Monte Bamboli lignite, type locality for *O. bambolii*. Several specimens of this species are known from Monte Bamboli, but only one fragment was tentatively assigned by Hürzeler & Engesser (1976) from Baccinello V2. By far the largest numbers of specimens have been found at V1 and Casteani, with one each published from Ribolla and Montemassi, and none from Acquanera. There are only minor differences between *Oreopithecus* from V1 and Casteani and those from Monte Bamboli (Rosenberger & Delson, in prep.). Combining the data from the several localities results in the faunal lists given in Table 1. Data provided by

Table 1 **Faunal lists from Late Miocene Maremma mammalian horizons**

	V1*	V2*	Cont. origin†	Known Range‡
Primates				
Oreopithecus bambolii Gervais, 1872	×	×	Af	Mar
Carnivora				
a small lutrine, undescribed	×			
Enhydriodon campanii Weithofer, 1888		×	Eu, As	Va–Tu
Hyaenarctos anthracitis Weithofer, 1888		×	Eu, A	As–Tu
a small carnivore, undescribed		×		
Insectivora				
a soricid, undescribed (new genus and species, fide Hürzeler and Engesser)	×			
Rodentia				
a cricetid (*Kowalskia?*)	×			
Valerimys aff. *vireti* (Schaub, 1938)	×		Eu	Tu
Anthracomys majori Schaub, 1938		×	Eu?	Mar
?*Apodemus* sp.		×	Eu?	
a very small murid, undescribed	×			
Anthracoglis marinoi Engesser, 1983	×	cf.		Mar
a glirid, new genus and species (Engesser, 1983)	×		Eu?	
Lagomorpha				
Paludotona etruria Dawson, 1959	×	cf.	Eu, As	Mar
Artiodactyla				
Maremmia haupti (Weithofer, 1888), an alcelaphine bovid	×		Af	Mar
Maremmia lorenzi (Hürzeler, 1983)		×	Af	Mar
Tyrrhenotragus gracillimus (Weithofer, 1888), a neotragine	cf.	×	Af	Mar
two undescribed bovids	×			
a giraffid, undescribed		×		
Eumaiochoerus etruscus (Michelotti, 1861)		×	Eu, As	Va–Tu
Anthracotheriid, ind.	×		Af?	
Chelonia				
Trionyx portisi Ristori, 1895	cf.	×	Eu, Af	
Emys depressa Ristori, 1895	×		Eu	
Emys campanii Ristori, 1895	×	×	Eu	
Emys parva Ristori, 1895	×		Eu	
Testudo sp.	×		Eu, Af, As	
Crocodilia				
Crocodilus bambolii Ristori, 1890	×	×	Af, Eu?	Mar

* V1 includes taxa known from Casteani, Ribolla, Montemassi and Acquanera; V2 includes Monte Bomboli taxa; almost all taxa are known from Baccinello.

† Probable continent of taxon's origin: Af, Africa; Eu, Europe; As, Asia.

‡ Known range of species or higher taxon: As, Astaracian; Va, Vallesian; Mar, Maremma sites only; Tu, Turolian (or equivalents outside Europe).

Hürzeler & Engesser (1976) are not sufficient to permit a separate listing of taxa for each locality.

The chronological placement of the Maremma faunas has been difficult to resolve until recently, not least because of their endemic character. The incompatibility of the "French" definition of the Mio-Pliocene boundary (based on marine concepts and also accepted in Italy), and the "Anglo-Germanic" conception (based on continental and paralic sequences) led earlier workers to place the faunas as either Early Pliocene (e.g., Thenius, 1959) or Late Miocene (Hürzeler, 1958). Lorenz (1968) described associated marine and brackish assemblages which led him to define the "Maremmian" mammalian phase as an equivalent of the Sarmatian of the Paratethyan region, with an estimated age of 13 Ma (million years). Hürzeler & Engesser (1976) reinterpreted the mammals to indicate a Turolian age, perhaps late in this interval. But the K-Ar date they reported (on an acidic tuff intercalated in level V2 near Roccalbegna—pers. comm. from J. C. Hunziker, the analyst) of 8·4 ± 0·4 Ma indicates an early to middle Turolian age for V2. Level V1 lies 150 m below V2 at Baccinello, and owing to the rapid rate of sedimentation of the largely detrital, alluvial and lacustrine deposits of the basin, it may not be much older than V2. It almost certainly falls within the Tortonian age of the marine time scale, but could be either late Vallesian or early Turolian in the mammalian scale. The occurrence of *Valerimys* aff. *vireti,* known also from the early Turolian locality of Mollon (France) may indicate the younger date. It is even possible that some of the difference in faunal composition is due to microhabitat distinction with little age separation. In either case, the two faunas are clearly closely related. In addition to shared taxa, *Anthracomys majori* may have been derived from *Valerimys* aff. *vireti* (Hürzeler & Engesser, 1976), and *Maremmia lorenzi* is a descendant of *M. haupti* (Hürzeler, 1983), if the two taxa are truly distinct.

On the other hand, the Maremma faunas are strikingly different from other Miocene European assemblages. Hürzeler and Engesser (1976) suggested an endemic, insular environment because of the relatively small number of species present, the scarcity of carnivores and the occurrence of some gigantic rodents. However, one of the characteristic effects of insularity, reduction in size of large mammals, is not obvious in the present case. *Maremmia* is a medium-sized alcelaphine and cannot be said to be dwarfed. Compared to V1 *M. haupti*, the younger *M. lorenzi* differs by its more hypsodont teeth and a pronounced reduction of its premolars, but the molars are larger. The result is that the length of the grinding surface of *M. lorenzi* is only 8% smaller than that of *M. haupti*. Thomas (1984) in fact considered that the two populations were conspecific. *Tyrrhenotragus* is of approximately the same size as other neotragines; it is represented by poor fragments from level V1 which are unsuitable for reliable comparisons with V2 specimens. Instead, it would appear that the mixed geographic origin of this local fauna, combined with a distinctive regional paleogeographic setting, is responsible for its unique nature.

The geographic source of the taxa has been much discussed. *Valerimys* of V1 is of European origin, and the occurrence in V1 of the charophyte *Tectochara etrusca* also supports (if weakly) a European connection. Hürzeler (1982) was unable to discern the origin of the suid *Eumaiochoerus etruscus,* but in our opinion, it is related to the European *Microstonyx*. The occurrence of this very abundant suid in Baccinello V2, by contrast to its total absence in level V1, provides evidence for at least two distinct phases of immigration from Europe (Hürzeler, 1983). The doubtful *Apodemus,* also restricted to level V2, seems to point the same way, but this murid is scarce in the fauna and its absence in level V1 may not be conclusive. In contrast, other elements of the Maremma local fauna are of African origin:

Oreopithecus (Harrison, 1985, 1986; Rosenberger & Delson, in prep.); the alcelaphine *Maremmia* (Hürzeler, 1983; Thomas, 1984); and the neotragine *Tyrrhenotragus* (Thomas, 1984). There is thus evidence of only one (early) phase of immigration from Africa, apparently followed by evolution in situ of *Maremmia,* but without appreciable change in the other faunal elements. Engesser (1976) drew attention to the close affinity between the Baccinello *Tyrrhenoglis* and a Pleistocene Sardinian species, but the derivation of this taxon is unknown.

From the ecological point of view, the faunal assemblage indicates a varied environment. The occurrence of lignites with crocodiles, turtles and a suspensory primate indicate a forested, possibly swampy, habitat, while the antelopes, murids and glirids (Engesser, 1983) suggest the presence of drier uplands nearby. This is supported by the analysis of the paleobotanical remains from the V1 lignite (Teichmüller, 1963), which include reeds, fern spores and swamp algae with rarer dry-forest pollen. Given the concentration of *Oreopithecus bambolii* in V1 layers at Baccinello and in other lignites in Maremma, but its scarcity in V2, it seems most likely that this primate was an inhabitant of the swampy forest biome.

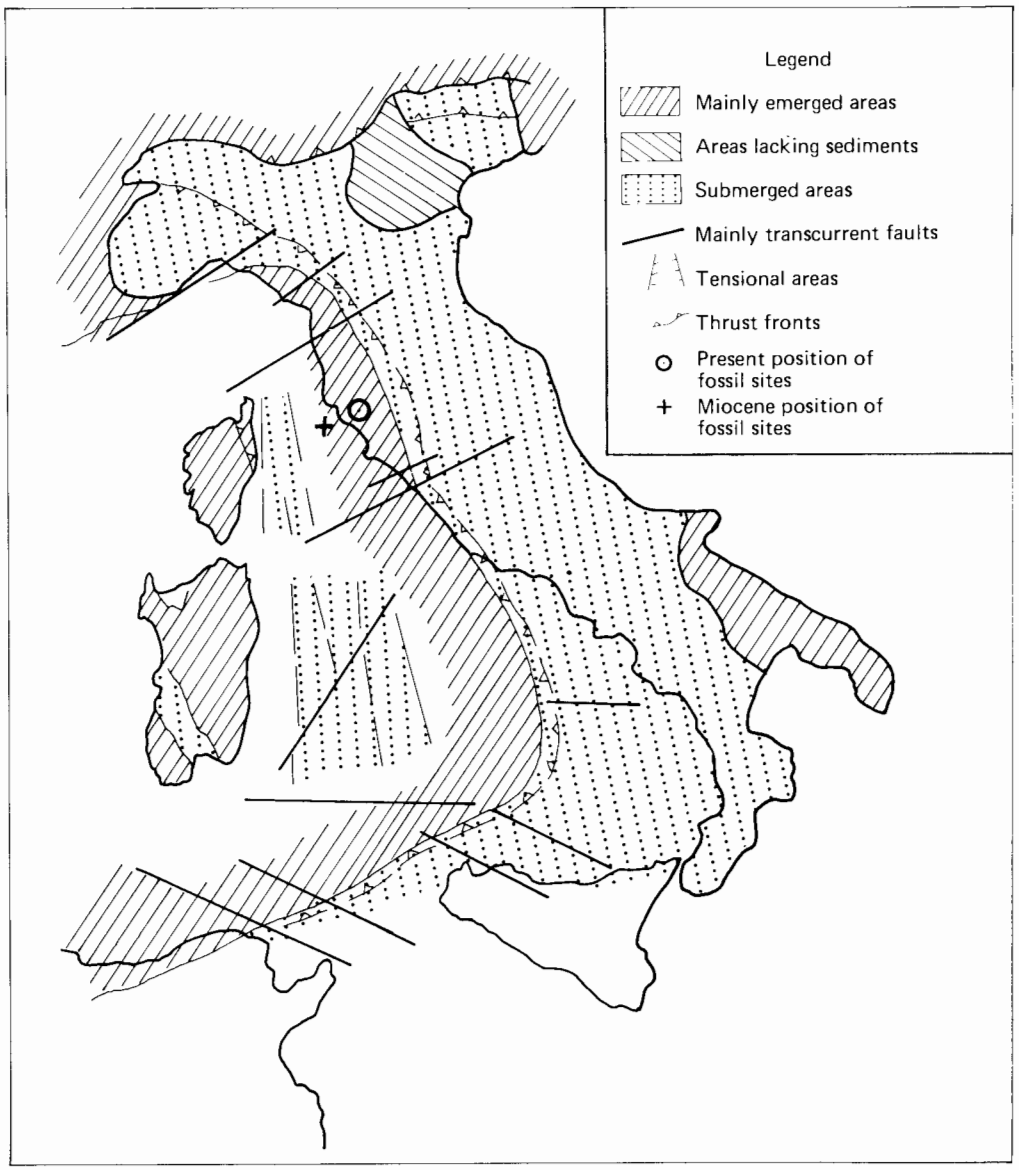
Regional Paleogeography

The presence in a single region of terrestrial mammals of European and African origin presupposes the existence of land bridges or other connections between southern Tuscany and the two main continental land masses. These connections were not necessarily contemporaneous; in fact, it seems rather that they were not. There is no evidence that the Maremma area ever acted as a real bridge between Europe and Africa, allowing migrants to move in either direction all the way from one continent to the other: instead they reached southern Tuscany and appear to have been stopped there.

The paleogeographic history of the Tyrrhenian area, and of the Mediterranean in general, was extremely complex during the Miocene, and a detailed reconstruction of its vicissitudes is a laborious task. As noted above, a team of Italian researchers is pursuing this problem (Boccaletti *et al.*, in press), and Figure 2 has been prepared by two of us (M. B. and G. M.) on the basis of these studies. In the Burdigalian (around 19 Ma), the Corsican–Sardinian block had reached its present position, ending its counterclockwise rotation. During the Middle Miocene, rifting began in the Tyrrhenian area, connected with a counterclockwise rotation of the Appennine area. Figure 2 represents the situation in the early Tortonian (11–10 Ma; earliest Late Miocene): the crustal spreading which led to the formation of the southern Tyrrhenian had already begun, and Corsica and Sardinia were isolated.

The result was folding along a belt running south from eastern Liguria and then swinging south-southeast through western Tuscany and the eastern part of the Tyrrenian area, continuing southward between lat. 40° and 39° and then swerving sharply west-southwest to join northern Tunisia. As suggested above by mammalian evidence, this belt was probably not all emergent at one time, but it may have provided a passageway from North Africa to southern Tuscany on the one side and from Tuscany through Liguria and the Maritime Alps to continental Europe on the other. Such travel would have taken place along a narrow and unstable strip of land (perhaps including islands) which may have acted as a filter to migrant faunas. This surely would have been one cause of the limited diversity of the Maremma assemblages. No relevant changes occurred after the

Figure 2. Paleogeographic reconstruction of the Perityrrhenian region during the early late Miocene, *ca* 11–10 Ma. As indicated in the text, this situation probably prevailed through 8 Ma as well.



early Tortonian until the main tectonic phase of the late Tortonian (about 8–7 Ma). The paleogeography of the interval from 10 to 8 Ma therefore did not differ substantially from the situation in the early Tortonian, except for local variation in the filter-bridge's connections.

Summary

By way of background to current studies of *Oreopithecus bambolii*, this paper has reviewed evidence for the age, environment and paleogeographic setting of the fossiliferous sites, here considered to represent the Maremma local fauna. *Oreopithecus* is known essentially from four deposits in southwest Tuscany, of which Baccinello is most important because it has yielded marine faunas reported by Lorenz (1968) in addition to three vertebrate horizons. Of these, the oldest, V1, is faunally similar to the Casteani, Ribolla and Montemassi localities with *Oreopithecus* (and to Acquanera, which lacks it). Slightly younger is Baccinello V2, dated at 8·4 ± 0·4 Ma, which shares faunal elements with Monte Bamboli, the *Oreopithecus* type locality (see Table 1). It is likely that V1 and its equivalents are of early Tortonian age in the marine scale, but could be as old as late Vallesian in terms of mammals, although V2 is early Turolian in age. The unique character of the Maremma sites, long noted by a variety of authors, was suggested by Hürzeler & Engesser (1976) to be partly due to island endemism, on the basis of the rarity of carnivores (and of taxa generally) and presence of very large rodents. This seems unlikely, given the lack of size reduction in larger mammals. On the other hand, it is clearly related to the mixture of taxa of African and European affinities. The African group, including *Oreopithecus*, *Maremmia* and *Tyrrhenotragus*, would appear to have entered the Tuscany region around the Vallesian-Turolian "transition". Two phases of European immigration are suggested by the presence of *Valerimys* in V1 and *Eumaiochoerus* (which we suggest is related to *Microstonyx*) only in V2. In terms of local environment, both lower vertebrates and paleobotanical evidence suggest forest and probably swamps in V1 time, which fits well with the skeletal adaptations for forelimb suspension of the rather common *Oreopithecus*.

The regional paleogeography has been reconstructed as part of a larger project (Boccaletti *et al.*, in press), and Figure 2 presents a pattern which probably held between 11–8 Ma. The most important feature is a complex folded belt passing through western Italy and into Tunisia. This zone is thought to have served as a "filter-bridge" permitting, at least on one occasion, the one-way passage of mammals from Africa into Tuscany. It is likely that another filter to the north of Maremma allowed European mammals to enter the region in at least two phases, probably at different times from when the African connection was operative.

Acknowledgements

We thank Dr Raymond L. Bernor and several anonymous reviewers for comments on earlier versions of this manuscript. This work was financially supported, in part, by PSC-CUNY grants (13610 and 6–63091) to Delson.

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