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Original article

The endemic bovids from Sardinia and the Balearic Islands: State of the art[☆]

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ABSTRACT

Bovids are not so common in endemic insular faunas and are mainly recorded in Southeast Asia, Japan and some Mediterranean islands. In the Western Mediterranean, endemic bovids have been recorded during the late Miocene in the Tusco-Sardinian palaeobioprovince (Baccinello–Cinigiano basin, South Tuscany, and Fiume Santo, north-western Sardinia). In the latest Neogene and Quaternary, bovids showing highly endemic features were restricted to the Balearic Islands and Sardinia, while Bovini only slightly reduced in size were present on Pianosa, Malta and Sicily. On Sardinia, the richest bovid sample comes from Monte Tuttavista (Orosei), where at least three species have been identified: *Asoletragus gentryi*, *Nesogoral* aff. *N. melonii*, and *Nesogoral* sp. 2. On Mallorca (Balearic Islands) six chronospecies belonging to the *Myotragus* endemic phylogenetic lineage have been described, spreading in age from the Early Pliocene to the Holocene. For decades, a close phylogenetic relationship between *Nesogoral* and *Myotragus* has been widely accepted by scholars. Morphological and biometrical differences shown by Balearic and Sardinian bovids have generally been regarded as the result of the evolution into two different island ecological systems, characterized by different inter and intra-guild selection pressures. Indeed, the more diversified environment of Sardinia, as well as the presence of other large mammals (similar-sized competitors belonging to the same guild and a running predator), increased the interspecific competition, forcing Sardinian bovids to exploit different resources and to occupy different niches, while *Myotragus* exploited under a monopoly regime the supply of resources available for large herbivores on the Eastern Balearic Islands. Nonetheless, new data suggest that *Nesogoral* and *Myotragus* possibly originated from different taxa.

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1. Introduction

Bovids are not so common in endemic insular faunas and are mainly recorded in Southeast Asia, Japan and some Mediterranean islands (Fig. 1). In Asia, fossil endemic bovids have been reported in the Early-Middle Pleistocene of Java (*Duboisia santeng*, *Bubalus palaeokerabau*, *Bibos palaesondaicus*, *Epileptobos groeneveldtii*), the Late Pleistocene-Holocene of Sulawesi (*Anoa* sp. = *Bubalus* sp.), the Middle and Late Pleistocene of Japan (*Bubalus* sp. and *Capricornis crispus/Capricornis* sp.), the Middle Pleistocene of Taiwan (*Bubalus* sp.), the Pleistocene-Holocene of Cebu (*Bubalus cebuensis*, with a body mass of 150–165 kg) and possibly Luzon (*Bubalus* sp.) (Van den Bergh et al., 2001; Croft et al., 2006; Ohdachi et al., 2009; Van der Geer et al., 2010; Rozzi and Palombo, in press; Rozzi et al., in press). Dwarf water buffaloes are still living in some Southeast

Asian islands: the tamaraw *Bubalus (Bubalus) mindorensis*, from Mindoro (Philippines archipelago), with an average weight of 300 kg, is less than half the body mass of the closest continental relative *Bubalus bubalis*; and *Bubalus depressicornis* and *B. quarlesi* from Sulawesi and Buton, with body masses from about 150 to 300 kg. Consistently with the evolutionary pattern shown by most of the fossil endemic bovids, they have short, squat limbs and horns cores significantly reduced in comparison to those of the mainland species.

In the Mediterranean area (Fig. 1), strongly endemic bovids were restricted to the Balearic Islands, maritime Tuscany and Sardinia (Hürzeler and Engesser, 1976; Abbazzi et al., 2008b; Palombo, 2009; Bover et al., 2010), while some bovids slightly reduced in size have been recorded in the Late Pleistocene of Pianosa (*Bos primigenius bubaloides*; Azzaroli, 1978), in the impoverished but balanced *Elephas mnaidriensis* (late Middle-early Late Pleistocene) and San Teodoro Cave-Contrada Pianetti Sicilian (Late Pleistocene, last glacial) faunal complexes (*Bos primigenius siciliae* and *Bison priscus siciliae*; Masini et al., 2008), and in Malta where *Bos* sp. is recorded in the “red earth layers” of

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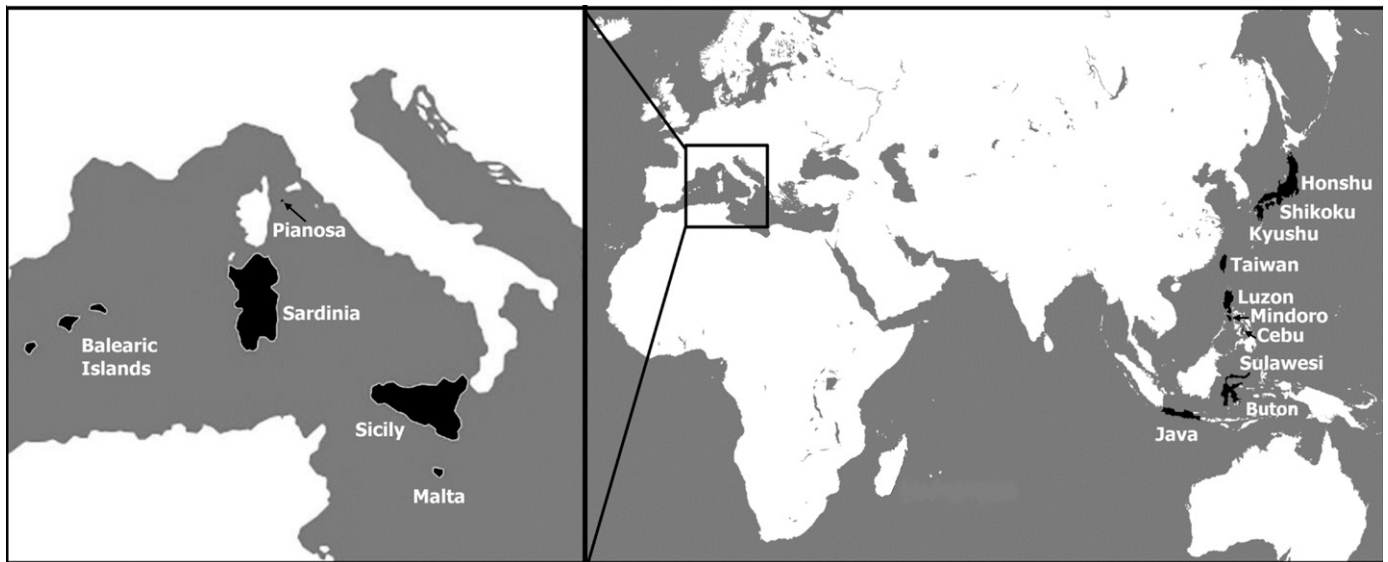


Fig. 1. Map of the main Eurasian Islands bearing fossil and living endemic bovids: Balearic Islands (*Myotragus*, Early Pliocene–Holocene), Sardinia (*Maremmia* cf. *M. lorenzi*, *Tyrrhenotragus gracillimus*, *Etruria viallii*, *Turritragus casteanensis*, and an undetermined taxon provisionally referred to ?Neotragini, Late Miocene; *Asoletragus gentryi* and bovids of *Nesogoral* group, Late Pliocene–Early Pleistocene), Sicily (*Bos primigenius siciliae* and *Bison priscus siciliae*, late Middle–Late Pleistocene), Pianosa (*Bos primigenius bubaloides*, Late Pleistocene), Malta (*Bos* sp., Late Pleistocene), Java (*Duboisia santeg*, *Bubalus palaeokerabau*, *Bibos palaeondaicus*, *Epileptobos groeneveldtii*, Early–Middle Pleistocene), Sulawesi and Buton (*Anoa* sp. = *Bubalus* sp., Late Pleistocene–Holocene; *Bubalus* (*Anoa*) *depressicornis* and *A. quarlesi*, living species), Cebu (*Bubalus cebuensis*, Pleistocene–Holocene), Mindoro (*Bubalus* (*Bubalis*) *mindorensis*, living species), Luzon (*Bubalus* sp., Pleistocene–Holocene), Taiwan (*Bubalus* sp., Middle Pleistocene; *Capricornis swinhoei*, living species), Japan (*Bubalus* sp. and *Capricornis crispus*/*Capricornis* sp., Middle–Late Pleistocene; *Capricornis crispus*, living species).

Ghar Dalam cave (last glacial) together with endemic elephants, hippos and deer (Hunt and Schembri, 1999).

Insular representatives of Bovinae that slightly reduced their size do not usually show marked endemic features; therefore the identification of their mainland ancestors is usually not tricky. This is not the case of the insular middle-sized endemic Antilopinae (*sensu Bibi et al.*, 2009), often represented by strongly modified taxa, making the distinction between apomorphies and plesiomorphies and the identification of the ancestral stock a difficult task. This is definitely true for the Plio–Pleistocene bovids from Sardinia and somehow for those from the Balearic Islands.

Based on recent discoveries and ongoing research, in this paper we present an overview of our knowledge on the late Cenozoic bovids from the Mediterranean area, focusing on the Plio–Pleistocene endemic lineages of Sardinia and the Balearic Islands in order to highlight and delve into still unsolved problematic issues regarding their systematics, phylogeny, and evolution.

2. Endemic bovids from Sardinia

The long, complex and still imperfectly known palaeogeographical history of the island makes the Sardinian faunal evolution absolutely unique with respect to that of the other Mediterranean insular faunas. During the Neogene and the Quaternary (from about the Burdigalian to the Late Pleistocene), several episodes of dispersal, mainly from the European bioprovince, but maybe also from Africa (see below), affected Sardinia, marking more or less important faunal changes that enable us to recognize successive biochronological complexes (Palombo, 2009). Some forerunners of the endemic taxa reached Sardinia by sweepstake routes, some others, including bovids, likely arrived when the island was connected to the mainland by discontinuous, ecologically selective, and temporarily emerged pathways. The fossil record of Sardinian bovids is rich and a number of endemic species have been recorded in quite diversified, but disharmonic faunas, ranging in age from the latest Miocene to the Early Pleistocene (Fig. 2), and including a number of endemic taxa, some of which showing a poor dispersal ability.

2.1. The latest Miocene Sardinian bovids

Bovids were absent in the unbalanced endemic fauna from Oschiri (Early Miocene, Olbia; Van der Made, 2008) and firstly appeared in the Late Miocene local faunal assemblage (LFA) of Fiume Santo (Sassari, north-western Sardinia). The fauna, including at least nine mammalian taxa (Cordy and Ginesu, 1994; Cordy et al., 1995; Abbazzi et al., 2008b), shows strong similarity with the endemic fauna from Baccinello–Cinigiano basin (maritime Tuscany), giving evidence of the presence during the Late Miocene of an isolated palaeobioprovince (a large island or an archipelago) inhabited by the so-called *Oreopithecus* fauna (Palombo, 2009; Rook et al., 2011). Two of the mammals present in the Fiume Santo LFA, the suid “*Eumaiocoer*” and the alcelaphine *Maremmia lorenzi*, first appeared in the level V2 of the Baccinello–Cinigiano stratigraphic succession (Hürzeler and Engesser, 1976). The presence of an approximate 7.55 myr-old ash layer between V1 and V2 levels, and palaeomagnetic data (Rook et al., 2011) indicate that V2 level likely deposited between about 7.1 and 6.7 Ma, providing a chronologic constraint for the Fiume Santo LFA.

Five Bovidae (*Maremmia* cf. *M. lorenzi*, *Tyrrhenotragus gracillimus*, *Etruria viallii*, *Turritragus casteanensis*, and an undetermined taxon provisionally referred to ?Neotragini) have been identified in the Fiume Santo LFA (Abbazzi et al., 2008b). The highly derived characters of most of these bovids make it difficult to ascertain their phylogenetic relationships and taxonomical status. *Maremmia* aff. *M. lorenzi* (Fig. 3), slightly larger and with somehow more advanced dental features than the specimens from the V2 level of Baccinello–Cinigiano, is the most common taxon in the Fiume Santo LFA. The middle-sized bovids of *Maremmia* lineage, *M. haupti* – known from the V1 level of the Baccinello–Cinigiano stratigraphic succession – and its descendent *M. lorenzi*, show latero-medially compressed horn-cores with anti-clockwise torsion on the right side and a kind of hollowing inside the pedicles, lower molars with undulating lingual walls, and an occlusal surface with an 8-shaped profile, matching the typical features found in Alcelaphini. The main peculiar morphological traits of *Maremmia* species are the very hypsodont dentition, the upper

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