The Plio-Pleistocene endemic bovids from the Western Mediterranean islands: knowledge, problems and perspectives*

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ABSTRACT: Bovids are unusual components of endemic insular faunas. From the Plio-Pleistocene of Mediterranean area recorded the well known *Myotragus balearicus* (and allies, Balearic Islands, Spain) and *Nesogoral* (Sardinia, Italy). This paper points out the similar features of these taxa, which are probably related to a continental common ancestor, as well as their peculiar morphologic aspects. The last features are the results of evolution taking place into two different island ecologic systems: the one of Balearic Islands and the one of Sardinia.

Key-words: *Plio-Pleistocene, Bovids, evolution, Mediterranean.*

ΠΕΡΙΛΗΨΗ: Τα Βοοειδή αποτελούν συνήθη στοιχεία στις ενδημικές νησιωτικές πανίδες. Από το Πλειο-Πλειστόκαινο της μεσογειακής περιοχής είναι γνωστά το *Myotragus balearicus* (και συγγενείς μορφές, Βαλεαρίδες Νήσοι, Ισπανία) και το *Nesogoral* (Σαρδηνία, Ιταλία). Αυτή η εργασία αναφέρει τα κοινά χαρακτηριστικά αυτών των μορφών τα οποία πιθανόν σχετίζονται με έναν κοινό ηπειρωτικό πρόγονο, καθώς και τους ιδιαίτερους μορφολογικούς τους χαρακτήρες. Αυτά τα τελευταία χαρακτηριστικά είναι αποτέλεσμα εξέλιξης που λαμβάνει χώρα σε δύο διαφορετικά νησιωτικά οικολογικά συστήματα: των Βαλεαρίδων Νήσων και της Σαρδηνίας.

Λέξεις-κλειδιά: *Πλειο-Πλειστόκαινο, Βοοειδή, εξέλιξη, Μεσόγειος.*

INTRODUCTION

Bovids are unusual components of endemic insular faunas and are only recorded in some Mediterranean and South East Asian islands. Plio-Pleistocene endemic bovids were not frequent in insular Mediterranean faunas (Fig. 1), but included some highly peculiar species, such as *Myotragus*, in the Balearic Islands, and the Sardinian bovids belonging to the *"Nesogoral"* group. Bovids of a relatively reduced size have also been reported in Late Pleistocene deposits of Sicily (*Bos primigenius siciliae* and *Bison priscus siciliae*) and have been claimed on Pianosa (*Bos primigenius buba-loides;* AZZAROLI, 1978). The degree of endemism of the Sicilian and Pianosan bovids was not marked —in agreement with the impoverished but quite diversified and balanced accompanying fauna (AZZAROLI, 1978; PALOMBO, 1996; BONFIGLIO *et al.,* 2001)— and as such will be excluded from this study. Outside the Mediterranean, endemic bovids are still living in some South East Asian islands. Significant differences can be found between continental Asian water buffalos and the modern taxa of the genus *Anoa*, which dwell on islands, in South-East Asia. The Tamaraw *Anoa mindorensis*, living on the homonymous island in the Philippines archipelago, is less than half the body mass of the closest continental relative, *Bubalus bubalis*: 300 kg as opposed to 950 kg (the average between 700 and 1200 kg; NOWAK, 1997). Other insular bovids, the anoas *A. depressicornis* and *A. quarlesi* from Sulawesi have body masses comprising between 150 and 300 kg. They have short, squat limbs and flat, triangular horn cores (NOWAK, 1997) which are reduced in comparison to those of the mainland species.

The most interesting and enigmatic bovids are found in the Plio-Pleistocene deposits of the Eastern Balearic Islands

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* Τα Πλειο-Πλειστοκαινικά ενδημικά βοοειδή από τις νήσους της δυτικής Μεσογείου: γνώση, προβλήματα και προοπτικές.

and Sardinia. Both lineages have been generally regarded as belonging to the Caprinae subfamily (*sensu* GENTRY, 1992), according to some cranial and dental features (see below), but these strongly modified taxa show n u m e r o u s apomorphies that obscure their phyletic relationships, and their ancestor/s as yet remain/s unknown. Recent molecular studies do not support the monophyly of the tribal groups within the Caprinae (e.g., GATESY *et al*., 1997; HASSANIN *et al*., 1998; MUCCI *et al*, 1998; HASSANIN & DOUZERY, 1990, 2003; LALUEZA-FOX *et al*., 2000, 2002), suggesting that the Caprini should be considered as a tribe inside the subfamily Antilopinae. Moreover, the suggested existence of a Rupicaprini or "Nemorhaedini" tribe as proposed by GLIOZZI & MALATESTA (1980) seems inconsistent with available molecular data.

The medium-sized Villafranchian species *Gallogoral meneghinii*, a caprine widely diffused in western Europe middle and early late Villafranchian local faunal assemblages (HEINTZ, 1964; GUÉRIN, 1965; DUVERNOIS & GUÉRIN, 1989), was considered as a possible forerunner, or regarded as a sister continental taxon. ALCOVER (1976) hypothesised that *Myotragus* and *Gallogoral* were closely related due to the high similarity of both genera, suggesting that the latter could have been the ancestor of the first. GLIOZZI & MALATESTA (1980) claimed that a direct descent of *Myotragus* from *Gallogoral* is unacceptable because Balearic bovids would have appeared earlier than their hypothetical ancestor, a view which is elsewhere accepted (e.g., ALCOVER *et al*., 1981). In these authors' opinion, the spreading to Europe of the ancestor of both endemic lineages and continental Villafranchian goat probably occured at the same time as the arrival of the Turolian fauna in connection with the diffusion of more arid environments.

Even if probably derived from the same taxon (or from closely related taxa), these bovids displayed a different evolutionary history in the Balearic Islands and in Sardinia.

The representatives of the *Myotragus* lineage were the only large mammals in the Eastern Balearic Islands (also known as Gymnesic Islands), recorded in highly impoverished, unbalanced faunas, which evolved in isolation for more than 5 million years before becoming extinct somewhere between 3700 and 2040 cal BC (BOVER & ALCOVER, 2003; QUINTANA *et al*., 2003; BOVER, 2004; Fig. 2).

On the other hand, the Sardinian bovids occurred in improverished but rather balanced faunas (Fig. 3), the so-called *"Nesogoral* complex", probably attributable to the Late Pliocene/Earliest Pleistocene. The *"Nesogoral* complex" seems to include two faunal assemblages: in the earlier there were small mammals (*Nesiotites* sp., *Talpa* sp., *Prolagus* sp., *Oryctolagus* aff. *O. lacosti, Rhagapodemus minor, Tyrrhenoglis* ssp.) and several large mammals (*Macaca* cf. *M. majori, Sus* aff. *S. sondaari*, and three bovids) including carnivores (*Pannonictis* sp., and possibly, *Chasmaporthetes melei* ROOK *et al*., 2004); in the later faunal complex, only one bovid seems to have survived together with the same, yet more advanced, small mammals, and with *Pannonictis* and *Macaca*. During the Early Pleistocene, most of the taxa belonging to the *"Nesogoral* complex" (*Tyrrenoglis, Sus,* bovids) had disappeared, being substituted by some new settlers, such as the vole *Tyrrhenicola* and the canid *Cynotherium*. Therefore —probably during the last Early Pleistocene— the ancestor of *"Praemegaceros" cazioti* reached Sardinia, completing the faunal turnover that led to the impoverished, unbalanced Middle Pleistocene endemic fauna (PALOMBO, this volume).

The most advanced Balearic species, *Myotragus balearicus* (Fig. 4), shows very peculiar features in its cranium,
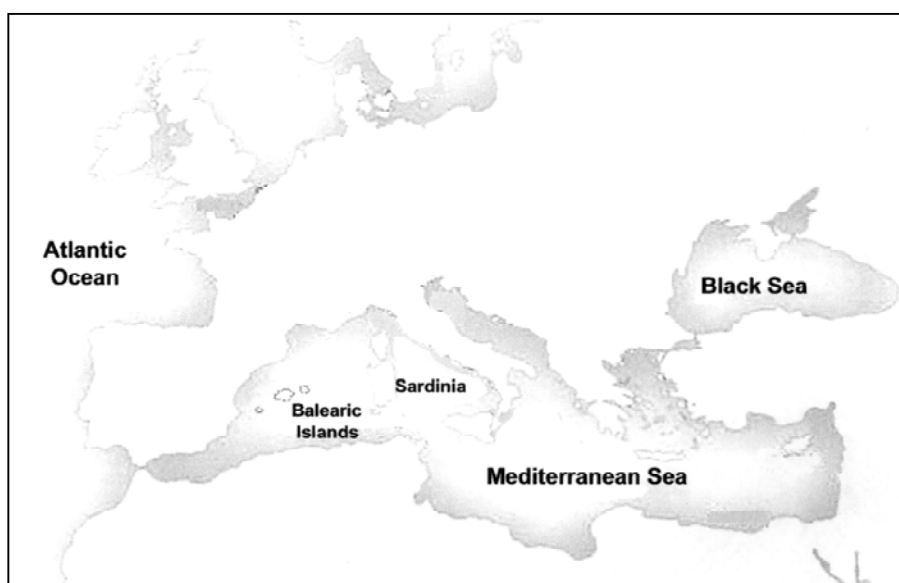

Fig. 1. Map of Mediterranean Sea with the position of the main islands bearing fossil bovids: Sardinia and Balearic Islands.
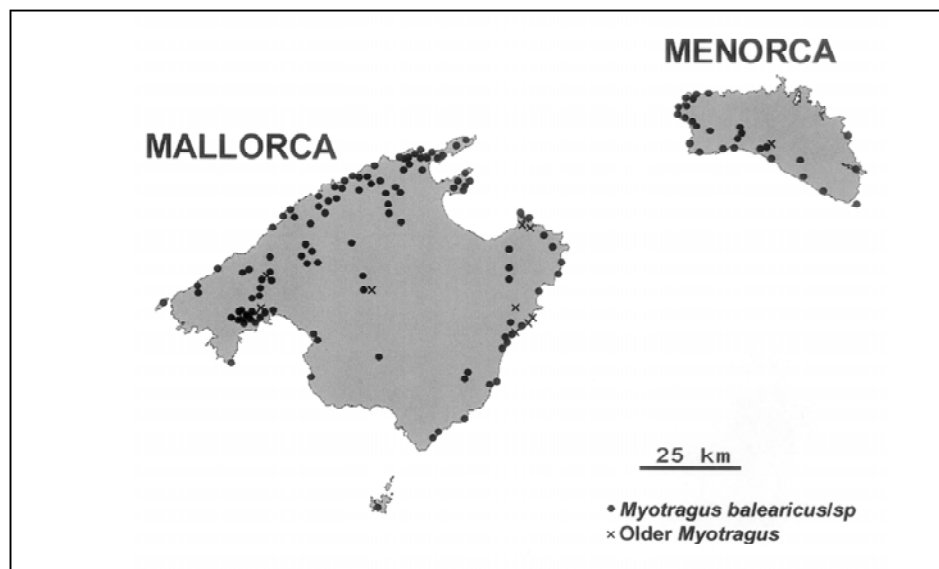
Fig. 2. Map of localities of *Myotragus* findings on Mallorca and Menorca (Balearic Islands).
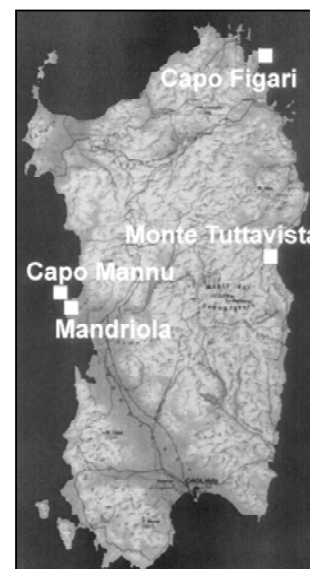

Fig. 3. Map of localities of
bovid findings on Sardinia.

dentition and body propotions. The orbits, in a shortened face, were small but located more frontally than those of recent bovids, allowing stereoscopic eyesight. The number of cheek-teeth was reduced with just one lower premolar (P_4) and two upper premolars (P^3 and P^4) in the adult stage (ANDREWS, 1915; ALCOVER *et*. *al*., 1981; BOVER & ALCOVER, 1999). The same pattern of reduction is found in the incisors, with just one ever-growing incisor in each jaw. The postcranial was also extremely modified: the leg bones were short and stout (BATE, 1909; ANDREWS, 1915; ALCOVER *et al*., 1981), distal tarsal bones were fused (ANDREWS, 1915; LEINDERS & SONDAAR, 1974) as were some carpal bones in a few individuals (BOVER, 2004). The metapodials were extraordinarily shortened (ANDREWS, 1915; ALCOVER *et al*., 1981). There was a great restriction in some joint movements (MOYY-SOLY, 1979; KÖHLER & MOYY-SOLY, 2001; BOVER, 2004) resulting in a perfect adaptation to economisation of energy and to slow and powerful locomotion on steep ground (SPOOR, 1988a, b; KÖHLER & MOYY-SOLY, 2001, 2004; BOVER, 2004).

Contrary to findings in *Myotragus*, in the Sardinian bovids the face was elongated, orbits were quite large and in a lateral position, no premolars were lost, incisors were not significantly modified, and the metapodial proportions did not differ greatly from those of continental caprines.

On the other hand, despite the variability in skull and mandible morphology of both Balearic and Sardinian species, the basic structure of the cranium supports the hypothesis that these bovids are closely related, probably sharing a common ancestral stock.

In this paper we explore the evolutionary pressures affecting the different evolution of the Plio-Pleistocene Mediterranean bovids in order to identify their putative causes. This paper points out preliminary results drawn from a Balearic – Sardinian bovids comparison, which allows us to explore the importance of the absence of terrestrial predators and the role of inter- and intra-specific competition as drivers of mammals' evolution in insular environments.

**BALEARIC AND SARDINIAN BOVIDS:
         AN OVERVIEW**

The Balearic bovids range in age from the Pliocene to the Holocene. It has been suggested that the two earliest species *M. pepgonellae* and *M. antiquus* should be included in a different genus, while *Myotragus* (*sensu stricto*) should be restricted to the upper Pliocene-Holocene species, *M. kopperi* (Fig. 5), *M. batei* (Fig. 6) and *M. balearicus* (BO-VER, 2004; BOVER & ALCOVER, in press). From Menorca *M. binigausensis* has also been reported (MOYY-SOLY & PONS-MOYY, 1980), although this species has recently been synonimized to *M. batei* (BOVER & ALCOVER, 2000).

Paleomagnetic data provide an age of about 2.6 Ma for *M. antiquus* found in layer J fo Cova de Canet (PONS-MOYY *et al*., 1979). No absolute datings are available for *M. pepgonellae*, but a chronology of Lower Pliocene has been proposed for the specimens beloning to this species (MOYY-SOLY & PONS-MOYY, 1982). *M. batei* has been considered as a Early Pleistocene species (Villafranchian; CRUSAFONT & ANGEL, 1966). More accurate dates are available for t h e more recent species, *M. balearicus*, which lived during the Late Pleistocene and became extinct somewhere inside the interval 3700-2040 cal BC, as indicated by ^{14}C data (RAMIS & ALCOVER, 2001; BOVER & ALCOVER, 2003; QUINTANA *et al*., 2003).

There is a general agreement in supposing that the continental ancestor of Balearic bovids possibly settled in Mallorca about 5.7-5.35 Ma B.P., during the Messinian fall

Fig. 4. *Myotragus balearicus*; dorsal (top) and lateral side (bottom). Scale bar 20 mm.

Fig. 5. *Myotragus kopperi*; dorsal (top) and lateral side (bottom). Scale bar 20 mm.

in sea level HSÜ *et al*., 1973, 1977; GAUTIER *et al*., 1994; KRIJGSMAN *et al*., 1999). After the Pliocene transgression (5.35 My) the Eastern Balearic Islands maintained a permanent insular condition and were inhabited by an unbalanced, heavily impoverished, and predator-free fauna composed of mammalian species belonging to a reduced number of lineages: a bovid (*Myotragus*), an insectivore of the *Nesiotites* genus, and a glirid of the genus *Hypnomys* in Mallorca (ALCOVER *et al*., 1981), and a glirid of the genus *Muscardinus* and a giant Leporidae only recorded on Menorca (AGUSTĘ *et al*., 1982; QUINTANA *et al*., 2004).

Under the peculiar ecological and new environmental conditions that characterized these medium-sized islands, Balearic bovids underwent important morphofunctional modifications and a reduction in size. The morphological and structural changes essentially affected dentition, sense organs and the locomotor system. In particular: modification of dentition such as the increase in hypsodoncy of incisors and molariforms and the reduction of the anterior cheek-teeth, increasing feeding efficacy on abrasive vegetation (ALCOVER *et al*., 1981; MOYY-SOLY & PONS-MOYY, 1982; BOVER & ALCOVER, 1999); the shift of the orbits from the typically lateral to the frontal position, improving perception of spatial depth (ALCOVER *et al*., 1981) and favouring movement on uneven ground; the reduction of the nasal cavity (BOVER & ALCOVER, 2000) and brain size (KÖHLER & MOYY-SOLY, 2004), reducing its metabolic expenses; and the very short metapodials and phalanges as well as the fusion of carpal and tarsal bones allowing *Myotragus* to reduce the energy costs of locomotion (e.g., KÖHLER & MOYY-SOLY, 2004; BOVER, 2004).

These modifications became more and more a c c e n t u a t e d from the earliest known species, *M. pepgonellae*, through the most advanced *M. balearicus*.

In Sardinia, bovids belonging to an endemic taxon have been recognised since the last century, when in 1911 DEHAUT established the new species *"Antilope (Nemorhaedus?)" melonii*, on an incomplete skull found in bone-breccia filling a karstic fissure at Capo Figari (North-Eastern Sardinia) (Fig. 7). During the first half of XXth century, FORSYTH MAJOR and Miss BATE collected other bovid specimens at Capo Figari, but it is doubtful as to whether such bones came from the same pocket which yielded the holotype or not. More recently, GLIOZZI & MALATESTA (1980) studied new-collected specimens and revised the material belonging to the BATE and MAJOR collections. The Italian palaeontologists established the genus *Nesogoral*, described as a small nemorhaedine (*sensu* GLIOZZI & MALATESTA, 1980), "...with almost straight horn-cores, extending backward on the same plane as the frontals, and very slightly diverging; dental formula 0I 0C 3P 3M upper and ?I ?C 3P 3M lower teeth; without lacrimal fossae; with a transversally arched palatine vault, steep maxillaries, high mandibles; and not notably shortened matapodials". After VAN DER MADE (1999), in bone breccias filling the karstic fissure called Capo Figari I, *Nesogoral* sp. was found to be present together with archaic small m a mmals, such as *T. figariensis* and *P. figaro*. An ESR age of about 1.807.500±20% years B.P. is valued on the basis of bovid tooth (MTOJI IKEYA, *fide* VAN DER MADE, 1999).

Bovid remains were also reported from deposits cropping out at the top of the Mandriola Formation (Capo

Fig. 6. *Myotragus batei*; dorsal (top) and lateral side (bottom). Scale bar 20 mm.

Fig. 7. *Nesogoral melonii*, (DEHAUT , 1911) holotype from Capo Figari (North-Eastern Sardinia). "Museo di Geologia e Paleontologia". Turin University. Photo by M. Paria. About at the natural size.

Mannu, Western-Central Sardi-nia, biozone MN 15, or to an earlier one, cfr. PE-CORINI *et al*., 1974; ANGELONE & KOTSAKIS, 2001; MELIS & PALOMBO, in prep.), and in the palaeosoils outcropping at the botoom of the Capo Mannu Pliocene Formation, where they occurred together with scanty remains of Leporidae and, probably, *Sus sondaari* (CARBONI & LECCA, 1995; VAN DER MADE, 1999; ABBAZZI *et al.,* 2004b). Scanty remains (one P_2, one M_1 and one distal end of tibia) ascribed to *Nesogoral* sp. were also reported by VAN DER MADE (1999) from the same locality.

Nesogoral species and indeterminate Bovidae have been also recorded from the karstic fissurae of Monte Tuttavista (Orosei, central Western Sardinia) (GINESU & CORDY, 1997; ARCA *et al*., 2000; SONDAAR, 2000; SONDAAR & VAN DER GEER, 2002), where in recent years more than 1500 bovid specimens have been collected from 6 fissures. A preliminary description of these bovids has been recently given by PALAMBO & VALLI (in ABBAZZI *et al*., 2004a). The preliminary analysis of the Monte Tuttavista bovids suggested that more than one taxon occurred in the same fossiliferous deposit. Moreover, the hypothesis that specimens from Capo Figari fissure fillings (specimens from DEHAUT, BATE, FORSYTH MAJOR and MALATESTA collection and new finding from Capo Figari 1, VAN DER MADE, 1999) actually belong to different taxa cannot be ruled out. Accordingly, the diagnosis given for *Nesogoral melonii* has to be reconsidered as well as the systematic attribution of all the Sardinian samples previously ascribed to the *Nesogoral* genus.

Due the fact that the Monte Tuttavista remains are mainly embedded in strongly cemented breccias, and that well preserved or complete postcranial bones are rare, PALOMBO & VALLI (in ABBAZZI *et al*., 2004a), in their preliminary analysis, took into consideration only cranial specimens.

Three different morphotypes have been described on the basis of shape and position of horn-cores, morphology of frontal bone, extension of pterygo-palatine fossa, wideness of the palate, arrangements of the tooth rows, development and shape of the palatine and premaxillary bones in front of the P^2, and position of the orbit sockets. Taking into account the description given by DEHAUT (1911) for *"Antilope (Nemo - rhaedus?)" melonii*, two of these morphotypes ("A" and "B") should be ascribed to *"Nesogoral"*(ABBAZZI *et al*., 2004a).

Morphotypes A and B can be definitely ascribed to the Caprinae (*sensu* GENTRY, 1992) on the basis of the occurrence of the frontal sinus as well as their horn and dental features (the upper molars present additional small cavities near the lingual edge of their occulsal surface, basal pillars between the lobes are absent, the M^3 metastyle have a large flange, and on the lower ones a transverse fold is present on the anterior part of the tooth).

Morphotype C (Bovidae gen. et sp. nov.) includes a single specimen, presumably belonging to a new genus,
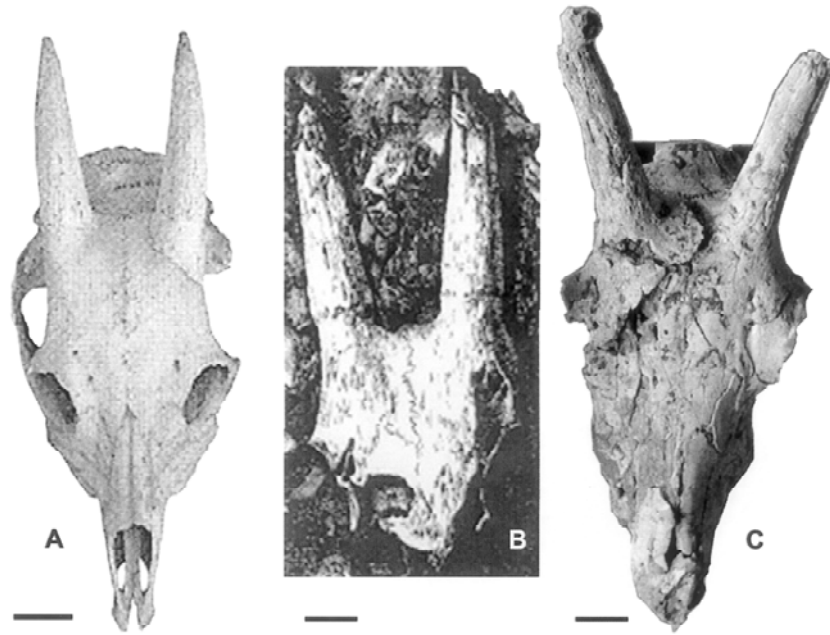
Fig. 8. Skull of insular bovids in dorsal side. A. *Myotragus balearicus*; B. *Nesogoral melonii*, holotype
(after DEHAUT, 1911, modified; C. *Nesogoral* morphotype A, from fossiliferous pocket "XI antilope",
Monte Tuttavista. Each scale bar is 2 cm.

characterised by a small size, stout horn-cores extending backward and jointed medially at their bases. It belongs to a bovid smaller than that previously described, and its peculiar morphology suggests that it represents a taxon distinct from all the Plio-Pleistocene bovid species already known in the Western Mediterranean (PALOMBO *et al*., in prep.).

The occurrence of different morphotypes were noted also for jaw, teeth (e.g., P_4 and M_3), long bones (e.g. distal epiphysis of humerus, olecranon, metapodials, etc.) and phalanges (PALOMBO, 2002a, b). Moreover, limb bones, especially metapodials and phalanges, show a combination of "Caprinae" and "non-Caprinae" features (such as slender metapodials, with more or less pronounced mediolateral compression of shaft, quite strong flanges on distal anterior surface, and elongated, mediolateral compressed first and second phalanges) (PALOMBO, 2002a, b).

DISCUSSION

The affinities and the differences between Balearic *Myotragus* and Sardinian *Nesogoral* genus have been noted since the first discoveries (e.g. ANDREWS, 1915; DEHAUT, 1920; JOLEAUD, 1926; VAUFREY, 1929) (Fig. 8). A major shared feature consists in the peculiar horn cores, straight, backwards directed, almost round in section, slightly divergent from the sagittal plane, and more or less parallel to the frontal surface. This trait is clearly displayed by the *Nesogoral melonii* holotype. However, among the skulls from Monte Tuttavista

fissurae, there is a specimen with slender, more divergent horn-cores (forming an angle of about 40°) and from Capo Figari there are some frontal fragments displaying this same horn core pattern. In *M. antiquus*, the horn-cores are roughly parallel. Moreover, as far as the horn-cores are concerned, in *Myotragus*, especially in *M. balearicus*, the horn-cores are inserted more backwards behind the orbits, especially in comparison to the skulls from Monte Tuttavista (morphotypes A and B). While in *M. pepgonellae* the orbits have a more lateral position, at least from *M. kopperi* the orbits are frontalized.

Other features shared by *Nesogoral* and the earliest known *Myotragus* species consist of the shape of the muzzle (in ventral and lateral view) and the shape of the occipital condyles. *Nesogoral* and the most advanced *Myotragus* species also share some characteristics that cannot be evaluated in *M. pepgonellae* and *M. antiquus*, such as the projection backwards of the saggital part of palatines and the relatively large size of the tympanic bullae and the auditory meatus. The most advanced *Myotragus* species displays more derived features. On the other hand, the neurocranium seems to have been less developed in *Myotragus balearicus* (KÖHLER & MOYY-SOLY, 2004) than in the Sardinian bovid. DECHASEAUX (1961) already noted differences in comparing encephala of *M. balearicus* and *Nesogoral* from Capo Figari which, in the author's opinion, were enough to exclude the identity of the two taxa.

Important differences between *Nesogoral* and *M. balearicus* concern the development of the facial region and muzzle (Fig. 8). They are cleary elongated and stout in Sar-

Fig. 9. *Nesogoral* sp.; metatarsals: A. & B. from the fossiliferous fissure "X ghiro", Monte Tuttavista; C. from the fossiliferous fissure "Cava X", Monte Tuttavista. Scale bar 5 cm.

dinian specimens (A and B morphotypes) and in *M. pepgonellae.* These features could be considered as archaic with respect to the apomorphic short, rather slender splacnocranium of *Myotragus balearicus*. The muzzle shortness might be related to some of the dentition traits, such as the reduction of the anterior teeth, and the increase in height of incisors and cheek teeth, probably related to increasingly abrasive vegetation. High masti catory efficiency was achieved by the Sardinian bovid by increasing hypsodonty and enlarging origin and insertion surfaces for masticatory muscles, as confirmed by the large origin of the masseteric muscle and unusually high, deep *angulur mandibulae*. Moreover, also in Sardinian specimens the occurrence of some reduced and perhaps non functional P_2 has been noted.

The propotion of long bones (especially metapodials) clearly makes bovids from the Eastern Balearic Islands different from the Sardinian ones. As has been pointed out by several authors (e.g. ALCOVER *et al*., 1981), probably after their first settlement, Balearic bovids reduced limblength by shortening metapodials and acquiring low-gear locomotion, a common adaptation in predator-free environments (SONDAAR, 1977).

The preliminary analysis of long bones found in Monte Tuttavista enables us to recognise differences in size, which

might be explained as sexual dimorphic features, and different morphologies (PALOMBO, 2002a, b), perhaps due to the occupancy of different niches. Either way, despite their morphological and dimensional variability, metapodials of Sardinian bovids were more or less elongated, sometimes also quite slender, with respect to continental caprines (Fig. 9). Moreover Sardinian bovids seem to have had long limbs as in animals whose behaviour requires speediness. Indeed, it is known that metatarsus/femur ratio and posterior limb length are correlated with running speed (e.g., GARLAND & JANIS, 1993; STEUDEL & BEATTIE, 1993). Moreover, longer limbs minimize energy consumption during running locomotion (see CHRISTIANSEN, 2002 and references therein). Accordingly, Balearic and Sardinian bovids minimized costs of locomotion by way of opposite limb proportion: *Myotragus* acquired a slow, powerful walking gait by reducing limb length through the marked shortness of metapodials and phalanges, and lack of shock-abasorbing mechanism in manus and pes (KÖHLER & MOYY-SOLY, 2004 and references therein). Its jumping and zigzag movements are largely constrained by the fusion of distal tarsal bones (LEINDERS & SONDAAR, 1974; SONDAAR, 1977; LEINDERS, 1979). In Sardinia, indeed, leg bones remained long, showing a more cursorial aptitude, with less modified limb morphology, and the distal tarsal b o n es remain unfused. Nevertheless, the preliminary (just indicative) values obtained for the femur/tibia and humerus/radius ratio in some *"Nesogoral"* specimens from Monte Tuttavista are similar to values calculated for *Myo - tragus balearicus* (Tab. 1).

To explore the causes of the morphofunctional traits exhibited by Balearic and Sardinian bovids, we have to analyse the e nvironmental conditions and the putative specific selection pressures affecting them. Changes in size of vertebrates once segregated in isolated geographic areas such as islands, and notably the dwarfism of large mammals, is a rather debated question. In the past decades, several authors have emphasized the role played by different factors to explain size changes in isolated areas: lack of selection pressure of large predators (e.g. THALER, 1973; SONDAAR, 1977; LOMOLINO, 1985), host-island surface (e.g. HEANEY, 1978; BURNESS *et al*., 2001), behavioural features or trophic requirements and metabolic rate (e.g., CASE, 1978; LAWLOR, 1982; BURNESS *et al*., 2001), genetic segregation and

TABLE 1

Ratio of the femur/tibia (F/T) and humerus/radius (H/R) for *Myotragus balearicus, Nesogoral* and selected Caprinae.
n=number of specimens.

SPECIES	F/T	n	H/R	n
Ovibos moschatus	112	1	101	2
Oreamnos americanus	95	1	103	1
Budorcas taxicolor	103	2	111	1
Capricornis crispus	87,5	1	103	0
Nemorhaedus goral	85	1	99,5	4
Capricornis sumatrensis	89	1	105	1
Myotragus balearicus	83,5	1	78,5	2
Nesogoral	85		75,3-87,0	

endogamy (MALATESTA, 1986), and also population density, overgrazing or overcrowding (e.g., THEODOROU, 1988; ROTH, 1990).

Actually, the Balearic Islands were characterised by a smaller area and a more limited carrying capacity than Sardinia and the environmental pressure must have been different in both territories. Nevertheless, the focal point to interpret the patterns of bovid evolution in Sardinia and Balearic Islands seems to have been the occurrence in Sardinia of a large carnivore, *Chasmaporthetes melei*, in an endemic insular faunal assemblage (ROOK *et al.*, 2004). Indeed, the unusual occurrence of large carnivores having a strictly carnivorous diet must have conditioned the structure of Sardinian Pliocene faunas and bovid evolution, while the opposite occurred in the free-carnivore Balearic environments.

Predator pressure is one of the most important factors affecting vigilance behaviours, locomotor patterns, and nervous system efficiency (see KÖHLER & MOYY-SOLY, 2004; BOVER, 2004, and references therein). It is worth noticing that *Myotragus* representatives acquired low-grear locomotion possibly just after their settlement on Balearic Islands, while the achievement of other modifications required more time.

Moreover, species diversity has been regarded related to the island area (MACARTHUR & WILSON, 1967). Small oceanic-like islands (sensu ALCOVER *et. al.*, 1998) are characterized by a reduction or absence of interspecific ecological competition, because of their low species diversity. Under such conditions (free-predator and competitor environments), some species can monopolise the resource supply of the island and their population dynamics must be regulated, at least partially, by intraspecific competition. This self-regulating population dynamics could have affected the *Myotragus* populations.

On the other hand, in Sardinia, more available niches were present, as well as some similar-sized competitors belonging to the same guild and a carnivore *(Chasmaportetes)*. All of this together suggests that the selection pressures must have been very different from those affecting the Eastern Balearic bovids.

The identification of a large-sized hyaena in the Sardinian *"Nesogoral* faunal complex" emerges as the evidence that enables us to clarify some key differences between evolutionary patterns in Balearic and Sardinian bovids: if some morphofunctional modifications exhibited by *Myotragus* are only possible in a carnivore-free environment, it is clear that the presence of a large predator acted as an evolutionary constraint, avoiding in Sardinian bovids any reduction of speed or vision system vigilance ability.

Besides, the more diversified environment of S a r d i n i a, as well as the presence of other large mammals, increased the interspecific competition in this island, forcing bovids to exploit different resources and to occupy different niches, perhaps even allowing a speciation process. *M y o t r a g u s*, on the contrary, exploited the supply of resources available for large herbivores on the Eastern Balearic Islands under a monopoly regime.

The strong morphological similarities shared by *Myotragus* (especially *M. pepgonellae*) and *Nesogoral* reinforce the claim of a close relationship. Probably both derived from the same ancestor stock, still unknown, which presumably spread to Sardinia and Mallorca during the Messinian. While the *Myotragus* lineage acquired a small size and underwent a highly peculiar evolution, no unquestionable evidence for a similar evolution has been obtained for the *Nesogoral* lineage.

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