

Estimating physical characteristics of neonate *Myotragus balearicus* (Artiodactyla, Caprinae)

Bover, P. & Alcover, J.A., 1999 - Estimating physical characteristics of neonate *Myotragus balearicus* (Artiodactyla, Caprinae) - in: Reumer, J.W.F. & De Vos, J. (eds.) - ELEPHANTS HAVE A SNORKEL! PAPERS IN HONOUR OF PAUL Y. SONDAAR - DEINSEA 7: 33-54 [ISSN 0923-9308]. Published 10 December 1999

Myotragus balearicus BATE, 1909 is a fossil dwarf bovid endemic to the Gymnesic Islands (Mallorca, Menorca and surrounding islets, Western Mediterranean Sea); it became extinct more than 4,000 years ago. Its neonate body dimensions have been studied comparing them with some extant neonate bovids. The small size of the adult specimens (shoulder height about 45-50 cm) is one of the most peculiar features displayed by *Myotragus balearicus*. From the identified neonate leg bones coming from three caves of Mallorca (Cova des Moro, Cova Estreta and Cova de Son Maiol) and one cave of Menorca (Cova C-2), an estimated shoulder height of 18 cm has been obtained for the Late Pleistocene neonate *Myotragus*. The difference in length of the bones of Pleistocene and Holocene *Myotragus*, being slightly more than 20 % shorter the latter, gives a shoulder height of 15 cm for Holocene neonates. The neonate *Myotragus* height was less than half the mother's shoulder height. This proportion differs substantially from the recorded ratio for the extant bovids. An estimated weight of 700-900 g for Late Pleistocene *Myotragus balearicus* neonates have been approached from similar body sized mammals. The small ratio (about 2%) between neonate and adult weight in *Myotragus balearicus* agrees with a suiform pattern, in a clear contrast to the typical ruminant pattern (where neonate weight is usually > 4%). Our estimate of the neonate size has been checked through the study of the dimensions of the birth canal in adult females.

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Keywords: *Myotragus balearicus*, neonate, body size, Balearic Islands, insular evolution, heterochrony.

INTRODUCTION

Information regarding the physical characteristics of neonate artiodactyls is scarce (e.g., Altman & Dittmer 1962, Eisenberg 1981, Verme 1985, Pöhlmeier 1985, Lochmiller *et al.* 1987, Braza *et al.* 1988, Saether & Gordon 1994). This lack of information is particularly acute for extinct artiodactyls. To our knowledge, the only available data on neonate extinct artiodactyls are the description of a few neonatal bones of *Megaceros cazioti* from Sardinia (Klein Hofmeijer 1996) and the description of two jaws of *Myotragus balearicus* (Waldren 1982, Bover & Alcover *in press*). There is no complete or general description of the neonate skeleton for any extinct artiodactyl.

The aim of this paper, written to commemorate the 65th birthday of Dr Paul Sondaar, is to present an approach to the physical characteristics of *Myotragus balearicus* BATE, 1909, at birth. This species is a very peculiar ruminant that lived in the Gymnesic Islands (Mallorca, Menorca, Cabrera and Sa Dragonera) until the arrival of humans (Alcover *et al.* 1981). *M. balearicus* displays a considerable amount of highly derived characters that have been interpreted as adaptations to the insular environments (Sondaar 1977, Alcover *et al.* 1981). Some knowledge about its general morphology comes from Andrews (1915), Adrover & Angel (1967) and Spoor (1988). It is one of the smallest

known Caprinae, at least in terms of body height. According to recent reconstruction, it reached approximately 45-50 cm at the shoulder in adult specimens (A in Table 1) (Quetglas & Bover, in press). However, we have obtained one skeleton, coming from the late Pleistocene of Cova des Moro, and belonging to an adult specimen, that reaches only about 22 cm of shoulder height. Other body size estimates were obtained by Andrews (1915) from the skeleton at the Natural History Museum of London and by Moyà-Solà (pers. comm.) from the skeleton at the Museu de Paleontologia 'M. Crusafont' of Sabadell (B and C, Table 1). The adult weight, as estimated by different authors, varies between 6 kg (minimum estimate provided by Waldren 1982) and 60 kg (maximum estimate provided by Köhler 1993) or even 70 kg (Alcover *et al.* in press). The minimum adult weight estimation of Waldren (1982) can be rejected, because it is clearly unfeasible. Spoor (1988) calculated that the weight of adults was between 30 and 40 kg for specimens of Würmian age (last ice age), whereas the Holocene specimens weighed between 20 and 30 kg. Alcover *et al.* (in press), from the length and diameter of long bones (Scott 1983), assign a weight to adult specimens of *Myotragus balearicus* (from different geological periods) between 13 and 20 kg for the smallest adult specimen known and between 50 and 70 kg for the normal sized late Pleistocene specimens.

METHODS

A research protocol has been developed to establish the general physiognomy of neonate *Myotragus balearicus*. Firstly, we studied neonate skeletons of several caprines (see the chapter of comparison material). We used the work by Benzie (1950), Smith (1956), Ratjová (1971, 1972a and b, 1973), Ratjová & Popesko (1971) and Pöhlmeier (1985), together with the direct study of neonate and juvenile bones of chamois, sheep, goats and mountain goats. The papers by Smith (1956) and Pöhlmeier (1985) allow us to establish

an upper size limit for the bones possibly belonging to neonates. It also allows to estimate the maximum age of bones whose ossification centres have not yet experienced their sequential fusions. The papers by Benzie (1950), Ratjová (1971, 1972a and b, 1973) and Ratjová & Popesko (1971) allow to establish a lower size limit for bones susceptible to belonging to neonates and to identify foetal bones. Thus, as a first approach we can establish a range of morphologies and sizes embracing the neonate condition, but including also some developed foetal bones as well as some up to 3-8 months old. We identified all the *Myotragus balearicus* bones that fall within this range. However, these criteria are rather inaccurate, so additional diagnostic characters of the neonate condition must be established for each bone.

Diagnostic characters, unrelated to size, of bone development at the time of birth have been identified through the comparison of material from living neonate ruminants (e.g., the bones of the neonate sheep illustrated at Figure 1). These characters are unrelated to size and were checked for each particular bone in all the comparison material, identifying the shared characters to all available neonate artiodactyls. To diagnose the *Myotragus balearicus* neonate bones, we

Table 1. Measurements (in cm) of *Myotragus balearicus* mounted skeletons: **A** - mounted skeleton from Cova Estreta, Mallorca (Quetglas & Bover in press); **B** - mounted skeleton in the exhibition of the Natural History Museum, London (Andrews 1915); **C** - mounted skeleton in the exhibition of the Museu de Paleontologia 'M. Crusafont', Sabadell (data from Moyà-Solà, pers.comm.).

	A	B	C
Greatest length	83.0	88.0	87
Shoulder height	47.5	49.0	50
Height to top of horns	49.9	63.0	59
Height to top of scapula	42.0	44.5	47
Height to top of pelvis	37.2	43.0	49

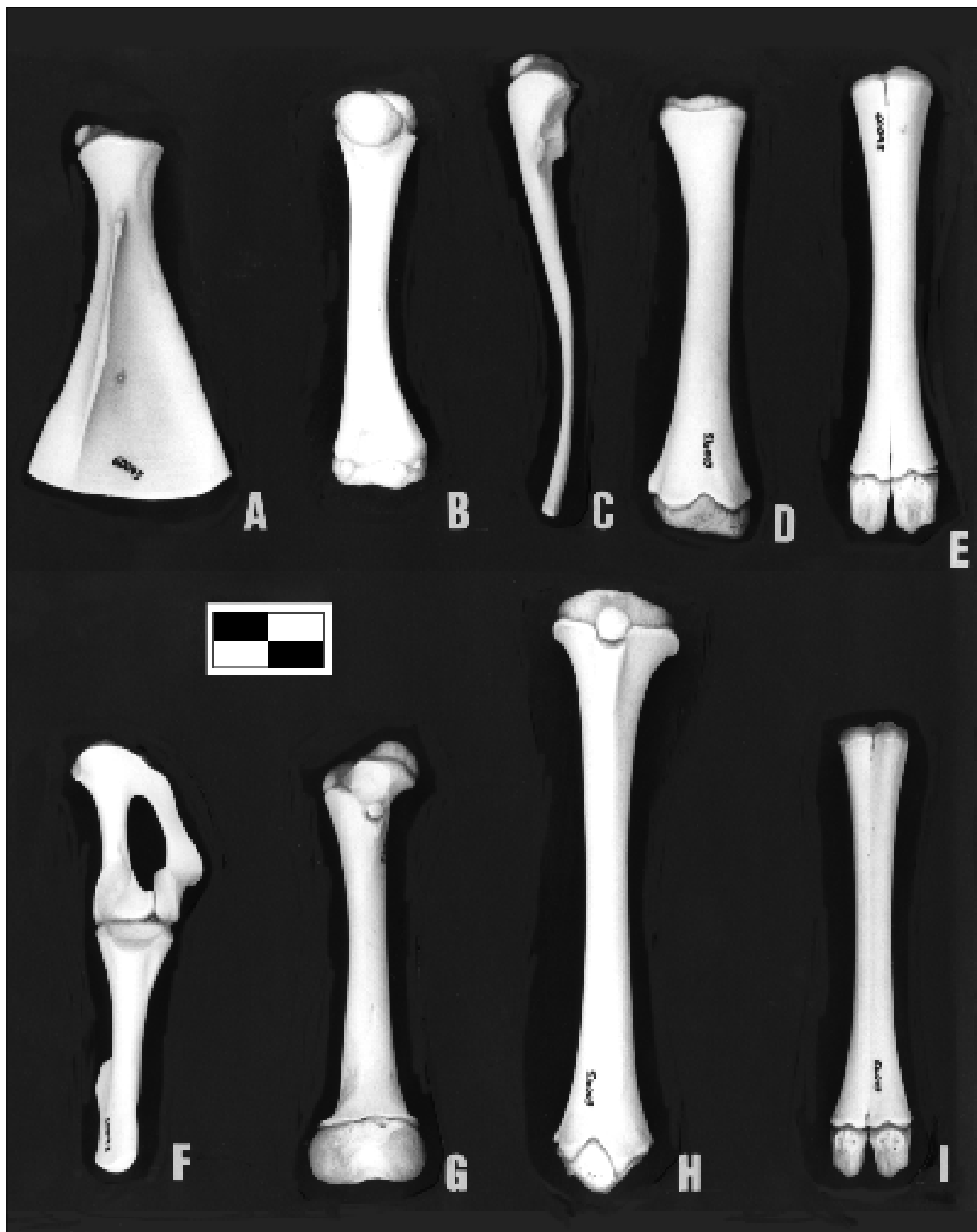


Figure 1 Neonate bones of *Ovis aries* MNIB 60093. The different ossification centres are clearly visible. **A:** Scapula, with two conspicuous ossification centres. **B:** Humerus, with six ossification centres. **C:** Ulna, with two conspicuous ossification centres, being the *processus styloideus ulnae* still cartilaginous (absent in the picture). **D:** Radius, with three ossification centres. **E:** Metacarpal os canon, with three ossification centres. **F:** Pelvis, with three ossification centres. **G:** Femur, with five ossification centres. **H:** Tibia, with four ossification centres. **I:** Metatarsal os canon, with three ossification centres. Scale: 20 mm.

used only those shared features that characterise the neonate stage in all the living species studied. We also used as comparative material the skeletons of 2-4 months old goats *Capra hircus* and mountain goats *Oreamnos americanus*. These skeletons allowed the establishment of an accurate limit for bone development. All bones of *Myotragus balearicus* displaying a more advanced stage of development than these 2-4 months aged skeletons were immediately deleted from the pool of possible neonates.

In a second stage, we carried out a detailed survey of the *Myotragus balearicus* bones exhibiting features characteristic of living neonate artiodactyls. We studied all the bones coming from the following sites: Cova Estreta, Cova des Moro, and Cova de Son Maiol in Mallorca, and Cova C-2 in Menorca. As no assembled neonate skeleton of *Myotragus balearicus* has been discovered until now, the diagnostic characters had to be checked for each bone. The heterochronic processes involved in *Myotragus* evolution (Bover & Alcover in press) introduce some uncertainties in our methods. In order to circumvent this source of error, fitting the articulations of anatomically adjacent bones tested the estimated age for each bone. In this way, a reasonable identification of the birth state was reached for long bones. The identi-

fied neonate long bones of *Myotragus balearicus* (see Appendix) have been individually measured (Fig. 4, Table 5). Later, we put these identified neonate bones in their anatomical upright resting position. The results of this procedure were used to estimate the live body parameters of neonate *Myotragus balearicus*. A complementary approach consisted in the identification of juvenile bones belonging to specimens several months old. The identification of these bones also contributed to establish an upper size limit for the bones of neonate specimens.

Finally, we checked the identification of the neonate bones using two external approaches. Firstly, we studied the pelvis size and shape in the adult *Myotragus balearicus* females. The foetus must pass through the pelvic cavity to become a neonate. In consequence, the size of the pelvic birth canal must be related to the maximum possible size for the foetus to be a neonate. Secondly, we estimated the position relative to the ground of the *Myotragus* udder. If juveniles sucked in an upright position, as is usual in bovids, their shoulder height must have been high enough to allow the mouth to reach the mammary glands. This second external approach is admittedly weak, and has been considered only as a rough estimate.

Table 2 Cranial measurements of recent caprine neonates (in mm).

Species	Condilobasal length	Skull height	Braincase width	Zygomatic width
<i>Ovis aries</i> MNIB 60093	110.9	46.6	52.6	55.4
<i>Ovis aries</i> MNIB 60094	117.1	46.8	53.5	60.7
<i>Ovis aries</i> MNIB 60097	108.3	48.3	53.6	59.6
<i>Capra hircus</i> MNIB 60088	93.0	45.4	51.5	50.7
<i>Capra hircus</i> MNIB 60089			52.9	55.8
<i>Capra hircus</i> MNIB 60090			56.6	55.5
<i>Rupicapra pyrenaica</i> MNIB 60091	90.1	44.6	47.6	48.1

MATERIAL

The studied *Myotragus balearicus* materials come from three caves of Mallorca [Cova Estreta and Cova des Moro (Late Pleistocene and Holocene) and Cova de Son Maiol (Late Pleistocene)] and one in Menorca [Cova C-2 (Late Pleistocene)]. After the first selection of juvenile bones (without fused epiphyses for the long bones, without teeth wear for dentaries, and without horn development in skulls), only a few of them have been identified as belonging to neonates. The list of identified neonate bones is presented in the Appendix. The acronyms of the collections where the materials studied at this work are curated, are as following:

AMNH	American Museum of Natural History
MNIB	Museu de la Naturalesa de les Illes Balears.

COMPARATIVE MATERIAL

Ovis aries (2 complete neonate skeletons, 0-2 days, MNIB 60093, 60094, 1 neonate skull and dentaries, 2 days, MNIB 60097), *Capra hircus* (3 incomplete skeletons of neonates probably belonging to the same unfeasible birth, MNIB 60088 - 60090; 1 incomplete skeleton aged 2-3 months old, MNIB 60096), *Rupicapra pyrenaica* (2 advanced foetal skeletons, MNIB 60091 - 60092), *Oreamnos americanus* (AMNH 128107, 1 skeleton aged 3-4 months old).

ESTABLISHMENT OF BONE STAGE DEVELOPMENT AT THE BIRTH

Jaw

At birth all the dissected fresh specimens of neonate artiodactyls present the teeth unerupted. Deciduous molars and incisors are both osteologically erupted (i.e., the teeth have emerged from bone), but actually they are not physiologically erupted, because they still remain under an epithelium layer.

Consequently, the neonate cheek teeth and incisors are completely unworn. The fresh eruption of the teeth occurs during the first

days after birth. It is only after this eruption when the teeth wear starts. For fossil specimens, tooth eruption refers always to teeth, which have emerged from bone, because the physiological definition is not useful. The unworn condition of the osteologically erupted cheek teeth and incisors is probably the best criterion to establish the birth age condition for a fossil jaw.

Bover & Alcover (in press, figure 3) identified a *Myotragus balearicus* jaw (MNIB 39318) that is considered to represent either the end of the foetal stage or a neonate. It has two incisiform teeth, the first one being wide and hypsodont, almost non-emerged, and the second one is smaller and is located at the back and above the former. The specimen has jugal teeth characteristic of dentary cheek teeth stage 1 of Bover & Alcover (in press), i.e., only dp3 and dp4 erupted (Fig. 6A). The mandibular length of this specimen is 53.1 mm. Waldren (1982) illustrated another specimen (SM-MO2-E-400) showing roughly the same dental development (with two incisiform teeth and dp3 and dp4). This specimen too can be considered to represent either the end of the foetal development or a neonate. Currently, this specimen is not in the paleontological collection of the Museu de Deia and it has not been available for this study. From the photograph presented by Waldren (1982), its estimated mandibular length is 47.6 mm. It is important to consider here that both dentaries are from the Late Pleistocene, therefore predating the Holocene period. The specimen from Cova de Moleta comes from a level with an estimate age of 23,400 yBP (Waldren 1982). The specimen of Cova de Son Maiol belongs to a population whose estimate geological age precedes the resolution power of the C14 method (P.Y. Sondaar, pers. comm.). The specimens of these populations are significantly at least 20 % bigger in size, in linear measurements, than those from the Holocene populations (Hamilton 1984, Marcus 1998).

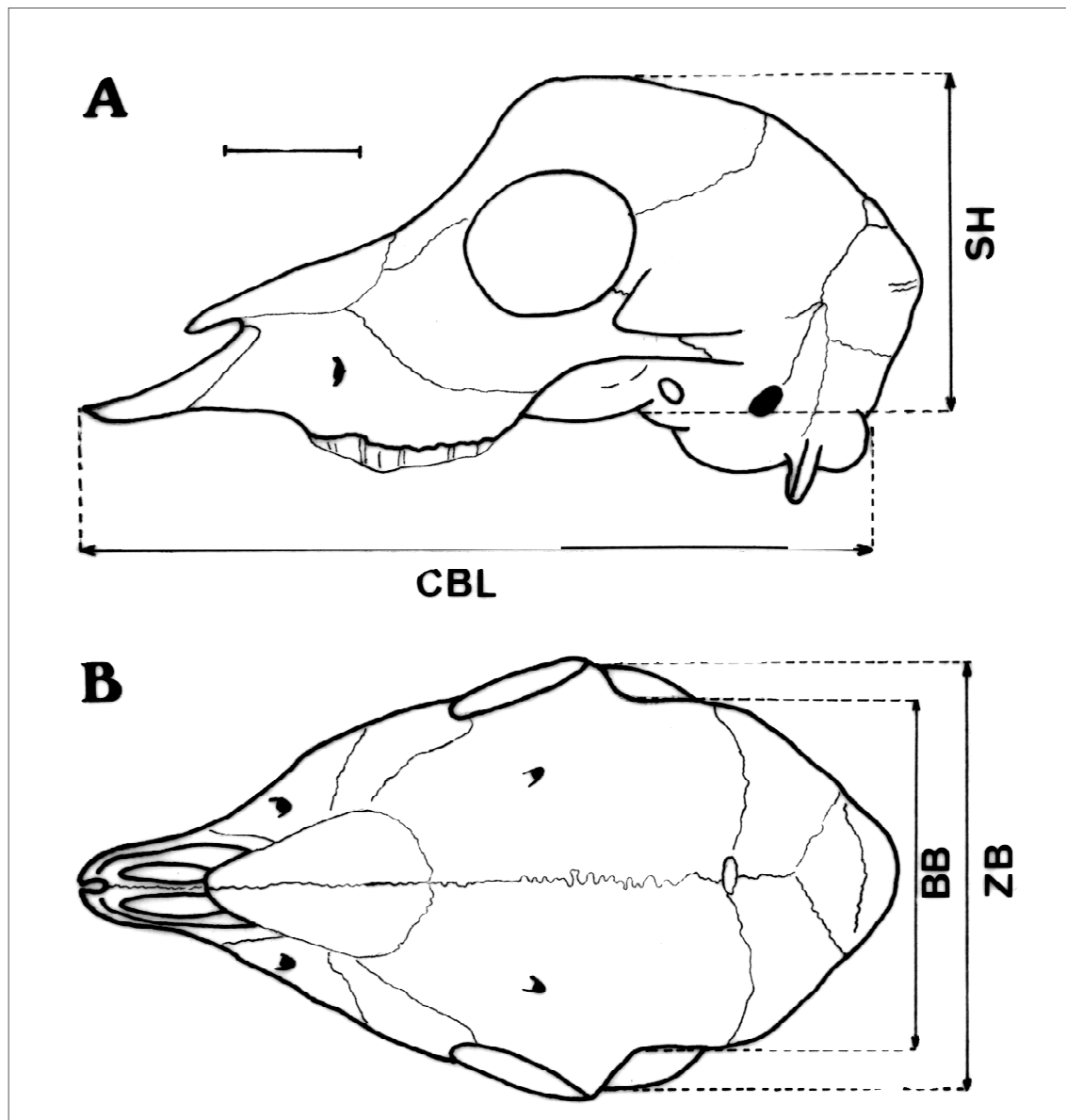


Figure 2 Neonate skull of *Ovis aries* MNIB 60093. **A** Lateral view. **B** Dorsal view. **CBL** Condilobasal length. **SH** Skull height. **BB** Braincase width. **ZB** Zygomatic width. Scale: 20 mm.

Skull

At the birth stage, all the artiodactyls considered lack horn cores on the skull. Even the neonate males of species with only horned males do not have any bone structure preceding adult horn cores. Neonate male sheep, goats or chamoises are absolutely hornless. The skull structure in neonate artiodactyls shows some clear morphological patterns.

The braincase is always very round (see Figure 2). The measurements of the neonate skulls (Table 2), allow us to calculate that the height of the skull is about 45 % of the condylobasal length (range: 50 % in *Rupicapra pyrenaica* to 42 % in *Ovis aries*) and 89 % of the width of the braincase (range: 93 % in *Rupicapra pyrenaica* to 87 % in *Ovis aries*). No complete neonate skulls of *Myotragus*

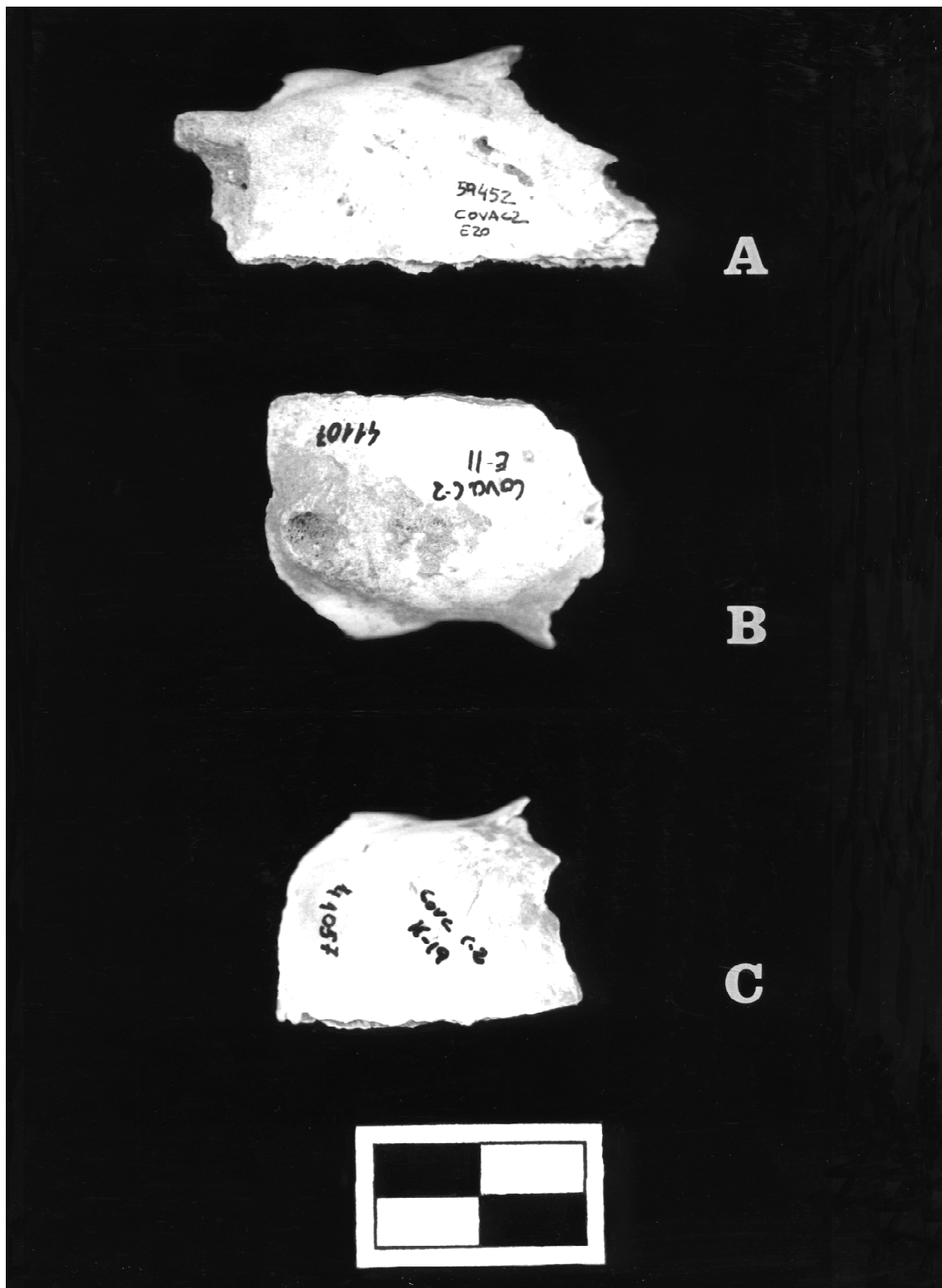


Figure 3 *Myotragus balearicus* frontal bones in frontal view. Right, distal part; left, proximal part. **A** MNIB 59452, a several months old specimen. **B** MNIB 41107, neonate specimen. **C** MNIB 41057, neonate specimen. Scale: 20 mm.

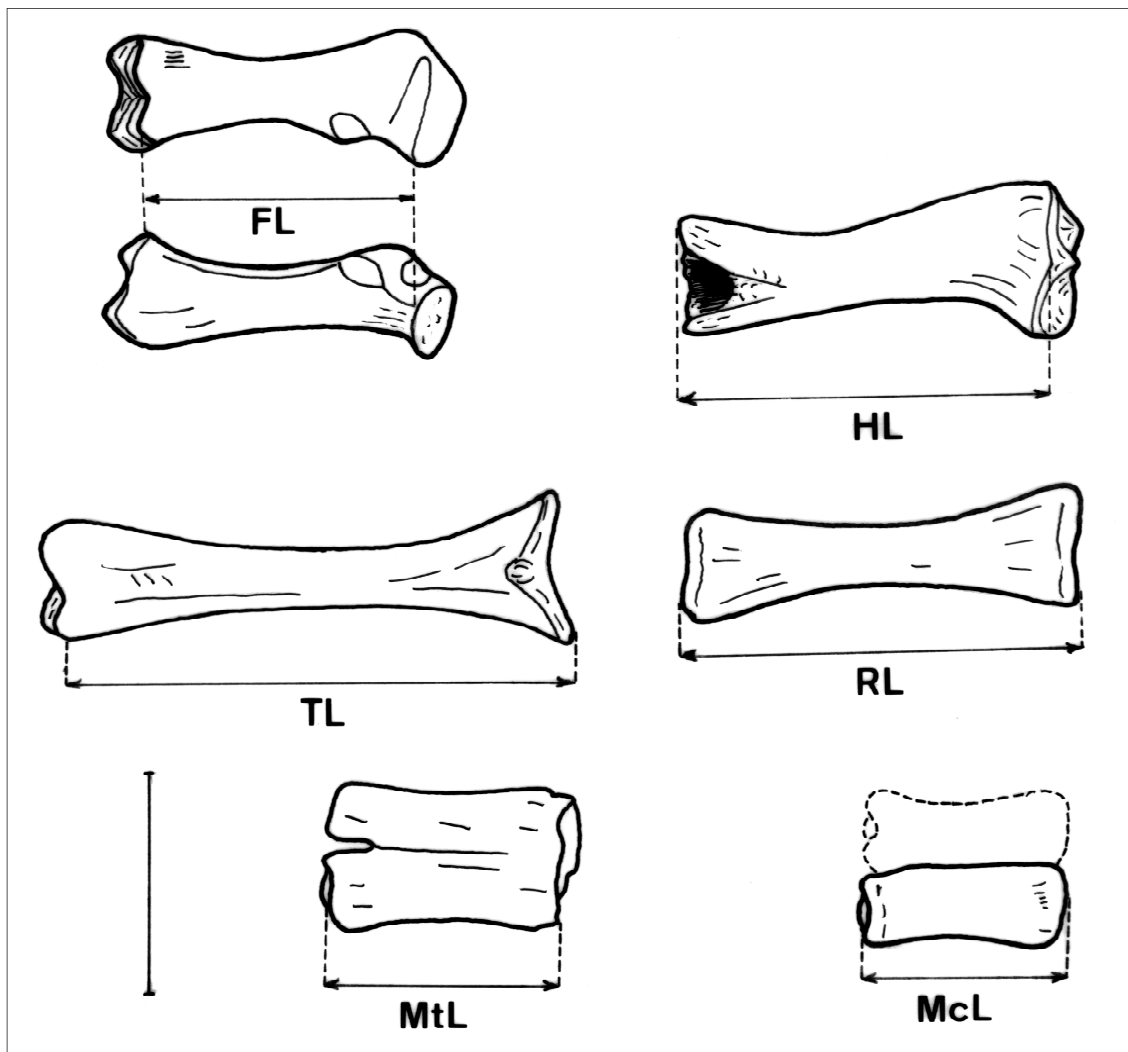


Figure 4 Long bone measurements of neonate *Myotragus balearicus*. **HL** Humerus length. **RL** Radius length. **McL** Metacarpal length. **F** Femur length. **T** Tibia length. **MtL** Metatarsal length. Scale: 20 mm.

balearicus are known, as expected from the unfused condition of the skull bones in other neonate artiodactyls. The preservation of the skull bones of neonates is highly unlikely. The bones are very fragile, as are those from young *Myotragus* specimens. Only in recent excavations the juvenile bones of the skull have been collected and identified. We identified only two frontal bones that can belong to neonates (MNIB 41057, 41107; Fig. 3). Both lack horn structures. Assuming that the relation between the width of the frontals and the zygomatic width is similar to that of the neonate skulls

available (Frontal width / Zygomatic width x 100 = 95), from these specimens (coming both from Cova C-2) we can establish that in Late Pleistocene neonate *Myotragus balearicus* the zygomatic width was about 41.0 mm.

There is a small sample of frontals with very small horn cores (e.g., specimen MNIB 59452, Fig. 3). They are attributed to very young *Myotragus balearicus*, some months aged, and not to neonates. These specimens are useful for establishing an upper size limit for neonates.

Humerus

Pöhlmeier (1985) established that in *Dama dama* at birth the humerus consists of six ossification centres. The same applies to *Ovis aries* (Smith 1956, see also our Figure 1), to *Capra hircus* (Dhingra & Tyagi 1970), to *Bos taurus* (Sisson & Grossman 1982) and so probably this is the rule for bovids. The main ossification centre is the *corpus humeri* (diaphysis). There are also two proximal centres, the *caput humerus* and the *tuberculum majus*, and three distal centres, the *condylus humeri*, and two epicondyles. The *epicondylus lateralis* and the *condylus humeri* are fused to the diaphysis at 4 months in *Dama dama*. Until 18 months in the *Dama dama*, and 4-11 months in *Ovis aries* and 6-11 months in *Capra hircus* there is no fusion between the diaphysis and the distal condyles. Humeri without fused *epicondylus lateralis* and *condylus humeri* are assumed to be of individuals aged less than 11 months (the maximum age for a such fusion in *Ovis aries* and *Capra hircus*). At least 51 (33 right, 18 left) specimens from the studied material belong to this category. Consequently, this criterion is not actually very accurate to establish neonatal character.

After the study of all the available neonates of the comparison material, we can establish a new criterion. In all the neonates studied, the proximal and distal surfaces of the diaphysis present a characteristic shape. Proximal surface consists of two concavities. The surface of these concavities is smooth (not wrinkled) and it contains a lot of irregularly disposed porosities with a diameter of over 100 µm. These porosities are visible on the proximal and distal surfaces of the diaphysis of all the neonate long bones (see SEM image in Figure 5A), but they disappear after some bone growth. A specimen of

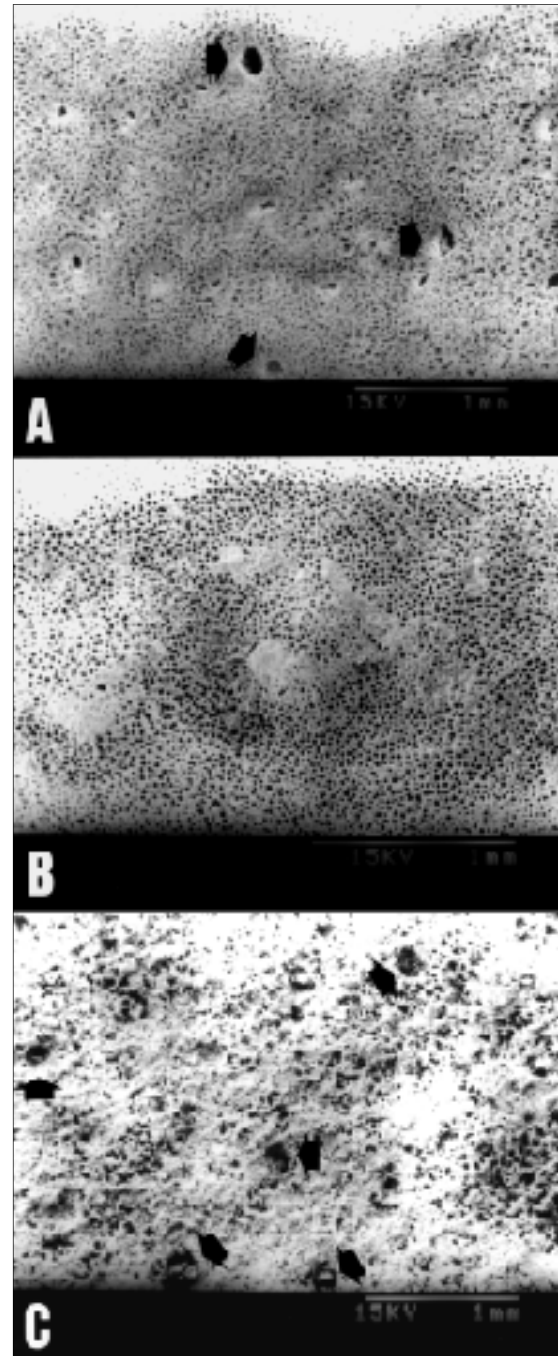


Figure 5 **A** SEM image of the proximal surface of the tibia diaphysis of a neonate *Ovis aries*, MNIB 60093. White arrows indicate the large porosities (diameter over 100 µm) observed in neonate bones. **B** SEM image of the proximal surface of the tibia diaphysis of a 3 month old *Capra hircus*, MNIB 60096. The large porosities are inconspicuous. **C** SEM image of the proximal surface of the radius diaphysis of neonate *Myotragus balearicus*, MNIB 41113. Arrows indicate the large porosities observed in neonate bones.

Capra hircus with an estimated age of about 2-3 months (MNIB 60096) presents these surfaces very wrinkled, without such porosities (see SEM image in Figure 5B). The specimen of *Oreamnos americanus* AMNH 128107, with an estimated age of 3-4 months, has the surfaces of the proximal and distal ends of the epiphysis displaying an intermediate pattern: they conserve on several points the smooth porosal surface combined with other points with a wrinkled surface without porosities. The significance of these porosities is unknown for us. Probably it is related with the important early growth of the bones of the juvenile bovids, with a very quick osteogenesis.

Radius

There are three ossification centres in the radius (Fig. 1). The main one is the *corpus radii* (diaphysis). The other two are the *caput radii* and the *trochlea radii*. Until 6-7 months in *Dama dama* there is no fusion between the *caput radii* and the diaphysis (Pöhlmeier 1985). In *Ovis aries* the fusion between the *caput radii* and the diaphysis start over 4 months (Smith 1956). For a more accurate diagnosis of the neonate bones, we used the same criterion as in humeral distal and proximal diaphysis surfaces. Both surfaces are smooth and with characteristic porosities in all the neonate specimens. By contrast, the *Capra hircus* MNIB 60096 presents both surfaces highly wrinkled. In *Oreamnos americanus* AMNH 128107 these surfaces are shaped similarly as those in MNIB 60096.

Ulna

Like in radius, there are three ossification centres in the ulna in *Dama dama* (Pöhlmeier 1985) and in *Ovis aries* (Fig. 1). The main one is the *corpus ulnae* (diaphysis). The other two correspond to the *tuber olecrani* and the *processus styloideus ulnae*. The fusion between the different parts of the ulna is delayed in comparison to the fusions recorded in the radius. The *tuber olecrani* and the diaphysis remain unfused until an age of 22

months in *Dama dama* (Pöhlmeier 1985) and 21 months in *Ovis aries* (Smith 1956). In *Capra hircus*, after Dhingra & Tyagi (1970), the ulna has only two centres of ossification at the birth, one for the olecranon and *corpus ulnae*, and the other one for the *tuberis olecrani*, being the *caput ulnae* still cartilaginous in the one-day old kid. The best diagnostic criterion for neonate ulna consists in its size concordance with the neonate radius. The neonate ulna is a very fragile bone. We have very few specimens of ulna that might belong to very young *Myotragus* according to the Pöhlmeier (1985) criteria. Nevertheless, their size is too big to correspond to the neonate radius, and consequently, their belonging to neonates can be excluded.

Metacarpal os canon

The metacarpal os canon comes from the fusion of metacarpals III and IV. This fusion generally occurs at the end of the foetal stage, but there are cases in which both metacarpals remain unfused at the birth (e.g., *Capra hircus*, MNIB 60088/89/90). The *caput metacarpale (epiphysis distalis)* remains unfused to the body of the bone until 24 months in *Dama dama*, 15-36 months in *Ovis aries* and 30-36 months in *Capra hircus* (Smith 1956, Pöhlmeier 1985). Consequently, this fusion cannot be considered as a good criterion for ageing neonate bones. We consider as neonate bones those metacarpal os canon with a proximal breadth similar to the distal breadth of the radius.

Scapula

Ontogenetically, the scapula originates from the fusion of three centres, the body of the scapula, the *tuberculum supraglenoideus* and the *processus coracoideus*. The latter two become fused first, but we have no data on the timing of this fusion. The literature about this first fusion is unclear (e.g., Smith 1956, Dhingra & Tyagi 1970, Pöhlmeier 1985). In our material (Fig. 1), we only recorded two ossification centres, the body of the scapula, and another one probably representing the

fusion of the *tuberculum supraglenoideus* and *processus coracoideus*. The fusion of the *tuberculum supraglenoidale* / *processus coracoideus* with the body of scapula occurs at an age of 15 months in *Dama dama*, 4,5-9 months in *Ovis aries*, 11 months in *Capra hircus* (Smith 1956, Pöhlmeier 1985), and 7-10 months in *Bos taurus* (Sisson & Grossman 1982).

First phalanx (fo re limb)

In *Ovis aries* this bone has only a proximal epiphysis which is fused before 10 months (Smith 1956).

Second phalanx (fo re limb)

In *Ovis aries* this bone has only a proximal epiphysis which is fused before 8 months (Smith 1956).

Femur

Smith (1956), Dhingra & Tyagi (1970) and Pöhlmeier (1985) established that at the birth the femur consists of five ossification centres (Fig. 1). The main one is the *corpus femoris* (diaphysis). There are also three proximal centres, the *trochanter major*, the *caput femoris* and the *trochanter minor*, and one distal centre, the distal epiphysis (coming from the intrauterine fusion of *condylus medialis* and *condylus lateralis*). During the growth, all the minor ossification centres are fused to the diaphysis. The fusions occur in a relatively advanced age. The *trochanter major* and the diaphysis are fused at 18-24 months in *Dama dama*, 11-19 months in *Ovis aries* and 36 months in *Capra hircus* (Pöhlmeier 1985) and in *Bos taurus* (Sisson & Grossman 1994). Like in the humerus, these criteria are not very accurate for the diagnosis of neonate femora. We used also the criterion of the shape and porosity of the proximal and distal surfaces of the *corpus femoris*. This criterion applies to all the neonate femurs of the recent comparative material we have, and it is not present in the 2-3 months old specimen MNIB 60096 of *Capra hircus*. The proximal and distal surfaces of the *Oreamnos america* -

nus AMNH 128107 aged 3-4 months display an intermediate condition.

Tibia

There are four ossification centres in the tibia (Fig. 1). The main one is the *corpus tibiae* (diaphysis). The other are the proximal epiphysis, the *tuberositas tibiae* and the *cochlea tibiae*. The fusion of these centres to the diaphysis occurs in an advanced age. The *cochlea tibiae* and the diaphysis are fused at 18 months in *Dama dama*, 15-16 months in *Ovis aries* and about 24 months in *Capra hircus* (Smith 1956, Pöhlmeier 1985). Like in the other long bones, these criteria are not very accurate for the diagnosis of neonate tibias. We used also the criterion of the shape and porosity of the proximal and distal surfaces. This criterion applies to the entire neonate tibia we have (Fig. 5A), and it is not present in the 2-3 months old specimen MNIB 60096 of *Capra hircus* (Fig. 5B). The proximal and distal surfaces of the *Oreamnos americanus* AMNH 128107 aged 3-4 months display an intermediate condition.

Also, at birth the length of the *corpus femoris* are, respectively, in *Rupicapra*, *Ovis* and *Capra* about 74.9 % (n = 1), 68.5 % (n = 2) and 72.7 % (n = 3) of the *corpus tibiae* length. As the adult ratio between the lengths of femur and tibia are 83 % in *Myotragus*, as compared to a ratio of 80 % in *Rupicapra* (n = 2), 83 % in *Capra* (n = 1), 84 % in *Nemorhaedus* (n = 1) and 86 % in *Ovis* (n = 4), we must expect that in neonate *Myotragus* the femur length must be about 73 % of the tibia length. The specimens identified as neonates on the basis of the shape and porosity of the epiphysarian surfaces are not in agreement with this prediction, but they are smaller (about 64 % in specimens coming from the same deposit, Cova C-2). Probably these figures indicate some peculiarities in the development of *Myotragus*.

Metatarsal os canon

The metatarsal os canon comes from the

Table 3 Adult and neonate body mass in selected artiodactyls. Sources: (1): Shaeter & Gordon (1994); (2): Eisenberg (1981); (3): Verme (1985); (4): Bover & Alcover, this paper. Shaeter & Gordon (1994) use the adult weight of the female, while data from Eisenberg (1981) do not specify the adult's sex. All the weights are in grams.

Species	Adult body mass (A)	Neonate mass (B)	A/B $\pm 10\%$	Source
Suiformes				
<i>Potamochoerus porcus</i>	35,600	960	3.68	(1)
<i>Sus scrofa</i>	147,000	2,300	1.6	(1)
<i>Microstictus anthracinus</i>	40,600	730	1.3	(1)
<i>Hippopotamus amphibius</i>	1415,000	42,500	3.0	(1)
<i>Moschus moschiferus</i>	372,000	4,900	1.8	(2)
Tylacina				
<i>Macropus macrurus</i>	42,000	5,000	13.2	(1)
Ruminantia				
<i>Tropus javanicus</i>	5,100	370	11.2	(1)
<i>Tropus tigris</i>	5,000	370	7.3	(2)
<i>Moschus moschiferus</i>	14,000	1,260	9.0	(1)
<i>Moschus moschiferus</i>	14,000	1,000	8.2	(1)
<i>Dama dama</i>	39,000	4,000	11.8	(1)
<i>Axis axis</i>	31,000	4,000	7.3	(1)
<i>Cervus canadensis</i>	210,000	16,400	7.1	(1)
<i>Cervus elaphus</i>	142,000	6,500	6.0	(1)
<i>Cervus elaphus</i>	71,000	4,900	6.7	(1)
<i>Cervus tigris</i>	81,000	3,200	4.2	(1)
<i>Cervus tigris</i>	171,000	9,400	5.5	(1)
<i>Elaphurus davidianus</i>	14,000	11,300	7.9	(1)
<i>Odocoileus hemionus</i>	51,000	3,400	6.3	(1)
<i>Odocoileus virginianus</i>	60,000	3,750	6.3	(3)
<i>Moschus moschiferus</i>	21,000	950	2.4	(1)
<i>Moschus moschiferus</i>	17,000	1,100	7.6	(1)
<i>Pudu pudu</i>	5,000	400	6.8	(2)
<i>Pudu pudu</i>	8,000	500	6.2	(1)
<i>Alces alces</i>	150,000	4,100	12.4	(1)
<i>Rangifer tarandus</i>	96,000	4,950	5.0	(1)
<i>Capreolus capreolus</i>	22,000	1,450	6.0	(1)
<i>Oreamya canadensis</i>	830,000	93,000	10.9	(1)
<i>Antilocapra americana</i>	4,000	2,800	6.8	(1)
<i>Tragelaphus oryx</i>	48,000	6,500	13.1	(1)
<i>Tragelaphus oryx</i>	25,000	3,400	13.1	(1)
<i>Taurotragus oryx</i>	525,000	30,400	5.8	(1)
<i>Syncerus caffer</i>	57,000	40,800	6.8	(1)
<i>Sylvestris griseus</i>	18,000	1,600	8.7	(1)
<i>Kobus ellipsiprymnus</i>	178,000	13,000	9.3	(1)
<i>Kobus ellipsiprymnus</i>	177,000	13,800	7.8	(1)
<i>Reevesia jelskii</i>	3,000	2,700	8.7	(1)
<i>Adelapha jelskii</i>	5,000	480	13.6	(1)
<i>Myxotrupa niger</i>	23,640	11,000	5.0	(2)
<i>Demalium dromas</i>	67,000	6,900	10.3	(1)
<i>Conocoryza taurina</i>	164,000	16,800	10.2	(1)
<i>Gazella gazelle</i>	4,300	6,35	14.1	(2)
<i>Aspicurus melanurus</i>	38,000	4,300	12.6	(1)
<i>Antelopea maragratia</i>	28,000	4,800	15.4	(1)
<i>Saiga tatarica</i>	28,000	3,200	11.9	(1)
<i>Rupicapra pyrenaica</i>	34,000	2,800	5.9	(4)
<i>Ovis montanus</i>	208,000	10,100	3.9	(1)
<i>Capra hircus</i>	68,000	2,200	3.7	(1)
<i>Capra ibex</i>	50,000	2,400	4.3	(1)
<i>Amurtagus ibex</i>	74,000	3,200	4.3	(1)
<i>Ovis arvensis</i>	58,000	3,800	6.0	(1)
<i>Ovis montanus</i>	7,000	4,00	3.8	(1)
<i>Ovis dalli</i>	66,000	3,480	5.4	(1)

fusion of metacarpals III and IV. This fusion generally occurs at the end of the foetal stage. The *caput metatarsale* (*epiphysis distale*) remains unfused to the body of the bone until 22 months in *Dama dama*, 15-24 months in *Ovis aries* and 24-36 months in *Capra hircus* (Smith 1956, Pöhlmeier 1985). This fusion cannot be considered as a good criterion for ageing neonate bones. We consider as neonate bones those metatarsal os canon with a proximal breadth similar to the distal breadth of the tibia.

Ossa coxae

The pelvis consists in three fused bones, ilium, ischium and pubis. At birth, they are unfused, being cartilaginous a great part of the acetabular cavity (Fig. 1). The synostosis in the acetabulum occurs at 12-15 months in *Dama dama*, 9-11 months in *Ovis aries*, 14-16 months in *Capra hircus* (Pöhlmeier 1985), and 7-10 months in *Bos taurus* (Sisson & Grossman 1994). Both left and right pelvis remain unfused until about 3 years in *Ovis aries* and *Capra hircus* and 8 years in *Dama dama* (Pöhlmeier 1985).

First phalanx (hind limb)

In *Ovis aries* this bone has only a proximal epiphysis which is fused before 9 months (Smith 1956).

Second phalanx (hind limb)

In *Ovis aries* this bone has only a proximal epiphysis which is fused before 6 months (Smith 1956).

WEIGHT AT BIRTH

Shaeter & Gordon (1994) furnish abundant documentation on the artiodactyl neonate weights. Other data on neonate weights are available from Eisenberg (1981) and Verme (1985). In Table 3 we present the adult and neonate body mass of selected artiodactyls. For living bovids, the neonate weight represents > 4% of the mother's weight (probably with the only exception of *Ovibos moschatus*, a short legged and massive species, in which

the neonate weight is about 3.5 - 3.9% of the mother's weight; Eisenberg 1981, Shaeter & Gordon 1994). The available data suggest that a neonate weight >4% of the mother's weight seems to be a general rule for all the ruminants. In contrast, for living suiforms, the neonate weight is usually about <2% of the mother's weight.

SHOULDER HEIGHT AT BIRTH

The information about the height at the shoulder of neonate artiodactyls is scarce and scattered (e.g., Braza *et al.* 1988). We have been unable to obtain global literature about this question. As a way to circumvent such a lack of information we analysed some published photographs as well as some movies (e.g., a movie on the reproduction of gnus). As it is widely known, it is possible to define two main groups of artiodactyls according the height at the shoulder of neonates. In Ruminantia, the height at the shoulder of neonates usually is higher than half the mother's shoulder height, while in Suiformes it is smaller than half the mother's shoulder height. The great shoulder height of the living neonate ruminants is a direct consequence of its long legs, and, more concrete, of the relative longer length of the autopodium.

RESULTS AND DISCUSSION

The existing data on bone growth in bovids (Smith 1956, Dhingra & Tyagi 1970, Sisson & Grossmann 1982, Pöhlmeier 1985) can be applied to the understanding of the physical characteristics of neonate *Myotragus balearicus*. Nevertheless, we must be especially cautious due to the existence of neotenic processes in *Myotragus* (Bover & Alcover in press). One such neotenic process affected the evolution of the incisiform dentition of *Myotragus*. Thus it is possible that heterochronic processes also affect other parts of the body. As in the evolution of other species (e.g., McKinney 1998), *Myotragus* evolution could have developed through a mosaic of alterations.



Figure 6 Dentaries in labial view of **A** neonate *Myotragus baleaicus*, MNIB 39318, and **B** adult *Oryctolagus cuniculus*, MNIB 702. Scale: 40 mm.

Table 4 Pelvis measurements of adult *Myotragus balearicus* females. **MBCB** Maximum birth canal breadth. **mBCB** Minimum birth canal breadth. **HBC** Height of the birth canal. **PSL** Pubic symphysis length. **TL** Total length. All the measurements in mm. See figure 7. Cova C2: MNIB 40783, 40215-8, 40851 (numbers represent different fragments of the same individual). Cova de Son Maiol: MNIB 39320. Cova Estreta: MNIB 51553.

Measurement	Cova C2	Son Maiol	Cova Estreta
MBCB	49.5	52.4	53.0
mBCB	51.1	59.8	62.1
HBC	31.8	43.6	37.5
PSL	30.2	42.7	37.4
TL	122.0	159.6	150.8

To estimate the physical characteristics of neonate *Myotragus*, our first approach comes from the dentary. At birth, an epithelium layer covers the teeth. Some teeth are osteologically erupted, but they are still unused and thus remain unworn. From our material, only one specimen (MNIB 39318) represents this stage. It belongs to a *Myotragus baleari* -

cus population (Cova de Son Maiol) from the late Pleistocene, where relatively robust adult specimens appear. Its length, 53.1 mm, is roughly similar to the mandibular length of a small rabbit (Fig. 6). Waldren (1982) illustrated another specimen of a similar age, coming from the lower levels of the Cova de Moleta. This specimen has not been available for study. Nevertheless, from the scale in the published photograph we estimate its mandibular length to be about 47.6 mm.

We have identified two frontals that surely belong to neonate specimens (Fig. 3). They have no sign of horns. The reconstruction of the shape of the skull from these frontals following the general skull shape of neonate chamoises, sheep and goats is highly consistent with the size of the dentary MNIB 39318.

The identified long bones can be used to establish the shoulder height of *Myotragus balearicus*. As with skull materials, to be consistent, it is important to consider the strati-

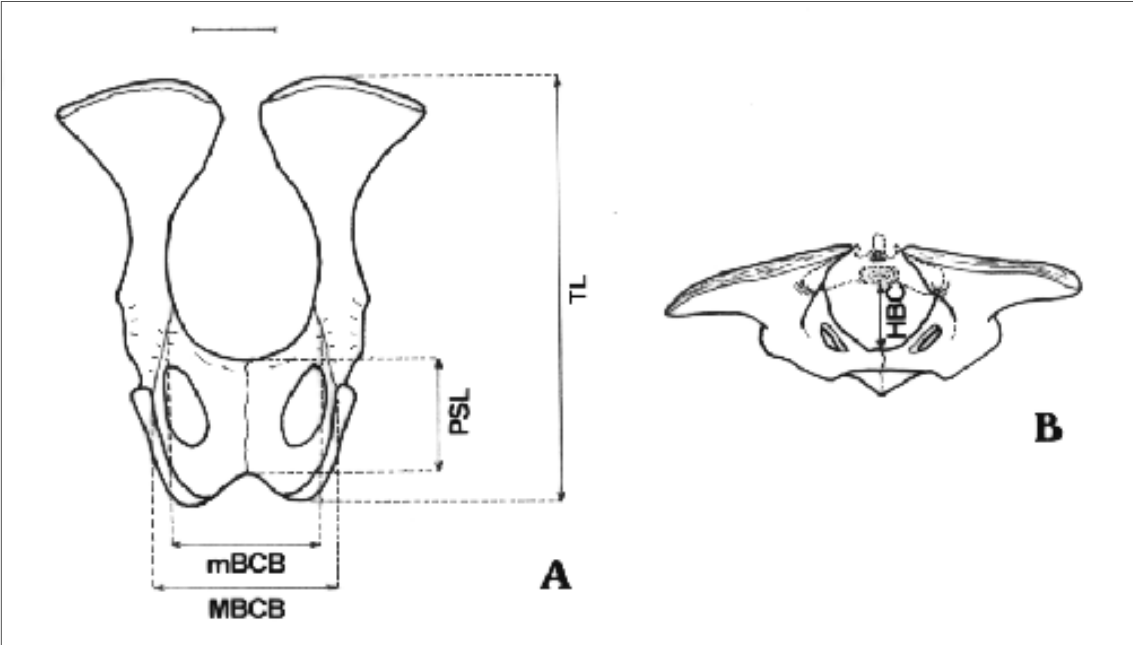


Figure 7: Measurements of the birth canal in the *Myotragus balearicus* pelvis. **MBCB** Maximum birth canal breadth. **mBCB** Minimum birth canal width. **HBC** Height of the birth canal. **PSL** Pubic symphysis length. **TL** Total length.

graphical age of these materials. At present we know that the adult specimens from the most recent Holocene level were at least 20 % smaller in long bone length than specimens from the late Pleistocene (e.g., Hamilton 1984, Marcus 1998). From the small sample of identified neonate bones, it is clear that the Holocene neonates were also smaller than the late Pleistocene ones. This size reduction probably affected the neonates in the same proportion as in the adult specimens, although we

have not enough material to confirm this point. Assuming that the temporal difference in size among neonates was of the same order as among adults, we can calculate from the length of long bones that the late Pleistocene *Myotragus balearicus* had a shoulder height at birth near 180 mm, while the neonate Holocene specimens reached only 150 mm. These estimates of neonate size are in agreement with the size of the birth canal in the female pelvis (Figs. 7 and 8, Table 4).

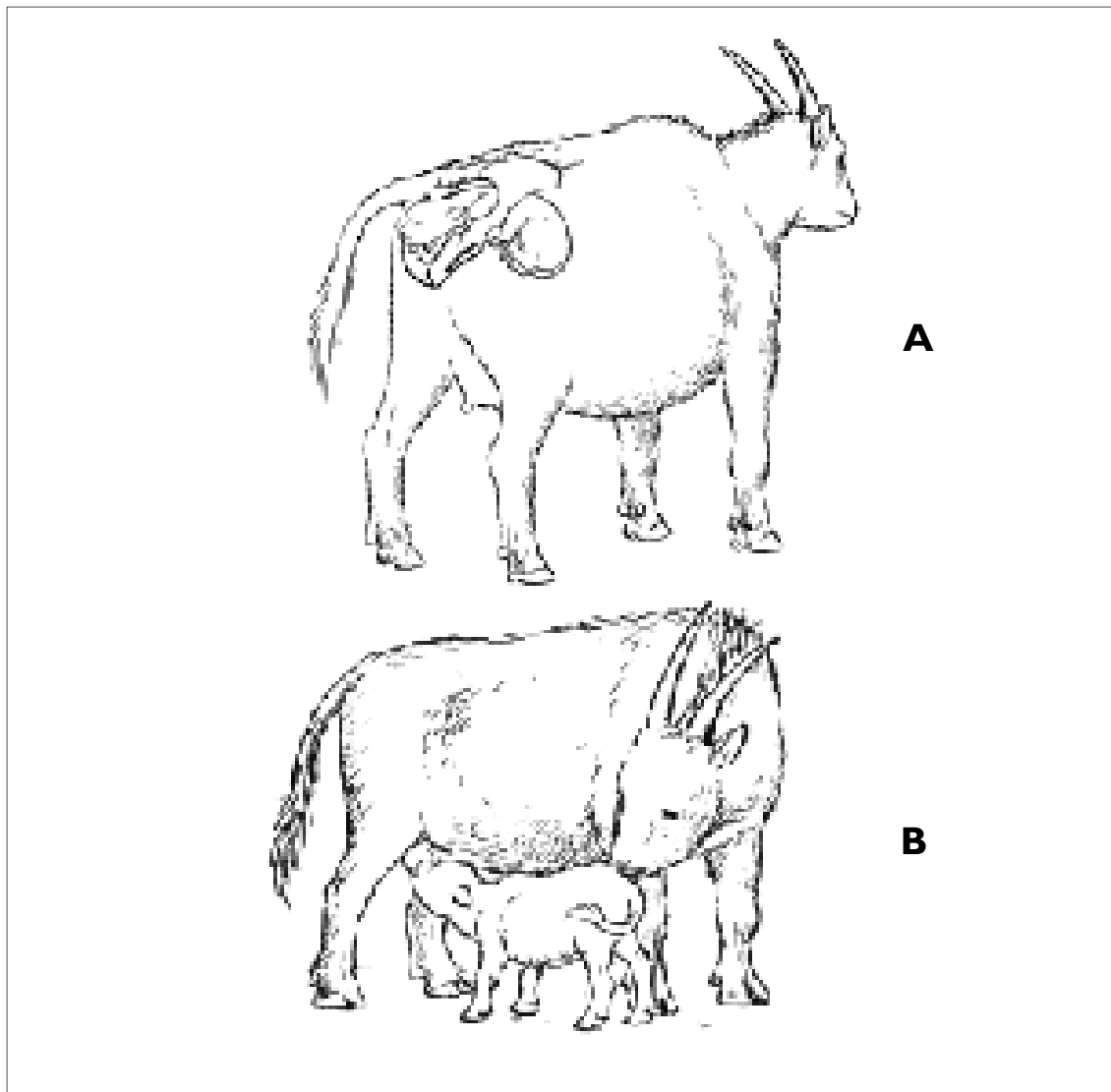


Figure 8. **A** An artistic view created by Aina Bonner of a *Myotragus balearicus* at birth, still inside its mother. The fore legs are very short and inconspicuous. **B** An artistic view of the first hours of the neonate *Myotragus balearicus*. Observe the ratio between the shoulder height of the mother and its kid.

Table 5 Measurements of neonate long bones (in mm). **ML** Mandibular length, from the mandibular condyle to the anterior part of the mandibular symphysis. **HL** Length of the humerus diaphysis. **RL** Length of the radius diaphysis. **MeL** Length of the metacarpal diaphysis. **FL** Length of the femur diaphysis. **TL** Length of the tibia diaphysis. **MeL** Length of the metatarsal diaphysis.

Species	ML	HL	RL	MeL	FL	TL	MeL
<i>Ovis aries</i>	81.5 n = 3	53.1 n = 2	75.8 n = 2	80.0 n = 2	70.9 n = 2	103.6 n = 2	83.2 n = 2
	78.8 - 86	61.3 - 64.4	71.0 - 80.6	78.7 - 81.4	67.7 - 74.2	103.3 - 103.9	81.7 - 84.7
<i>Capra hircus</i>	65.3 n = 2	56.7 n = 3	63.9 n = 3	49.6 n = 3	63.3 n = 3	86.2 n = 3	53.3 n = 3
	65.3 - 65.4	54.0 - 60.7	60.9 - 69.6	47.8 - 53	60.1 - 69.1	82.2 - 93.9	50.9 - 57.7
<i>Rupicapra pyrenaica</i>	64.4 n = 1	50.8 n = 1	68.0 n = 1	61.5 n = 1	68.3 n = 1	91.1 n = 1	68.6 n = 1
<i>Myotragus balearicus</i> (Late Pleistocene)	53.7 n = 1		37.4 n = 4	20.1 n = 5	31.7 n = 4	49.5 n = 2	23.3 n = 3
			34.0 - 40.9	16.2 - 23.4	31.0 - 32.4		18.7 - 25.8
<i>Myotragus balearicus</i> (Holocene)		31.5 n = 3		17.7 n = 1	30.9 n = 2	38.3 n = 1	23.0 n = 4
		28.1 - 34.0			28.8 - 33.0		20.2 - 25.9

In the adult females from the late Pleistocene population of Cova de Son Maiol, this canal was 52 x 44 mm, while in the adult females from the Holocene populations of Cova Estreta and Cova C-2, this canal was about 53 x 37 mm and 50 x 32 mm, respectively (see Table 4). The estimated size of neonates is about the maximum possible size to cross the birth canal in the adult female pelvis (Fig. 8).

Usually, bovids have neonates that reach a shoulder height taller than one half the mother's shoulders height. We concluded that the shoulder height of neonate *Myotragus balearicus*, was only about 30 % of the mother's (Fig. 8). This is an unexpected result of our research, showing that in this respect *Myotragus balearicus* was more similar to suids (where shoulder height of neonates is less than one half the mother's shoulder height) than to other bovids. Unfortunately, no data are available on the shoulder height of neonates of *Ovibos moschatus*, a short-legged bovid with neonates displaying a relatively small weight.

Neonate bovids are usually characterised by very long legs. The legs of neonate bovids have a very long autopodium, proportionally longer than in adults. The configuration of the neonate legs in mainland bovids is consistent with the precocial walking behaviour of the bovid kids, generally associated to an escape strategy from mammal predators. The 'following' behaviour of the young bovids is in contrast to the hiding behaviour in different cervid fawns (e.g., Carl & Robbins 1988), but both behavioral patterns are considered as strategies for neonatal defence or predator avoidance (Lent 1974). *Myotragus balearicus* lived in an environment free of terrestrial carnivores. Selective pressures modelling neonatal behaviour must be considered taking this into account. Living in an environment without mammalian carnivores, the selective pressure for neonatal defence or predator avoidance must have been irrelevant, in contrast with the mainland bovids. In *Myotragus balearicus*, the autopodium of adults is highly reduced. This anatomical feature has been related to the absence of mammal predators (Sondaar 1977, Alcover

et al. 1981). From our neonate materials, it is clear that the shortening of the autopodium in *Myotragus balearicus* represents an important heterochronic change. The length of the diaphysis of the metacarpal os canon in *Myotragus balearicus* neonates only represents about 20 % of the limb length (estimated as diaphysis femur length + diaphysis tibia length + diaphysis metacarpal os canon length). This proportion is considerably larger in other caprines: 36.6 % in *Ovis aries*, 29.2 % in *Capra hircus* and 32.3 % in *Rupicapra rupicapra*.

Our estimate of shoulder height in *Myotragus balearicus* neonates is consistent also with the estimated height above the ground of the mother's udder. Whether the young *Myotragus balearicus* sucked the mammary glands while the mother was upright, as usual in bovids, or while the mother lay on the ground, as usual in pigs and dogs, remains unknown.

The weight of neonate *Myotragus balearicus* cannot be approached from the width and/or length of the diaphyses of the long bones, the usual way to estimate it in artiodactyls (Scott 1983, 1990). Scott's formulae yield an estimate with a very wide range, from 0.1 kg to 8 kg. In fact, the applicability of this approach is questionable even for extant neonate artiodactyls, for which a great variability of results was obtained. The known weight of a male *Rupicapra pyrenaica* neonate is 2 kg. The best approach to this weight from the measurements of long bones and the use of the Scott's formulae comes from the femur and tibia lengths. Scott (1983, 1994) suggests the stylopodium bones as the most useful to estimate artiodactyl weights. Thus, femur length has been selected to estimate the weight of the *Myotragus balearicus* neonates. The length of the diaphysis of long bones of the stylopodium and zygopodium of neonate *Rupicapra* are about twice that of *Myotragus* bones. For femur lengths, the use of Scott's formulae gives for the late Pleistocene

Myotragus balearicus neonates a weight of 200-260 g. Nevertheless, these figures must be considered clearly as underestimates of the actual neonate weight, because *Myotragus* bones are clearly, even in the neonate stage, more robust than its counterparts in other living artiodactyls. Thus, we consider that the actual weight of neonate *M. balearicus* must have been undoubtedly higher. Using the Scott's formula for suids, a weight of about 330-440 g can be estimated from femur lengths. In our opinion, even these figures are underestimates, because the bones of neonate *Myotragus* are even more robust than the bones of a neonate pig. These estimates are suggesting than the *Myotragus balearicus* neonates weighted the same as an adult brown rat (*Rattus norvegicus*), but nevertheless the size of their bones are clearly bigger. The jaw of the upper Pleistocene neonate *Myotragus balearicus* is roughly similar in size to a rabbit (*Oryctolagus cuniculus*) (Fig. 6). Also the long bones are of a roughly similar length to those of a rabbit. An estimated weight of 700-900 g can be approached from our materials for the late Pleistocene specimens while for Holocene specimens the weight must have been less than 500-600 g. Of course, the long bones of *Myotragus balearicus* are more robust than the corresponding rabbit bones, but the body weight of a rabbit always includes the viscera contents, while the weight of the neonate *Myotragus balearicus* has been estimated assuming that neonate has empty viscera.

This estimated weight represents probably about 2 % of the mother's weight. In this respect, *Myotragus balearicus* was also unusual. The neonate weight for ungulates is closely correlated with the mother's weight (Robbins & Robbins 1979, Saether & Gordon 1994; see Table 3). Usually, the neonate weight for bovids is > 4 % of its mother's weight. This seems not to be the case for *Myotragus balearicus*. In contrast with ruminants, the Suina in general produce relatively small offspring (Frädrich 1967). For

some suids the weight of the neonate is less than 2% of the mother's weight. For example, in *Sus scrofa*, *Potamochoerus porcus* and *Phacochoerus ethiopicus* the ratio between the weight of the neonate and that of its mother is 1.6%, 2.0% and 1.3% respectively (see Saether & Gordon 1994 and Table 3). The weight of neonate *Myotragus balearicus* relative to the mother's weight was similar to these figures. Whether this small size of neonates was related to larger litter size, as is the case in suids, is currently unknown. Although litter size in ungulates is inversely related to the relative neonate weight, *Myotragus balearicus* may have also been an exception to this rule.

It is also difficult to make an accurate estimate of the timing of intra-uterine development and the gestation, another life history parameter usually correlated with neonate body size. *Myotragus balearicus* could also represent an exception to this rule. A possible reproductive strategy for *Myotragus balearicus* can be suggested. This highly modified insular species, that was surely a K-strategist, lived in a stable environment with very poor productivity. As a consequence, its metabolic rates may have been very low. In this context, its reproductive strategy may have involved reduction in energy investment for reproduction. This could mean having the minimum litter size (one calf per litter, exceptionally two), a long intra-uterine growth at a very slow growth rate, and a very small size of the neonates. This scenario is currently only speculative, but is in agreement with the current knowledge of insular evolution.

The birth of *Myotragus balearicus* was probably different to the usual ruminant birth. At the time of birth, the front legs appear first, and the head appears only when the front legs are in part outside. The shortened legs of the neonate *Myotragus balearicus* suggest that this event may also have been peculiar in this species (Fig. 8).

Another point that remains insufficiently known in *Myotragus balearicus* is the possible sexual dimorphism at birth. In some species, like *Dama dama*, statistically significant differences in the size of males and females have been recorded for neonates (Braza *et al.* 1968). In our opinion, *Myotragus balearicus*, a highly dimorphic species at the adult stage, probably displayed some sexual dimorphism in size from birth. Nevertheless, in order to establish this accurately it will be necessary to exhume additional neonate materials.

ACKNOWLEDGEMENTS

Firstly, we are highly indebted to Dr Paul Sondaar (Rotterdam) for his leadership work on insular vertebrate evolution. During one year we shared with him stimulating discussions about the methodology of the work and on *Myotragus* evolution. Dr Peter Weesie (Groningen) obtained for us the book of Pöhlmeier (1985). Dr Damià Jaume Llabrés, Damià Jaume Bosch (Ciutat de Mallorca) and Mr Mateu Bennàssar (Manacor) gives us three neonate sheep, Dr Carlos Nores (Oviedo) two foetal chamoises, and Mr Pere Arnau (Ciutadella de Menorca) three neonate goats. The last also discovered the Cova C-2, a very important deposit for this study. We are indebted also to Dr Ross MacPhee and Dr Clare Flemming (American Museum of Natural History, New York) for the loan of the youngest *Oreamnos americanus* of the AMNH collection. We thank Aina Bonner (Boston) for the drawings of Figure 8. Ms Bernadette Canut (Montferrer) help us with some veterinary literature. Ms Marta Macias (Ciutat de Mallorca) obtained for us important literature. Mr Ferran Hierro (Ciutat de Mallorca) obtained the SEM images of Figure 5. Dr Salvador Moyà (Sabadell) gave us the linear measurements of the skeleton mounted at Sabadell. Miquel Trias (Ciutat de Mallorca) and José Antonio Encinas (Pollença) discovered the Mallorcan deposits that delivered an important part of the studied material. Dr Cristian R. Altaba (Ciutat de Mallorca) and Ms Aina Bonner (Boston) con-

siderably improved the English of our first version. The studied material has been exhumed in excavations authorised by and partially financed with funding from the Conselleria de Cultura del Consell Insular de Mallorca and the Conselleria de Cultura del Consell Insular de Menorca. This paper is included in Research Project DGICYT PB97-1173. One of the authors (P.B.) received a fellowship from the Conselleria d'Educació i Cultura del Govern Balear.

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received 15 January 1999

APPENDIX Identified neonate bones of *Myotragus balearicus*. All collection numbers are referred to the vertebrate collection 'Museu de la Naturalia de les Illes Balears', Ciutat de Mallorca (acronym: MNIB).

Collection number	Bone	Locality	Side	Square and level	Age
46253	Humerus	Cova Estreta	Left	O 7 -50/60	Holocene
46582	Humerus	Cova Estreta	Left	O 7 -50/70	Holocene
50585	Humerus	Cova Estreta	Right	L6 surface	Holocene
41047	Radius	Cova C-2	Left	K 15	Late Pleistocene
41113	Radius	Cova C-2	Left	B 11	Late Pleistocene
41442	Radius	Cova C-2	Left	Laminader entre 12 i 13	Late Pleistocene
41385	Radius	Cova C-2	Right	U 12	Late Pleistocene
41384	Metacarpal	Cova Estreta	Left	Devorantiu 1	Late Pleistocene
41385	Metacarpal	Cova Estreta	Left	Devorantiu 1	Late Pleistocene
51946	Metacarpal	Cova Estreta	Left	N 8 n 2	Holocene
51804	Metacarpal	Cova Estreta	Right	Gal 2 Gorg	Late Pleistocene
51462	Metacarpal	Cova Estreta	Left	Devorantiu 1	Late Pleistocene
51460	Metacarpal	Cova C-2	Right	Sala Gran 2	Late Pleistocene
40366	Femur	Cova C-2	Right	B 22	Late Pleistocene
40712	Femur	Cova C-2	Left	B 10	Late Pleistocene
40750	Femur	Cova C-2	Left	B 14	Late Pleistocene
41457	Femur	Cova C-2	Right	F 14	Late Pleistocene
45151	Femur	Cova Estreta	Right	O 7 -50/70	Holocene
51609	Femur	Cova Estreta	Left	M 6 n	Holocene
41028	Tibia	Cova C-2	Right	K 19	Late Pleistocene
46025	Tibia	Cova Estreta	Left	L 4	Holocene (estimated)
58124	Tibia	Cova des Moro	Left	Unknown	Late Pleistocene(estimated)
37972	Metatarsal	Cova des Moro	Left	U 3 -70/100	Holocene
38133	Metatarsal	Cova des Moro	Right	Unknown	Late Pleistocene (estimated)
50952	Metatarsal	Cova Estreta	Right	L 7 n 1	Holocene
50983	Metatarsal	Cova Estreta	Left	Gal 2 Gorg	Late Pleistocene
51066	Metatarsal	Cova Estreta	Right	Gal 2 Gorg	Late Pleistocene
51823	Metatarsal	Cova Estreta	Left	M 8 n 1	Holocene
51842	Metatarsal	Cova Estreta	Right	L 4 -120/140	Holocene
59454	Scapula	Cova C-2	Right	Sala Gran 1	Late Pleistocene
59183	Scapula	Cova C-2	Right	Unknown	Late Pleistocene
41057	Frontal	Cova C-2	Left	K 9	Late Pleistocene
41107	Frontal	Cova C-2	Right	B 11	Late Pleistocene
53508	Frontal	Cova Estreta	Left	Gal 2 Gorg	Late Pleistocene
59452	Frontal	Cova C-2	Left	B 20	Late Pleistocene
39318	Dentary	Cova de Son Maiol	Left	Unknown	Late Pleistocene
55776	3 rd Phalange	Cova Estreta		Gal 2, Gorg	Late Pleistocene
55844	3 rd Phalange	Cova Estreta		N 8 n 1	Holocene
43447	3 rd Phalange	Cova Estreta		Devorantiu 1	Late Pleistocene
44086	3 rd Phalange	Cova Estreta		M 6 n 2	Holocene
55777	3 rd Phalange	Cova Estreta		M 3 n 1	Holocene
55809	3 rd Phalange	Cova Estreta		Gal 2, final	Late Pleistocene
55738	2 nd Phalange	Cova Estreta		Gal 2, Gorg	Late Pleistocene
56200	2 nd Phalange	Cova Estreta		Devorantiu 1	Late Pleistocene
55540	1 st Phalange	Cova Estreta		Gal 2, Gorg	Late Pleistocene
55545	1 st Phalange	Cova Estreta		Gal 2, Gorg	Late Pleistocene
55548	1 st Phalange	Cova Estreta		Gal 2, Gorg	Late Pleistocene
55499	1 st Phalange	Cova Estreta		M 3 n 1	Holocene
55546	1 st Phalange	Cova Estreta		Gal 2, Gorg	Late Pleistocene

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