

THE OLFACTORY ABILITY OF *MYOTRAGUS BALEARICUS*: PRELIMINARY NOTES

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Resum

Als mamífers insulars fòssils s'ha observat una reducció relativa de la mida del cervell. *Myotragus balearicus*, el bòvid nan de les Balears, no va ser una excepció, i la petita mida del cervell podria haver afectat a la capacitat d'algun dels seus sentits. Aquest és el cas de la capacitat olfactiva. S'han estudiat les làmines criboses de diferents espècies de bòvids i d'altres grups taxonòmics. La làmina cribosa és un envà prim i petit que està travessat pels nervis que connecten l'epiteli olfatori (a la cavitat nasal) i el bulb olfatori del cervell. Cada una de les ramificacions del nervi que travessen aquest envà produeixen un orifici en ell, de forma que les espècies amb una gran capacitat olfactiva tenen una làmina cribosa altament perforada (e.g., *Canis familiaris*), mentre que les espècies amb una capacitat olfactiva relativament minvada tenen un nombre d'orificis reduït (e.g., *Phoca vitulina*).

Si se compara la làmina cribosa de *Myotragus balearicus* amb la d'altres bòvids actuals, es pot observar que la densitat d'orificis és considerablement menor que el de les altres espècies de bòvids estudiades. Per tant, es pot inferir que l'espècie tenia una pèrdua de capacitat olfactiva. El nombre i densitat d'orificis de la làmina cribosa de *Myotragus* és inclús menor que el de les espècies amb cervells petits (com *Madoqua kirki*). Aquesta característica podria estar relacionada amb la manca de depredadors terrestres a les illes on va viure aquest animal (absència de carnívors). A les illes Gimnèsies no era necessària una gran capacitat olfactiva per a detectar un atac per part de depredadors, i l'orientació frontalitzada de les òrbites oculars de *Myotragus* ha estat també relacionada a aquesta manca de depredadors. No s'ha trobat cap efecte de la inclinació de la làmina cribosa sobre la capacitat olfactiva. Aquesta capacitat olfactiva minvada derivada de l'estudi de la làmina cribosa s'adiu amb la mida reduïda dels bulbs olfactoris en els molles endocranials estudiats.

Només a *Oribos moschatus* el nombre d'orificis de la làmina cribosa és semblant al registrat a *Myotragus*. Aquest fet podria estar relacionat amb el comportament defensiu peculiar d'aquesta espècie davant d'atacs de depredadors. Quan un grup es atacat per un depredador (bàsicament llops), se situen tots junts, en forma de cercle o semicercle, amb les cries a l'interior. Per tant, per a aquesta espècie, sembla ser més important un comportament defensiu que no un comportament de fugida.

Paraules clau: *Myotragus balearicus*, capacitat olfactiva, òrgans dels sentits, bòvids, Illes Gimnèsies.

Abstract

In insular fossil mammals a relative reduction of the brain size has been quoted. *Myotragus balearicus*, the dwarf fossil bovid from Balearic Islands, was not an exception, and the small size of its brain could affect the capacity of some of its senses. This is the case of the olfactory capacity. We studied the criba nasalis of different bovid species' and of other taxonomic groups. The criba nasalis is an small and thin septum crossed by the nerves that connect the olfactory epithelium (in the nasal cavity) and the olfactory bulb of the brain. Everyone of the nerves that cross the septum produces an orifice on it, so that the species with a great olfactory ability have a criba nasalis highly perforated (e.g., *Canis familiaris*), while in the species with a scarce olfactory ability the number of orifices is reduced (e.g., *Phoca vitulina*).

If we compare the criba nasalis of *Myotragus balearicus* and extant bovids we observe that the orifices density in the fossil species is considerably lesser than in the other studied bovids. A lost of olfactory ability can be consequently inferred. The number and density of orifices in the criba nasalis of *Myotragus* is even smaller than in some small-brained species (as *Madoqua kirki*). This feature could be related to the terrestrial predator free environment where this animal lived (carnivores absence). In Gymnesic Islands there was not necessary a good olfactory ability to detect predators before they attacked, and the frontal orientation of the eye sockets in *Myotragus* has been also related to this lack of predators. We have not found any effect of the inclination of the criba nasalis on the olfactory ability. The small olfactory ability derived from the study of the criba nasalis is consistent with the small-sized olfactory bulbs in the studied brain casts.

Only in *Oribos moschatus* the number of orifices in the criba nasalis is close to that recorded in *Myotragus*. This could be related to the peculiar defensive behaviour of this species against predators. When a herd is approached by a putative predator (mainly wolves), they bunch together, in the form of a circle or semicircle with the calves inside. Then, for this species is seems more important the defensive behaviour than the escape.

Key words: *Myotragus balearicus*, olfactory ability, sense organs, bovids, Gymnesic Islands.

INTRODUCTION

Evolution in isolated conditions entailed a series of extraordinary morphological changes in fossil vertebrate species (e.g., Caloi *et al.*, 1988; Caloi & Palombo, 1990; Alcover *et al.*, 1999; Alcover, 2004). Among these morphological changes we find those affecting the nervous system. Evidently, in fossils, as a general rule, there are no conserved remains of the soft structures of the nervous system, however, the prints and foramina left by the brain and nerves in the bones can be evaluated. There are many scientific works which study the brain of fossil species by the elaboration of endocranial moulds with different techniques (e.g., Holloway, 1978). Apart from the studies on endocranial volume, which is so important in the evolution of primates, and more specifically in Hominids (e.g., Holloway, 1968; Tobias, 1975), there is a series of studies evaluating the circumvolutions of the skull caused by the shape of the brain (e.g., Dechaseaux, 1961; Accordi & Palombo, 1971).

In insular fossil mammals a relative reduction in brain size has been detected (e.g., Fleagle, 1988 in *Oreopithecus*; Quintana, 2002, in the giant leporid of Menorca). *Myotragus balearicus*, the Balearic fossil dwarf bovid, is no exception (Köhler & Moyà-Solà, 2004). In *M. balearicus* the ocular orbits are relatively frontalised, making stereoscopic vision possible (Alcover *et al.*, 1981). The frontalisation of the ocular orbits observed for the genus *Myotragus* has been associated with the lack of terrestrial predators in the islands where it lived, making lateral orbits unnecessary (as can be seen in present day bovid species). Furthermore, it has been recently observed that the size of the ocular orbits is relatively small in *M. balearicus* (Köhler & Moyà-Solà, 2004).

The reduction in brain size could have affected the capacity of some of its senses. In this work we evaluate the olfactory capacity. The relationship between the olfactory bulb of the brain and the olfactory capacity has been known for a long time (see review of current literature on the subject made by Xu *et al.*, 2000).

To such an effect, we have studied the lamina cribrosa (or cribriform plate) of *M. balearicus* and have compared it with the different species of bovids and other taxonomic groups. The lamina cribrosa is a small, thin plate located in the ethmoid bone in the skull (see Fig. 1), separating the cranial cavity from the nasal cavity. This plate is divided (seen from the inside of the skull) into two surfaces by the *crista galli*. This plate is perforated by ramifications of the olfactory nerve which connect the olfactory epithelium (in the nasal cavity) to the olfactory bulb of the brain (located in the front part of the neurocranium). Each of the nervous ramifications which perforate the plate do so through a foramen. Embryologically, the ossification of this area is posterior to the innervation, therefore, these nervous ramifications are the ones that are already present in the foetus (Tolosa, 1980), without there being any posterior variations due to environmental motives. It seems that species with a great olfactory capacity have a highly perforated lamina cribrosa (e.g., *Canis familiaris*), whereas in species with a lesser olfactory capacity, the number of perforations is reduced (e.g., *Phoca vitulina*). What is more, in species

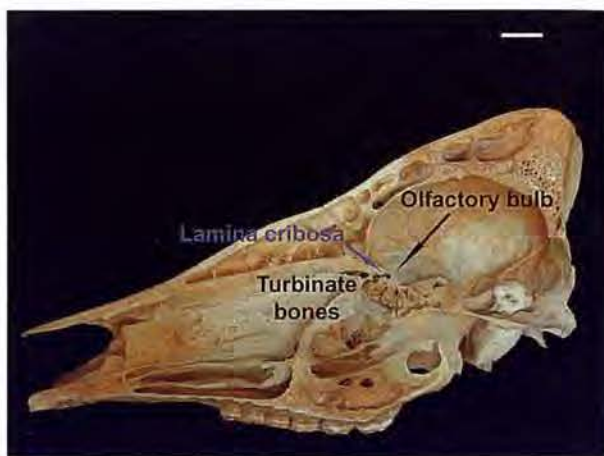


Fig. 1. *Tayassu pecari* skull (NMNH 269185) in which the anatomical position of lamina cribrosa is showed. This lamina is an small septum that separates olfactory bulb and the olfactory epithelium located in the nasal cavity. Scale bar, 2 cm.

Fig. 1. Crani de *Tayassu pecari* (NMNH 269185) on s'ha situat anatòmicament la posició de la làmina cribrosa. Aquesta làmina és un envà prim que separa el bulb olfatori de l'epiteli olfatori situat a la cavitat nasal. Escala, 2 cm.

with a highly developed olfactory capacity (such as *Canis*), the position of the lamina cribrosa is oblique with respect to the saggital plane, a fact which leads to increasing its surface, thus allowing the passage of a larger number of nervous ramifications, whereas in *Phoca*, the shape of the lamina cribrosa is practically perpendicular to the saggital plane of the skull.

MATERIALS AND METHODS

The materials from present day species used in this study are deposited in the vertebrate collection of the Mammal Division of the National Museum of Natural History-Smithsonian Institution in Washington, D.C. (USA), acronym (NMNH). In this collection there is an important quantity of skulls from different species, in which the top of the neurocranium has been removed, leaving the area of the lamina cribrosa clearly visible. This fact has been taken advantage of to take the photographs and measurements used in this study. Table 1 gives a relation of the materials from the living species studied. So as to compare the lamina cribrosa of the different species, we selected, out of the ones in which it was possible to directly observe this part of the inside of the skull, (1) those bearing some sort of relation to *Myotragus* (*Oreamnos*, *Ovibos*, *Nemorhaedus*, *Ovis*, Lalueza *et al.*, 2000, 2002), (2) those of a similar size (*Madoqua*), (3) those which, due to their large size, did not depend strictly on their sense of smell as an anti-predatory strategy (*Syncerus*, *Taurotragus*) and (4) the supposed extreme cases according to the development of the olfactory capacity) of lamina cribrosa morphology (*Canis*, *Phoca*, *Monachus*).

From the collection of vertebrates MNIB (Museu de la Naturalesa de les Illes Balears, Palma de Mallorca) we studied the skull of a sheep (*Ovis aries*, MNIB 85104) and a dog (*Canis familiaris*, MNIB 85103) in which a transversal cut was made just behind the ocular orbits in order to be able to observe the lamina cribrosa. Furthermore, a skull of

Ovis aries (MNIB 85107) and one of *Canis familiaris* (MNIB 85106) were cut in a horizontal section so as to observe the position of the lamina cribrosa in dorsal view.

As regards the materials of *M. balearicus* studied, 4 skulls were used in which the lamina cribrosa was visible (MNIB 5222, 85108 and 85109 and an unnumbered example from Cova des Moro), and observations were carried out using laparoscopic techniques (with a rigid Storz optic of Ø 4 mm) in three others (MNIB 5213, 48139 and 51345). Only in two cases, MNIB 5222 and 85109, was an incision with a small saw made so as to observe the area under study. The quantity of skulls and skull fragments of *M. balearicus* deposited in the MNIB collection is important, but for different reasons it was not possible to study all of them: the most common motive being the fragmentation of the lamina cribrosa due to the fact that it is such a thin, delicate lamina. One of the other habitual motives is the fact that the plate is covered by a layer of concreted sediment, and could be destroyed by an attempt at cleaning (both via mechanical and chemical means). In some cases the concretions are placed in such a way that they obstruct the foramina in the lamina cribrosa, a fact which makes its evaluation difficult. Neither was it possible to study the lamina cribrosa of the oldest species of the *Myotragus* genus. As well as the scarcity of skulls, the few that there are, are either so fragmented, or are surrounded by an extraordinarily hard matrix, which makes it very difficult to clean them.

An attempt was made to correlate the measurements of the lamina cribrosa and the skulls of the different species studied. The *M. balearicus* skulls used to study the lamina cribrosa are incomplete and it was not possible to measure condylobasal length in any of them. Therefore, in the case of *M. balearicus* only the parameters related to the nasal area and the lamina cribrosa can be assessed. The measurements carried out are the following (Fig. 2):

AmCR: Width of the Lamina Cribrosa. Maximum width measured in the area of union between the olfactory bulb and the rest of the brain. It is measured from the *crista galli* to the side of the concavity of the olfactory bulb.

- AICR: Height of the Lamina Cribrosa. Maximum height measured in the area of union between the olfactory bulb and the rest of the brain. It is measured from the ventral end to the dorsal end of the concavity of the olfactory bulb.

- CBL: Condylobasal Length. Length measured between the front of the premaxillary bones and the caudal part of the occipital condyles (Von Den Driesch, 1976).

- AmN: Nasal Width. Width of the maxillary bones measured at the height of the base of the first upper premolar present (P² in present day bovids and P¹ in *M. balearicus*).

- Angle of the Lamina Cribrosa: angle made by the side of the *crista galli* with the roof of the palate, in lateral view.

The total measurement of the lamina cribrosa is complicated to carry out without destroying the skulls studied. In fact, the AmCR and AICR measurements were carried out in the area of union between the olfactory bulb of the brain and the rest of the brain hence it is an indirect measurement of the transversal size of the olfactory bulb.

SPECIES	COL	NUM
ARTIODACTYLA		
<i>Cephalophus leucocephalus</i>	NMNH	220389
<i>Hemitragus jemlahicus</i>	NMNH	49884
<i>Litocranius walleri</i>	NMNH	164034
<i>Madoqua kirkii</i>	NMNH	396306
<i>Madoqua kirkii</i>	NMNH	538106
<i>Nemorhaedus goral</i>	NMNH	259411
<i>Neotragus pygmaeus</i>	NMNH	467679
<i>Neotragus pygmaeus</i>	NMNH	467686
<i>Oreamnos americanus</i>	NMNH	218758
<i>Oreamnos americanus</i>	NMNH	218789
<i>Oreamnos americanus</i>	NMNH	201003
<i>Oreamnos americanus</i>	NMNH	201002
<i>Oreamnos americanus</i>	NMNH	287532
<i>Oreamnos americanus</i>	NMNH	287553
<i>Oreamnos americanus</i>	NMNH	287552
<i>Ovibos moschatus</i>	NMNH	6251
<i>Ovibos moschatus</i>	NMNH	120921
<i>Ovis aries</i>	MNIB	85104
<i>Ovis aries</i>	MNIB	85107
<i>Ovis canadensis</i>	NMNH	3668
<i>Ovis canadensis</i>	NMNH	244189
<i>Ovis canadensis</i>	NMNH	218006
<i>Saiga tatarica</i>	NMNH	336265
<i>Syncerus caffer</i>	NMNH	220129
<i>Taurotragus oryx</i>	NMNH	199548
<i>Tayassu pecari</i>	NMNH	269185
<i>Tayassu tajacu</i>	NMNH	499758
CARNIVORA		
<i>Canis familiaris</i>	MNIB	85103
<i>Canis familiaris</i>	MNIB	85106
<i>Canis familiaris</i>	NMNH	20851
<i>Monachus tropicalis</i>	NMNH	100357
<i>Phoca vitulina</i>	NMNH	504110
<i>Phoca vitulina</i>	NMNH	550060
MARSUPIALIA		
<i>Vombatus ursinus</i>	NMNH	19566

Table 1. List of extant species in which lamina cribrosa has been studied.

Taula 1. Llistat d'espècies actuals a les que s'ha estudiat la làmina cribrosa.

The angle of the lamina cribrosa was calculated in the skulls which were sectioned in such a way that it was possible to stick a small rod on the *crista galli* and another on the palate. After taking digital photos in the lateral view, the angle between the two sticks was calculated using the Photoshop 6.0 programme. The length measurements were carried out with a Kern callibre (precision, 0.02 mm).

The task of measuring the number of foramina perforating the lamina cribrosa, or calculating the surface they occupy with respect to the total surface of the lamina cribrosa has, so far, turned out to be very complicated, without it being possible to establish methodology which can give us very precise results. The main complication of measuring the number of foramina, is that each foramen which can be seen with the naked eye in the first layer of the plate is subdivided into others (a variable number) as we look on the inside using a stereomicroscope. This fact, together with the irregular surface of the plate also complicates very much the measurement of the surface occupied by these foramina. Hence, in this work we make only an anatomical description of the plate, trying to give an accurate illustration of the features observed, but without presenting the measurements pertaining to the foramina observed. The differences between species are clear enough to be defined using categories based on the number and distribution of the perforations in the lamina cribrosa by direct visual estimation. The quantification of these features will have to be made after finding an adequate method to carry out the measurements so as not to introduce significant errors.

RESULTS

The region of the lamina cribrosa shows different distributions of foramina for the passage of the ramifications of the olfactory nerve. Using a sheep's skull (*Ovis aries*, MNIB 85104, Fig. 3) as a model to describe this distribution in bovids, it can be observed, in caudal view (see Fig. 3), that the lamina cribrosa is made up of two highly perforated regions, separated, as mentioned above, by quite a highly developed saggital crest, the *crista galli* (in *Canis familiaris* this crest is a very thin, very slightly developed lamina). These two perforated areas are slightly concave in the bovids studied. In each of these areas a row of parallel perforations can be found, just by the *crista galli*. These perforations are the largest ones observed in the lamina cribrosa. On the lateral side of this row a more or less oval region can be found with a low number of perforations with a very small diameter. In the rest of the lamina cribrosa a multitude of uniformly distributed perforations with varying diameters can be seen, although at the lower margin, upper margin and in the centre of the lamina cribrosa small accumulations of perforations with a wider diameter can be observed (similar to the row of perforations by the *crista galli*). The lamina cribrosa has a perpendicular saggital orientation if the skull is observed in dorsal view (Fig 5).

To serve as an example of the lamina cribrosa of a species with a high olfactory capacity, we used *Canis*

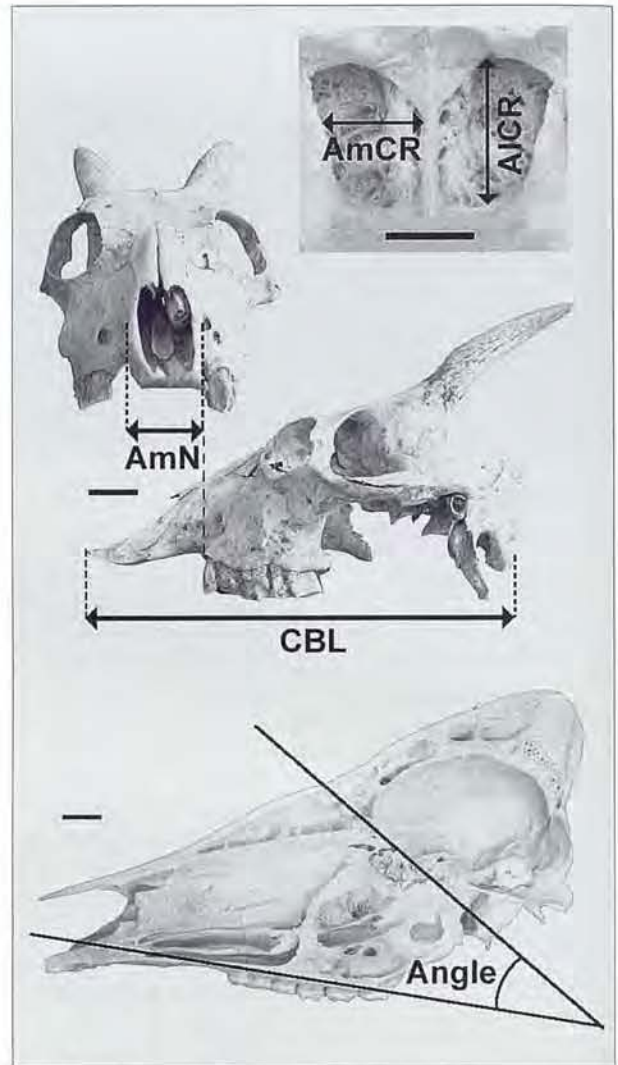


Fig. 2. Measurements made on nasal region. AICR: Lamina cribrosa Height; AmCR: Lamina cribrosa Breadth (measurements shown on an *Oreamnos americanus* skull, NMNH 201002). AmN: Nasal Breadth; CBL: Condilobasal Length (measurements shown on a *M. balearicus* skull (sn, Cova des Tancats). Angle: Angle of Lamina cribrosa (measurement shown on a *Tayassu pecari* skull, NMNH 269185). Scale bar, 2 cm.

Fig. 2. Mesures realitzades a la regió nasal. AICR: Alçada de la Làmina Cribrosa; AmCR: Amplada de la Làmina Cribosa (mesures il·lustrades sobre un crani d'*Oreamnos americanus*, NMNH 201002). AmN: Amplada Nasal; CBL: Longitud Còndilo-Basal (mesures il·lustrades sobre un crani de *M. balearicus* (sn, Cova des Tancats). Angle: Angle de la Làmina Cribrosa (mesures il·lustrades sobre un crani de *Tayassu pecari*, NMNH 269185). Escala, 2 cm.

familiaris (MNIB 85103, Fig. 4). The lamina cribrosa, if a horizontal cut is made in the skull in dorsal view, is "V"-shaped, with the vertex facing towards the area of the nasal cavity (Fig. 5). In this vertex we find a very thin *crista galli*, flanked by a row of large perforations (as happens in the bovids). The slightly perforated area is not as centrally placed as in the bovids, but is found in the upper margin of each perforated area. The rest of the lamina cribrosa is very highly perforated (more than in *Ovis*). The perforations are of a large diameter, in general, but without reaching the dimension of the perforations of the rows adjacent to the *crista galli*.

Among the species in which the olfactory capacity does not seem to be as important (if compared, for instance, with the fissipedes) it is worth noting the pinnipeds in which the sense of smell seems to be related to short-distance recognition between mothers and young and to territorial behaviour and reproduction (Ryg *et al.*, 1992; Insley *et al.*, 2003), and not to the search for food or to anti-predatory conduct. As an example of a species with a reduced olfactory capacity, we used *Phoca vitulina* (NMNH 504110, Fig. 6). The lamina cribrosa of *Phoca* is very flat and practically perpendicular to the sagittal plane of the skull, in dorsal view. The number of perforations is extraordinarily low. Just as happens in the other groups, the lamina cribrosa is separated by a *crista galli*, which in this case is very highly developed. There are no rows of foramina adjacent to the crest, rather only one single elongated foramen can be seen (at times reduced in size) on each side, parallel to the *crista galli*. Along the peripheral line of the lamina cribrosa different groups comprising a small number of foramina can be found, surrounding areas without perforations.

If the lamina cribrosa of *M. balearicus* and present day bovids are compared it can be seen that the density of foramina in this fossil species is considerably lower than in the other bovids studied. In *M. balearicus*, the number of perforations parallel to the *crista galli* seems to be lower in all the cases studied (Fig. 7). The central part of each lobule of the plate either has no perforations or, if it has, they are very few and very small. This central part, in some of the skulls, is made up of a protuberance (e.g., MNIB 5213, Fig. 7.A), however, in other cases this surface is more or less flat (e.g., MNIB 5222, Fig. 7.C). In the peripheral area on each side of the plate there is an abundant number of perforations which are distributed more or less uniformly (Fig. 7). Another of the relevant characteristics with respect to the other bovids studied is that in *Myotragus* there are no perforations in the lateral peripheral walls of the concavity where the olfactory bulb is situated, so this part of the brain can only have received nervous endings from the frontal part of the plate (see Fig. 7).

Apart from studying the morphology of this area in the bovids related to *Myotragus*, so as to evaluate the possible effect of size on this region, we observed the lamina cribrosa from two small-sized bovids, *Madoqua kirkii* and *Neotragus pygmaeus*. In these two species we can see a similar pattern of foramina, broadly speaking, to that described for *Ovis*. As a result, the number and density of foramina in the lamina cribrosa of *Myotragus* is also lower than in species with a small brain (such as *Madoqua kirkii*).

Regarding the nearest relatives of *Myotragus* (*Oreamnos*, *Capricornis*, *Nemorhaedus*, *Budorcas*, *Ovibos*), it is worth pointing out that the morphology of the lamina cribrosa follows the pattern observed in *Ovis*, with only one exception. In *Ovibos moschatus* the pattern of the number of foramina in the lamina cribrosa is comparable to that documented in *Myotragus*. Just as happens in the fossil bovid species, the two *Ovibos moschatus* skulls studied (NMNH 6251 and 120921) have a central area in each part of the lamina cribrosa which is only very slightly perforated. They have a row parallel to the *crista galli*, whereas the rest of the perforations are situated in the peripheral areas of the plate.

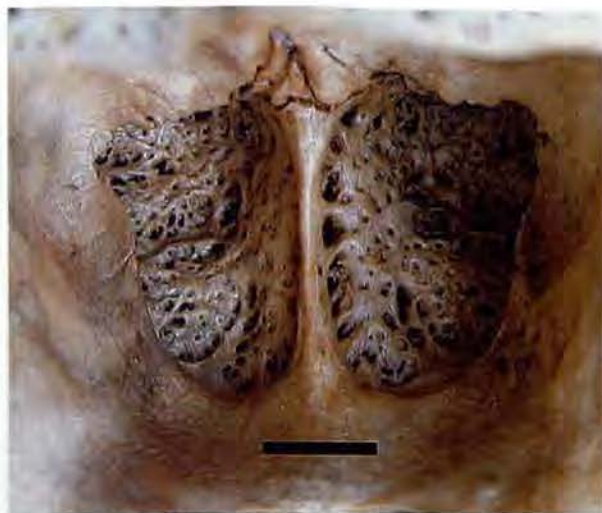


Fig. 3. Detail of the lamina cribrosa of *Ovis aries* MNIB 85104. The median ridge that divides the lamina cribrosa is the *crista galli*. Scale bar, 1 cm.

Fig. 3. Detall de la làmina cribrosa d'*Ovis aries* MNIB 85104. La cresta sagital que separa les dues làmines perforades és la *crista galli*. Escala, 1 cm.



Fig. 4. Detail of the lamina cribrosa of *Canis familiaris* MNIB 85103. The *crista galli* is not much developed in this species. Scale bar, 1 cm.

Fig. 4. Detall de la làmina cribrosa de *Canis familiaris* MNIB 85103. La *crista galli* està molt poc desenvolupada en aquesta espècie. Escala, 1 cm.

In order to classify the different morphologies of the perforations in the lamina cribrosa observed we defined four categories based on the analysis of the number and distribution of the perforations produced by the passage of the nerves. These are:

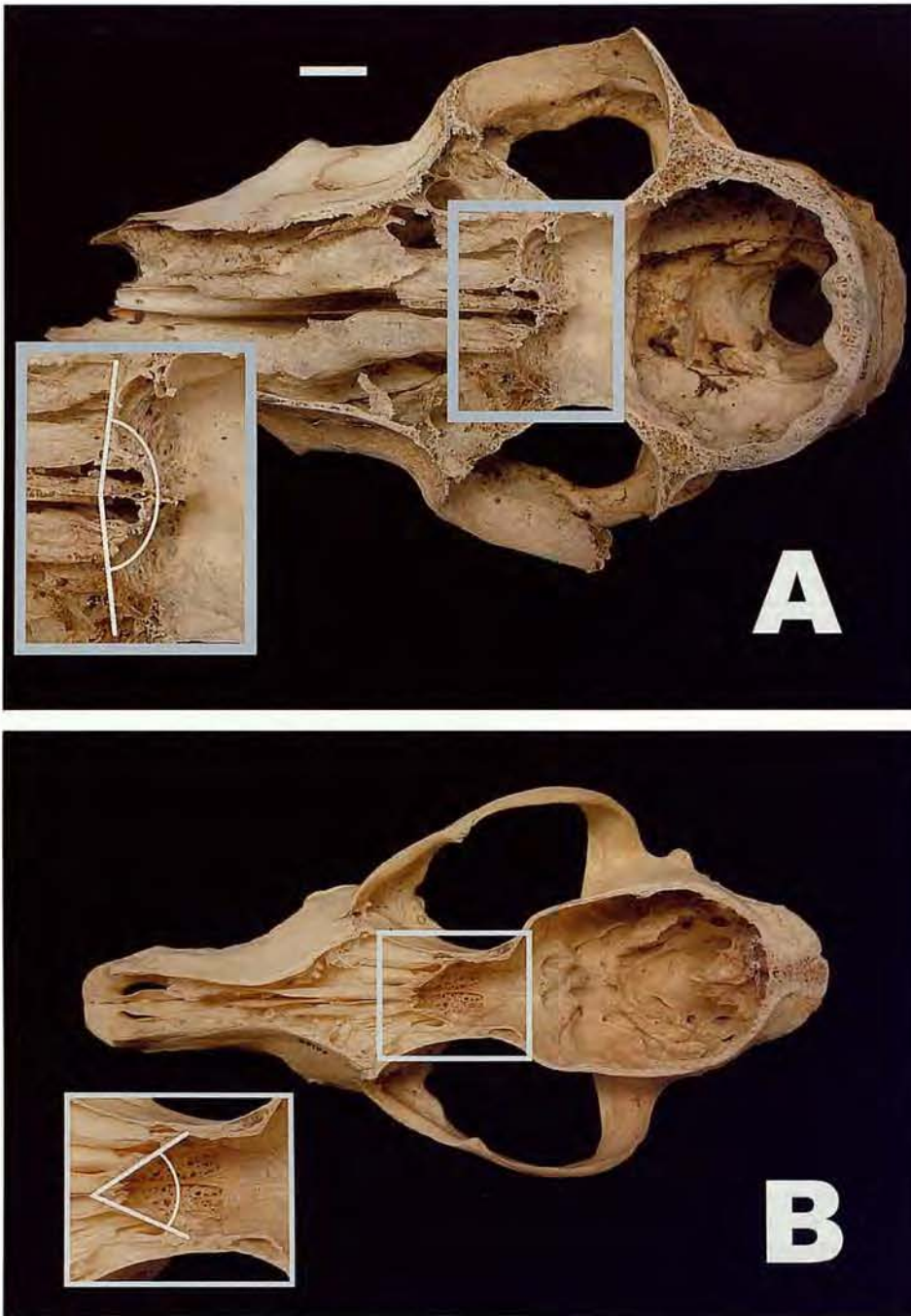


Fig. 5. Skulls with removed dorsal region of neurocranium. A: *Ovis aries* MNIB 85107. B: *Canis familiaris* MNIB 85106. Detail, lower left part of each skull, position of lamina cribrosa in each species. While in *Canis* the position of the lamina is oblique in relation to sagittal plane, in *Ovis*, the lamina is positioned in a transverse plane. Scale bar, 2 cm.

Fig. 5. Cranis amb la regió dorsal del neurocrani seccionada. A: *Ovis aries* MNIB 85107. B: *Canis familiaris* MNIB 85106. En detall, a la part inferior esquerra de cada crani, l'orientació de la làmina cribrosa a cada espècie. Mentre que a *Canis* la posició de la làmina és obliqua respecte al pla sagital, a *Ovis*, la làmina està situada en un pla transversal. Escala, 2 cm.

- Category 1: numerous perforations distributed uniformly on the whole surface of the lamina cribrosa (except for the row of larger foramina on each side of the *crista galli*, see above). This is the case of *Nemorhaedus goral* (see Fig. 8).
- Category 2: numerous perforations distributed nearly uniformly on the whole surface of the lamina cribrosa (except for the row of larger foramina on each side of the *crista galli*), with a small region which is very slightly or not at all perforated in the central area of each side of the plate. For instance *Ovis aries* (see Fig. 3).
- Category 3: reduced number of perforations, distributed in peripheral areas of the lamina cribrosa (except for the row of larger holes on each side of the

crista galli). The non-perforated central area occupies an important surface area on each side of the plate. By way of example, *Ovibos moschatus* (see Fig. 9).

- Category 4: extraordinarily reduced number of perforations distributed in the peripheral area of the lamina cribrosa. The most representative case studied is that of the pinnipeds, for instance *Phoca vitulina* (see Fig. 6).

Table 2 relates the species of present day mammals studied according to their morphology and distribution of the perforations in the lamina cribrosa.

The measurements carried out in bovids are presented in Table 3. Only in the case of the AmCR/AICR index (lamina cribrosa width/lamina cribrosa height) does there seem to be any differences in *M. balearicus*, which

basically respond to the more rounded morphology of the area of the olfactory bulb, like in *Nemorhaedus goral*, *Syncerus caffer*, *Taurotragus oryx* and *Ovis aries*. The greatest values of the AmCR/AmN index (lamina cribrosa height/nasal width) are produced in *M. balearicus*, basically due to the reduced nasal width in this species. Moreover, we observe considerable variability in practically all the indexes calculated in which there are more than one individual per species.

The angles calculated for the different species studied do not indicate any type of outstanding anatomical particularity. In fact, the angle formed by the lamina cribrosa seems to be more related to the anatomical posture of the animal, always so as to make the plate perpendicular to the nasal cavity. In humans for instance, with a bipedal posture, the lamina cribrosa is situated horizontally (Tolosa, 1980).

Morphologically the lamina cribrosa of *M. balearicus* is included in category 3, in agreement with the morphology and distribution of the foramina in the lamina cribrosa.

DISCUSSION

The morphology of the lamina cribrosa of *M. balearicus* clearly indicates a reduction in the olfactory capacity of the species in relation to other caprines or other similar-sized bovids. The only species of artiodactyl studied which has a similar morphology is *Ovibos moschatus*. This reduction in the olfactory capacity could be related to the terrestrial predator free environment where *Myotragus* lived (absence of carnivorous mammals). In the Gymnesics Islands a great olfactory capacity was not necessary in order to detect terrestrial predators. The reduced olfactory capacity of the species inferred by our study is in agreement with the small size of the olfactory bulb of the *Myotragus* brain revealed by the study of many skulls (e.g., Dechaseaux, 1961).

Category	Species
1	<i>Madoqua kirkii</i> , <i>Nemorhaedus goral</i> , <i>Canis familiaris</i>
2	<i>Hemitragus jemlahicus</i> , <i>Litocranius walleri</i> , <i>Neotragus pygmaeus</i> , <i>Oreamnos americanus</i> , <i>Ovis aries</i> , <i>Ovis canadensis</i> , <i>Syncerus caffer</i> , <i>Taurotragus oryx</i>
3	<i>Ovibos moschatus</i> , <i>Vombatus ursinus</i>
4	<i>Monachus tropicalis</i> , <i>Phoca vitulina</i>

Table 2. List of mammal species studied, ordered by category of morphology and distribution of lamina cribrosa foramina. Bold, Bovidae species.

Taula 2. Relació de les espècies de mamífers estudiats segons la seva categoria de la morfologia i distribució de les perforacions de la làmina cribrosa. En negreta es posen les espècies pertanyents a la família Bovidae.



Fig. 6. Detail of the lamina cribrosa of *Phoca vitulina* NMNH 504110. Number of foramina is reduced. Scale bar, 1 cm.

Fig. 6. Detall de la làmina cribrosa de *Phoca vitulina* NMNH 504110. El nombre de perforacions està molt reduït. Escala, 1 cm.

It would seem logical to believe that the absence of predators living in the Balearic Islands could be related to the supposed reduction in the olfactory capacity of *M. balearicus*. Among the species of living bovids, the anti-predatory strategy before attack is basically guided by the location of possible predators by sight and hearing, above all in species in open habitats and savannahs (Carl & Robbins, 1988). Small species of bovids living in closed habitats of dense woods use their sense of smell in an important way to locate predators (Macho & Williamson, 2002).

As far as the sense of smell is concerned as a response to food stimuli, it must be said that it has not yet been studied as regards skull morphology and even less regarding the lamina cribrosa in bovids. What is known is the importance of the use of smell for reproductive times and to follow the herd (Nowak & Paradiso, 1984).

What is more, it is worth bearing in mind how the relative reduction of brain size observed in *M. balearicus* (Köhler & Moyà-Solà, 2004) could have affected the morphology observed for the lamina cribrosa. Kaas (2000) states that an evolutionary increase in brain size produces both an increase in the number of neurons and in their size (which is reflected in a change in nerve size). The same author states that a reduction in the number of neurons due to a reduction in brain size could, basically, produce an important problem. A certain number of neurons is necessary so that a function can be executed correctly. A loss in neurons could cause certain circuits not to be func-

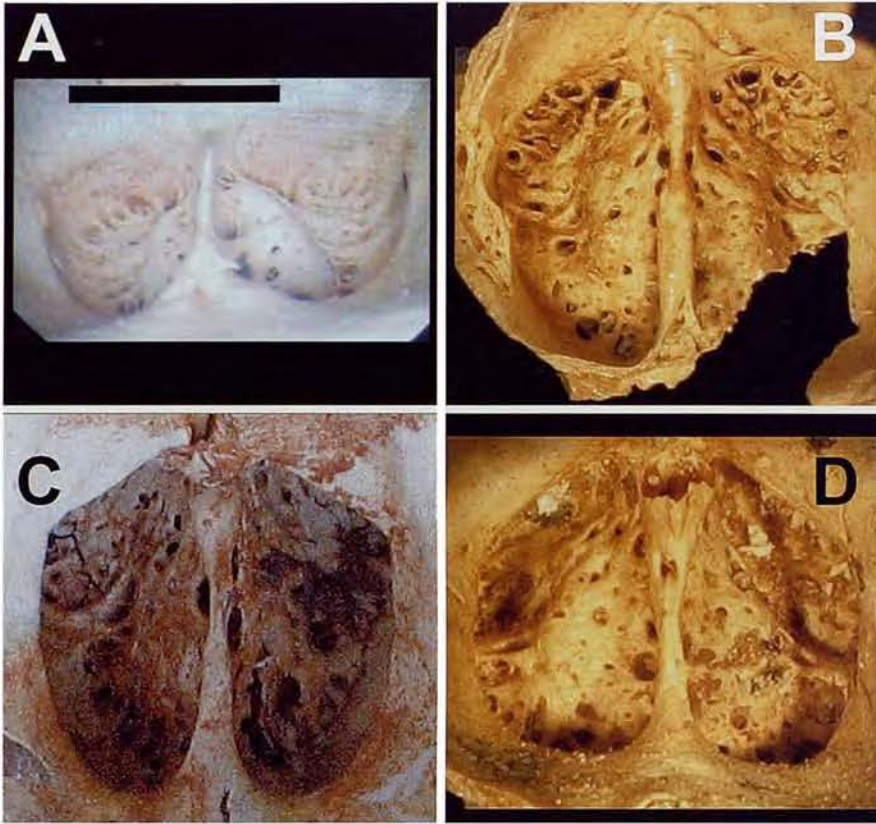


Fig. 7. Detail of the lamina cribrosa of some *M. balearicus* skulls. A: MNIB 5213; B: without number; C: MNIB 5222; D: MNIB 85109. On the MNIB 5213 skull (A) the bulk near *crista galli* can be seen. The lower number of foramina is also noted. Scale bar, 1 cm.

Fig. 7. Detall de la làmina cribrosa de diversos cranis de *M. balearicus*. A: MNIB 5213; B: sense numerar; C: MNIB 5222; D: MNIB 85109. Al crani MNIB 5213 (A) es pot observar l'abultament que presenta devora la *crista galli*. També es poden apreciar el nombre reduït de perforacions. Escala, 1 cm.

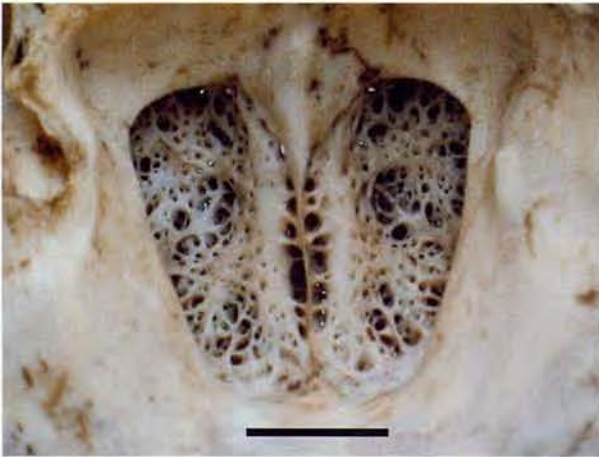


Fig. 8. Detail of the lamina cribrosa of *Nemorhaedus goral* NMNH 259411. Foramina are uniformly distributed in the lamina cribrosa. Scale bar, 1 cm.

Fig. 8. Detall de la làmina cribrosa de *Nemorhaedus goral* NMNH 259411. Les perforacions estan repartides de forma uniforme per la làmina. Escala, 1 cm.



Fig. 9. Detail of the lamina cribrosa of *Ovibos moschatus* NMNH 6251. This species shows a similar morphology of lamina cribrosa than that of *M. balearicus*. Scale bar, 1 cm.

Fig. 9. Detall de la làmina cribrosa d'*Ovibos moschatus* NMNH 6251. Aquesta espècie presenta una morfologia de la làmina similar a la de *M. balearicus*. Escala, 1 cm.

tional, with all the negative consequences that this would produce. Once this point has been reached, one solution is to completely abandon some circuits in order to keep others functional (Kaas, 2000). The intrinsic effect of the reduction in brain size in *M. balearicus* does not seem to have been the main cause of the reduction in nervous connections with the olfactory epithelium. Other species,

with proportionally larger brains than *M. balearicus*, such as pinnipeds and the bovid *Ovibos moschatus* have either a lower or similar number of ramifications of the olfactory nerves as the Balearic fossil caprine. On the other hand, small-brained species (*Madoqua kirkii*, *Neotragus pygmaeus*) have a very highly perforated lamina cribrosa (categories 1 and 2 respectively).

Seeing the information provided, it can be concluded that the olfactory capacity of *M. balearicus* was lessened, a fact which is quite possibly linked to the lack of predatory mammals in the Balearics. *Aquila chrysaetos* has been identified as a possible predator of *M. balearicus* young (Arnau *et al.*, 2000; Alcover *et al.*, 2004). The pressure of bird predation on a medium-sized mammal is not as hard as the pressure of predation from a mammal (e.g., Worthy & Holdaway, 2002). The detection of a flying predator is not made by smell, but rather by sight or by hearing.

M. balearicus was very possibly capable of eating any type of plant (Bover, 2004). As the current state of knowledge stands, the reduction in olfactory capacity cannot be related to feeding, even though it cannot be excluded that it may have had some sort of effect on the selection of the most nutritional parts of plants.

Ovibos moschatus also has a certain reduction in olfactory capacity. Interpreting this fact proves to be complicated. The fact that in *Ovibos moschatus* the number of foramina in the lamina cribrosa is similar to *M. balearicus* could be related to the peculiar defensive behaviour of

the species in the presence of predators. When a group of *O. moschatus* is attacked by a predator (basically wolves), the individuals in the group have singular defensive behaviour: they all group together, forming a circle or semicircle with the young on the inside of the group (Nowak & Paradiso, 1984). In this species a collective defensive strategy seems to be more important than fleeing behaviour in the presence of terrestrial predators.

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SPECIES	COL	NUM	AmCR	AICR	CBL	AmN	AmN/CBL	AmCR/AICR	AmCR/AmN	AICR/AmN	ANGLE	CAT.
<i>Oreamnos americanus</i>	NMNH	218758	14,18	20,00	274,84	47,92	0,174	0,709	0,296	0,417	60,4	2
<i>Oreamnos americanus</i>	NMNH	218789	10,13	15,34	306,64	47,28	0,154	0,660	0,214	0,324	52,0	2
<i>Oreamnos americanus</i>	NMNH	201003	12,40	15,84	249,84	35,28	0,141	0,783	0,351	0,449	54,9	2
<i>Oreamnos americanus</i>	NMNH	201002	12,70	17,92	245,80	38,48	0,156	0,708	0,330	0,466	68,6	2
<i>Oreamnos americanus</i>	NMNH	287532	13,14	20,14	270,00	44,38	0,164	0,652	0,296	0,454	52,7	2
<i>Oreamnos americanus</i>	NMNH	287553	14,22	19,70	271,14	44,24	0,163	0,722	0,321	0,445	60,3	2
<i>Oreamnos americanus</i>	NMNH	287552	11,54	18,54	271,90	45,96	0,169	0,622	0,251	0,403	64,6	2
<i>Nemorhaedus goral</i>	NMNH	259411	11,90	21,68	192,92	32,12	0,166	0,549	0,370	0,675	80,3	1
<i>Ovibos moschatus</i>	NMNH	6251	14,02	21,94	457,70	86,04	0,188	0,639	0,163	0,255	63,0	3
<i>Ovibos moschatus</i>	NMNH	120921	17,02	26,56	469,12	98,34	0,209	0,941	0,173	0,270	43,8	3
<i>Syncerus caffer</i>	NMNH	220129	16,56	28,30	400,60	73,80	0,184	0,585	0,224	0,383	72,4	2
<i>Taurotragus oryx</i>	NMNH	199548	16,66	30,72	422,36	71,88	0,170	0,542	0,232	0,427	63,4	2
<i>Madoqua kirkii</i>	NMNH	396306	-	-	112,28	14,80	0,132	-	-	-	67,3	1
<i>Madoqua kirkii</i>	NMNH	538106	-	-	104,80	12,40	0,118	-	-	-	58,0	1
<i>Saiga tatarica</i>	NMNH	336265	14,68	19,16	210,30	28,66	0,136	0,766	0,512	0,669	76,7	2
<i>Tayassu tajacu</i>	NMNH	499758	10,82	16,66	195,90	35,88	0,183	0,649	0,302	0,464	38,0	2
<i>Ovis aries</i>	MNIB	85104	11,04	21,06	-	31,8	-	0,524	0,347	0,662	74,5	2
<i>Ovis canadensis</i>	NMNH	244189	13,90	19,54	257,96	44,94	0,174	0,711	0,309	0,435	70,1	2
<i>Ovis canadensis</i>	NMNH	218006	15,86	23,20	311,12	60,36	0,194	0,684	0,263	0,384	76,3	2
<i>Myotragus balearicus</i>	MNIB	5222	6,18	12	-	17,18	-	0,515	0,360	0,698	54,7	3
<i>Myotragus balearicus</i>	MNIB	SN	7,53	13,78	-	20,94	-	0,546	0,359	0,658	60,5	3
<i>Myotragus balearicus</i>	MNIB	SN	6,14	10,30	-	-	-	0,596	-	-	-	3

Table 3. Result of the measurements (in mm) proposed in this paper for the different species studied. AmCR: Lamina cribrosa Breadth, AICR: Lamina cribrosa Height; CBL: Condilobasal Length; AmN: Nasal Breadth. In this table indexes and categories according to lamina cribrosa morphology (CAT) are also shown. NMNH: National Museum of Natural History (Washington, D.C.); MNIB: Museu de la Naturalesa de les Illes Balears (Palma).

Taula 3. Valors obtinguts de les mesures (en mm) considerades per a les diferents espècies estudiades. AmCR: Amplada de la Làmina Cribrosa, AICR: Alçada de la Làmina Cribrosa; CBL: Longitud Còndilo Basal; AmN: Amplada Nasal. Es presenten els valors dels índexos estudiats, així com les categories que s'han establert en base a la morfologia de la làmina cribrosa (CAT). NMNH: National Museum of Natural History (Washington, D.C.); MNIB: Museu de la Naturalesa de les Illes Balears (Palma).

REFERENCES

- Accordi, F.S. & Palombo, M.R. 1971. Morfologia endocranica degli elefanti nani pleistocenici di Spinagallo (Siracusa) e comparazione con l'endocrania di *Elephas antiquus*. *Accad. Naz. Lincei, Rend. Sc. Fis. Mat. Nat.*, 51: 111-124.
- Alcover, J.A. 2004. Tendencias evolutivas de los vertebrados en las islas. In Fernández-Palacios, J.M. & Morici, C. (eds.), *Ecología Insular*: 277-304. Ed. AEET y Cabildo Insular de La Palma. La Palma, Islas Canarias.
- Alcover, J.A., Moyà-Solà, S. & Pons-Moyà, J. 1981. *Les Quimeres del Passat. Els Vertebrats Fòssils del Plió-Quaternari de les Balears i Pitiüses*. Edit. Moll. Palma de Mallorca. *Monografies Científiques*, 1: 1-260.
- Alcover, J.A., Bover, P. & Seguí, B. 1999. Una aproximació a la paleoecologia de les illes. *Monografies de la Societat d'Història Natural de les Balears*, 6/ *Monografies Institut d'Estudis Baleàrics*, 66: 169-204.
- Alcover, J.A., Bover, P., Escandell, M.J., López-Garí, J.M., Marlasca, R. & Ramis, D. 2004. Els superdepredadors de la fauna pleistocènica de Menorca i Formentera. *Endins*, 26: 53-57.
- Arnau, P., Bover, P., Seguí, B. & Alcover, J.A. 2000. Sobre alguns jaciments de *Myotragus balearicus* Bate 1909 (*Artiodactyla*, *Caprinae*) de tafonomia infreqüent. *Endins*, 23: 89-100.
- Bate, D.M.A. 1909. Preliminary note on a new artiodactyle from Mallorca *Myotragus balearicus*, gen. et sp. nov. *Geological Magazine*, Dec. 5, 6: 385-389.
- Bover, P. 2004. *Noves aportacions al coneixement del gènere Myotragus Bate, 1909 (Artiodactyla, Caprinae) de les Illes Balears*. PhD Thesis. Universitat de les Illes Balears. Palma de Mallorca. 469 pp.
- Caloi, L. & Palombo, M.R. 1990. Pleistocene herbivores of Mediterranean islands. *Hystrix*, 2: 87-100.
- Caloi, L., Kotsakis, T. & Palombo, M.R. 1988. La fauna a vertebrati del Pleistocene delle isole del Mediterraneo. *Bull. Ecol.*, 19 (2-3): 131-152.
- Carl, G.R. & Robbins, C.T. 1988. The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. *Can. J. Zool.*, 66: 239-246.
- Dechaseaux, C. 1961. Moulages endocraniennes de bovidés fossiles. *Ann. Paleont.*, 47: 51-73.
- Fleagle, J.G. 1988. *Primate adaptation and evolution*. Academic Press. London and New York.
- Holloway, R.L. 1968. The evolution of the primate brain: some aspects of quantitative relations. *Brain Res.*, 7: 121-172.
- Holloway, R.L. 1978. The relevance of endocasts for studying primate brain evolution. In Noback, C.R. (ed.), *Sensory systems in primates*: 181-200. Plenum Press. New York.
- Insley, S.J., Phillips, A.V. & Charrier, I. 2003. A review of social recognition in pinnipeds. *Aquatic Mammals*, 29.2: 181-201.
- Kaas, J.H. 2000. Why is brain size so important: design problems and solutions as neocortex gets bigger or smaller. *Brain and Mind*, 1: 7-23.
- Köhler, M. & Moyà-Solà, S. 2004. Reduction of brain size reduction and sense organs in the fossil insular bovid *Myotragus*. *Brain, Behavior and Evolution*, 63: 125-140.
- Lalueza-Fox, C., Bertranpetit, J., Alcover, J.A., Shailer, N. & Hagelberg, E. 2000. Mitochondrial DNA from *Myotragus balearicus*, an extinct bovid from the Balearic Islands. *Journal of Experimental Zoology (Molecular & Developmental Evolution)*, 288: 56-62.
- Lalueza-Fox, C., Saphiro, B., Bover, P., Alcover, J.A. & Bertranpetit, J. 2002. Molecular phylogeny and evolution of the extinct bovid *Myotragus balearicus*. *Molecular Phylogenetics and Evolution*, 25: 501-510.
- Macho, G.A. & Williamson, D.K. 2002. The effects of ecology on life history strategies and metabolic disturbances during development: an example from the African bovines. *Biol. J. Linnean Soc.*, 75: 271-279.
- Nowak, R.M. & Paradiso, J.L. 1984. *Walker's Mammals of the World, 4th Edition*. John Hopkins University Press. Baltimore & London.
- Quintana, J. 2002. *Estudio morfológico y funcional del cráneo y la mandíbula de Nuralagus rex*. Memòria d'investigació. Universitat Autònoma de Barcelona.
- Ryg, M., Solberg, Y., Lydersen, C. & Smith, T.G. 1992. The scent of rutting male ringed seals (*Phoca hispida*). *J. Zool. Lond.*, 226: 681-689.
- Tobias, P.V. 1975. Brain evolution in the Hominoidea. In Tuttle, R.H. (ed.), *Primate functional anatomy and evolution*: 353-392. Mouton. The Hague.
- Tolosa, F. 1980. *Anatomia y embriología de los componentes nerviosos de la fosa pterigoidea*. Tesi Doctoral. Universitat de Barcelona.
- Von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletin*, 1: 1-117.
- Worthy, T.H. & Holdaway, R.N. 2002. *The lost world of the moa. Prehistoric life of New Zealand*. Indiana Univ. Press. Indiana. 718 pp.
- Xu, F., Greer, C.A. & Shepherd, G.M. 2000. Odor maps in the olfactory bulb. *J. Comp. Neurology*, 422: 489-495.