

CARPAL BONES, CARPAL FUSIONS AND FOOTPRINTS OF *MYOTRAGUS*: CLUES FOR LOCOMOTION AND BEHAVIOR

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Resum

Algunes de les característiques anatòmiques de les extremitats de *Myotragus balearicus* demostren que aquesta espècie presentava una locomoció anomenada de "marxes curtes". Entre aquestes característiques cal destacar la fusió del complex naviculocuboide als cuneïforms gran i petit i al metatars, la pròpia morfologia dels ossos de les extremitats, amb ossos molt robusts i amb àrees d'inserció muscular i lligamentosa molt importants. Totes aquestes característiques s'han interpretat com una forma d'establir les articulacions degut a un gran pes corporal en relació a l'alçada del cos, en detriment d'una locomoció més cursorial. A més, s'han obtingut alguns ossos procedents de l'excavació dels jaciments de la cova Estreta (Pollença, Mallorca) i la cova des Moro (Manacor, Mallorca) que presenten unes característiques que s'adiuen amb les interpretacions més a dalt presentades. En concret, s'ha obtingut un os resultant de la fusió de l'escafoide i el semilunar, i un os resultant de la fusió del pisiforme i el cuneïforme. Actualment, només es disposa de dos exemplars del primer tipus de fusió i un del segon tipus. Cap d'aquests ossos sembla ser patològic, i no presenten cap tipus de creixement ossi a la zona de fusió. La fusió de l'escafoide i el semilunar, i la fusió del cuneïforme i el pisiforme semblen provocar una limitació de moviment, i juntament amb les característiques d'altres articulacions (bàsicament de l'extremitat anterior), demostren que les extremitats no estaven situades just davall del cos, tal com passa a quasi tots els bòvids actuals. De nou, sembla que aquestes fusions (juntament amb la robustesa dels ossos del carp) estan relacionades amb l'adquisició d'una major estabilitat de les articulacions.

Les petjades i els rastres poden ser importants fonts d'informació pel que fa a la locomoció i comportament d'espècies fòssil i actuals. A pesar de que es disposa d'una considerable quantitat de petjades de *Myotragus*, només es poden seguir i mesurar molts pocs rastres o pistes. En concret, els jaciments de s'Estret des Temps i ses Piquetes a Santanyí (Mallorca) han proporcionat tres rastres que s'han estudiat aquí en detall. La mesura de la longitud de passa, l'amplada entre extremitats (anterior i posterior) i l'orientació dels potons pot donar algunes pistes sobre la locomoció i el disseny corporal d'aquesta espècie. L'angle dels peus (cap a fora) de *M. balearicus* és considerablement superior a la dels altres espècies d'ungulats estudiades, com *Cervus elaphus* i *Ovis aries*. Aquesta mesura, juntament amb la relativa separació de les extremitats (relacionada amb la longitud de passa), indiquen que les extremitats d'aquesta espècie no estaven situades just davall del cos durant la marxa (com a quasi tots els bòvids actuals), tal com se pot inferir a partir d'altres característiques anatòmiques.

Paraules clau: *Myotragus* - locomoció - ossos del carp - fusions òssies - rastres - etologia.

Abstract

Some of the anatomical features of the *Myotragus balearicus* limb bones show that this species displayed a "low gear" locomotion. These features are the fusion of the naviculocuboïd complex to the large and small cuneiforms and to the metatarsal bone, limb bones morphology and very stout leg bones with important muscular and ligament insertions. All these features have been identified as a way to stabilise the joints due to a great body mass in relation with the body height, in detriment of a cursorial locomotion. From the excavation of deposits as Cova Estreta (Pollença, Mallorca) and Cova des Moro (Manacor, Mallorca) several bones have been obtained displaying undescribed features that agree with the above explained proposal. Specifically, it has been obtained a bone produced as the result of the fusion of scaphoid and lunar and a bone result of the fusion of pisiform and cuneiform. For the present, only have been obtained two specimens of the former case and just one of the later. None of the bones seem to be pathologic, and they do not show any kind of bone regrowth in the fusion zone. Fused scaphoid and lunar, and fused cuneiform and pisiform, seems to limit this movement, and together with anatomical characteristics of other joints (mainly in the fore leg), shows that the legs were not placed just under the body, as the almost all the extant bovids. Again, it seems that these fusions (together with the stoutness of the carpal bones) are also related with the stability of the joint.

Tracks and trackways can be important sources of information on locomotion and behaviour of fossil (and extant) species. Although a considerable amount of *Myotragus* footprints are available, just few trackways can be followed and measured. Particularly, the deposits of s'Estret des Temps and Ses Piquetes in Santanyí (Mallorca) have furnished three trackways that have been here studied in detail. The measurement of path length, width between limbs (fore and hind limbs) and feet orientation can give some clues on locomotion and body design of this species. The feet angle (outwards) of *M. balearicus* is considerably larger than in other ungulate species studied, as *Cervus elaphus* and *Ovis aries*. This measurement together with the relative separation of the limbs (related to the path length) show that the limbs of this species were not positioned just under the body during walking (as almost all the extant bovids), as can be inferred from other anatomical characteristics.

Key words: *Myotragus* - locomotion - carpal bones - bone fusions - trackways - ethology.

INTRODUCTION

The anatomic characteristics of *M. balearicus* bones have been studied by different authors. The main aim of these studies was to determine what the effects of the acquisition of derived characteristics were on locomotion and on the body design of *M. balearicus* (Leinders & Sondaar, 1974; Sondaar, 1977; Leinders, 1979; Moyà-Solà, 1979; Alcover *et al.*, 1981; Spoor, 1988a and b; Köhler, 1993; Köhler & Moyà-Solà, 2001). All the studies into the functional morphology of the limbs have reached conclusions along the same lines. The main inference consists of the fact that *M. balearicus* must have had a non-cursorial type of locomotion (*sensu* Gambaryan, 1974), more graviportal, characterized as slow locomotion, but with great power (called "low gear" locomotion by Sondaar, 1977). The short, robust metapodials seem to indicate great stability in the stride (Alcover, 1976; Sondaar, 1977), while the robustness of the long, proximal limb bones (femur, humerus, tibia and fibula) could be related to a greater resistance to breakage (Alcover *et al.*, 1981).

Similar adaptations to those observed in *M. balearicus* have been documented in other species. For instance, the insular fossil hippopotamus *Phanourios minutus* has an important reduction in the size of different distal limb bones (e.g., Sondaar, 1977). In the Pleistocene cervid fossil found in Crete, *Cervus cretensis*, short, robust metapodials have been observed, which must have given great stability to the stride (Sondaar, 1977).

One of the anatomical areas that has been most studied is the digital region of *M. balearicus*. The peculiar morphology of the articular areas between the metapodials and the proximal phalange (with very slightly marked sagittal crests on the distal articular facet of the metapodials, and articulations with a very small palmar-dorsal surface), and between the different phalanges (very flat surfaces, without a great articular surface), was interpreted as proof of limited flexion capacity in the metapodial-phalange and interphalangeal articulations. What is more, this anatomical characteristic also seems to indicate a reduction in the capacity to absorb the shock produced in this area during jumping or running (Leinders, 1979). For this reason, the capacity to jump would be very limited in the species, and locomotion would be of a much slower, more powerful and peaceful nature. This would be in agreement with other works (Köhler, 1993; Köhler & Moyà-Solà, 2001).

Another part of the hind limb of *M. balearicus* that has been studied is the tarsal region. One of the most singular features in *M. balearicus* is the fusion of the naviculoboid complex with the small cuneiform and with the great cuneiform. The bone resulting from the fusion of the three distal tarsals is fused to the metatarsal in most of the adult specimens of *M. balearicus* (Bate, 1909; Andrews, 1915; Alcover *et al.*, 1981; Spoor, 1988b). The fusion of these bones has been interpreted as a way of stabilising the articulations in this area, with the consequent loss of the capacity to perform zigzag movements while running (Leinders & Sondaar, 1974). These movements are very important in bovids, so as to avoid being captured by a running predator. This zigzag movement is caused by the contraction of the *musculus peroneus lon-*

gus, which transmits a small rotation movement to the metatarsal caused by the small cuneiform. In an environment lacking in terrestrial predators, it seems that this type of fleeing mechanism is not necessary, thus evolutionally favouring the stabilisation of the articulations (Leinders & Sondaar, 1974).

In fact, as regards this bone, Howell (1944) had already interpreted the progressive fusion of the different elements of the distal tarsal bones during the evolution of artiodactyls as a mechanism to restrict movement to one plane alone. *M. balearicus* would represent the extreme case known of movement restrictions in this sense.

Fusions of the tarsal bones are known in other insular fossil artiodactyls, although to a lesser extent than in *M. balearicus*. In *Cervus cretensis* from the Pleistocene in Crete different tarsal bone fusions have been found (Sondaar, 1977). They have also been described in another insular fossil species, *Hoplitomeryx* from the Miocene in *Gargano* (Leinders & Sondaar, 1974; Van der Geer, 1999).

The anatomical changes produced in the calcaneus of *M. balearicus* serve to reduce the muscular tension in this area, thus favouring greater tarsal stability and decreasing the danger of breakages and injuries. Moyà-Solà (1979) observed great roughness in the calcaneus for the strong insertion of ligaments, which provide a greater rigidity to the tarsus (above all in the calcaneus-talus articulation).

The talus has also been the object of a series of functional interpretations, in comparison with the insular deer *Hoplitomeryx* and with continental artiodactyls (Van der Geer, 1999). Its peculiar morphology, with an important lateral distortion (in anterior view, *sensu* DeGusta & Vrba, 2003, the upper part of the talus is laterally displaced), was interpreted as being related to a loss in muscular power and a rise in stability. This author also explains that the peculiar form of the talus could be related to a convergent position of the proximal bones in the hind limbs due to the fact of having a very large abdomen. A relative separation of the limbs was also postulated by Spoor (1988b).

One way of verifying some of the anatomical characteristics of the limbs, and at the same time, one of the indirect ways of inferring locomotor aspects of a fossil species, is the study of footprints and trails left in sediment. Prints, trails and tracks can be important sources of information as far as locomotion and the behaviour of fossil and extant species are concerned (e.g., deer counts, Mayle *et al.*, 2000), and have provided important information in the case of dinosaurs (e.g., Gillette & Lockley, 1991; Lockley & Hunt, 1995). In the Pleistocene-age calcareous eolianite in the south-east coast of Mallorca a series of *Myotragus balearicus* trails were found and attributed to the ichnospecies *Bifipides aeolis* (Fornós *et al.*, 2002). The first findings of footprint remains of this bovid were made in Santanyí (Fornós & Pons-Moyà, 1982), and these studies are not resumed until Fornós *et al.* (2002). These authors gave a detailed description of the *Myotragus* tracks and trackways characteristics, especially from the Upper Pleistocene of Mallorca. In Menorca, ichnites of one of the accompanying species, the rodent *Eliomys sp.*, and also trails of *Myotragus*, were found (Quintana, 1993). Recently, Quintana & Arnau (2004) have analysed and studied a trail and other footprints of the fossil rodent found in a cave in Menorca.

MATERIALS AND METHODS

Although different nomenclatures have been erected to name the carpal bones (e.g., Barone, 1968; May, 1970; Sisson & Grossman, 1982; Schaller, 1992), in this paper will be used those proposed by Yalden (1971). The used names for each bone are:

Magnum for *os carpale II et III*, *os trapezoideo-capitatum*, fused second and third carpal bones.

Unciform for *os carpale IV*, *os hamatum*, fourth carpal bone.

Cuneiform for *os carpi ulnare*, *os triquetrum*, ulnar carpal bone.

Lunar for *os carpi intermedium*, *os lunatum*, intermediate carpal bone.

Scaphoid for *os carpi radiale*, *os scaphoideum*, radial carpal bone.

Pisiform for *os carpi accesorium*, *os pisiforme*, accessory carpal bone.

The *Myotragus* bones studied in this work come mainly from two deposits in which a lot of *Myotragus balearicus* bones have been obtained, the Cova Estreta (Pollença, Mallorca) (Encinas & Alcover, 1997) and the Cova des Moro (Manacor, Mallorca) (Trias, 2000). The number of carpal bones of each deposit is 318 (87 scaphoids, 76 lunars, 38 cuneiforms, 68 magnums, 45 unciforms and 4 pisiforms) and of 72 (17 scaphoids, 15 lunars, 4 cuneiforms, 22 magnums, 12 unciforms and 2 pisiforms), respectively. Additionally, more bones from other deposits have been studied. From these deposits a lesser number of bones has been obtained. For example, the Cova de Son Maiol (Palma, Mallorca) with 38 bones (7 scaphoids, 12 lunars, 4 cuneiforms, 8 magnums, 5 unciforms and 2 pisiforms) and the Cova C-2 (Ciutadella, Menorca) with 5 bones (2 scaphoids, 1 lunar, 1 magnum and 1 unciform). All these bones are curated in the vertebrate collection MNIB and their catalogue numbers are related in Bover (2004).

As a comparison material the carpal bones of several species taxonomically related to *Myotragus* genus have been studied. The acronyms of the studied material are:

AMNH: American Museum of Natural History (New York, USA).

NMNH: National Museum of Natural History-Smithsonian Institution (Washington D.C., USA)

MNCN: Museo Nacional de Ciencias Naturales (Madrid, Spain)

MZB: Museu de Zoologia de Barcelona (Barcelona, Spain)

MNIB: Museu de la Naturalesa de les Illes Balears (Mallorca, Spain)

The extant species studied are: *Ammotragus lervia* (MZB 94-0661 and 97-0680), *Bos taurus* (MNIB 48177 and 48292), *Bison bison* (AMNH 3754 and 98954 and NMNH 839 and 22664), *Budorcas taxicolor* (AMNH 57013, 57014, 57016 and 57017 and NMNH 259079), *Capra hircus* (MNIB 39996, 40000, 48167-48175, 48208-48212, 48222, 48223, 60096, 60148, 60149, 65277 and 73196), *Capra pyrenaica* (MZB 94-0682), *Capricornis crispus* (AMNH 165685 and NMNH 20934), *Capricornis sumatrensis* (NMNH 258670 and 259025), *Nemorhaedus goral* (AMNH 43001, 43004 and 110481), *Oreamnos ame-*

ricanus (AMNH 35286, 35492, 35786 and 130223), *Ovibos moschatus* (AMNH 35588, 35612, 80095, 100058 and 202866), *Ovis aries* (MNIB 39997-39999, 48176, 48181, 60098, 60147, 60150, 73865 and 73866), *Ovis musimon* (MZB 92-0233), *Rupicapra pyrenaica* (MNCN 2218 and 2271 and MNIB 60091, 60092 and 65276), *Rupicapra rupicapra* (MZB 98-0258 and 98-0259).

Although there is a considerable quantity of *Myotragus* footprints available (sometimes to excess, defined as myoturbation in Fornós *et al.*, 2002), only very few trails can actually be followed and measured which seem, clearly, to be the trail made by an isolated individual. Specifically, the sites in S'Estret des Temps and Ses Piquetes in Santanyí (Fornós & Pons-Moyà, 1982; Fornós *et al.*, 2002) have provided three trails that can be studied in detail. We have also included in this work the measurements obtained by Quintana (1993) of the *Myotragus* trails in Menorca.

The measurements carried out are (Fig. 1):

- Stride Length (SL): distance measured between two homologous points of two footprints belonging to the same foot, that is, the distance covered by one limb.
- Trail Width (TW): distance between two imaginary lines traced between the outside of two footprints on each side. This measurement serves to infer the transversal distance between two limbs.
- Feet Angle (FA): angle made from two lines, one parallel to the direction of the animal's stride and the other parallel to the line of separation of the two toes in each hoof.
- Trail Index (TI): the result of the SL/TW division. This index enables us to compare the trails of different species.

Only in the cases of our own measurements have we obtained values in cm of the SL and TW, due to the fact that in the literature the trail is only drawn or photographed, without any real values. Thus, we have taken values obtained from the photos to calculate the TI.

These measurements can provide information as to the locomotion and body design of this species (Bover, 2004). As material for comparison we used the trails of extant bovids which can be found in Cabrera (1997) and in the literature on the trails of extant species (Bang & Dahlström, 1975). What is more, we carried out measurements on the trails of sheep (*Ovis aries*) in the farm of Son Cotoner d'Avall (Puigpunyent, Mallorca) and goats (*Capra hircus*) in the area of Cala Sant Vicenç (Pollença, Mallorca).

RESULTS

The carpal bones of *M. balearicus* were not described in detail by Andrews (1915). Only Spoor (1988b) mentions that they have normal proportions, although he does observe that the *stop-facets* of the distal area are well developed, a characteristic which gives more stability to the articulation. This author states that the flexion of the proximal and ulnar carpal articulations are less than 90° and 75°, respectively, calculated by Yalden (1971) in different bovids.

Here we present a more detailed description of the carpal bones in *M. balearicus* as there is no complete one available. We have also compared the morphology of these bones with that of different species of bovids.

All the carpal bones have, as happens with other bones in *M. balearicus*, a high degree of robustness. In general, all the carpal bones in *M. balearicus* have a proximal-distal compression, a fact which causes the areas of ligament insertion to be much more important than in other caprines (Fig. 2 and 3). This compression is also present in *Oreamnos americanus* and in *Ovibos moschatus*, albeit to a lesser degree.

The anatomical description of each part of the carpal bones will be done for each margin of each bone and not according to the view from which it is observed.

The description is always carried out using the bones of *Myotragus balearicus* as a reference.

Scaphoid

Proximal margin

The articulation surface with the distal epiphysis of the radius is "S"-shaped in flexor-extensor view [FES, according to Yalden, (1971)], although the articulation surfaces have a more abrupt relief, that is, the different articulation areas are separated by crests which are more or less developed (Fig. 2C).

In the proximal part, the highest prominence on this surface, which articulates with the fossa for this prominence in the distal part of the radius, is not rounded, neither is it surrounded by more articular surface (not in all cases) (Fig. 2a), rather there are basically three morphologies:

- In front of the prominence there is a transversally convex-shaped articular surface, (as happens in *Capra hircus*), but much more acute.

- In some cases, the articular surface can become transformed into a crest which joins the more dorsal margin (extensor margin) of the scaphoid with the prominence (similar to *Oreamnos americanus*) (Fig. 3a1-4). The dorsal prominence is more elevated than or at the same height as the palmar.

- In four of the pieces observed in Cova Estreta (MNIB 44841, 50128, 53352 and 55935) there is no articular surface in front of the prominence, but rather the prominence forms an apical margin, which means a restriction in the extensor movement.

The medial prominence is very well-developed (Fig. 2b), as happens in *Oreamnos americanus* (Fig. 3a1), projecting towards the axis of the limb, fitting with a notch in the proximal-medial margin of the lunar. In *Nemorhaedus goral* this medial prominence is also quite well marked. It is not so well marked in the other caprines studied.

Lateral margin

The distance between the fossas of the dorsal and ventral sides in some cases is proportionally less than in the other caprines. The articular facet is rounder (Fig. 2c) and is more ventrally developed. Its orientation is different; it is not as parasagittal, but rather takes a proximal-dorsal-lateral orientation.

On the distal-palmar side there is a very pointed prominence (absent in *Oreamnos americanus* and rounded in *Capra hircus*), which has an articular facet facing in a proximal-palmar direction. This is absent in practically all the species studied and serves as an articulation with the lunar (Fig. 2d). Only in *Ovibos moschatus* can a ridge be found sticking out of the lateral articular area (Fig. 3c1). In the other extant species this articulation is not there since the dorsal crest of the magnum impedes it. In *Capricornis sumatrensis* this articular surface is quite large, but does not have this articular ridge.

Distal margin

The main difference is that the prominence explained by the lateral margin, means that the distal contact surface with the magnum is larger, which means that there are restrictions to the movement between the scaphoid and the lunar.

The articulation area with the magnum is "S"-shaped (Fig. 2e). The concave part is more rounded and is at times cup-shaped because the lateral edge is closed. The convex part (dorsal) is, proportionally, much smaller

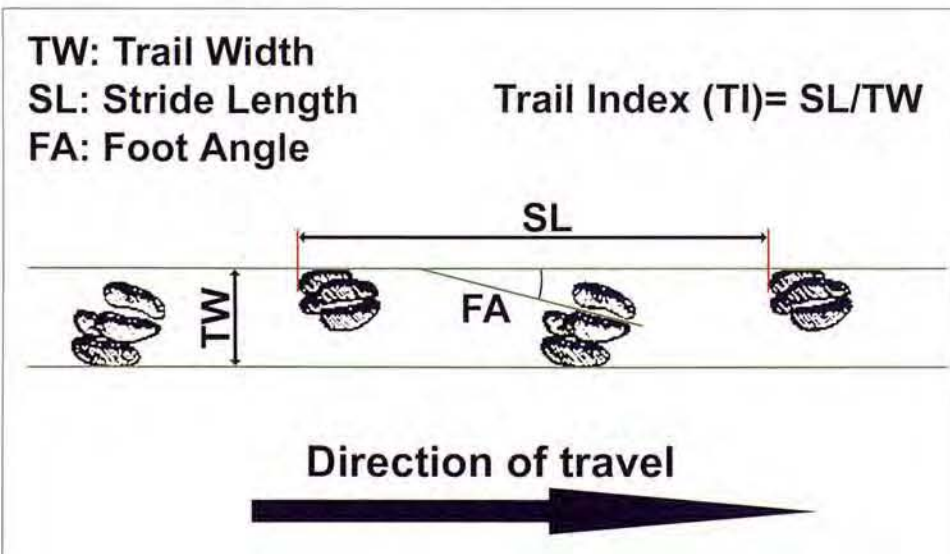


Fig. 1. Measurements on trackways of the different species studied.

Fig. 1. Mesures réalisées sobre les petjades de les diferents espècies estudiades.

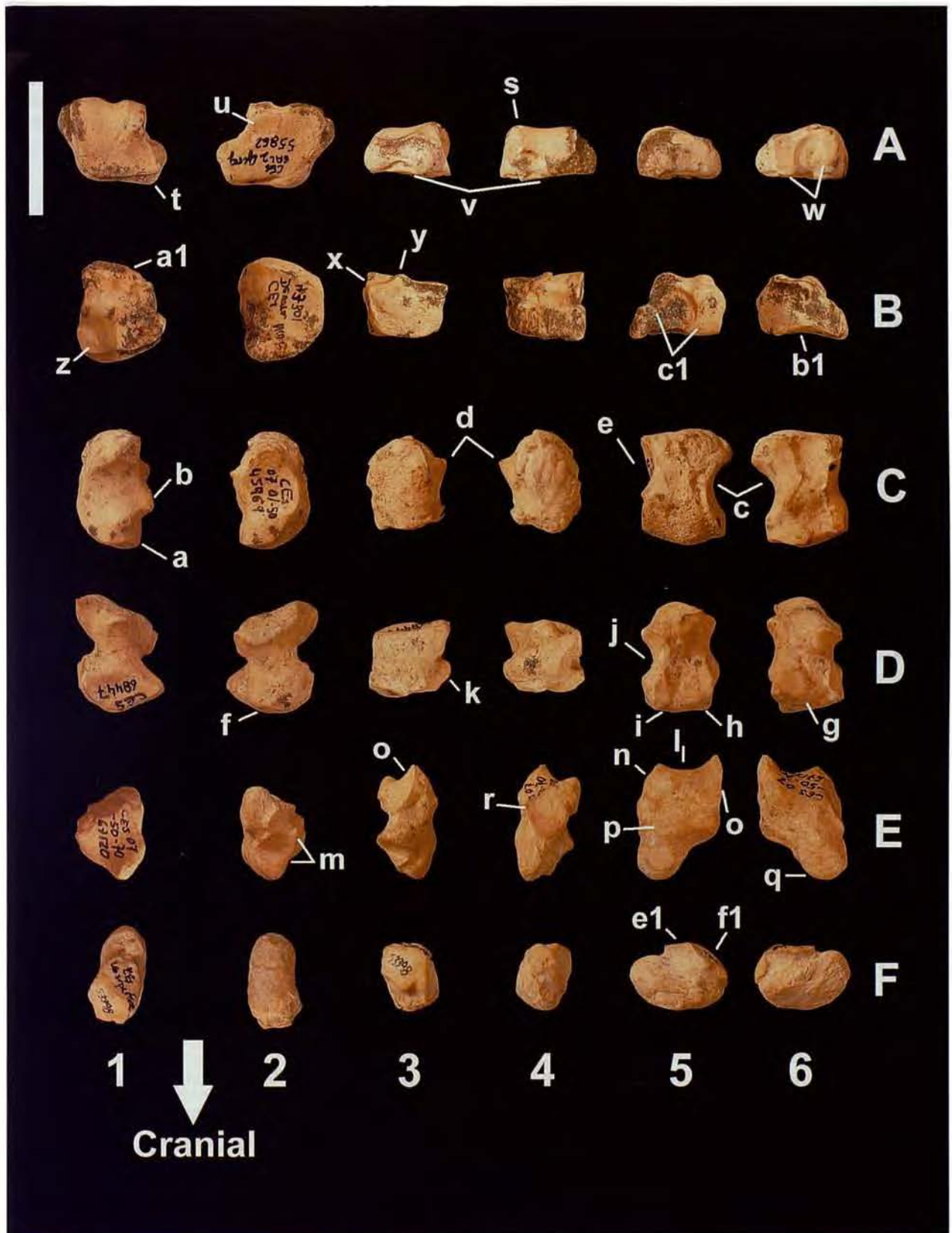


Fig. 2. *M. balearicus* carpal bones. A: left magnum MNIB 55682. B: right unciform (inverted photos) MNIB 43301. C: left scaphoid MNIB 68447. D: left lunar MNIB 45969. E: left cuneiform MNIB 67120. F: left pisiform MNIB 53398. 1: proximal view; 2: distal view; 3: dorsal view; 4: palmar view; 5: medial view; 6: lateral view. Cranial part for 1 and 2 views is indicated. Small letters explained in text. Scale bar 2 cm.

Fig. 2. Ossos del carp de *M. balearicus*. A: capitatotrapezoide esquerre MNIB 55682. B: unciforme dret (fotos invertides) MNIB 43301. C: escafoide esquerre MNIB 68447. D: semilunar esquerre MNIB 45969. E: cuneiforme esquerre MNIB 67120. F: pisiforme esquerre MNIB 53398. 1: norma proximal; 2: norma distal; 3: norma dorsal; 4: norma palmar; 5: norma medial; 6: norma lateral. Se situa la part cranial de l'animal per a les normes 1 i 2. Les lletres en minúscules s'expliquen al text. Escala 2 cm.

than in the other species studied. In *Budorcas taxicolor* this articulation surface is not "S"-shaped, but rather flat in its dorsal region (where it has a crest), and is even slightly concave (Fig. 3b2).

Medial margin

The insertion surfaces of the different ligaments are much more developed than in the rest of the caprines.

Lunar

In general, the aspect of this bone in *M. balearicus* is really robust (as in *Budorcas taxicolor*), and the crests which separate the smooth articulation areas are not very well-marked (Fig. 2D). This is, in general, the aspect also in different species studied (*Capra hircus*, *Ovis aries*, *Capricornis crispus* and *C. sumatrensis*, *Nemorhaedus goral* and *Ovibos moschatus*), but above all in *Budorcas taxicolor*, in which, for instance, the proximal articulation surface is quite flat and the distal ones are hard to distinguish, due to the fact that there is no clear crest to mark them (Fig. 3c). On the other hand, in *Oreamnos americanus* the crests are marked, although not exaggeratedly (Fig. 3a5-7).

Proximal margin

There is no significant differential feature in comparison with the other caprines.

Distal margin

This has a relatively well-developed dorsal prominence (Fig. 2f). This is likely to be related to restrictions in carpus extension movements.

The ventral channel of articulation with the magnum and unciform is more excavated and closed than in the other caprines (Fig. 2j). In some cases the distal dorsal facet (which is more rounded in shape) and the proximal dorsal facet are also joined with an articular bridge.

The distal lateral articular facet is directed and oriented more towards the lateral side than in the rest of the caprines studied (Fig. 2k).

Lateral margin

In *Capra*, the distal articulation surface is separated from the palmar side by a crest which extends transversally to the sagittal plane. In *Oreamnos* and *M. balearicus* this articulation surface is not continuous, as in *Capra hircus* and *Ovis aries*, becoming thinner towards the palmar side but rather it forms a very thick, broad surface on the dorsal side (Fig. 2g), tapering very slowly, disappearing in some cases, and even, at times, there is only a circular or triangular surface left on the palmar side.

There is an articular facet on the distal palmar side which articulates with the cuneiform.

Medial margin

There is a small articular facet for articulation with the scaphoid (Fig. 2h), which corresponds with the aforementioned lateral prominence of the scaphoid. In *Ovibos moschatus* there is also an articular surface on the lunar for this scaphoid prominence (Fig. 3c3-4). The central fossa is deeper.

The notch in the ulnar proximal margin is more marked due to, just as has been explained with the scaphoid, a more intimate articulation with this bone (Fig. 2i). Due to the presence of this notch, the dorsal and palmar articular facets of the proximal area are separated and do not form a continuum, as happens in the species with which it has been compared.

Cuneiform

Proximal margin

No great differences with respect to the other species studied are observed (Fig. 2E).

The articular surface with the ulna is flatter, that is, the articular sulcus is not as deep (Fig. 2l).

Distal margin

In general, the articular surface with the unciform is broader in an ulnar-lateral direction than in the other caprines (Fig. 2m). The articular surface of the distal-palmar spur is reduced, with the facet taking on a more medial orientation (Fig. 2m).

In two cases, (MNIB 56293 and 43304) the articular surfaces of the sulcus and the spur, are of more or less the same breadth, taking, however, a more medial orientation.

Medial margin

The proximal articular surface with the lunar is reduced, above all on the palmar side (Fig. 2n), even disappearing in some cases. The dorsal area is proportionally wider in a proximal-distal direction than in other caprines (Fig. 2o), except in *Capra hircus*, where it is similar, but with a much thinner dorsal area.

The central articular surface is, in general, smaller, circular and oriented in a more palmar way (Fig. 2p). Specimen MNIB 43304 does not have this surface.

Lateral margin

The surface is smoother than in the other caprines. In *Oreamnos americanus* there are several very well-marked crests which are absent in *Myotragus* and *Capra*.

The spur which articulates with the unciform does not end in a sharp point, but is rounded (Fig. 2q). The articular sulcus with the unciform is less deep and has a small articular surface.

Dorsal margin

There are few differences with respect to the other species studied.

In *Oreamnos americanus* the crests for the insertion of ligaments are very well developed. In *Myotragus* there are none, and the surface is not as abrupt.

Palmar margin

In general, the articulation surface for the pisiform is more rounded and broader in medial-lateral direction than in the other caprines (Fig. 2r). It is a concave surface on all sides. In *Oreamnos americanus* it is convex in lateral-medial direction. In *Capra hircus* it is concave dorsal-ventrally and convex in lateral-medial direction, just as happens in *Budorcas*, *Nemorhaedus goral* and *Capricornis crispus*.

Magnum

The magnum looks like being compressed proximal-distally, with a degree of compression greater than that observed in other caprines (Fig. 2A). Due to this compression the areas for insertion of ligaments are well developed. In this case, the magnum in *Capricornis sumatrensis* and *Nemorhaedus goral* also has a slight dorsal-ventral compression, but it is not as evident as in *Ovibos* or *Oreamnos*.

Proximal margin

As happens in other species studied (*Capricornis sumatrensis*, *Ovibos*) (Fig. 3c7), the crest and the separation prominence of the articulation surfaces for the scaphoid and the lunar are very low (Fig. 2s), not too well marked, so that in *M. balearicus* this allows a certain caudal contact of the scaphoid and the lunar. In *Oreamnos* (Fig. 3a13), *Budorcas*, *Capra hircus*, *Ovis aries* and *Capricornis crispus* (Fig. 3d1) this crest is quite high and is well marked.



Fig. 3. Comparison carpal bones (all bones, left side). a: *Oreamnos americanus* AMNH 130223; b: *Budorcas taxicolor* AMNH 57017; c: *Ovibos moschatus* AMNH 100058; d: *Capricornis crispus* AMNH 165685; e: *Capricornis sumatrensis* NMNH 258670. a1: scaphoid, proximal view; a2: scaphoid, distal view; a3: scaphoid, medial view; a4: scaphoid, lateral view; a5: lunar, distal view; a6: lunar, medial view; a7: lunar, lateral view; a8: cuneiform, lateral view; a9: cuneiform, medial view; a10: magnum, proximal view; a11: magnum, distal view; a12: magnum, dorsal view; a13: magnum, palmar view; a14: unciform, proximal view; a15: unciform, distal view; a16: unciform, lateral view; a17: unciform, medial view; a18: pisiform, lateral view; a19: pisiform, medial view. b1: scaphoid, proximal view; b2: scaphoid, lateral view; b3: lunar, lateral view. c1: scaphoid, proximal view; c2: scaphoid, lateral view; c3: lunar, medial view; c4: lunar, proximal view; c5: cuneiform, dorsal view; c6: magnum, proximal view; c7: magnum, dorsal view; c8: magnum, medial view; c9: unciform, dorsal view; c10: unciform, medial view; c11: unciform, proximal view; c12: pisiform, medial view. d1: magnum, lateral view. e1: magnum, dorsal view. Scale bar 2 cm.

Fig. 3. Ossos del carp de comparació (tots els ossos dels costat esquerre). a: *Oreamnos americanus* AMNH 130223; b: *Budorcas taxicolor* AMNH 57017; c: *Ovibos moschatus* AMNH 100058; d: *Capricornis crispus* AMNH 165685; e: *Capricornis sumatrensis* NMNH 258670. a1: escafoide, norma proximal; a2: escafoide, norma distal; a3: escafoide, norma medial; a4: escafoide, norma lateral; a5: semilunar, norma distal; a6: semilunar, norma medial; a7: semilunar, norma lateral; a8: cuneiforme, norma lateral; a9: cuneiforme, norma medial; a10: capitatotrapezoide, norma proximal; a11: capitatotrapezoide, norma distal; a12: capitatotrapezoide, norma dorsal; a13: capitatotrapezoide, norma palmar; a14: unciforme, norma proximal; a15: unciforme, norma distal; a16: unciforme, norma lateral; a17: unciforme, norma medial; a18: pisiforme, norma lateral; a19: pisiforme, norma medial. b1: escafoide, norma proximal; b2: escafoide, norma lateral; b3: semilunar, norma medial; c1: escafoide, norma proximal; c2: escafoide, norma lateral; c3: semilunar, norma medial; c4: semilunar, norma proximal; c5: cuneiforme, norma dorsal; c6: capitatotrapezoide, norma proximal; c7: capitatotrapezoide, norma dorsal; c8: capitatotrapezoide, norma medial; c9: unciforme, norma dorsal; c10: unciforme, norma medial; c11: unciforme, norma proximal; c12: pisiforme, norma medial. d1: capitatotrapezoide, norma lateral. e1: capitatotrapezoide, norma dorsal. Escala 2 cm.

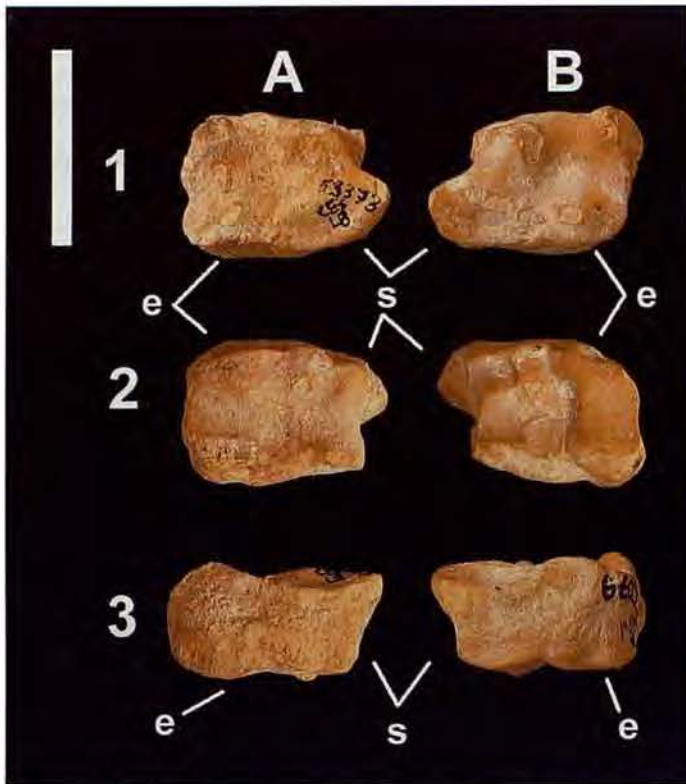


Fig. 4. Fused scaphoids and lunars of *M. balearicus*. A: left scapho-lunar MNIB 53378. B: right scapho-lunar MNIB 53379. 1: proximal view; 2: distal view; 3: dorsal view; 4: palmar view; 5: lateral view; 6: medial view. s: lunar; e: scaphoid. Scale bar 2 cm.

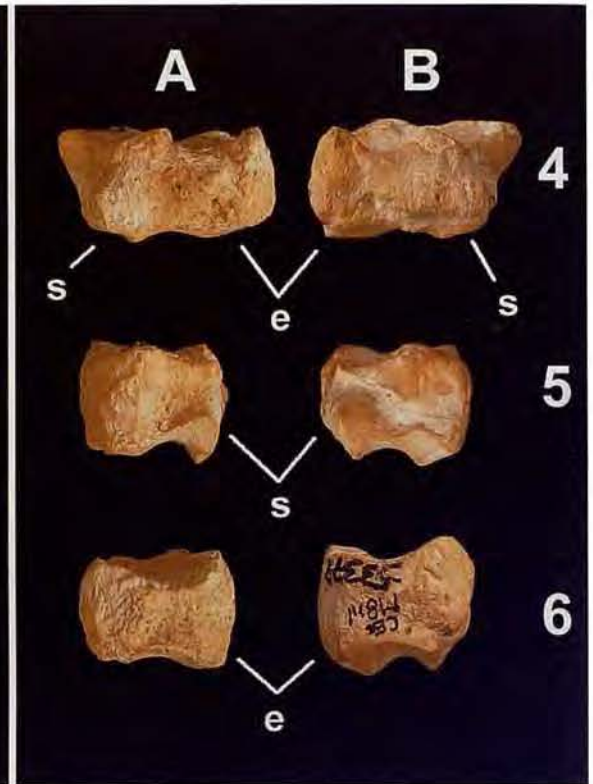


Fig. 4. Escafoïdes i semilunars fusionats de *M. balearicus*. A: escafo-semilunar esquerre MNIB 53378. B: escafo-semilunar dret MNIB 53379. 1: norma proximal; 2: norma distal; 3: norma dorsal; 4: norma palmar; 5: norma lateral; 6: norma medial. s: semilunar; e: escafoïde. Escala 2 cm.

The perimeter of the magnum in *M. balearicus* in proximal view is more square than in the other caprines studied.

Specimen MNIB 53360 has a fossa on the articular surface which can not be observed in the other specimens, and which probably represents a sinovial mark.

The medial dorsal margin is well developed (Fig. 2t) and is ulnarly longer than the palmar.

Distal margin

In general, as happens in extant species, the articulation surface with the metacarpus follows the shape of the bone. It is basically concave in most extant caprines, although the surface edges are more irregular.

The distal non-articular region is larger (Fig. 2u), deeper and more irregular than in the other caprines.

The articulation surface in *M. balearicus* is flat (like in *Capricornis sumatrensis*), and even has a small concavity which would act as a *stop-facet* (Fig. 2v). There is no possibility of magnum/metacarpus flexion, contrary to what happens in extant species, which have a convex surface which allows a certain degree of flexion [20° according to Yalden (1971)]. In *Capricornis crispus* there is an articular facet in this area which penetrates within the region of the non-articular shallow fossa of the metacarpus, whereas in *Ovibos* there is a small concavity on the lateral-palmar tip which gives it an S-shape.

Lateral margin

There are, in all the species studied (Fig. 3), basically

two articular facets: a more or less developed, square dorsal facet and another palmar one which follows the curvature of the crest (Fig. 2w). In *M. balearicus* the dorsal surface is smaller and is oriented in medial-proximal direction (obliquely) and not medially, which allows the unciform to slightly overlap with the magnum. The palmar articular facet is generally smaller and is limited to the proximal-palmar tip. In some cases it sticks out in a distal-palmar direction thus acquiring a semi-lunar shape. In this posterior articular region, in *Ovibos*, there is a small prominence. In *Oreamnos* there is no type of ridge or prominence.

In *Budorcas*, the dorsal articular surface is sloped, offering a sort of support to the unciform (just as can be seen in *M. balearicus*).

Unciform

The unciform is robust and is proximal-distally compressed, just as happened with the magnum (Fig. 2B). The ligament insertion areas are well marked.

Proximal margin

The proximal articular surface for the unciform, on its more palmar side, does not have such a lateral orientation as the other caprines (Fig. 3C11), but rather it takes a more palmar orientation (Fig. 2x). The crest limiting this articulation surface is also laterally deviated.

The separation crest between the two articulation surfaces for the unciform and the lunar, in general, is not

very well developed (like in *Capricornis sumatrensis*, *Ovibos*, *Budorcas*), except in its more palmar position (Fig. 2y), in which it is well marked (but not as much as in *Oreamnos americanus*, *Capricornis crispus*, *Capra hircus*, *Ovis aries*, in which it is a protuberant crest).

The articulation surface for the lunar is proportionally broader transversally than in other species (Fig. 2z).

The groove under the lateral-medial crest is very deep, above all on the medial side (Fig. 2a1). The palmar ridge where this groove can be found is only slightly developed (as in *Oreamnos*, *Capra hircus* and *Ovis aries*), contrary to what happens in *Ovibos* and, to a lesser extent, in *Budorcas* (Fig. 3c10) and *Nemorhaedus goral* (in the latter case, the ridge gives off a distal projection).

Distal margin

The surface is concave in dorsal-palmar direction, as happens in *Oreamnos americanus*, *Budorcas*, but in *M. balearicus* it is even more so (Fig. 2b1). In *Capra hircus* it is flat or slightly convex.

Medial margin

There are generally two articular bands with the magnum, which coincide with the articular areas of the latter.

In *M. balearicus* there is a dorsal articular area, which is square and obliquely oriented, in distal-medial direction, coinciding with the morphology of this surface corresponding to the magnum (Fig. 2c1).

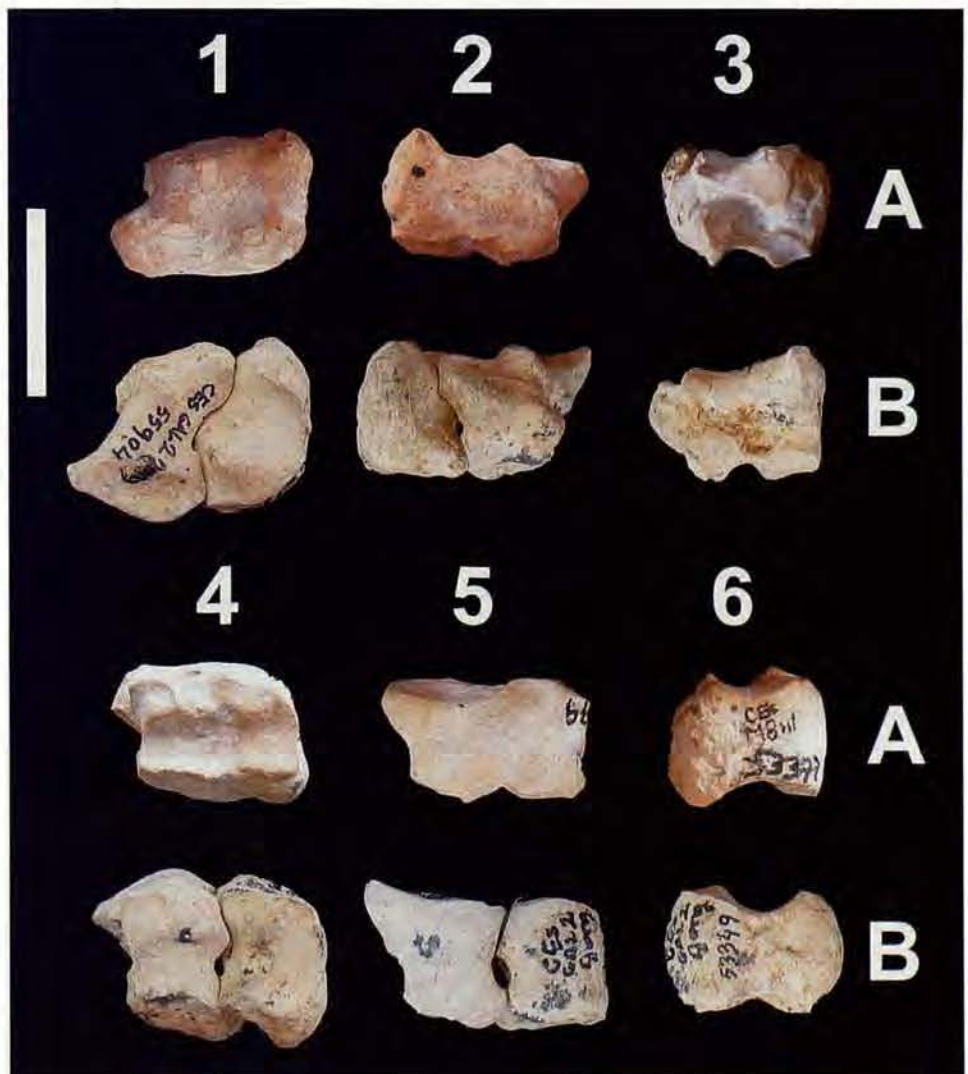
This dorsal articulation surface of the unciform connects, in most bones, with the proximal-palmar articulation surface of the same bone, which is semi-lunar (Fig. 2d1). At times it has a ridge following the palmar margin of the bone (Fig. 2c1).

Pisiform

In general it has a more globular shape than in other caprines (Fig. 2F). The size of the articular surface with the cuneiform is smaller (Fig. 2e1), whereas the articulation surface with the distal tip of the ulna is greater (Fig. 2f1). At times the two articular surfaces are the same size (e.g., MNIB 43297). In *M. balearicus* a clear separation can be seen between these two articular surfaces, whereas in *Oreamnos* this separation is not as clear (Fig. 3a19). In *Capricornis crispus* and *Nemorhaedus goral* the articulation with the ulna is practically inappreciable, whereas in *Budorcas* this articulation surface is very small and is situated on a dorsally projecting spur (Fig. 312). In the

Fig. 5. Comparison between (A) right scapho-lunar MNIB 53379 and (B) articulated right scaphoid MNIB 53349 and right lunar MNIB 55904 of *M. balearicus*. 1: proximal view; 2: palmar view; 3: lateral view; 4: distal view; 5: dorsal view; 6: medial view. Scale bar 2 cm.

Fig. 5. Comparació entre (A) escafo-semilunar dret MNIB 53379 i (B) escafoide dret MNIB 53349 i semilunar dret MNIB 55904 articulats de *M. balearicus*. 1: norma proximal; 2: norma palmar; 3: norma lateral; 4: norma distal; 5: norma dorsal; 6: norma medial. Escala 2 cm.



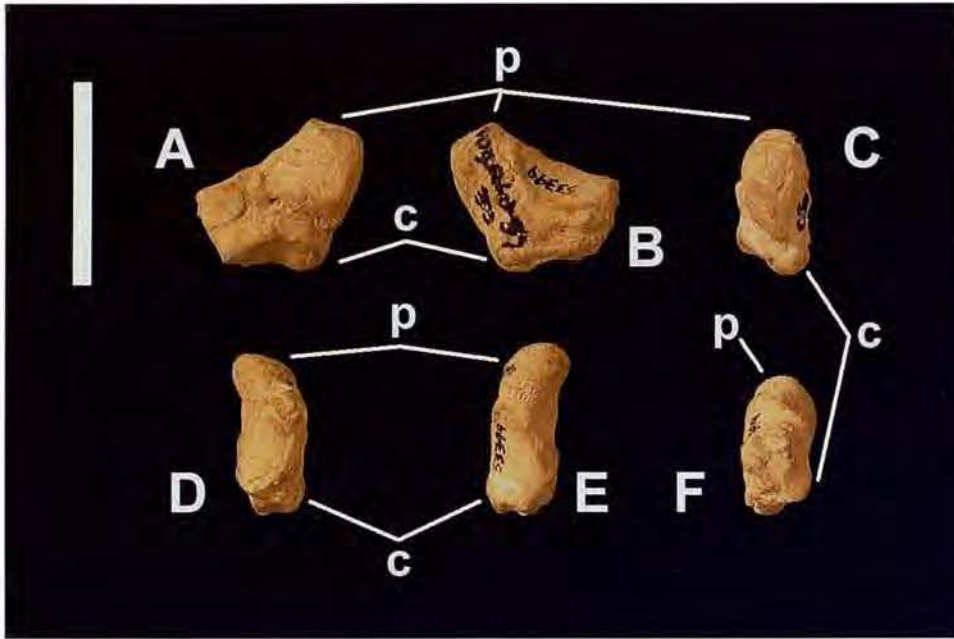


Fig. 6. Fused right cuneiform and pisiform of *M. balearicus* MNIB 53399. A: medial view; B: lateral view; C: palmar view; D: distal view; E: proximal view; F: dorsal view. Lower part of photo is the cranial side for D and E. p: pisiform; c: cuneiform. Scale bar 2 cm.

Fig. 6. Cuneiforme i pisiforme drets fusionats de *M. balearicus* MNIB 53399. A: norma medial; B: norma lateral; C: norma palmar; D: norma distal; E: norma proximal; F: norma dorsal. La part inferior de la foto seria la part cranial per a D i E. p: pisiforme; c: cuneiforme. Escala 2 cm.

extant caprines studied there are differences between the morphology of the articulation surface with the cuneiform: in *Capricornis crispus* it is convex, in *Capricornis sumatrensis* it is flat and in *Budorcas* it is wavy.

Carpal fusions

In Cova Estreta (Pollença, Mallorca) two *M. balearicus* bones have been obtained which were not identified until a short time ago. They are two small, robust, prism-shaped bones (MNIB 53378 and 53378, Fig. 4) measuring 19.82 x 11.66 x 14.46 mm and 21.06 x 11.06 x 14.76 mm, respectively. An in-depth study, comparing their morphology with the different *M. balearicus* bones of this size, has enabled their identification as a bone resulting from the fusion of a scaphoid and a lunar by their anatomical region of contact (see Fig. 5). Specifically, MNIB 53378 is the fusion of a left scaphoid and lunar and MNIB 53379 is the fusion of a right scaphoid and lunar. On their dorsal side, the fusion is produced even as regards the scapholunar ligament insertion area. On the palmar edge, the radius-lunar and scapholunar-magnum ligament insertion areas are very marked and rough. Their union area does not have any type of bone re-growth or any type of arthritic osteologic pathology. For this reason, it would seem that this fusion is natural and does not present any type of pathological situation.

Another bone obtained which has a very highly modified morphology is specimen MNIB 53399 (Cova Estreta, Pollença). This is a right cuneiform which has a bony prominence in the pisiform articulation area (Fig. 6). Once studied in detail, it was possible to identify that, actually, this bony prominence is the pisiform itself, which is fused in its natural articular region with the cuneiform. In this case neither does there appear to be any type of bone re-growth. The articular area for the ulna is continuous from the cuneiform to the pisiform, and the ligament insertion areas also form a continuous structure.

Among the carpal bones obtained from the excavation of this same cave there is another bone with a previously unobserved morphology. This is specimen MNIB 56300. Even though we have identified it as a carpal bone, we have been unable to diagnose with precision which bone it is (Fig. 7). It is a bone which has some articular areas which look like the three bones in the proximal row of the carpus (scaphoid, lunar and cuneiform), basically due to the morphology of the different articular facets and crests. On one of its lateral sides there are no articular areas, so we can discount it being a lunar. If it were a cuneiform it would have a totally modified articular facet for the ulna, divided into two very clear facets. What is more, the articular facet for the unciform would be situated in an medial and not distal position like in normal specimens. In the case of it being a scaphoid we would find a similar situation. The articular facet with the radius would have more than one surface, and the articulation surface with the magnum would also be ulnarly oriented. As a result, it has not been possible to diagnose which bone we are dealing with (scaphoid or cuneiform). Neither has another altered bone been found that could be associated with it.

Tracks and trackways

The measurements obtained for the different trails studied, defined in the section on materials and methods, are related in Table 1.

The foot angle (radial rotation of the foot) of *M. balearicus* is considerably greater than the angles of the other species studied, like the cervids and domestic caprines in Mallorca (*Ovis aries* and *Capra hircus*).

Another of the parameters measured of the trails made by extant bovids which differ significantly with respect to *Myotragus* is the width of the trail (a characteristic already observed by Quintana, 1993). The distinction between the footprints made by the fore and hind limbs are difficult to distinguish in the case of the trails of *Myo-*

tragus, since the sediment in which the animal walked was soft (sand) and many of the footprints are made up of only one mark. However, in some cases, as Fornós *et al.* (2002) also explain, it is possible to distinguish the mark of the footprint of the hind limb situated on the mark (but slightly behind) the footprint of the fore limb. Contrary to what happens with the trails of the extant comparison species, the width of the trails of *Myotragus* is proportionally greater (see Table 1, Fig. 8, Index TI). Whereas the TI index in *M. balearicus* acquires values between 2.1 and 2.9, in *Sus* it is slightly above 3 and in the extant bovids and cervids studied the TI value is greater than 4, with the greatest value calculated for *Odocoileus hemionus* (5.9). In proportion, the width of the trail with respect to the length of the stride is greater in *M. balearicus*. This measurement, together with the anatomic arrangement of the limbs established from the study of the femur, suggests that the limbs of this species were not as near the sagittal plane during gait as in the species they have been compared with. Spoor (1988b) already mentions this particularity for the species.

DISCUSSION

The observations made about the different anatomical particularities of the carpal bones of *M. balearicus* corroborate, in a general way, what had already been observed by other authors (e.g., Alcover *et al.*, 1981; Spoor, 1988b; Köhler, 1993; Köhler & Moyà-Solà, 2001). The fact that in *M. balearicus* there are prominent, rough regions of muscular and ligament insertions in the different bones both in the fore and hind limb, indicate that the collateral ligaments were of an important length, and must have contributed in an important way to stabilising the articulations. This fact can be observed clearly in the



Fig. 7. Non identified modified carpal bone of *M. balearicus* MNIB 56300. Could be a scaphoid or a cuneiform. Scale bar 2 cm.

Fig. 7. Os modificat del carp no identificat de *M. balearicus* MNIB 56300. Pot tractar-se d'un escafoide o d'un cuneiforme. Escala 2 cm.

carpal bones, which have a proximal-distally compressed aspect. The thickening of the edges where the ligaments were inserted between the different carpal bones, and between the carpal bones and adjacent bones, must be understood as the important relevance of these ligaments in providing stability in an area prone to suffering injuries, like the different carpal articulations. In fact, a certain reduction in the flexion capacity in this articulation is also observed (Spoor, 1988b).

The other observations made in the carpus are also in agreement with this, as is the case of the synostosis observed in this area. Synostoses are bony unions between bones which usually have mobile or semi mobile articulations. They could be of congenital, traumatic or other type of origin. Carpal synostoses are extraordinarily rare, and we are unaware of cases previously described in bovids. The registered cases of fusion between the scaphoid and the lunar and between the cuneiform and

SPECIES	TI	FA	SOURCE
BOVIDAE			
<i>Ovis aries</i>	4,58	8	Unpublished
<i>Capra hircus</i>	4,49	7,5	Unpublished
<i>M. balearicus</i> (S'Estret des Temps)	2,78	14	Unpublished
<i>M. balearicus</i> (S'Estret des Temps)	2,84	-	Unpublished
<i>M. balearicus</i> (Ses Piquetes)	2,13	15	Unpublished
<i>M. balearicus</i> (Penyes d'Alparico)	2,46	-	Quintana (1993)
SUIDAE			
<i>Sus scrofa</i>	3,21	-	Bang i Dahlström (1975)
CERVIDAE			
<i>Odocoileus hemionus</i>	5,9	7	Cabrera (1997)
<i>Cervus elaphus</i>	4,5	9	Bang i Dahlström (1975)
<i>Cervus elaphus</i>	5,4	-	Cabrera (1997)

Table 1. Values for Trail Index (TI) and Feet Angle (FA) of the different species studied. Source of the tracks pictures or photos measured is indicated.

Taula 1. Valors de l'Índex de Rastre (TI) i de l'Angle del Peu (FA) de les diferents espècies estudiades. S'indica la font de les fotos o dibuixos dels rastres mesurats.



Fig. 8. Example of *M. balearicus* trackways from s'Estret des Temps (Mallorca).

Fig. 8. Exemple de rastres de *M. balearicus* de s'Estret des Temps (Mallorca).

pisiform are few and far between, and do not allow us to talk about an evolutionary tendency towards the appearance of these synostoses, however neither can the beginning of these tendencies be excluded (even more so if we take into account the existence of tarsal fusion precedence). What it does seem to be able to exclude is that these fusions could be of traumatic origin. According to Yalden (1970, 1971), ungulates have a separate scaphoid and lunar in order to allow a certain ulnar deviation of the fore limb so as to facilitate the passage of leg behind leg during the protraction movement without them coming into contact. The fusion of the scaphoid and lunar, and the fusion of the cuneiform and the pisiform, observed in *M. balearicus* seem to limit this movement. If we observe an associated carpus in *M. balearicus*, the mobility of the lunar and the scaphoid separately is different. Whereas the scaphoid-magnum articulation permits a flexion of around 55°, the lunar-unciform articulation only allows a flexion of 40°, caused, apart from by a lesser articular surface of the unciform, by a caudal ridge which limits the flexor movement of the lunar. If the lunar fuses with the scaphoid, the angle of flexion between the distal carpal row and proximal row is reduced to 40°, much smaller than the 75° which can be observed in extant ruminants (Yalden, 1971). Spoor (1988b) previously observed that there was an important reduction in the articulation angle of the two carpal articulations, but he did not quantify it.

The fusion of the pisiform and the cuneiform is more difficult to interpret clearly. The pisiform basically acts as sesamoid bone for the flexors *carpi ulnaris* and *carpi radialis* (Sisson & Grossman, 1982). The restriction in the movement of the pisiform-cuneiform articulation, not only in the specimen that had these fused bones, but also in the ones that have non-fused bones, due to the reduction in the articular areas registered in *M. baleari-*

cus in a general way, seems to produce a similar effect to the fusion between the lunar and the scaphoid. The rigidity that could be produced by having a cuneiform with limited movement, with respect to the distal epiphysis of the ulna, has a smaller ulna articular movement, and therefore, a smaller ulnar deviation.

The articular facets of the different carpal bones, some flat, some without an articular movement and some with eminences which act as *stop-facets*, indicate the reduction in mobility and lack of general flexion capacity in the area.

The lack of capacity for ulnar deviation, to avoid the two limbs hitting each other when one moves in front of the other when walking, agrees with the lateral separation of the radius with respect to the humerus (Bover, 2004). Spoor (1988b) also previously detected a separation of the front limbs with respect to the sagittal plane of the body based on the inclination of the articular trochlea of the humerus with the radius. This separation can now be confirmed, both as far as the fore limb and the hind limb are concerned (based on the morphology, amongst others, of the radius-humerus articulation and the distal and proximal regions of the femur, respectively; Bover, 2004). It is not possible to know whether the fusion of these carpal bones would have become a generalised evolutionary tendency in all the populations of *M. balearicus*, basically since there are only two conserved examples of scapholunar fusion (out of tens of specimens obtained for each of these bones) and one example of pisiform-cuneiform fusion. Either way, the rigidity caused from the morphology of ligament insertion and of the different carpal articular regions, indicates that this gave an important stability to this limb. What is more, as has already been said, other evolutionary patterns of the species have also led to fusions which restrict locomotor movements (e.g., distal tarsal fusions).

Therefore, in summary, some articular anatomical characteristics of the fore limb indicate that they were not positioned just under the body, as happens in nearly all the other extant bovids, but rather they were situated more laterally (Spoor, 1988b; Bover, 2004). Thus, it seems that these fusions (together with the robustness of the carpal bones) are related to greater stability in the articulations, with greater muscular power, and with slow, but powerful movements, all in all, with "low gear" locomotion (Sondaar, 1977). The acquisition of this type of locomotion could have been evolutionarily favoured for different reasons. Firstly, the lack of predators in the Gimnesics would have allowed the loss of anti-predatory anatomical and ethological characteristics (Leinders & Sondaar, 1974; Sondaar, 1977; Leinders, 1979; Moyà-Solà, 1979; Alcover *et al.*, 1981; Spoor 1988a and b; Köhler, 1993; Köhler & Moyà-Solà, 2001; Bover, 2004; Bover & Tolosa, 2005). Secondly, there could have been some sort of relationship with the acquisition of locomotion adapted to a more mountainous habitat (Andrews, 1915; Leinders, 1979). Thirdly, slow locomotion could be important in energy saving processes, as has been observed in certain parameters studied in the species (e.g., Köhler & Moyà-Solà, 2004). And finally, the anatomical characteristics observed could be related to the acquisition of a relatively high weight of the species with respect to its size (Alcover *et al.*, 1999; Bover, 2004).

We have been able to corroborate the separation of both limbs in *M. balearicus* with respect to the sagittal plane of the body of the animal with the study of the footprints and trails left by individuals of this species in different sediments in *Mallorca* and *Menorca*. The TI index in *M. balearicus* is nearly half that of the species of cervids and bovids studied, and is inferior to the suids studied. This indicates that, proportionally, the trails left by *M. balearicus*, are transversally broader than in the species with which they were compared. Quintana (1993) previously stated that the trails that an individual of *M. balearicus* left in the sediments of the Penyes d'Alparic in *Menorca* are more similar to those of *Sus* than other artiodactyls, such as *Cervus*.

As far as the trails of *M. balearicus* are concerned, the significance of the FA values, foot angle with respect to the axis of the animal's gait, is not clear. The greatest values in this species with respect to the other species studied indicate that the feet were rotated laterally. Either way, the measurement of this angle entails a series of problems due to the fact that there is no clear separation between the two hooves in the trails studied.

There are other sites near fossilised dunes that have provided other types of trails attributed to *Myotragus*. These are the cases of the sites in *Cala Figuera* (Calvià, *Mallorca*) and *Son Mulet* (Llucmajor, *Mallorca*) where considerable quantities of coprolites can be observed in the eolianite. These coprolites, together with the footprints, show that *Myotragus* has some sort of attraction and/or preference to these areas. The presence of possible "fossil" sources of water resources very near these areas or the presence of fresh vegetation could express the attraction of the species for these areas.

Although the considerable amount of *Myotragus* tracks and trackways in Pleistocene dunes, the findings of *Myotragus* bones in these kind of deposits are not abundant (Muntaner & Cuerda, 1956; Muntaner, 1957).

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