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On the astragalus of the Miocene endemic deer *Hoplitomeryx* from the Gargano (Italy)

This report compares the astragalus of the endemic deer *Hoplitomeryx* (Gargano, Miocene) with that of a number of recent and fossil ruminants. It appears that the profile of the dorsal border deviates from the expected situation. In addition, in many astragali the axis through the cranial and the caudal half meet each other at an angle, yielding an oblique appearance. This situation resembles that of *Myotragus balearicus*, another endemic ruminant from the Mediterranean. A probable explanation is the decrease of muscular power needed, and the increase of stability, in relation to the convergence of the upper legs, due to a larger abdomen. *Hoplitomeryx* certainly was neither a runner nor a jumper.

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INTRODUCTION

Once upon a time, a five-horned deer lived on the Gargano Island, now part of South Italy. Its fossils were discovered in the Mio/Pliocene sediments in karstic fissure fillings in the late sixties and subsequent years (Freudenthal 1971). After collecting and preservation, Leinders (1984) described the cranial fragments as belonging to a new cervid family Hoplitomerycidae, a new genus *Hoplitomeryx*, and a new species *H. matthei*. The postcranial elements have not been described yet. They show many typical endemic features, such as the functional fusion of the navico-cuboid with the metatarsus of the type as described by Leinders & Sondaar (1974), shortening of a number of metapodia (Alcover 1976) and in one case the fusion of both malleoli with the tibia. These characteristics could help to understand the evolutionary processes that took place on islands in general (*sensu* Sondaar 1977) and the Miocene Mediterranean islands in particular.

In this paper the astragali of *Hoplitomeryx* are described. As there are clear mutual differences, it is very likely that they belong to more than one type or species, maybe chrono-types, each probably with a different habitat and/or diet, and consequently with a different locomotion, which then should be indicated by morphological differences. In the present study the focus is on similarities, as dissimilarities will be part of a later study, that includes all postcranial elements.

MATERIAL

There is a number of determining characters with the help of which Boesneck *et al.* (1964) and Heintz (1970) were able to distinguish taxa from each other, respectively goat from sheep, and cervids from bovids. These characters are taken as a starting point for the present study. The studied material and the material used for comparison are stored in the National Museum of Natural History, Leiden

(The Netherlands). They include the following species:

Hoplitomeryx sp., *Axis axis, Duboisia santeng, Bison priscus, Bos primigenus, Megaloceros giganteus, Alces alces, Candiacervus ropalophorus, Cervus elaphus, Eucladoceros tegulensis, Cervus rhenanus, Capreolus capreolus, Rangifer tarandus, Ovis aries, Capra hircus,* and *Sus scrofa.*

The last three species have also been studied from private collections. *Myotragus balearicus* BATE, 1909 is stored in the 'Institut Mediterran d'Estudis Avançats', Palma de Mallorca (Balearics, Spain). The *Hoplitomeryx* material consists of 72 astragali, from twenty different localities within the Gargano region.

BIOMETRY

Observation

The massivety index 100 x DT-distal/L appears to be a rather good discriminator between sheep and goat, with some overlap

and no sex dimorphism at all (Boesneck 1964: 101). The DT-distal is the width of the caput, or lower trochlea, of the astragalus. The length is the maximum length of the lateral, or external side. DT-distal is indicated with a by Boesneck (1964, in fig. 58: 102), and with GG' by Hue (1907, plate 14, fig. 3); length is resp. b and LL', same figures. If we compare Boesneck's figures with ours, we get the result as given in Table 1. Data from *Myotragus* are provided by P. Bover (Institut Mediterrani d'Estudis Avancats, Palma de Mallorca, Spain); data from *Candiacervus ropalophorus* were calculated on the basis of data from John de Vos (Naturalis, Leiden, The Netherlands).

From the scatter diagram (Fig. 1) it becomes clear that the individual *Hoplitomeryx* localities each contain a range of variation of the massivety index, in other words, there is no such thing as locality specificity of the massivety index. Based on this, a division into

Table 1   Massivety index of some ruminants. Island endemics are indicated with an asterisk *.

Species	n	range	range size	mean
C. ropalophorus size 2	37	51,3-64,2	12,9	59
C. capreolus	2	59,7-60	0,3	59,9
M. antiquus, Cova des Fum	7	56,5-65,2	8,7	60,6
D. santeng	8	57,9-69,2	11,3	60,9
B. taurus	13	57-67,5	10,5	61,4
E. tegulensis	9	58-63,4	5,4	61,6
M. balearicus, Cova des Moro	20	57,3-66,9	9,6	61,8
M. balearicus, Cova de son Maiol	10	58,2-65,4	7,2	61,8
C. rhenanus	10	56-64	8	61,9
R. tarandus	5	61-67	6	61,9
C. hircus	>70	56,5-68,5	12	62
C. ropalophorus size 1	55	58,4-67	8,6	62
M. balearicus, Cova Estreta	20	55,6-70,2	14,6	62,4
C. elaphus	14	59,6-68,3	8,7	63,3
M. kopperi, Pedrera de s'Onix	10	60,3-68,5	8,2	63,5
C. hircus, dwarf	3	63,8-66	2,2	64
M. giganteus	20	57,6-71,2	13,6	64,2
O. aries	>100	60-71	11	65
Hoplitomeryx	41	58,9-72,9	14	65
Bison priscus	21	55,1-69,7	14,6	65,1

several types is impossible. All taxa show a rather wide range, probably due to the fact that it is impossible to determine age with astragali, as there is no epiphysis. Consequently, large juveniles and small adults cannot be discriminated; the same is true for young males and full-grown females (Klein Hofmeijer 1996: 195), although Boesneck *et al.* (1964) couldn't find a sexual dimorphism. With fossils, it may prove possible to assign the light and porous specimen to juvenile animals. If this is done with *Candiacervus ropalophorus* size group 2, the massivety index is 64,4 (N=8, range 61,1-70,3). However, also taphonomic factors might result in light and porous specimens.

The mean for *Hoplitomeryx* lies at 65, which indicates that the modal *Hoplitomeryx* has a more massive astragalus than *Capra hircus*, the endemic *Candiacervus ropalophorus* and *Myotragus balearicus*; is equally massive as *Ovis aries*, but less massive than *Bison priscus*.

Discussion

It is remarkable that the continuous *Hoplitomeryx* range is larger than most other taxa. This may be due to the fact that the collection consists of more than one type, as in the case of *Capra* and *Ovis* (Boesneck *et al.* 1964, took 18 different goat races and 33 sheep races from all over the world). However, the range of dwarf *Capra* falls within the normal *Capra* range, so one would expect the dwarfed endemic *Hoplitomeryx* also fall within the colonisers range. Another conclusion might be that we deal with several species, not with several types. We get the same picture as we lump *Ovis aries* and *Capra hircus* together; in that case we get a range of 15,5. In doing so, we disregard the fact that islands and continents might show a different type of evolution.

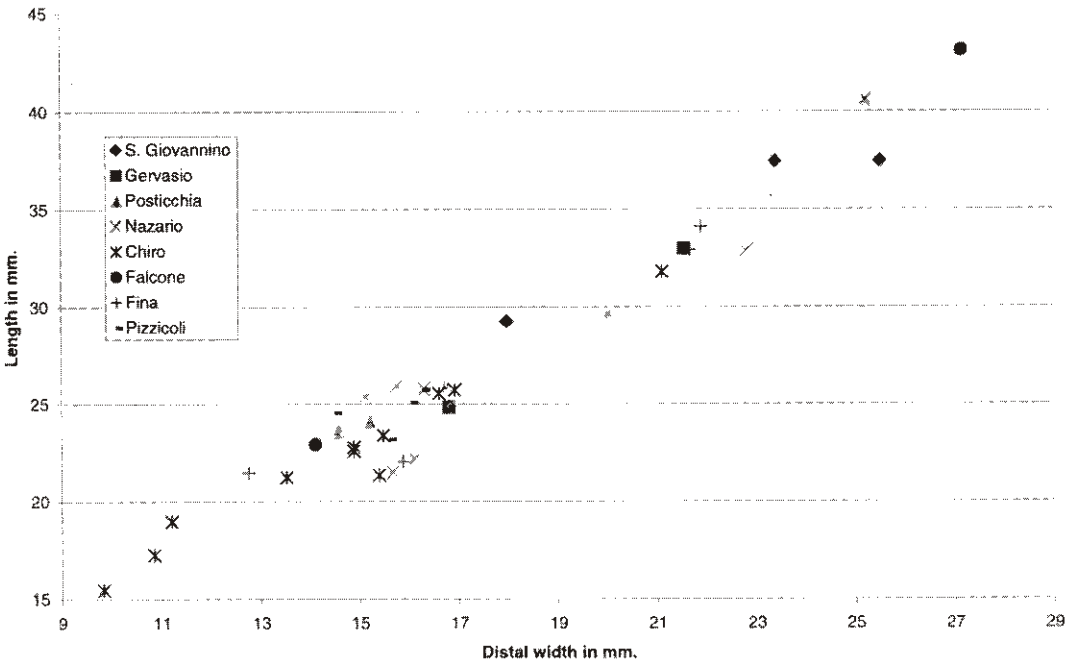A comparable island situation is provided by *Myotragus balearicus* from Cova Estreta.

Figure 1 Massivety index of the *Hoplitomeryx* astragalus.

Myotragus balearicus from the Pleistocene is further evolved than *Myotragus kopperi* from the Late Pliocene/Early Pleistocene. The last species is, in its turn, a descendant of *Myotragus antiquus* from the early Late Pliocene, regarding the trend to monophyodonty and ever-growing incisiform series (Bover & Alcover in press, Alcover *et al.* 1981). *Myotragus balearicus* from Cova de son Maiol (Late Pleistocene) is older than those from Cova des Moro (Holocene; Moyá-Solá 1979: 89) and Cova Estreta (Bover & Alcover in press). As we can notice, there is an increase of massivety in *Myotragus*, although *Myotragus kopperi* somewhat disturbs the picture. At the same time the variability in the most recent *Myotragus balearicus* has increased considerably. Only the largest continental artiodactyle species, *Megaloceros giganteus* and *Bison priscus*, have a similarly wide range. An explanation for this fact on the continent may be the increase in sex and age differences in large species. Another explanation may be the composition of the populations: whereas the species with a smaller range appear to be found in well-defined, small localities, the others are not. They might consist of specimens originating from different herds or, even worse, from different times.

The increase in massivety is also seen in *Candiacervus*, where size 1 is smaller than size 2. Both have shortened metapodals. However, the restricted variation within size 1 is striking, see also its metatarsals (De Vos 1979: 70). The larger range is found in size 2, which is found at the site of Liko, where also size groups 3, 4 and 6 were found. This fact might explain part of the variation in the astragali, as ontogenetic age cannot be determined (Klein Hofmeijer 1996: 195), which might result in a confusion of young individuals of size 3 with adult individuals of size 2.

The high variability in *Hoplitomeryx* is of the same order as the most recent *M. balearicus* and *Candiacervus ropalophorus* size 2, indicating the co-existence of several types. The

massivety is large compared to other cervids, so their locomotion must have been powerful, probably characterised by endurance, but not very swift; the 'low gear locomotion' *sensu* Sondaar (1977). The massivety, however, doesn't tell us much about stability, a factor that accompanies the low gear type of locomotion.

MORPHOLOGY OF THE DISTAL BORDER

Starting point

The morphological differences between cervids and bovids as shown by Heintz (1970) might be used as a factor in the classification of *Hoplitomeryx*. Heintz (1970) chose *Gazellospira torticornis* and *Cervus pardinensis* as examples for, respectively, bovids and cervids. Heintz himself already was aware of the problem of discriminating these two families, as he wrote not to have found any evidence for a good criterion to distinguish the astragalus of cervids from that of bovids (Heintz 1970: 49). The only differential criteria that can be applied more or less to the Villafranchian ruminants are to be found at the level of the lower trochlea. The cervid transverse profile of the distal part of the lower trochlea has the following characteristics (Heintz 1970: 49-50): (1) the horizontal part of the external condyle suddenly ascends to the median gorge; (2) the position of the median gorge is shifted a bit medially; (3) the internal condyle is smaller than the external one, and ascends progressively to the median gorge.

Contrarily, the bovid astragalus has a more symmetrical profile, with equally large condyles, that both ascend progressively and regularly to the median gorge, which occupies a median position.

Observation

When we look at the undamaged *Hoplitomeryx* astragali (n=50), we see that 16 specimens have a convex external condyle,

whereas 18 specimens have only a very small flat area on the external condyle; 16 specimens could not be discriminated properly. The differences are, however, marginally. Specimens with a convex condyle are from San Giovannino (n=3), Gervasio (2), Nazario 2A (1), Chiro D2 (1), Chiro D3 (2), Chiro 28A (1), Falcone 2B (1), Fina N (2), and Gargano (3). Specimens with a horizontal area are from Gervasio (2), Posticchia (1), Nazario 4 (4), Chiro D3 (1), Chiro D1 (1), Chiro 29 (1), Posticchia 5 (1), Nazario 2B (1), Nazario 3 (1), Pizzicoli 12 (2), and Gargano (3). The internal condyles are round or end horizontally, and do not ascend medially; they are cut off abruptly. The round external condyle is unique for cervids, but is found in bovids like *Gazellospira torticornis* and the endemic *Myotragus*. Another endemic deer, *Candiacervus ropalophorus*, has a flat area on the external condyle. *Cervus pardinensis* and *Cervus philisi philisi* are the most comparable cervids in this respect, with their slightly convex external condyles. The non-ascending internal condyle is of the *Cervus* type.

Discussion

As we have seen above, the differences often are not as obvious as Heintz (1970) shows, so the navico-cuboid, or the basitarsale is useful as additional discriminator. In comparing the various astragali, it appeared that most astragali show a mixture of bovid and cervid characteristics. In none of the bovid species a sharp median gorge could be found as depicted by Heinz (1970) for *Gazellospira torticornis*, except for some *Myotragus balearicus* specimens (Cova Estreta). The median gorge is always placed asymmetrically, except in *Bos taurus* and *Gazellospira torticornis*, where we find a symmetry.

Almost all external condyles appear to have a flat area that has a latero-distal orientation as in some *Bos primigenius* and *Ovis aries*, or that is horizontal, as in other *Bos primigenius*, *Bos taurus* and most cervids, or

that has a latero-proximal orientation as in *Cervus cusanus*, *Cervus perrieri* and some *Myotragus balearicus* specimens (Cova Estreta, Cova de Son Maiol). The only round, or convex external condyle seems to be found in some *Myotragus balearicus* (Cova Estreta, Cova de Son Maiol) and in some *Hoplitomeryx*. The flat area on the external condyle ascends abruptly to the median gorge in most cervids and in *Ovis*, whereas it ascends gradually in *Bison priscus*, *Bos primigenius*, *Bos taurus*, *Cervus pardinensis* and *Cervus philisi philisi*. The interior condyle ascends medially, reaching almost or exactly the same level as the median gorge, with a corresponding broadening of the medial part of the basitarsale, in the bovids, in *Alces alces* and *Rangifer tarandus*. It seems to be cut off, without reaching the level of the median gorge, or ends horizontally in most cervids. In *Cervus ramosus ramosus* an *Ovis*-like interior ascending condyle is found, however, not with a corresponding broadening in the basitarsale. The interior condyle is round in *Bison priscus*, *Bos primigenius*, *Bos taurus*, *Myotragus balearicus* (in some specimens even ascending beyond the level of the median gorge), *Rangifer tarandus*, *Alces alces*, and *Megaloceros giganteus*. It is elliptical in *Ovis aries*, *Cervus ramosus ramosus*, and *Cervus perrieri*, and with a flat area in *Cervus elaphus*, *Eucladoceros ctenoides*, *Cervus rhenanus*, *Cervcus pardinensis*, *Cervus cusanus*, *Cervus phisili phisili* and *Eucladoceros senezensis senezensis*. In short, it seems that differences in the morphology of the distal border might tell us more about the functional aspects than about the taxonomy.

MORPHOLOGY OF THE MEDIAN AXIS

Observation

What strikes most is the fact that the median axis of the proximal and the distal condyles are in line in all ruminants available in Leiden. Whereas the very same median axes

in the *Hoplitomeryx* specimens cross each other somewhere lateral of the median, and meet each other at an angle. These astragali therefore have a rather distorted appearance, seen from dorsal. This appears to be a specific *Hoplitomeryx* characteristic. In *Myotragus*, a comparable situation is found, but to a lesser degree as regards the proximal part (Fig. 2). The obliqueness is not the same in all specimens and attracts attention, particularly when the specimens are aligned in a row. There are 26 specimens clearly oblique, 8 specimens that are only slightly oblique. Three types can be distinguished:

type 1 is clearly oblique, and has no flat area on the external condyle; it is found in S. Giovannino (3), Gervasio (2), Nazario 2A (1), Chiro D3 (2), Chiro D2 (1), Chiro 28A (1), Falcone 2B (1), Fina N (2), and unknown localities (3);

type 2 is slightly oblique, and has a flat area on the external condyle; it is found in Nazario 4 (3), Chiro D1 (1), Posticchia 5 (1), Nazario 3 (1), Pizzicoli 12 (1), and an unknown locality (1);

type 3 is clearly oblique, and has a flat area on the external condyle; it is found in Gervasio (2), Posticchia (1), Nazario 4 (1), Chiro D3 (1), Chiro 29 (1), Nazario 2B (1), Pizzicoli 12 (1), and unknown localities (2).

The most clearly oblique specimens are, for example, the left astragalus RGM 425.331 (Gervasio), the right astragalus RGM 425.421 (Fina N), and the left astragalus RGM 425.424 (Fina N) (all type 1). The obliqueness of especially the first two goes in the direction of recent *Sus scrofa* and the extinct Protoceratidae (see Patton & Taylor 1973: 385).

Discussion
If the proximal trochlea is oblique, then the distal one has to be oblique as well, although mirrored in the dorso-volar plane, to guarantee the vector of the stress line. But which advantage has this obliqueness? Some oblique specimens have a flat area on the distal external condyle, where others have not. The difference between the two Fina N specimens, which have almost exactly the same dimension, lies in the profile of the distal border. In the one the median gorge is much

Figure 2 The astragalus of (left) *Myotragus balearicus* (from Cova Estreta, number CES 51369), and (right) *Hoplitomeryx* (from Fina N, number RGM 425.421).
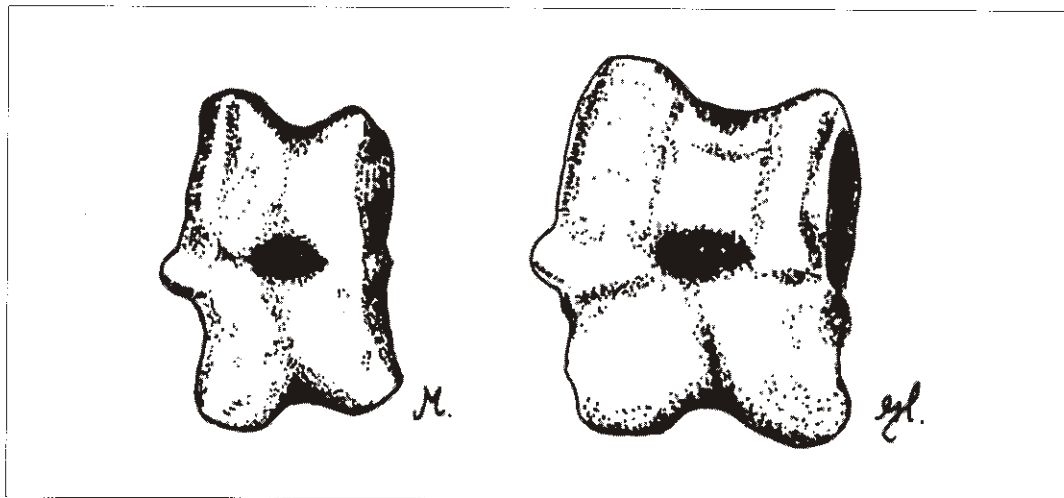
deeper, and the external condyle is round, while the border is more flat in the other, with the external condyle more gradually descending than round. This is an important observation, because the form and properties of the distal border seem to have nothing to do with the obliqueness. The result of the obliqueness is that the lower leg converges to the median, in other words, the animal was O-legged at the level of the ankle, in *Hoplitomeryx* even more than in *Myotragus*. It can be seen as a correction of the diverging femur and tibia, so that the axis through the phalanxes is vertical again. This decreases stability, increases speed, and, very important, reduces the muscular power needed. In *Sus*, this form makes quick and sharp turns possible, without spraining of the ankle. In *Hoplitomeryx* and *Myotragus* turning is highly improbable, as the fusion of the grand cuneiform with the navico-cuboid in *Myotragus* and the further fusion of this complex with the metatarsus in *Hoplitomeryx* result in gain of stability, but loss of zig-zag movements (Leinders & Sondaar, 1974). The zig-zag movements are further prevented in at least one *Hoplitomeryx* specimen by the fusion of the os malleolare with the tibia (RGM 261.517, S. Giovannino). Alcover (1976) and Sondaar (1977) relate the morphology of the tarsus of *M. balearicus* with the adaptation to an environment where the lack of carnivores and the presence of a mountainous area favour the development of this special type of locomotion. The greater strength, stability and stiffness of the tarsal joint is more advantageous than speed and allows more possibilities of movements (see also Moyá-Solá 1979: 90).

Divergence of femur-tibia is seen in dwarfed herbivores, due to the relatively large abdomen. Further enlargement of the abdomen is necessary in cases where food is scarce and difficult to digest, a situation not improbable on a karstic island (see also the situation in *Myotragus*, which even ate the toxic *Buxus* (Alcover *et al.* in press). The very muscular

aspect of the lateral side of the astragalus in both *Hoplitomeryx* and *Myotragus* indicates a significant muscular action, in other words, climbing and maybe also jumping, in a mountainous region, carrying a relatively large body mass.

RELATION TO OTHER SKELETAL ELEMENTS

Tibia
The small tibia RGM 425.144 (Chiro D1), which resembles *Axis axis* as to the S-curved shape but which measures only about two-third of this deer, only fits to the clearly oblique astragali of type 3, the best with RGM 261.746 (Gervasio). The distal articulatory facets are deeper in *Axis axis* than in RGM 425.144, which means less pronounced proximal condyles of the astragalus, and consequently less dorsal-plantar flexibility than in *Axis axis*. The muscle *M. tibialis cranialis* must have been well-developed: the proximal fossa on the dorsal side, lateral from the crista tibiae is deeper than in *Axis axis*. The action of this muscle is extension of digit II, and rotation of the foot in a lateral direction. Development of this muscle indicates a powerful thrust, which is contradicted by less pronounced astragalus condyles, or a divergence of the tibia. The distal tibia RGM 261.756 (Gervasio) differs from RGM 425.144: no clear muscular fossa, wider and shallower middle part between both trochlea-fossae, dorsal plain not concave but simply straight, even more straight than in *Ovis aries*. Still, an oblique astragalus likes RGM 425.421 (type 1, Fina N) fits very well. This means that here both flexibility and strength are restricted. The distal tibiae that fit the type 2 astragali also fit the type 1 astragali, as could be expected regarding the distal articulation which resembles that of tibia RGM 261.756. Their distal part are all rather broad (medio-lateral), have a rather broad middle part between the fossae for the trochleae (in the larger specimens relatively broader), that are not markedly deep. Fitting tibiae are from

S. Giovannino (where astragalus type 1 is found), Chiro D3 (where astragalus types 1 and 3 are found), and Stazione Poggio (no astragali). Here, too, flexibility is clearly restricted.

There is one unique distal tibia, RGM 261.517 (S. Giovannino), where the lateral and medial malleoli are equally strong developed (both ossae malleolare here fused to tibia), and bent slightly inward, so that the articulation area is surrounded at all sides by a high wall. It will be difficult to squeeze in an astragalus. The only possibility is from the plantar side. It is clearly not an ankylotic joint, as the articulation areas are well developed and undamaged. The fossae for the trochleae are deep, the bridge in the middle is small, and has an oblique orientation. As regards the fossae, the medial proximal condyle of the astragalus must be higher than the lateral, but not much. A rather well-fitting specimen is RGM 261.746 (Gervasio). Flexion is possible to the same degree, or even a bit further, than in *Ovis aries*, however, with a much greater stability. Extension is possible as far as about 10 or 15 degrees beyond the vertical position. Luxation to medial or lateral is excluded definitely. Extension in *Ovis aries* beyond the vertical position is impossible. There are two solutions to explain this adaptation: this *Hoplitomeryx* is either more plantigrade than recent sheep, in which case phalanxes may provide the solution, or is an excellent good jumper, in which case the knee may provide the solution. Both aspects will be dealt with in the near future.

Metatarso-navico-cuboid
The possible flexion turns out to be quite normal, as can be concluded from the combination of the oblique RGM 177.933 (type 3) and the even more oblique RGM 425.029 (type 1) with the fitting metatarsal RGM 261.215 (Posticchia 5). Another ad-hoc combination is the clearly oblique astragalus RGM 425.331 (Gervasio) with the relatively

muscular metatarsal RGM 425.334 (Gervasio). What strikes furthermore is that on this medium sized metatarsal the longitudinal sulcus on the proximal part of the volar diaphyse proceeds in proximal direction beyond the foramen nutricium, and thus on the navico-cuboid part, till almost the proximal border. This phenomenon is hardly detectable on RGM 261.101 (Nazario 4), and a bit more clearly on RGM 261.215 (Posticchia 5). The oblique left astragalus RGM 425.424 (type 1; Fina N) fits very well to the fairly deviant, quite well-muscled left metatarsus RGM 260.917 from S. Giovannino Low. The type 1 oblique astragali RGM 425.424 (Fina N) and RGM 425.331 (Gervasio) fit very well to the well-muscled metatarsal RGM 260.917 (S.Giov. Low) and RGM 425.334 (Gervasio) respectively.

The type of metatarsal that fits on RGM 261.746 (Gervasio) [this astragalus also fits to the S-shaped, muscular tibia RGM 425.144 (Chiro D1)] is, for example, the complete and not well-muscled, shortened RGM 261.101 (S.Giovannino). Other fitting specimen are RGM 425.102 (Chiro 28), and RGM 177.930 (Gargano), that both have approximately the same appearance as RGM 261.101. Specimen RGM 178.518 (S. Giov.) fits astragalus RGM 425.424 (type 1; Fina N) very well. To sum up, flexibility of the lower part of the ankle joint is normal, in contrast to that of the upper part of the ankle. Lower parts of the legs have a muscular aspect, indicating flexion and extension of the toes.

Remarks on the chronology
Freudenthal (1976) established a chronological order between the different fissures on the basis of evolutionary changes in molars of *Microtia*. Ballman (1976) and De Giuli *et al.* (1985) added some more fissures to the scheme on the basis of, respectively, birds and micromammals. Unfortunately there are many fissures that were not taken into account. If other factors played a role in the taphonomy, such as predators, and type and

location of the fissure, then an order that fits for a certain genus may prove to be false for another. This can already be seen in the Cricetidae line in Freudenthal (1976: 12-13). Taking the massivety of the astragalus into account, we see that there is no increase between the localities. This is in conflict with the thesis of a chronology between the localities, unless we accept the idea that *Hoplitomeryx* was already in a final adaptational stage, as regards the massivety of the astragalus.

Considering the profile of the distal border, it might be that there is a certain difference between the localities or 'layers' in this respect, as only Gervasio and Chiro D3 contain both types, and Nazario 2A differs from Nazario 2B. This should be in line with other characteristics. The combination of this feature with the degree of obliqueness results in the three different types. If we accept the evolution of a normal cervid type with a flat area on the external condyle (types 2 and 3) to a new type with a convex, *Myotragus*-like external condyle (type 1), and at the same time the evolution of only slight obliqueness (type 2) to notorious obliqueness (type 1), with clear obliqueness as intermediary stage (type 3), then the chronology would be as follows:

Late: S. Giovannino, Nazario 2A, Chiro D2, Chiro 28A, Falcone 2B, Fina N
Middle to Late: Gervasio, Chiro D3
Middle: Posticchia, Chiro 29, Nazario 2B
Early to Middle: Nazario 4, Pizzicoli 12
Early: Chiro D1, Posticchia 5, Nazario 3

However, there is also the possibility of coexisting herds, each with a different habitat. This is indicated if we consider the other post-cranial elements as well. For example, the shortened metatarsals are found in Posticchia 5 and Nazario 4, whereas normal metatarsals are found in S. Giovannino (both upper and low) and Fina N. Metacarpals, too, cannot consolidate the idea of chronology, as

the shortened specimens are from Gervasio, and the normal specimens from S. Giovannino (both upper and lower) and Nazario 4. So, normal metacarpals and shortened metatarsals are found together in Nazario 4, and oblique astragali with a convex external condyle are found together with metatarsals of normal length. If Nazario 2A and 2B are of approximately the same age as Nazario 2 in Freudenthal (1976), then the two types coexisted at already an early stage.

If we take the fitting bones into consideration, we see that a Chiro D1 tibia fits a Gervasio astragalus, a Gervasio tibia fits a Fina N astragalus, and finally that a Gervasio astragalus, a Chiro D1 tibia, a S. Giovannino metatarsal and a Chiro 28 metatarsal fit perfectly well. Their time distance cannot have been very large, if we accept the above chronology.

GENERAL DISCUSSION AND CONCLUSION

Concerning the massivety index, the average *Hoplitomeryx* has a more massive astragalus than *Capra hircus*, *Candiacervus ropalophorus* and *Myotragus balearicus*, equally massive as *Ovis aries*, but less massive than *Bison priscus*. Concerning the morphology of the distal border, the *Hoplitomeryx* astragalus belongs to the cervids, as none of the specimens show a clearly ascending internal condyle. Only bovids show this latter phenomenon, in addition to *Alces alces* and *Rangifer tarandus*, which also have a bovid-like internal astragalus condyle and corresponding basitarsale. This can be explained by the functionality of this construction, as it gives more support medially and consequently more stability in a muddy environment (*Alces alces*), during running on frozen or otherwise very firm plains with many irregularities (*Rangifer tarandus* and some bovids, like *Gazellospira torticornis*), or climbing (other bovids, like *Ovis aries* and *Myotragus balearicus*). In such environments, ankles are very easily sprained. *Hoplitomeryx* obviously

didn't have such problems, which is a bit surprising as the avifauna indicates a karstic landscape: a dry, rather open area with low, bushlike flora and a limited growth of trees (Ballmann 1976). The walking level in such an environment is not horizontal, and full of holes and sharp fissures. Maybe the stability was ensured by the other characteristic: the lack of the horizontal plane in half the specimens, just as in the runner *Gazellospira torticornis* and the climber *Myotragus balearicus*, and to a lesser degree in *Cervus pardinensis* and *Cervus philisi philisi*. One reasonable functional explanation of this feature at the moment is the increase of stability, as a round condyle can hardly move transversally. Such an articulation can only make movements in dorso-plantar direction. Zigzag movements are unlikely then, but spraining during running, climbing and jumping will hardly occur, if ever. Speed is lost, but stability is gained. Another functional explanation lies in the direction of the vectors through the bone. In the case of a clear horizontal plane, like in *Eucladoceros senezensis*, the gravity vector goes vertical through the bone, and acts on the horizontal plane. A convex area means extra bone substance at the median, thus there must have been more stress on the external condyle, as bone grows only under pressure or tension. This stress can be a result of convergence of the feet, of landing after jumping, of a larger body mass or a combination of factors. In *M. balearicus*, the increased body mass, caused by a larger rumen volume due to the digestion of *Buxus* (Alcover *et al.* in press), may be the most probable factor. In *Hoplitomeryx* the jumping would have been the main factor, if only the elongated patella and the muscular aspect of the lateral side of the astragalus and the tibiae were taken into account, as both indicate a heavy stress on the extensors. The obliqueness of the astragalus, which is a clear characteristic of *Hoplitomeryx* and of many *Myotragus*, reveals the true reason for the extensor action: convergence of the lower leg to

compensate for the divergence of the upper leg due to a larger abdomen. This convergence avoids further muscular strength needed, and increases stability. In *M. balearicus* there is even more stability, resulting from the round internal condyle; in *Hoplitomeryx* this is not the case, although here the convergence is more pronounced.

Considering the differences and agreements between the localities, we cannot find a proof for a clear chronology for *Hoplitomeryx*. If there is a certain chronology, then it is for *Hoplitomeryx* not as clear as it is for *Microtia* (Freudenthal 1976). The several types are distributed between the localities, without a clear preference for one type per locality, as in the case of *Candiacervus ropalophorus* from Crete and *Myotragus* from Mallorca. Assuming the localities to be filled in a relatively short time with a mixture of materials contradicts the findings of Freudenthal (1976). Thus, *Hoplitomeryx* must have been fully developed into several types already in an early stage, and these types seem to have co-existed, providing an example of adaptive radiation. For convenience, these types can be described as different species, but in that case we have to realise that these species have a completely different evolution and origin than continental, or 'real' species. According to Van Bemmel (1973: 295), these different species can have lived in the same region and time, as different species of Cervidae occurring in the same habitat under natural conditions are, as a rule, of considerably different size. In the case of exception to this rule, for instance *Rucervus duvauceli* and *Rusa unicolor* in some parts of India, the species occupy different ecological niches or in some cases a slightly different habitat (Van Bemmel 1973: 295). The *Hoplitomeryx* types differ in size (normal situation) and/or in morphology (Indian situation).

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