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THE POSTCRANIAL OF THE DEER *HOPLITOMERYX* (PLIOCENE; ITALY): ANOTHER EXAMPLE OF ADAPTIVE RADIATION ON EASTERN MEDITERRANEAN ISLANDS

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Resum

Durant el Plíocè, a l'illa de Gargano (costa sudest d'Itàlia) va evolucionar una fauna vertebrada altament endèmica. Aquesta fauna comprenia, entre d'altres, el eriçó gegant *Deinogalerix*, l'òliba gegant *Tyto gigantea*, el hàmster gegant *Hattomys*, i el cèrvol *Hoplitomeryx* amb cinc banyes i canins superiors en forma de sabre (tipus mòsquid). Els materials esquelètics d'*Hoplitomeryx* formen un grup heterogeni, amb quatre classes de talla; dintre de les classes de talla poden estar presents diferents morfotipus. Totes les classes de talla comparteixen els mateixos trets típics d'*Hoplitomeryx*. Aquests són: una banya nasal central i un parell de banyes orbitals en punxa, canines sortints, fusió completa del navicocuboide amb el metatarsià, acanaladura metatarsiana distalment tancada, astràgal sense costats paral·lels, i una ròtula allargada. Les dife-rents classes de talla es troben repartides de forma igual a les fissures excavades, i a llavors no es poden considerar cronotipus. La hipòte-si d'un arxipèlag consistent en diferents illes on a cada una d'elles hi hagués un morfotipus no s'ha pogut confirmar.

La situació de diferents morfotipus coexistint a una illa té un paral·lel amb *Candiacervus* (Pleistocè, Creta, Gràcia). Les opinions sobre la seva taxonomia són diverses, i actualment prevaleixen dos models: un gènere per a vuit morfotipus o, alter-nativament, dos gèneres per a cinc espècies. El segon model només es basa en les proporcions dels membres, però aquestes són característiques taxonòmiques invàlides per als endemismes insulars, ja que canvien sota la influència de factors ambien-tals diferents dels continentals. També a *Hoplitomeryx* els morfotipus difereixen en les proporcions dels membres, però en aquest cas resulta improbable que provinguin de diferents ancestres, ja que en aquest cas els ancestres haurien d'haver com-partit els trets hoplitomerícids típics. La morfoesfera d'*Hoplitomeryx* és massa coherent com per suposar dos o més ances-tres, i indica un origen monofilètic de tots els morfotipus.

En lloc d'això, la gran variació s'explica com a un exemple de radiació adaptativa, que va començar quan l'ancestre miocènic va colonitzar l'illa. L'espectre de nínxols buits degué promoure la seva radiació en diferents tipus tròfics, conduint a una diferenciació d'*Hoplitomeryx*. La manca compartida de mamífers depredadors grans i l'oferta limitada d'aliment a tots els nínxols degué promoure el desenvolupament de trets derivats secundaris a totes les classes de talla.

Paraules clau: Gargano, endemisme, *Candiacervus, Cervus astylodon,* fauna de *Microtia*.

Summary

During the Pliocene a highly endemic vertebrate fauna evolved on Gargano Island (south-east coast of Italy), compri-sing amongst others the giant hedgehog *Deinogalerix*, the giant barn owl *Tyto gigantea*, the giant hamster *Hattomys*, and the prongdeer *Hoplitomeryx* with five horns and sabrelike ('moschid' type) upper canines. The *Hoplitomeryx* skeletal material forms a he-terogenous group, containing four size groups; within the size groups different morphotypes may be present. All size groups share the same typical *Hoplitomeryx* features. These are: one central nasal horn and a pair of pronged orbital horns, protruding canines, complete fusion of the navicocuboid with the metatarsal, distally closed metatarsal gully, a non-parallel-sided astragalus, and an elongated patella. The different size groups are equally distributed over the excavated fis-sures, and are therefore not to be considered chronotypes. The hypothesis of an archipelago consisting of different islands each with its own morphotype cannot be confirmed.

The situation with several co-existing morphotypes on an island is paralleled by *Candiacervus* (Pleistocene, Crete, Greece). Opinions about its taxonomy differ, and at present two models prevail: one genus for eight morphotypes, or alter-natively, two genera for five species. The second model is based upon limb proportions only, but these are invalid taxonomic features for island endemics, as they change under influence of environmental factors that differ from the mainland. Also in *Hoplitomeryx* the morphotypes differ in limb proportions, but here different ancestors are unlikely, because in that case they all ancestors must have shared the typical hoplitomerycid features. The morphosphere of *Hoplitomeryx* is too coherent to assume two or more different ancestors, and indicates a monophyletic origin of all morphotypes.

The large variation is instead explained as an example of adaptive radiation, starting when the Miocene ancestor colo-nized the island. The range of empty niches promoted its radiation into several trophic types, yielding a differentiation in *Hoplitomeryx*. The shared lack of large mammalian predators and the limited amount of food in all niches promoted the development of secondary features in all size groups (apomorphies).

Keywords: Gargano, endemism, *Candiacervus, Cervus astylodon, Microtia* fauna.

Introduction

The Gargano fauna

Once upon a time, the five-horned deer *Hoplitomeryx matthei* Leinders, 1984 (Fig. 1) lived on the Gargano Island, now part of the east coast of South Italy. Its fossilized remains were retrieved in the late sixties and subsequent years (Freudenthal, 1971) from reworked reddish, massive or crudely stratified silty-sandy clays (*terre rosse*), which partially fill the paleo-karstic fissures in the Mesozoic limestone substrate and that are on their turn overlain by Late-Pliocene-Early Pleistocene sediments of a subsequently marine, shallow water and terrigenous origin (Abbazzi *et al.*, 1996). In this way a buried paleo-karst (*sensu* Bosak *et al.*, 1989) originated. The fauna from the paleokarst fillings is known as *Microtia* fauna after the endemic murid of the region. Later, after the regression and continentalization of the area, a second karstic cycle started in de late Early Pleistocene, the neokarst, which removed part of the paleokarst fill (Abazzi *et al.*, 1996). In this paper, I focus only on the *Microtia* fauna from the Early Pliocene paleokarst fillings.

Hoplitomeryx was not the only inhabitant of the Early Pliocene palaeoisland; many remains of other vertebrates have been found in the paleokarst fills as well. The other mammals that have been identified and described can be divided into genera and species that are truly endemic to the Gargano only, and species that are more wide-spread. The true endemic genera are the soricid *Deinogalerix* Freudenthal, 1972 with five species, amongst which the giant *D. koeningswaldi* with a skull length of approximately 20 cm (Freudenthal, 1972; Butler, 1980), the murid *Microtia* Freudenthal, 1976, which appears to be the only burrowing murine genus known till now (Parra *et al.*, 1999), and which radiated into at least three lineages of different size, and of which the largest, *M. magna*, has a skull length of about 10 cm (Freudenthal, 1976), the huge glirid *Stertomys laticristatus* Daams & Freudenthal, 1985, and the hamster *Hattomys* Freudenthal, 1985, with three species. True endemic species, belonging to wider spread genera, are the otter *Paralutra garganensis* (Willemsen, 1983) and the ochotonids *Prolagus imperialis* (Mazza, 1987) and *P. apricenicus* (Mazza, 1987), of which the largest, *P. imperialis*, is larger than any other known *Prolagus* species (Mazza, 1987). The mammals that are also found in other regions are the arvicolid *Apodemus gorafensis* (Ruiz Bustos *et al.*, 1984), and the three hamsters *Cricetulodon, Megacricetodon, Cricetus* (Freudenthal, 1985).

Also the sky above the Gargano was not empty, and was filled with at least the following birds (Ballmann, 1973, 1976): the endemic eagle *Garganoaetus* Ballmann, 1973 with three species, the barn owl *Tyto* with three species, of which the largest, the endemic *T. gigantea* (Ballmann, 1973), was about twice as large as the living *Bubu bubo*, a true owl possibly of the genus *Strix*, and the Eurasian pigeon *Columba omnisanctorum* and gull *Apus wetmorei*.

The age of the Gargano

The age of these fossiliferous sediments is still under discussion (Abbazzi *et al.*, 1996; Zafonte & Masini, 1992; De Giuli *et al.*, 1986). The first datation of the *terrae rossae* was based upon a combination of stratigraphy and microfauna. In these studies, the calcarenite overlying the karst system is considered to have been deposited during the Tortonian, or Vallesian - early Turolian Mammal Age (Freudenthal, 1971, 1976; D' Alessandro *et al.*, 1979), and therefore the fissure deposits were supposed to range from late Vallesian (MN 10) to early Turolian (MN 11), which was confirmed by the microfaunal evolutionary stage in the view of Freudenthal (1971, 1972, 1976). A younger age than in first instance is assumed by De Giuli & Torre (1984a, 1984b) and De Giuli *et al.* (1985, 1986, 1987), who propose the Late Turolian (Messinian, MN 13), or early Ruscinian (MN 14) as period during which the endemic fauna evolved. Freudenthal (1985) also adjusts his earlier estimation to the Messinian, on the basis of the cricetids. Other studies are based exclusively on faunal elements, such as Ballmann (1973), who gives a post-quem age of Late Aragonian, MN 7/8 on the basis of avifauna. De Giuli *et al.* (1986) give a post-quem date of latest Turolian (MN 13) on the basis of the occurrence of a true *Apodemus (A. gorafensis)*, a widely distributed taxon in the Early Pliocene onwards (Martín Suarez & Mein, 1998); the first *Apodemus* occurs in the Eastern Mediterranean at the beginning of the Late Miocene (Koufos, 2001). De Guili *et al.* (1985) consider Monte Gargano as part of a larger structural unit, the so-
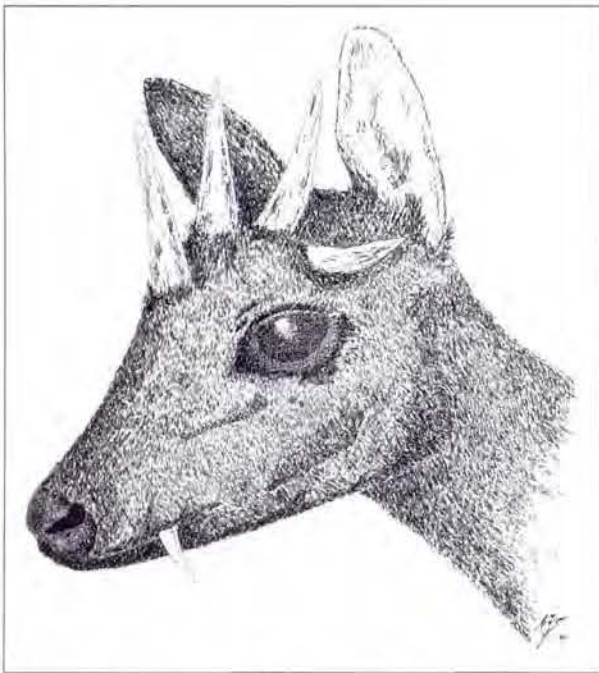

Fig. 1. The deer *Hoplitomeryx matthei* Leinders, 1984 is characterised by its five horns (one nasal horn and two pronghorns on each orbit). Its fossils are found in the *terre rosse* of the paleokarst fissures of the Gargano (South Italy), associated with other faunal elements, known as the *Microtia* fauna.

Fig. 1. El cèrvol Hoplitomeryx matthei *Leinders, 1984 es caracteritza per tenir cinc banyes (una banya nasal i dues punxes sobre cada òrbita). Els seus fòssils es troben a bretxes paleocàrstiques vermelloses de Gargano (Sud d'Itàlia), associats amb altres elements faunístics, coneguts com a la fauna de* Microtia.

called Apulo Dalmatic Realm, which gradually got disrupted and submerged from the earliest Miocene to the Early Pleistocene, with a temporary major regression in the earliest Pliocene or Messinian, and a smaller, local regression in the Middle Pliocene (*Globorotalia* gr. *crassaformis* zone; Valleri, 1984), documented by field geological data, which resulted in the almost complete submersion of the foreland in the Late Pliocene - Early Pleistocene (De Giuli & Torre, 1984a; De Giuli *et al.*, 1985; Valleri, 1984). During the Pleistocene, the regional uplift caused the emergence and continentalization of the foreland (Ricchetti *et al.*, 1992). The Messinian-earliest Pliocene regression is considered probably the time of the last large fauna immigration (Torre, 1986). A detailed biogeostratigraphic study is made by Abbazzi *et al.* (1996), who define eight units, ranging from late Miocene to Middle Pleistocene. The oldest unit (1) is a facies of residual red silty clays, *terre rosse*, which are the fillings of the paleokarst. The next five units are breccia facies, with successive *Globorotalia punticulata* and *G. inflata*, of which the second is rich in mollusks, including marine taxa. The next unit is terrigenous, and consists of sands and pelites with marine mollusks. The last, eight unit is again a filling, now of the neokarst, represented by alternating finely stratified sands and pelites. Unit 1, containing the *Microtia* fauna with endemic taxa, is assigned a Late Miocene - Early Pliocene age, whereas Unit 7 coincides with the Plio-Pleistocene boundary; Unit 8 contains a late Villafranchian fauna, and is therefore assigned a late Early Pleistocene age. During the neokarst cycle, most of the fillings of the Paleokarst were washed out and/or reworked (Abbazzi *et al.*, 1996), which makes proper stratigraphic and evolutionary approaches extremely risky. Unit 1 is found in many sites spread over the region, whereas Unit 8 is constricted to Pirro Nord and Cava Dell' Erba (community of Apricena), the area where F16 and F17 are assigned to the Unit 1 finds. It is not completely clear if the marine Tortonian sediments effectively overlie the fossiliferous horizon, and furthermore, the study is local (quarries between Apricena and Poggio Imperiale), and Abbazzi *et al.* (1996) strongly advise not to extrapolate the stratigraphic data to a larger scale, for example the entire Gargano area, due to the complexity of the stratigraphic relationships in the Gargano, in which extremely dynamic paleogeographic conditions were governed by structural activity. In other words, the only observation that remains valid is that the Unit 1 endemic *Microtia* fauna predates the Unit 8 latest Villafranchian fauna, but the absolute age is still unclear.

Diagnosis of *Hoplitomeryx*

Leinders (1984) described the cranial and dental material of the Gargano artiodactyls, and established a new cervid family Hoplitomerycidae, a new genus *Hoplitomeryx*, and a new species *matthei*. The most striking characteristic of the Hoplitomerycidae is the presence of five horns (Fig. 1), of which one projects between the eyes on the caudal part of the nasals. The other four arise in pairs above the orbit, and can be considered pronged horns, hence the name prongdeer was suggested (Van der Geer, in press). Other characters are a large bulla tympanica, a non-pneumatized skull roof, the

large, flaring and sabre-like upper canines, lack of P1 and P2 inf., a non-molarized P4 inf., a variable degree of hypsodonty, and an M3 inf. with large, bicuspid third lobe. *Hoplitomeryx* had a short, massive snout, more anteriorly positioned orbits, and a double lacrimal orifice on the rim of the orbit. Some artiodactyl material (amongst others, an orbital horncore, a fused metatarso-cubonavicular, and some molars) discovered in the Turolian (Late Miocene) Scontrone fauna (Maiella, Abruzzo National Park, Central Italy) has also been attributed to *Hoplitomeryx* (Mazza & Rustioni, 1996; Rustioni *et al.*, 1992).

The postcranial elements of *Hoplitomeryx* have not been described yet in full detail, but they are remarkably homogenuous in their morphology. They show many typical endemic features, such as the fusion of the navico-cuboid with the metatarsus, described as a functional adaptation by Leinders & Sondaar (1974), shortening of some metapodials as described for *Myotragus* (Sondaar, 1977) and in one case the fusion of both malleoli with the tibia, which has till now been reported only for one other species: *Myotragus* (Bover, 2003; Bover *et al.*, this volume). Other diagnostic features are the non-parallel sided astragalus (Van der Geer, 1999) and the extremely elongated patella (Van der Geer, in press); these are explained as a return to a less derived condition, favored by the absence of predators and the lack of abundant food (Van der Geer, in press).

The size of the *Hoplitomeryx* postcranial material is on the contrary less homogenuous, and seems to form a heterogenous group, containing at least four size classes. The sizes are not restricted to specific fissures, and an equally distribution over the fissures instead seems to be more the case. In most fissures, more than one size is represented. Due to the often fragmentary character of the material, and the relative scarcity of the material, it is at the moment not possible to recognize all size classes in each limb element, in particular the largest sizes. Large specimens are always incomplete, and as a remarkable detail, the largest size is represented by juveniles only. The total number of size groups is therefore a combination of the groups defined per limb element,

In this article only the metapodals are described in more detail, as an illustration of the process of adaptive radiation, which is supposed to be the underlying drive behind the speciation of *Hoplitomeryx*. The other limb bones follow the same pattern, and will be dealt with in a future paper.

Explanation of increased size range

The increased size range with separate size groups as observed in endemic insular taxa is usually explained in terms of allopatric speciation, which implies the existence of an archipelago, e.g. the famous Darwin's Finches on the Galápagos Islands. The Pliocene island Monte Gargano (Italy) has been considered part of a larger archipelago (Apulo-Dalmatic Realm) in relation to the micromammals (De Giuli & Torre, 1984; De Giuli *et al.*, 1985, 1987) and the ochotonid *Prolagus* (Mazza, 1987) to explain the presence of several sister taxa that evolved in a relatively short time. Another explanation is the occurrence of more than one invasions, e.g. as suggested for the deer *Candiacervus* on Crete (Kuss, 1975; De Vos, 1984,

however cf. De Vos, 1996, 2000; Capasso Barbato, 1992; Caloi & Palombo, 1996) and the rodents on the Monte Gargano (Freudenthal, 1976).

In the archipelago hypothesis, it does not explain sufficiently why sister taxa are found together on one and the same island. In the multiple invasion hypothesis, it is no explanation as to where and why this new sister taxon evolved. In both cases it is not clear why the sister taxa wait with migration untill full speciation has taken place.

What we see is only the end result, consisting of a range of taxa, closely related; when the variety is large and the genetic distance small, the term flock is used (e.g. Greenwood, 1974; Echelle & Kornfield, 1984, and references therein). The radiation into morphotypes can be compared to the medium scale, medium term radiations (e.g. the radiation of the antlered deer in Eurasia), and on its turn with the large scale, long term radiations (e.g. the radiation of the marsupials in South America and Australia; Woodburne & Case, 1996). The main driving force

in all cases is the urge to occupy free ecological niches. The resulting speciation can be explained best in terms of sympatric speciation (De Vos & Van der Geer, 2002).

MATERIAL

Hoplitomeryx

For the description are used: 47 adult metatarsals, 6 juvenile metatarsals, 55 adult metacarpals, all RGM numbers; stored at Naturalis, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; 3 unnumberd metatarsals (field numbers P77/4, F8 and 25.9.83 Fina F9), and 1 unnumbered metacarpal (field number P77/4), all four stored at Museum of Geology and Paleontology, University of Florence, Italy)
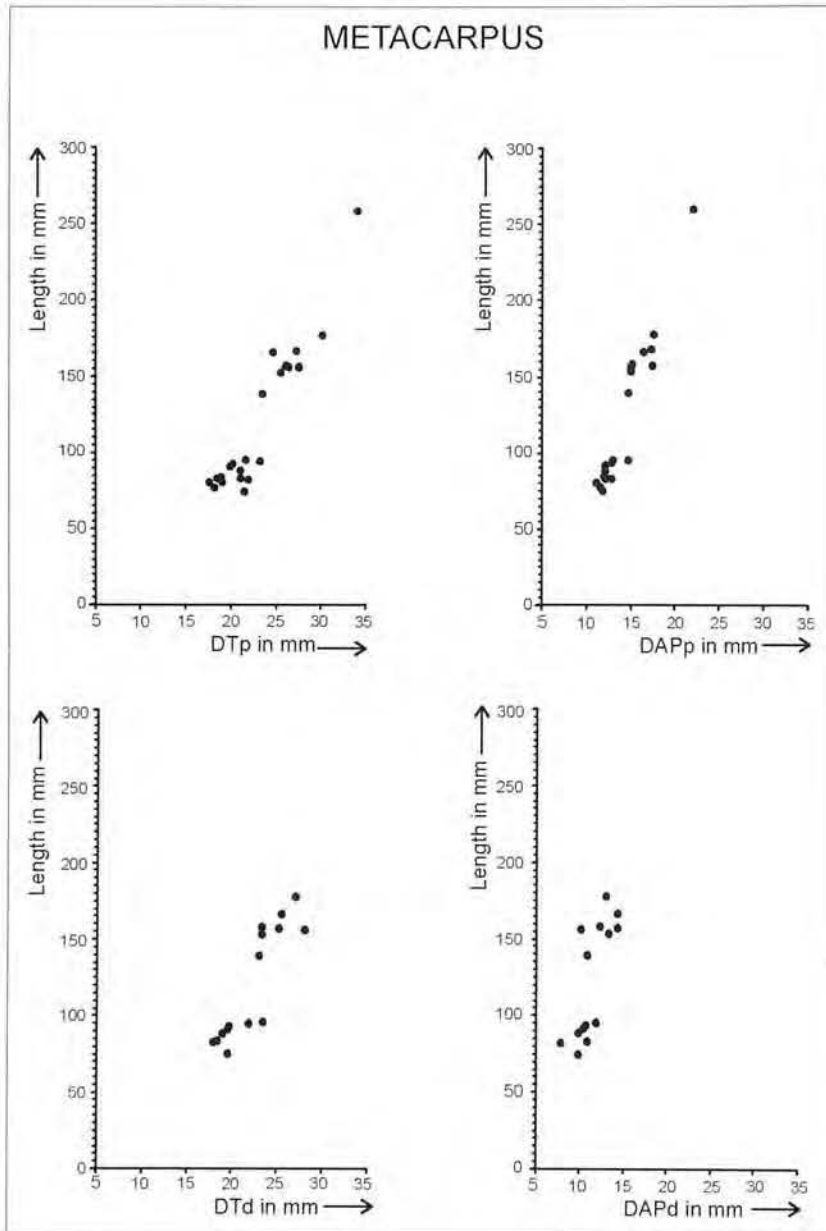

Fig. 2. The four different massivity diagrams of adult metacarpals of *Hoplitomeryx* show three (massivity proximal end) or two (massivity distal end) size groups. DTp = proximal width; DAPp = proximal depth; DTd = distal width; DAPd = distal depth.

*Fig. 2. Els quatre diagrames de massivitat diferent de metacarpians adults d'*Hoplitomeryx *mostren tres (extrem proximal de massivitat) o dues (extrem distal de massivitat) classes de talla. DTp = amplària proximal; DAPp = fondària proximal; DTd = amplària distal; DAPd = fondària distal.*

Comparison material

The following species have been used for comparison, in alphabetical order:

Alces alces (Fairbanks, Alaska, Rancholabrean; F:AM BX276 and 2 others, drawer with F:AM 8309-1933, n=6); *Antilocapra americana* (North America, recent; FMNH 14239, FMNH 57217, FMNH 74239); *Axis axis* (Pleistocene, Java; Coll. Dubois, nos. 5376, 5593, 6089, 6258, 9853, 9861); *Blastomeryx* (Trinity River; F:AM CRO 60-1752); *Candiacervus* size 2 (Liko Cave, Crete, Pleistocene; LiB n=20, LiC n=20, Li-C n.n. complete leg); *Cervalces* (Rancholabrean, Alaska; F:AM 527); *Cervus elaphus* (Rancholabrean, Alaska; drawer with F:AM 34672, n=5); *Cervus kendengis* (Pleistocene, Java; Coll. Dubois nos. 6459 and 6471); *Cranioceras granti* (Clarendonian, Nebraska; F:AM 31716, n=7); *Eumeryx culminis* (Mongolia, Middle Rupelian; AMNH 19147, cast of type); *Ovis aries* (n=5, own collection); *Rangifer tarandus* (Fairbanks, Alaska, Rancholabran; F:AM A 591 (complete postcranial skeleton), drawer with A 473 (n-12), drawer with F:AM 120-6244 (n=8), and F:AM 2204-1951).

THE *HOPLITOMERYX* METACARPUS

Introduction

Metacarpals of *Hoplitomeryx* have been recovered from the following fissures in the Gargano, in alphabetical order: Chiro 1, Chiro 2, Chiro 4, Chiro 10B, Chiro 12, Chiro 14b, Chiro 27, Chiro 29, Chiro D1, Chiro D3, Falcone 2A, Fina D, Fina H, Fina K, Fina N, Gervasio 1, Nazario 4, Pizzicolli 4, Pizzicolli 12, S. Giovannino, S. Giovannino Low, Trefossi 2A, Trefossi F26.

To determine full-grown stage, the pattern as described for *Dama dama* (after Pöhlmeyer, 1985) is followed. At birth the distal epiphysis is unfused, and consists of two separate condyles. At the end of the sixth month the two condyles are fused. At 20 months the dis-

tal epiphysis starts to fuse with the diaphysis, and at the end of the second year this fusion is complete. *Megaloceros cazioti* (="*Megaceroides*" *cazioti, Dama cazioti*) follows the same pattern (Klein-Hofmeijer, 1996), and the same appears to be true for *Candiacervus* size 1 (= *Candiacervus ropalophorus*) (Biskop, 1978). It is therefore reasonable to accept the same pattern for *Hoplitomeryx*, but not necessarily with the same growth speed. Specimens without distal end cannot be determined on ontogenetic stage, and are therefore discarded from the size estimations.

Metacarpal size

Measured are maximal length, proximal width and depth, and distal width and depth. Length is measured from the most proximal end of the proximal articulation till the distalmost end of the trochlea. Proximal depth (DAPp) and proximal width (DTp) are both the maximum values as measured on the articulation area. Distal depth (DAPd) and distal width (DTd) are both the maximum values as measured on the distal epiphysial fusion line. Measurements on the distal articulation itself, the trochlea, are found to be too subjective, and in many cases impossible due to fragmentation.

Length of the adult *Hoplitomeryx* metacarpals appears to vary between about 74,4 mm and 259 mm (average 118,7 mm). Proximal depth varies between 9 mm and 22 mm (average 13,8 mm); proximal width (DTp) between 12 mm and 34 mm (average 22,3 mm). Distal depth (DAPd) varies between 9,2 mm and 18,2 mm (average 11,8 mm); distal width (DTd) between 18 mm and 31,5 mm (average 21,8 mm).

In the massivity diagrams of the adult specimens, three groups can be discerned (Fig. 2; Fig. 3). The low number of larger, complete specimens may lead to artificial groups, which as a consequence would disappear if more specimens could be measured. A fourth group is not represented by an adult specimen, but by a juvenile trochlea, which is significantly larger than any of the adult specimens, with a DAPd 22,2 mm and a DTd 36,6 mm (for the adult range, see above).

Fig.. 3. Proximal massivity (transversal diameter against length) clearly shows three size groups. The smallest specimens are laterally compressed at midshaft, while the larger specimens are straight.

Fig. 3. *La massivitat proximal (diàmetre transvers respecte la llargària) mostra clarament tres classes de talla. Els espècimens més petits estan clarament comprimits enmig de la canya, mentre que els espècimens més grans són rectes.*
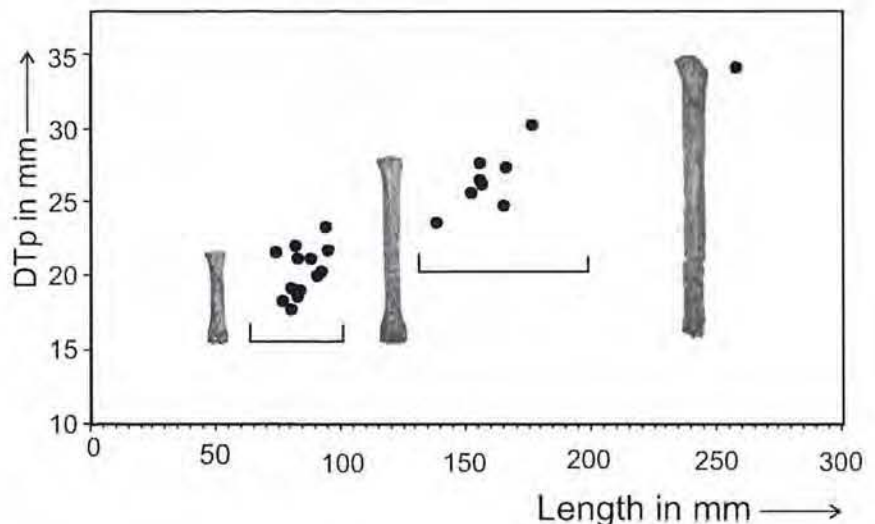
The massivity indexes (DT/L) gradually increases from large to small specimens, as is also observed in *Candiacervus* (after De Vos, 1979), but run a bit ahead, in other words, the smaller specimens are relatively more massive. Another observation is that in the diagram with DAPp/L plotted against DTp/L, two clouds can be discerned, which shows that the smaller specimens are more square than the larger specimens, which are clearly more broad (DT) than deep (DAP). The smallest specimens are therefore not only shortened, but also more square in cross-section.

Four sizes groups can be discerned within the available material, based upon the maximum length. These groups are the following, from small to large:

Size 1. Length varies between 74,4 mm and 95 mm with an average of 85,5 mm (N=14). Proximal depth (DAPp) varies between 11 mm and 14,6 (average 12,1 mm), proximal width (DTp) between 17,6 mm and 23,2 mm (average 19,9 mm). Distal depth (DAPd) varies

between 10 mm and 12 mm (average 10,9 mm), distal width (DTd) between 18,3 mm and 23,4 mm (average 20,2 mm). The average distal massivity DTd/L is 0,24.

The length of this size group corresponds to that of *Cervus astylodon* size G3 (range 80-89 mm) of Kume (Ryukyu Islands, Japan; after Matsumoto & Otsuka, 2000), and to *Candiacervus* size 1 (range 88,4-114,1 mm; after De Vos, 1979). The distal massivity corresponds to that of *Candiacervus* sizes 1 and 2 (range 0,21-0,24).

Size 2. Length varies between 139 mm and 177 mm with an average of 158,9 mm (N=8). Proximal depth (DAPp) varies between 14,6 mm and 17,5 mm (average 16,0 mm), proximal width (DTp) between 23,5 mm and 30,1 mm (average 26,4 mm). Distal depth (DAPd) varies between 10,3 mm and 14,4 mm (average 12,7 mm), distal width (DTd) between 23,0 mm and 28,0 mm (average 25,0 mm). The average distal massivity DTd/L is 0,16.

The length of this size group corresponds to that of *Candiacervus* size 3 (range 131,0-144,2 mm; after De Vos,
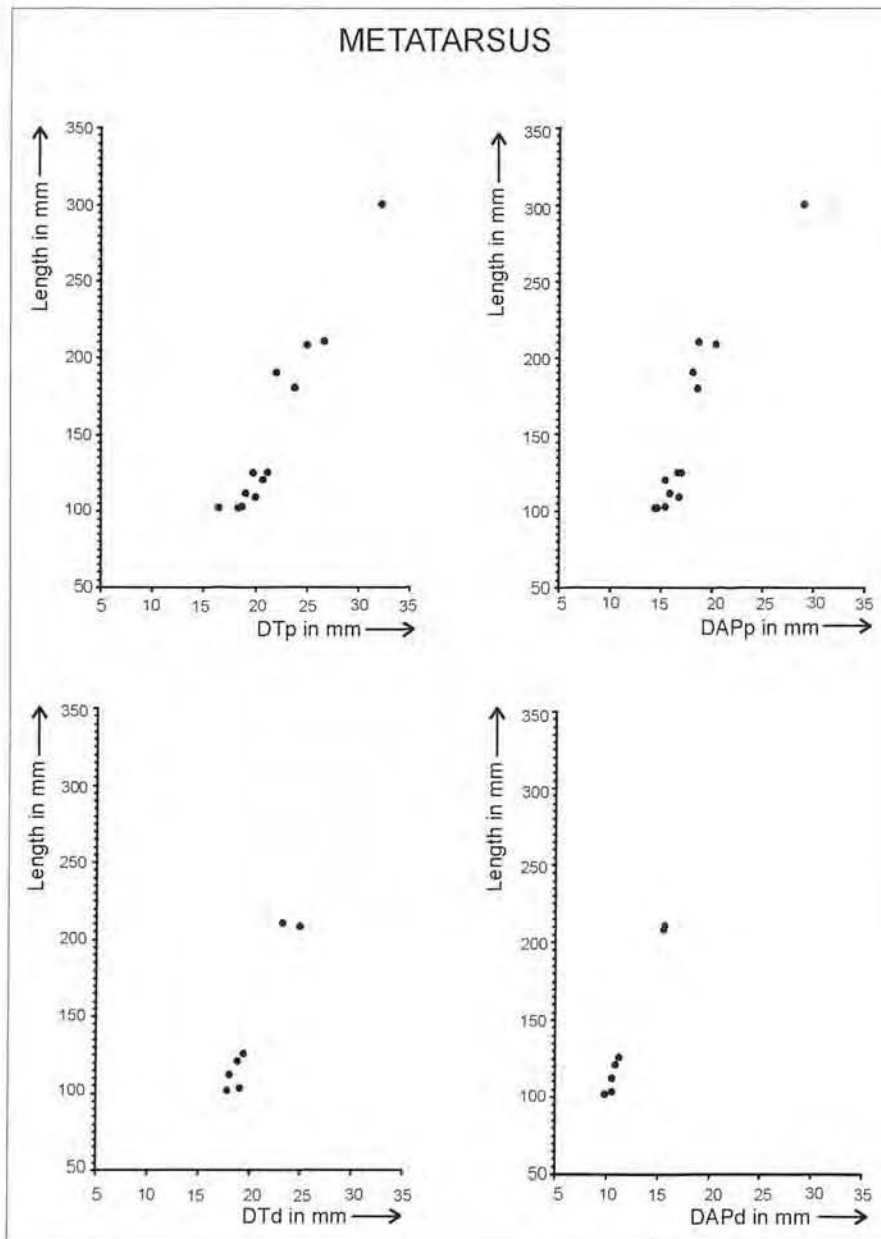

Fig. 4. The four different massivity diagrams of adult metatarsals of *Hoplitomeryx* show three (massivity proximal end) or two (massivity distal end) size groups. DTp = proximal width; DAPp = proximal depth; DTd = distal width; DAPd = distal depth.

Fig. 4. Els quatre diagrames de massivitat diferent de metatarsians adults d'Hoplitomeryx mostren tres (massivitat de l' extrem proximal) o dues (massivitat de l'extrem distal) classes de talla. DTp = amplària proximal; DAPp = fondària proximal; DTd = amplària distal; DAPd = fondària distal.

1979), to that of *Cervus astylodon* size G1 (140 mm; after Matsumoto & Otsuka, 2000) from Ryukyu Islands, Japan, and to that of the living Japanese deer *Cervus nippon keramae* (range 140-155 mm; after Matsumoto & Otsuka, 2000). The distal massivity corresponds to that of *Candiacervus* sizes 4 and 5 combined (range 0,14-0,17), to *Cervus elaphus* (0,15-0,17), and *Rusa unicolor* (0,16).

Size 3. The length of specimens of this size group may be about 259 mm (only one specimen), with a proximal depth (DAPp) of 19,5-22 mm (two specimens), and a proximal width (DTp) of about 33,4-34 mm (two specimens). Distal depth is about 18,2 mm, and distal width about DTd 31,5 mm, but there is only one specimen available. The distal massivity DTd/L would then be about 0,12, which corresponds to *Capreolus capreolus* (0,12-0,13).

The length of this size group seems to correspond to the size of *Candiacervus* size 5 (range 262 mm-284 mm; after Kotsakis *et al.*, 1976), but the proximal and distal diameters are lower, for example the proximal DT is about 38 mm (after Capasso Barbato, 1988, table 7)

Size 4. This size group is not represented by measurable adult specimens, but its existence is without doubt, as the largest juvenile trochlea epiphysis is already clearly larger than any adult trochlea. The specimen in question has already at this stage (no fusion started yet) a distal depth (DAPd) of 22,2 mm, and a distal width (DTd) of 36,6 mm. This size corresponds probably to that *Candiacervus* size 6, but no metacarpals were found. However, the increase in DTd of the metatarsal between size 5 and 6 is about 20% (calculated with data from Kotsakis *et al.*, 1976); it is logic to assume that the same takes place in the DTd of the metacarpal, too. In *Hoplitomeryx* an increase of 20% can be observed in the metacarpal DTd from size 3 to size 4. For the moment I therefore compare *Hoplitomeryx* metacarpals of size 4 to *Candiacervus* size 6.

Morphology of the metacarpal

The morphology of the metacarpus shows some uniform features, shared by all *Hoplitomeryx* specimens, but also some differences. The shared characters are the following. The groove on the dorsal surface for the interosseus muscle covers the proximal one third of the shaft or the proximal two third. The trochlea of *Hoplitomeryx* is inclined as in deer, with the lateral trochlea extending further than the medial one, or straight as in bovids, with the lateral and medial trochlea extending equally far.

The *Hoplitomeryx* specimens are, however, not homogeneous in the configuration of the proximal articulation, and four morphotypes can be discerned if we take the features into account with which cervids are distinguished from bovids (*sensu* Heintz, 1970). These morphotypes are irrespective of size, and are the following:

Morphotype 1. The crest ends in the central fossa, and makes an angle of about 30 degrees with the dorso-palmar axis. The fossa lies more or less central, and makes no contact with the palmar surface. This pattern is not only typical for *Cervus* (Heintz, 1970), but is also found in the other modern cervoids *Antilocapra americana* and *Rangifer tarandus*, and even in the very distantly related *Cranioceras granti*. The crest may be continued palmar of the fossa, as in some *Axis axis* (Coll. Dub. no. 5593).

Morphotype 2. The separating crest ends in central fossa, and runs more or less dorso-palmar following the DAP-axis; the fossa lies central, and the contact area between the lateral and medial articulation is minimal. The difference with morphotype 1 is the angle of the crest compared to the DAP-axis; it may be thus nothing more than a variety of the typical cervoid pattern, in which the lateral component increased in importance (= weight bearing). This configuration is typical for the Tokunoshima-type of *Cervus astylodon* from Ryukyu Islands, Japan (Matsumoto & Otsuka, 2000), and is also seen in *Alces alces* and *Cervalces*. The crest may be continued palmar of the fossa, as in *Cervalces*. In some specimens, the fossa borders the palmar surface.

Morphotype 3. The crest runs parallel to the border of the fossa, and ends somewhere within the lateral facet. The crest runs more or less dorso-palmar along the DAP-axis, and the fossa borders the palmar surface. This pattern is seen in the Kume-type of *Cervus astylodon*.

Morphotype 4. The crest runs parallel to the border of the fossa, along the DAP-axis, and ends at the palmar surface, as in bovids. In a way this morphotype is an elaboration of the former type. This pattern is seen in the Okinawa-type *of Cervus astylodon*, and is typical for bovids, e.g. *Gazellospira torticornis* (Heintz 1970: 33, fig.26), *Ovis aries* and *Myotragus balearicus*.

THE *HOPLITOMERYX* METATARSUS

Introduction

Metatarsals of *Hoplitomeryx* have been recovered from the following fissures in the Gargano, in alphabetical order: Chiro 10c, Chiro 23, Chiro 28, Chiro 28a, Chiro 29, Chiro 30, Chiro D1, Chiro D3, F8, Fina F9, Fina N, Gervasio 1, Nazario 1, Nazario 3, Nazario 4, Pizzicoli 1, Pizzicoli 4, Pizzicoli 12, Posticchia 1B, Posticchia 5, S. Giovannino, S. Giovannino Low, Trefossi 1.

To determine the ontogenetic stage of the metatarsals, the fusion pattern as described for *Dama dama* (after Pöhlmeyer, 1985) are followed. At time of birth the distal epiphysis is unfused, and consists of two separated condyles. At the beginning of the fourth month they become fused, and at month 22 the distal epiphysis fuses with the diaphysis. The pattern of fusion is confirmed by the data for *Megaloceros cazioti* (Klein-Hofmeijer, 1996), and by *Candiacervus cretensis* from Gerani layer 4: there are specimens with two separated condyles, larger specimens with a single distal epiphysis, and again larger specimens with a visible fusion line.

For the time of fusion of the navicocuboid with the metatarsal, no data for other insular species are available. It appears that in *Hoplitomeryx* this fusion takes place already before the fusion of the distal epiphysis with the shaft. This is evidenced by RGM 178.258 (Chiro 3) and RGM 178.534 (Nazario 3), where the distal epiphysis is still unfused, and the fusion line between navicocuboid and metatarsal already hardly visible, to the degree as seen in adult specimens. The earliest developmental stage is represented by RGM 178.261 (Chiro 3)

and RGM 178.659 (Fina K), where the condyles are separated and no fusion has yet taken place with the cubonavicoid. At this stage the proximal articulation is developed as in *Dama dama*, which means that the lateral and medial facet are developed,whereas the other two facets are not.

Metatarsal size

Measured are maximal length, proximal width and depth, and distal width and depth. Length is measured from the top of the internal point of the cubonavicular element (which is in all cases firmly fused to the cannon bone, with no trace of a fusion line in adults), till the distalmost end of the trochlea. Proximal depth (DAPp) and proximal width (DTp) are both the maximum values as measured on the cubonavicular part. Distal depth (DAPd) and distal width (DTd) are both the maximum values as measured on the distal epiphysial fusion line. Measurements on the distal articulation itself, the trochlea, are found to be too subjective, and in many cases impossible due to fragmentation.

The length of the *Hoplitomeryx* metatarsal varies between about 420 and 102 mm (average 174 mm). Proximal depth varies between 13,1 mm and 29,1 mm (average 16,4 mm); proximal width (DTp) between 16,5 mm and 32,3 mm (average 20,6 mm). Distal depth (DAPd) varies between 9,9 mm and 17,1 mm (average 12,2 mm); distal width (DTd) between 16,9 mm and 26,0 mm (average 20,2 mm).

All measurements fall within a large range, especially those of the smaller half of the collection, but with some discontinuities; three or two groups can be discerned in the scatter diagrams (Fig. 4). The low number of complete specimens may lead to artificial groups, which as a consequence would disappear if more specimens could be measured.

The massivity indexes (DT/L) gradually increase from large to small specimens, as is also observed in *Candiacervus* (after De Vos, 1979).

The shapes (DAP/DT) of the distal and proximal ends show a gradual change along the size scale. The smaller the specimens, the more square they become; in other words, the ends remain more or less the same while the length decreases. If we divide the shape by maximal length, it appears that this allometric ratio runs a bit behind along the length scale: the smallest specimens have a relatively slightly larger DAPp than the largest specimens, and at the same time a relatively smaller DAPd.

The size groups are the following, from small to large:

Size 1. Length varies between 102 mm and 125 mm, with an average of 112,2 mm (N=8). The massivity proximal varies between 0,16 and 0,18 (average 0,17), and distal between 0,16 and 0,19 (average 0,17). The length of this group corresponds to that of *Candiacervus* size 1 (range 110 mm-131 mm, without the cubonavicular bone; after De Vos, 1979), but also includes smaller specimens than ever found in *Candiacervus*. Such small specimens, and even smaller ones, occur in *Cervus astylodon* from Ryukyu Islands, Japan, where the smallest length is 76 mm (after Matsumoto & Otsuka, 2000). A dis-

tal massivity of 0,16-0,19 is also found in *Rangifer tarandus* and *Candiacervus* sizes 1 to 3 (after De Vos, 1979).

Size 2. Length varies between 180 mm and 210 mm, with an average of 199,6 (N=5). The massivity proximal varies between 0,12 and 0,13 (average 0,13), and distal between 0,11 and 0,12 (average 0,12). This size class is comparable to *Candiacervus* size 3 of De Vos (1979), which has a metatarsal length (without cubonavicular) of 180 mm. It is also comparable to *Megaloceros cazioti*, which has a metatarsal length between 185 mm and 217 mm, without the cubonavicular (after Klein Hofmeijer, 1996). A distal massivity of 0,11-0,12 is also found in *Capreolus capreolus*, *Moschus* and *Candiacervus* size 6 (after De Vos, 1979).

Size 3. This size class is not represented by a complete specimen, but is likely to be present, seen the presence of a large proximal part of about one and a half times that of the former size (rgm 178.553). The estimated length would than be about 300 mm., but this is only true in case this proximal part belongs to a full grown individual. The massivity proximal is 0,11, distal it is unknown. This size is, tentatively, comparable to that of *Candiacervus* size 5 of De Vos (1979), which has a metatarsal length (excl. cubonavicular) of about 304 mm (after Kotsakis *et al.*, 1976).

Size 4. This size class is not represented by an adult specimen, but the juvenile shaft rgm 425.055 exceeds the largest available specimen, and is already its unfused stage twice as large. The estimated full grown length therefore is at least 420 mm. The massivity proximal is unknown, distal it is about 0,08. This size is comparable to that of *Candiacervus* size 6, which has a length (excl. cubonavicular) of about 406 mm (after Kotsakis *et al.*, 1976).

Morphology of the cannon bone

All *Hoplitomeryx* full-grown metatarsals, without exception, show a complete fusion with the navicocubocuneiform, elongated specimens as well as shortened specimens. As such, complete fusion can be considered a synapomorphic character of all morphotypes of *Hoplitomeryx*. This is unique, as in other described island artiodactyls this is not the case. The percentage of total fusion is 0% in *Megaloceros cazioti* from Sardegna, Italy (after Klein-Hofmeijer, 1996), 0% in *Cervus astylodon* from the Ryukyu Islands, Japan (after Matsumoto & Otsuka, 2000), both species Late Pleistocene, 6% in *Candiacervus ropalophorus* (= *C.* size 1) from Gerani 4 Cave, Crete (De Vos, 1979). In *Myotragus balearicus* this percentage differs according to locality and age: 40% in Cova de Son Maiol, 50% in Cova de Llenaire, which are both late Late Pleistocene, 60% in Cova des Moro and 80% in Cova de Moleta, which are both Holocene (Moyá-Solá, 1979:89).

In proximal view, there is a difference between the *Hoplitomeryx* specimens as regards the configuration of the fossae. Three configurations seem to be present. Two fossae can be present, where the fossae are located in the non-articulatory surface, interno-dorsal of both facets. One single fossa can be present, located within the lateral facet. No fossae can be present. The first configuration is seen in some bovids, e.g. *Ovis*; the third configuration is observed in deer (e.g. *Candiacervus* size 2 from Liko,

Crete; *Rangifer tarandus*), dromomerycids (*Cranioceras granti*), but also in *Myotragus balearicus*. The second configuration is new, and maybe a variation of the first type.

In general, the morphology of the distal articulation is strikingly similar in all *Hoplitomeryx* specimens, irrespective of size. In all specimens the trochlea is complete, whereby the condyls extend slightly further on plantar side than on dorsal side. In almost all specimens the lateral condyl extends clearly further distal than medial condyl; as an exception they extend equally far. In almost all specimens the condyls are parallel to each other; in exceptional cases they diverge or converge. The lateral surface of the distal epiphysis is always diverging.

The same distal articulation is seen in *Axis axis*. In *Rangifer* the extension varies from clearly further to not at all. In *Alces alces* there is hardly an extension or not at all. In *Cervus kendengis* (Pleistocene, Java) the lateral condyl extends further than the medial condyl (Coll. Dubois nos. 5406, 6501, 6502), or they extend both equally far (Coll. Dubois no. 6982). *Hoplitomeryx* follows a *Cervus* pattern, including the rare exceptions.

All *Hoplitomeryx* specimens have a square cross-section, laterally compressed, and most specimens miss a clear volar sulcus. The smallest specimens have a convex plantar surface. The same shape can be observed in *Cervus kendengis*, *Axis axis*, *Candiacervus*.

As to the development of the muscular groove at the plantar surface, there is a gradual range from moderate robust with a weak or even indistinct muscular groove till robust with a pronounced muscular groove. The majority of specimens is moderate robust, and only about one third of the specimens shows the pronounced groove. There is no relation between development of the groove and length.

In all *Hoplitomeryx* specimens the medial ridge along the sulcus interosseus is higher than the lateral border, ranging from only slightly higher to clearly higher. In rare cases the development is so strong that the medial border is even convex at about one third from the proximal end.

In *Axis axis* from Java and *Candiacervus* size 2 from Liko Cave, Crete, the medial border is only slightly higher than the lateral border. In *Rangifer tarandus* the medial border is clearly higher than the lateral border.

The gully on the dorsal surface of the shaft of the metatarsal bone is distally closed in all *Hoplitomeryx* specimens, as typical for deer (Heintz, 1963). This is not only true for the genus *Cervus*, but already for the very early relative *Eumeryx*, which otherwise differs a great deal from eucervoids. The closed gully is also found in *Antilocapra*, and in the telemetacarpal cervoids (*Blastomeryx*, *Rangifer*, *Alces*).

In all *Hoplitomeryx* specimens the dorsal gully is pronounced, and extends proximally till somewhere in the cubonavicular, in any case at a point proximally of the fusion between metatarsal and the cubo-navicular bone. In cervids as a rule, the gully ends in the fossa just proximal of the distal epiphysis in cervids, whereas the gully continues till the end in bovids (Heintz, 1963). This is confirmed by *Rangifer tarandus*, but not by *Candiacervus* size 2 from Liko Cave, Crete; in the latter the gully also extends till the proximal articulation. In *Antilocapra americana* the gully also extends till the proximal end.

Size groups

To summarize, in both the metacarpals and the metatarsals of *Hoplitomeryx* four size groups are discerned, which are comparable in size, from small to large, to the Cretan deer *Candiacervus* size 1, size 3, size 5 and size 6, as we saw above.

Remarks on the chronology

The four size groups and the different morphotypes are equally distributed over the excavated fissures, and are therefore not considered chronotypes. The hypothesis of an archipelago consisting of different islands each with its own morphotype, cannot be confirmed on the basis of *Hoplitomeryx*. For example, shortened metatarsals are found in Posticchia 5 and Nazario 4, whereas normal sized metatarsals are found in S. Giovannino (both upper and low) and Fina N. The former two fissures are supposed to be of an older age than the latter (Freudenthal, 1976; De Giuli, 1986; Abbazzi *et al.*, 1993). 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. Gervasio is supposed to be older than the latter two fissures. Normal-sized metacarpals and shortened metatarsals are found together in Nazario 4. Also the astragalus contradicts the given chronology (Van der Geer, 1999). 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 but also a Chiro 28 metatarsal fit perfectly well. Their time distance cannot have been very large. The only way to accept the rodent-based chronology is a fully developed radiation in *Hoplitomeryx* already in an early stage.

Other examples

The situation with several co-existing morphotypes on an island finds already a perfect parallel in the Gargano itself: all mammalian and avian taxa appear to be represented by three to five species, different in size and/or morpology. If all fissures would have contained only one species at the time, a morphological change during the ages would be the most parsimonous solution. That is, however, not the case, as the majority of fissures yields more than one species of each genus.

Is the situation with co-existing size groups unique for the Gargano? No, it is not unique at all, but appears to be just another example of what happens on islands of all times. Where the mainlands host a range of genera and species, the islands host a range of species and morphotypes. A good example is provided by the Pleistocene deer *Candiacervus* of Crete. A huge amount of fossils have been recovered, so that statistics are useful. It appears that *Candiacervus* bones show a statistically significant large variation, so that six size groups can be reliably distinguished (De Vos, 1979). The taxonomical phramework (for a complete overview, see Dermitzakis & De Vos, 1987 and De Vos, 2000), is still under discussion, and two theories prevail concerning its phylogenetic sta-

tus: one monophyletic genus *Candiacervus* (De Vos, 2000), or two paraphyletic genera *Megaloceros* and *Cervus* (Capasso Barbato, 1988; 1992) or *Megaceroides* and ?*Pseudodama* (Caloi & Palombo, 1996). Irrespective of the taxonomical problems, the eight Cretan deer types in any case differ clearly too much to assume a similar ecological niche; more likely is the hypothesis of different niches. On the ground of body proportions, molar morphology and wear pattern, the specialist trophic niches occupied by the eight taxa might, tentatively, be summarized as follows: grassy food or prickly bushes on a rocky hill (*Candiacervus* sizes 1 and 2), grasses on a steppe-like plain (*Candiacervus* size 3), leaves and branches in a forest, like red deer (*Candiacervus* size 4), leaf-like food and soft bushes in a forested terrain with many obstacles (*Candiacervus* sizes 5 and 6) (De Vos & Van der Geer, 2002).

It is strange that theories based on radiation instead of on linear evolution are only reluctantly accepted for mammals. A factor may be the absence of a good testing facility. For fishes for example this is much easier: experiments not only in vitro but also in vivo can be done, and the process behind changes can be followed step by step. A lot of research has been done on the haplochromine cichlid fishes of the East African Great Lakes. These fishes can be compared to colonizers of a new island, as they entered a new and still unoccupied lake. Lake Victoria was filled about 14,000 years ago, due to the creation of the Rif Valley, which started to arise from 750,000 years ago. Immediately after the formation of the lake, a host of adaptive zones became available. The entering of a zone with free niches gave the cichlids the possibility to radiate beyond the degree seen in related cichlids. The haplochromine species flock of Lake Victoria is a good example of recent speciation, which took place in less than 200.000 years (Meyer *et al.*, 1990). The rapid adaptive radiation resulted in a wide range of trophotypes (Fryer & Iles, 1972; Greenwood, 1974; Barel *et al.*, 1977; Witte, 1981; Keenleyside, 1991). Initially they differed little from their immediate reverine ancestors, and there is no evidence of significant new morphological changes that facilitated their differentiation into many trophic levels; rather they capitalised on a biological versatility already present (Liem & Osse, 1975). The cichlids were obviously capable of a much higher rate of speciation than were other fish in the East African Great Lakes, and were able to differentiate into many different trophic levels with a minimum of morphological change (Carroll, 1997). It resulted mainly in differences in the mouth, which gradually became adapted to different types of food: detritus, fishes, shells, crabs, insects, phytoplankton, zooplankton.

For taxonomy, such radiations as seen in the cichlids are a disaster, as taxonomy deals with fixed, clearly defined subunits of the observable world, whereas in reality such a species flock approaches a continuum. The taxonomical problems become evident through the many revisions and reconsiderations of the classification of the haplochromine cichlids (e.g. Greenwood, 1981; Witte & Witte-Maas, 1981; Hoogerhoud, 1984; Van Oijen, 1991). This reminds us of the taxonomical problems with *Candiacervus*, with Darwin's finches, and maybe soon with *Hoplitomeryx*, as soon as more material has been described in full and scholars start to fit it into a phylogenetic scheme.

DISCUSSION AND CONCLUSION

In *Hoplitomeryx* the four size groups differ in limb proportions, as is the case in *Candiacervus* from Crete and *Cervus astylodon* from Ryukyu Islands, Japan. In the case of *Hoplitomeryx* the assumption of different ancestral genera is unlikely, because in that case the separate ancestors must have shared the typical hoplitomerycid features. The morposphere of *Hoplitomeryx* is too coherent to assume two or more different ancestors.

The large variation could be explained through adaptive radiation (as in Darwin's finches on the Galápagos), that gradually evolved after the Miocene pre-antler stage cervoid entered the island. The range of empty niches promoted the radiation into several trophic types, and caused the differentiation in *Hoplitomeryx*. The lack of large mammalian predators and the limited amount of food in all niches promoted the fast development into morphotypes. This is demonstrated by Darwin's finches, which are limited in numbers primarily by their food supply in the absence of predators; in such a case, adaptations in feeding methods are likely to be of special importance in determining the survival of the species, and the absence of predators may well have accelerated their adaptive radiation (Lack, 1947: 114). An alternative hypothesis explaining the occurrence of several sympatric species is that of multiple speciation on an archipelago of relatively close islands, with a later island merging. This can be excluded on geological grounds (Abbazzi *et al.*, 1996).

Interspecific competition for food and area is therefore at the present stage of knowledge the only reasonable hypothesis to explain the different size groups observed for the *Hoplitomeryx* groups. This appears also to be true for some mainland rodent communities (Dayan & Simberloff, 1994; Parra *et al.*, 1999), so why not for larger mammals, such as cervoids. As a matter of fact, different species of Cervidae occurring in the same mainland habitat under natural conditions are, as a rule, of considerable 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).

If we explain the different size groups of *Hoplitomeryx* and *Candiacervus* as the outcome of an adaptive radiation in an area with originally empty ecological niches, we automatically assume a narrow genetic base for the whole genus, in contrast to a mainland genus like *Cervus*.

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