

The effect of insularity on the Eastern Mediterranean early cervoid *Hoplitomeryx*: The study of the forelimb

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Abstract

Island studies increase our understanding of the effects of habitat fragmentation. The study of the Tertiary paleo-island Gargano is an important contribution, because of the long-term isolation under less fluctuating climatic conditions, free from anthropogenic influences; such a situation does not exist in the Quaternary period nor in the Holocene period. This makes the Gargano a unique case to study the effects of insularity in isolation. Here, a highly endemic, unbalanced vertebrate fauna evolved including the five-horned deer *Hoplitomeryx*. Its post-cranial material contains four size groups, based on the metapodals. In this study, the humerus and radius are described. The question whether the morphotypes are chronomorphs or ecomorphs is addressed. Sexual dimorphism is ruled out as the underlying principle of size separation in this case, based upon body mass estimations and data from living deer. Chronomorphs is the best explanation for the *Megaloceros cazioti* lineage (Pleistocene, Sardinia) and the *Myotragus balearicus* lineage (Pliocene–Holocene, Mallorca). Ecomorphs are a better explanation for the size groups of *Candiacervus* (Pleistocene, Crete) and *Cervus astylodon* (Pleistocene, Ryukyu Islands). An adaptive radiation into several trophic types took place, promoted by the ecological meltdown of the ancestral niche. The drive behind this speciation is increased interspecific competition. For *Hoplitomeryx*, although the hypothesis of chronomorphs cannot be discarded, that of ecomorphs seems most likely, based upon the coexistence of two or more size groups per fissure, and upon the presence of a huge morphotype, larger than mainland species, in the younger fissures.

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1. Introduction

1.1. The island rule

Fossil island faunas provide a special case of the effects of evolution on a taxon. For new colonizers on an empty island, isolated from the rest of the world, otherwise unexplored possibilities in adaptation to a new environment are suddenly open. But the picture is not honey and milk, at least not for the large herbivores such as deer. The initial lack of large predators and food competitors leads to a population explosion, and that on its turn inevitably results in overgrazing and the loss of vegetation—an ecological meltdown. In order to escape certain death, the herbivores have no other option than to start eating something else, in other words, to explore new ecological

niches, apart from a general advancement in more economic energy and nutrient strategies. Those who are able to do so, will survive, and eventually, their offspring may gradually develop adaptations to the new niche in order to compete better.

The general pattern or trend on islands according to which the larger mammal species, such as proboscideans and artiodactyls, gradually develop towards a dwarf size, and the smaller mammal species, such as rodents and hares, towards a giant size is already well-known for half a century (e.g. Foster, 1964; Hooijer, 1967; Van Valen, 1973; Carlquist, 1974; Sondaar, 1977; Heaney, 1978; Lomolino, 1985), and has recently been reviewed (for living taxa, Lomolino, 2005; Lomolino et al., 2005; for extinct taxa, Palombo, 2005 and references therein). This graded trend is supposed to be related to characteristics of the taxon itself: morphological, physiological and behavioral traits influencing resource requirements, interspecific interactions and immigration abilities—and of the island—primary productivity, available resources, isolation (Lomolino, 2005). The

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emerging body size patterns are, however, not always straightforward (see, e.g. Raia et al., 2003; Meiri et al., 2006; Raia and Meiri, 2006), due to the many factors involved, and the different approaches. Continuing research of island vertebrates is therefore indeed needed (Lomolino, 2005, p. 1684), and the study of extinct island faunas could provide additional information. The fact that in most cases the ancestral taxon of an extinct species is not known is not as problematic as it seems at first sight, since the studies of Case (1978) and Lawlor (1982) indicate that size evolution is more dependent on biological attributes of the taxon itself than on ancestral body size. Interestingly, this implies that a large deer only has to ‘travel’ a longer distance along the regression line to reach dwarf size, but that eventually, he ends up at the same point as any other deer.

For the paleo-island Gargano, now a promontory at South Italy’s east coast but an island during the Late Miocene and Early Pliocene, the only larger species to test the island rule, is the five-horned deer *Hoplitomeryx* Leinders, 1984. The effect of insularity on the Gargano fauna is remarkable, and unique in its extent. The study of this fauna can contribute to our knowledge of similar effects seen in Quaternary species. The two advantages of using a Tertiary species to test patterns seen in Quaternary species is that, firstly, any anthropogenic interference can be excluded, and secondly, that effects of Ice Ages—resulting in more frequent sea level rises and falls—are non-existent as well, which implies a possibly much longer isolation and evolution under more constant influences. Indeed, it has been shown that regions with a smaller amplitude of climatic change harbor a larger number of endemic species (Jansson, 2003); the Gargano case confirms this pattern. The effects of insularity can thus be studied here separated from the effects of changing paleoclimate, paleogeography and anthropogenic impact.

1.2 The spectacular Gargano fauna

Practically all mammals of the Gargano show extraordinary morphological signs of insularity. Most of the genera are restricted to the Gargano. These are the soricid *Deinogalerix* Freudenthal, 1972 with five species, amongst which the giant species *D. koeningswaldi* with its skull length of approximately 20 cm (Freudenthal, 1972; Butler, 1980) is probably the largest insectivore ever found; the murid *Mikrotia* Freudenthal, 1976 (*Mikrotia* is nomen novum for *Microtia*; see Freudenthal, 2006) which appears to be the only burrowing murine genus known till now (Parra et al., 1999), and of which the largest, *M. magna*, has a skull length of about 10 cm (Freudenthal, 1976); the giant glirid *Stertomyx* Daams and Freudenthal, 1985 with three species (Freudenthal & Martín-Suárez, 2006) and finally, the giant hamster *Hattomys* Freudenthal, 1985, with several species, which cannot be delimited sharply (Freudenthal, 1985, p. 46). Other genera have a much wider distribution, and are only restricted to the Gargano on a species level. These are the otter *Paralutra garganensis*

Willemsen, 1983, which is larger than the mainland species *P. jaegeri* (Willemsen, 1983); the ochotonids *Prolagus imperialis* Mazza, 1987 and *P. apricenicus* Mazza, 1987, of which the first species is larger than any other known *Prolagus* species (Freudenthal, 1971; Mazza, 1987) and the glirid *Dryomys apulus* Freudenthal and Martín-Suárez, 2006. Again, others are found even on species level elsewhere. These non-endemic species are the arvicolid *Apodemus gorafensis* Ruiz Bustos et al., 1984 and the three hamsters *Cricetulodon*, *Megacricetodon* and *Cricetus* (Freudenthal, 1985).

Also, the avifauna contained endemic elements such as the giant eagle *Garganoaetus* Ballmann, 1973 with three species, and the barn owl *Tyto* Billberg, 1828 with three species, of which the largest, *T. gigantea* Ballmann, 1973, was about twice as large as the living *Bubo bubo* Linnaeus, 1758 (Ballmann, 1973). Large endemic owls are also recorded, with possibly two species, *Strix perpasta* and a *Strigidarum* (Ballmann, 1973). Also a vulture may have been present (Ballmann, 1976, p. 39). Other birds, e.g. the pigeon *Columba omnisanctorum* and the swift *Apus wetmorei*, are not endemic. The reptilians are represented by a crocodile of African origin, *Crocodylus* sp. (Kotsakis, Delfino & Piras, 2004), but whether this species shows endemic characters or not, is unknown.

1.3 The case of *Hoplitomeryx*

The drive behind the dwarfism (nanism) and the gigantism is explained differently by different authors, for example, decreased predation (Heaney, 1978), physiological optimal body size (Brown et al., 1993; Damuth, 1993), resource limitation and decreased interspecific competition (Lomolino, 1985). It seems likely that the situation differs from island to island, and from taxon to taxon. In this paper, I focus on the Gargano and on *Hoplitomeryx*, and the possible drives behind its evolution.

For the Gargano, part of the paleo-island Apulia-Abruzzi during the Late Miocene–Early Pliocene, the hypothesis of decreased predation can be seriously doubted, because for the deer *Hoplitomeryx*, the giant eagle *Garganoaetus* and the crocodiles *Crocodylus* sp. must have constituted a severe danger, either in the open zones or at drinking places, respectively. For the micromammals, there were the giant owls of the genus *Tyto* and the insectivore *Deinogalerix*, which included micromammals into its diet (Freudenthal, 1972).

In case the hypothesis of optimal body size is valid for *Hoplitomeryx*, I expect its eventual body size to be roughly similar to that of other extinct island artiodactyls, which evolved long enough under isolation. In this hypothesis, different sizes represent chronospecies, in which the largest specimens are the oldest, and the smallest the youngest (in geological age).

The hypothesis of resource limitation will not be addressed here, but taken for granted.

The observation that most Pleistocene insular genera not only contain dwarf (or giant in the case of micromammals)

species, but also normal-sized or even giant (or small in the case of micromammals) species is sometimes explained as adaptive radiation, an attempt to occupy more and new ecological niches (Dermitzakis and De Vos, 1987; De Vos and Van der Geer, 2002). In the case of the murid *Mikrotia*, the drive behind this radiation is interspecific competition, as on the mainland (Millien-Parra, 2000). Difference with the mainland is that competition is now between different species of one and the same genus, whereas on the mainland it is between different genera. For the murid *Mikrotia*, this resulted in three different lineages, present in the fissures of the age of Chiro 27 or younger (Freudenthal, 1976, Fig. 4; Millien and Jaeger, 2001, Fig. 3). Such a situation might be valid for the ruminant *Hoplitomeryx* as well. The initial overgrazing and the resulting resource limitation pushed the survivors to enter new niches, but since this is valid for all survivors, a competition must have been unavoidable. The intragenetic competition eventually led to a radiation into different size classes and morphotypes, each adapted to its own ecological niche. This hypothesis implies that different sizes are contemporaneous with each other.

In this paper, I focus on the long bones of the forelimb. Data on the metacarpals were taken from a previous study (Van der Geer, 2005a); data on the humerus and radius are presented here for the first time.

2. Regional setting

The Gargano region is a promontory on the southeast coast of Italy, province of Apulia, Puglia, and consists of a block of uplifted Jurassic and Cretaceous limestones; this carbonate block descends into the Foggia Graben in the west, which graben separates the Gargano from the main Italian mountain ridges (Freudenthal, 1971), is part of the slightly deformed foreland of the southern Apennine thrust belt (Bosellini et al., 1999) and is part of the Adriatic Plate (Delle Rose et al., 2004). During the Late Miocene and Early Pliocene, however, the Gargano was an island. This was concluded from findings of fossil remains of an endemic, unbalanced fauna (Freudenthal, 1971), the so-called *Mikrotia* fauna. The fossils were found in buried paleo-karstic fissures in the Mesozoic limestone substrate, which are overlain by Late Pliocene–Early Pleistocene sediments of a subsequently marine, shallow water and terrigenous origin (Abbazzi et al., 1996). From the Early Pleistocene, the region was interested by a general uplifting (Doglioni et al., 1994), resulting in the regression and continentalization of the area, after which a second karstic cycle (neokarst) started in the late Early Pleistocene, which removed part of the paleokarst fill (Abbazzi et al., 1996). The fossiliferous fissures are for the greater part situated in the area between the villages of Poggio Imperiale, Apricena and San Nazario (province of Foggia).

Late Miocene land mammal faunas of Italy indicate the presence of three separate paleobioprovinces. Between 11 and 9 ma, the Gargano belongs to the Apulia portion of the

Apulia-Abruzzi paleobioprovince (also Apulo-Abruzzi, in Kotsakis et al., 2004), which was located on the Adriatic side of the Apennines (Rook et al., 2000). This province formed either one large island, or alternatively, a series of islands. Vertebrate remains found at Scontrone, which is part of the Abruzzi portion, are ascribed to the same endemic fossil assemblage as those from the Gargano (Rustioni et al., 1992; Mazza and Rustioni, 1996; Rook et al., 1999). Between 7 and 4 ma, the Gargano portion got isolated from the Abruzzi portion, and kept emerged until the early Pliocene (Mazza et al., 1995; Rook et al., 2000). The subsequent Pliocene flooding of the Mediterranean around 5 Ma ago greatly reduced the emerged areas, and most likely led to the extinction of the endemic fauna of the Gargano.

3. Phylogenetic position of *Hoplitomeryx*

3.1. 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, of which one projects between the eyes on the caudal part of the nasals (Fig. 1). The other four arise in pairs above the orbit and can be considered pronged horns, hence the name prongdeer was suggested (Van der Geer, 2005b). Hoplitomerycidae are further characterized by the presence of large, flaring and sabre-like canines in the upper jaw (Fig. 2).

The other diagnostic features of *Hoplitomeryx* are a large and smooth-surfaced auditory bulla; a non-pneumatized skull roof; absence of lower p1 and p2; a non-molarized lower p4; a variable degree of hypsodonty; absence of pli-*Palaeomeryx* on the lower molars; a lower m3 with large, bicuspid third lobe; a short, massive snout; more anteriorly positioned orbits and a double lacrimal orifice on the rim of the orbit (Leinders, 1984). Post-cranial characters are complete distal metapodal keels, complete fusion of the navicuboid with the metatarsus, distally closed metatarsal gully, shortening of some metapodals (Leinders, 1984), a non-parallel sided astragal (Van der Geer, 1999) and an extremely elongated patella (Van der Geer, 2005b).

Five morphotypes seem to be present in the cranial material, based on the horncore and the ear region, but their sizes differ not so much, except for ear region type III, which is much larger, while still juvenile (Leinders, 1984). Differences in size of the dental elements are larger than those observed in the cranial fragments (Leinders, 1984). Six morphotypes might be present in the dental material (personal communication; Paul Mazza to author; July 2, 2003).

The size of the *Hoplitomeryx* post-cranial material is not homogeneous, but ranges from pygmy size to extremely large. Four size classes can be discerned to date, based

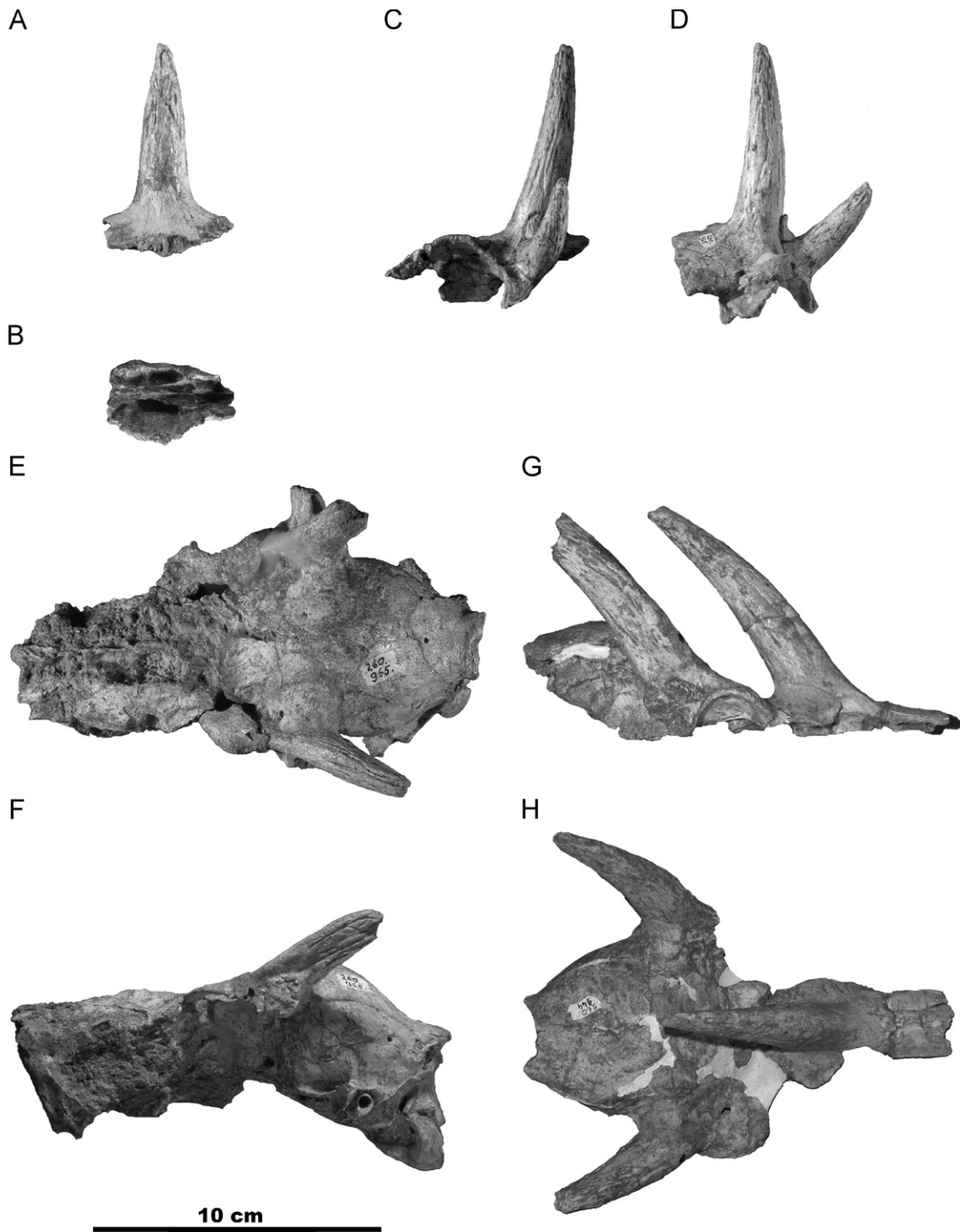


Fig. 1. Skull and horn materials of *Hoplitomeryx* are highly endemic, and seem more or less similar in all size classes, with only some minor differences: (A) nasal horncore type II, rgm 260.902 from San Giovannino, lateral view; (B) same, ventral view; the nasal septum continues into the horn; (C) orbital pronged horncore type II, rgm 260.945 from San Giovannino, lateral view; (D) same, posterior view; (E) type skull with orbital horncores, rgm 260.965 from Pirro 11a, dorsal view; (F) same, lateral view (left side); (G) skull roof and nasalia with orbital and nasal horncores, rgm 260.944 from San Giovannino, lateral view (right side) and (H) same, dorsal view. Scale bar = 10 cm.

upon length and proximal diameters of the metacarpals and metatarsals (Van der Geer, 2005a) (Fig. 3). Interestingly, the largest size class is represented by juvenile material only, and it may be that the largest cranial

fragment (ear region type III; juvenile) can be associated with it. The metacarpal length (LMc) and the metatarsal length (LMt) of the four size groups are as follows (from small to large): size 1, LMc = 74.4–95 mm



Fig. 2. Artist impression of the head of *Hoplitomeryx*, characterized by its pairs of orbital horns, a nasal horn and protruding upper canines. Drawing by Van der Geer.

(average 85.5 mm), LMt = 102–125 mm (average 112.2 mm); size 2, LMc = 139–177 mm (average 158.9 mm), LMt = 180–210 mm (average 199.6 mm); size 3, LMc = c. 259 mm, LMt = c. 300 mm and size 4 is represented by juvenile fragments only. LMt may exceed 420 mm; LMc cannot be estimated.

3.2 Differential diagnosis

Within the infraorder Pecora, Hoplitomerycidae differ from Cervidae and Moschidae (sensu Janis and Scott, 1987, p. 78) by the presence of non-deciduous horncore-like cranial appendages, from Bovidae and Giraffidae by the presence of two lacrimal orifices on the orbital rim and the closed dorsal metatarsal gully, from Bovidae by the presence of upper canines, and from Giraffidae by the non-bilobed lower canine, a sabre-like upper canine and the presence of a non-pneumatized skull roof.

Nasal horncores are unique to date in artiodactyls. Only members of the non-Pecoran family Protoceratidae bear

them, but their nasal horn shows a clear twist; this morphology has nothing to do with that which is present in *Hoplitomeryx*. The dromomerycid *Sinclairiomeryx* (Frick, 1937) has paired nasal bosses, again unlike the horn of *Hoplitomeryx*. Supra-orbital horncores are much less rare, and are shared with Dromomerycidae and Antilocapridae (including Merycodontinae).

Within the Eucervoidea (sensu Janis and Scott, 1987), Hoplitomerycidae further differ from Antilocaprinae by the presence of upper canines, more brachyodont dentition, the lack of a lower p2 and by bifurcation of the orbital horncore directly at the basis instead of more distally; from most Merycodontinae by bifurcation of the orbital horncore directly at the basis (shared, however, with *Stockoceros* Skinner, 1942 and *Hayoceros* Skinner, 1942 instead of more distally; from Palaeomerycidae by a non-molarized lower p4; from *Palaeomeryx* Von Meyer (1851) by the absence of a lower p2 and the absence of pli-*Palaeomeryx* in lower molars and from Dromomerycinae

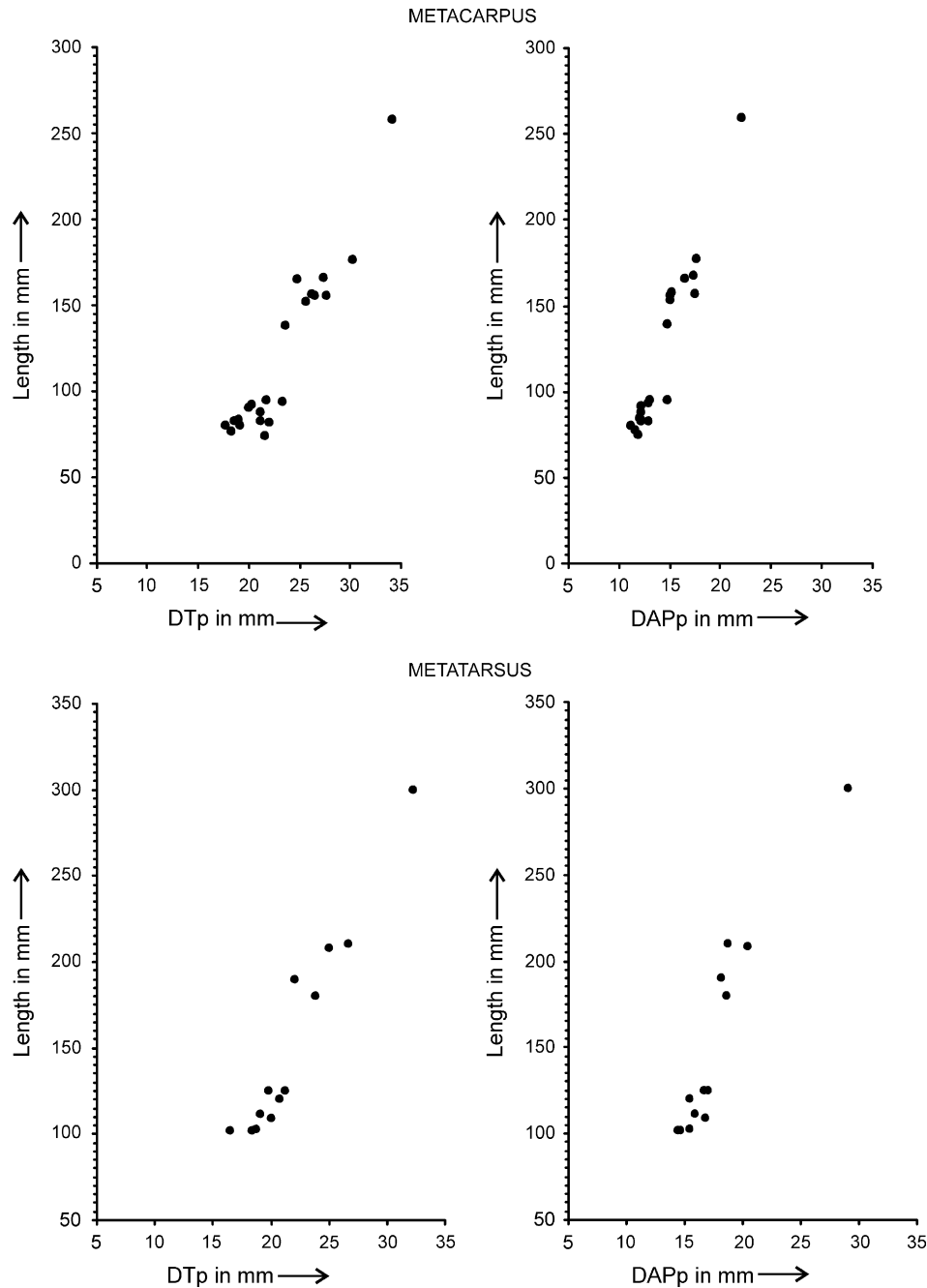


Fig. 3. Bivariate diagrams of the adult metacarpus and metatarsus of *Hoplitomeryx*. If length (y-axes) is plotted against proximal transverse diameter (DTP) and antero-posterior diameter (DAPP) (x-axes), we see three separate groups. The fourth and largest size group is represented by juvenile specimens only, and is therefore not represented in the diagrams.

by the smaller angle between the basicranial and palatal plane. In this angle, *Hoplitomeryx* is only similar to *Capreolus capreolus* Linnaeus, 1758; *Tragulus Pallas, 1779* and possibly *Micromeryx* Lartet, 1851. Finally, *Hoplitomeryx* differs from *Amphimoschus* Bourgeois, 1873—suggested as its closest relative by Leinders (1984)—by the presence of cranial appendages, loss of lower p2, a non-bifurcated protocone, weakly developed entostyle and ectostylid (Leinders, 1984) and from *Micromeryx*—sug-

gested as its close relative by Moyà-Solà et al. (1999)—by the presence of cranial appendages, a non-molarized lower p4, and double lacrimal orifices.

3.3. Potential parallel characters

A number of diagnostic characters of *Hoplitomeryx* may represent parallel evolved characters. These are, apart from the cranial appendages and the flaring upper canines, the

dorsally closed metatarsal gully, the fused navicocuboid, the non-parallel sided astragal, the elongated patella and possibly also the absence of the pli-*Palaeomeryx* in the lower molars.

The closed metatarsal gully is observed in Cervidae and in Antilocapridae, but also in tragulids like *Hyemoschus*. The combination of closed dorsal metatarsal gully and the presence of two orbits on the lacrimal rim validates the transfer of Antilocapridae from Bovoidea to Cervoidea (Leinders and Heintz, 1980; Ginsburg, 1985; Janis and Scott, 1987; Gentry, 2000; see, however, Hernández Fernández and Vrba (2005), according to whom Antilocapridae and Giraffidae form together the superfamily Giraffoidea). The closed gully may thus have developed more than once.

The fused metatarso-navicocuboid is a condition shared with other island ruminants (Leinders and Sondaar, 1974; Leinders, 1984; Van der Geer, 2005b), in deer (*Candiacervus* Kuss, 1975) as well as in bovids (*Myotragus* Bate, 1909). This indicates a secondary derived parallel character, which cannot inform about phylogeny.

The non-parallel sided astragal is seen in living tragulids, in extinct hypertragulids, leptomerycids, protoceratids, but also in suids, which indicates a reversal to the primitive condition (Van der Geer, 2005b), possibly evolved in parallel with other insular ruminants. This is confirmed by *Myotragus balearicus* Bate, 1909, in which insular species the astragal is slightly non-parallel sided, although not to the degree as seen in *Hoplitomeryx* (Van der Geer, 1999).

The elongated patella is shared with tragulids; this, too, is best explained as due to endemic insular adaptations, and not necessarily of phylogenetic importance (Van der Geer, 2005b).

The absence of the pli-*Palaeomeryx*, finally, seems more related to the higher degree of hypsodonty than to phylogeny, since this fold is typically only expressed on brachyodont molars (Janis and Scott, 1987). A higher degree of hypsodonty is no exception for endemic insular herbivore species (Van der Geer, 2005b), and in that case, the lack of the *Palaeomeryx*-fold indirectly, too. The same is valid for the loss of premolars; this may be a parallelism as well.

3.4. Remarks on phylogeny

The phylogeny of Hoplitomerycidae cannot be solved at the present stage of knowledge, because some diagnostic characters are parallelisms, based on adaptation. The phylogeny of many other cervid taxa are poorly understood as well, due to the rarity of complete skeletons or rich post-cranial material, and there is not even a clear consensus of the interfamilial relationships of the living Pecora (Hernández Fernández and Vrba, 2005, and references therein). In this paper, I do not intend to solve the phylogenetic position of *Hoplitomeryx*, and I assume for the present that *Hoplitomerycidae* indeed constitute a family on its own, as an early member of the Cervoidea. This is, however, by no means certain, and also a lower phylogenetic position, as holdover of a primitive ruminant stock is possible (Mazza and Rustioni, 1996). There is no

strong evidence for including *Micromeryx* and *Amphimoschus* as sister taxa in Hoplitomerycidae.

4. Materials and method

4.1. *Hoplitomeryx* material

The studied materials of *Hoplitomeryx* are stored in Nationaal Natuurhistorisch Museum Naturalis, Leiden, the Netherlands, and have as acronym 'rgm', followed by a number of six digits. An additional radius (n.n., 'F1') has been measured at Dipartimento di Scienze della Terra, Università di Firenze, Florence, Italy. All studied materials come from fissure fillings at the Gargano promontory (province of Foggia, Puglia, Italy).

Remains of the humeri of *Hoplitomeryx* have been found in the following fissures (in alphabetical order): Chiro 2S, Chiro 5a, Chiro 10a, Chiro 20a, Chiro 20e, Chiro 28A, Chiro 30, Chiro D3, Fina H, Fina N, Gervasio 1, Pizzicoli 1, Pizzicoli 4, Pizzicoli 12, Posticchia 1B, Rinascita 1, San Giovannino, San Giovannino Low, and San Nazario 4.

Complete humeri are not present within the collection, due to the rather fragile nature of this element; the most complete specimen is rgm 260.950 (San Giovannino); only the condyle and distal-most part of the shaft are missing. Two other relatively complete specimens (rgm 260.953 and rgm 261.761, both from San Giovannino) are heavily damaged; the first is flattened by pressure, the second lacks the complete medial surface. The most resistant part of the humerus is the condyle and indeed much more distal parts have been preserved than proximal parts. Complete proximal parts, including head and greater tubercle, are extremely rare, as in most fossil collections.

Remains of radii of *Hoplitomeryx* come from the following fissures (in alphabetical order): Aucelli 2, Biancone 2, Chiro 2, Chiro 2N, Chiro 3, Chiro 5A, Chiro 5B, Chiro 10A, Chiro 10C, Chiro 12, Chiro 14B, Chiro 20A, Chiro 21, Chiro 26, Chiro 27, Chiro 28A, Chiro 29, Chiro 30, Chiro 30B, Chiro D1, Chiro D2, Falcone 2A, Fina H, Fina N, Gervasio 1, San Nazario 1, San Nazario 4, Pizzicoli 1, Pizzicoli 12, Posticchia 1B, San Giovannino, San Giovannino Low.

Three complete radii (rgm 260.916, rgm 178.499 and rgm 260.860, all from San Giovannino) and one almost complete radius (rgm 261.803 from Chiro 28a) are present among the material.

4.2. Estimation of ontogenetic age

Related to the problems of bone fragmentation is the estimation of the ontogenetic age of the specimens. Only complete specimens with fused epiphyses can be called adult, but since these are missing, we have to work with incomplete specimens. When we know the sequence of fusions of a skeletal element, we can estimate its ontogenetic stage. For the present, I follow the ontogenetic stages as they are described for *Dama dama* Linnaeus, 1758

by Pöhlmeier (1985), by lack of ontogenetic data for extinct cervoids. The pattern of *Hoplitomeryx* is, however, not expected to differ much from *Dama*, if at all. This is inferred from the order of fusion of the distal centers of the humerus, which follows different patterns among cervids. For example, in *Megaloceros cazioti* (Depéret, 1897) the condyle is already firmly fused to the shaft before the epicondyles fuse (Klein Hofmeijer, 1996). In *Candiacervus ropalophorus* De Vos, 1984 (e.g. G4–915 from Gerani Cave, Crete, Greece) on the other hand, the pattern of *Dama* is followed, as is also the case in *Hoplitomeryx* specimen rgm 178.236 (Chiro 3; unfused condyle with both epicondyles fused). Also, the order of fusions in the radius is not likely to deviate, as in both *C. ropalophorus* (own observation) and *M. cazioti* (Klein Hofmeijer, 1996) the order is that as in *D. dama*; for *Hoplitomeryx*, I expect no difference.

4.2.1. The humerus

The fusion of the six ossification centers takes place at approximately the following ages in *D. dama*: the lateral epicondyle fuses with the condyle after 4 months, the medial epicondyle fuses with the condyle after 10 months, the condyle fuses with the shaft 18 months, the great tubercle fuses with the shaft at 2 years of age and the head finally fuses with the shaft at 3 years of age in females and at 6 years of age in males.

The fusion sequence unfortunately implies that the distal halves, of which there are so many, cannot be assigned properly an age older than 18 months, the age of the complete fusion of the condyle with the shaft. Yet, I include these parts into this research, because it appears that further length growth of the humeral shaft after the complete fusion of the condyle seems to be at the most one-sixth more, estimated from the data on *M. cazioti* (as given by Klein Hofmeijer, 1996), which implies that the error of including specimens of this subadult stage is acceptable.

Taking this into account, the following ontogenetic groups are represented by the humeri. Adult stage: six proximal parts, and the three almost complete specimens; adult or subadult: 29 distal parts, six distal fragments, a distal half associated with a separated partial head and many fragments; juvenile: a proximal shaft ending in unfused epiphyseal line, combined with a distal shaft with fused condyle, two complete, unfused heads, two proximal shaft parts with unfused epiphyseal line; ontogenetic stage unknown: 24 distal fragments, 18 shaft fragments, 11 proximal fragments.

4.2.2. The radius

At birth, radius and ulna are not connected, and have unfused proximal and distal epiphyses. At the age of 5 months in *D. dama*, the proximal epiphysis of the radius starts fusing to its diaphysis and by the age of 7 months, the suture has disappeared. At the age of 22 months, the proximal apophysis of the ulna (tuber olecrani) fuses with the olecranon. At the age of 2 years, the distal epiphysis of the radius and that of the ulna start to fuse with the

respective shafts. Early in the third year, the distal radius and distal ulna shafts start to connect in males, and half a year later in females. In the fourth year, this radius–ulna connection is firm, without noticeable difference between males and females. Length growth stops at the age of 2 years, before the distal connection between radius and ulna.

Since length growth stops when the distal epiphyses start to fuse, all distal fragments with complete fused epiphyses are considered adult. The same is true for proximal fragments with traces of fusion between radius and ulna, because this fusion starts only after the distal epiphyses are fused. Distal shafts that show no trace of the ulna cannot be aged properly, because they may represent juveniles at a stage before the connection between radius and ulna, or (sub)adults of a group that does not develop such firm connections anyway.

Taking this into account, the following ontogenetic groups are represented by the radii. Adult: 25 proximal parts, 19 distal parts, two shaft fragments, the three complete radii, and the almost complete radius; juvenile: five proximal parts, four distal parts, and four complete shafts; ontogenetic stage unknown: four proximal parts, seven proximal fragments, three distal fragments, and 11 shaft parts.

4.3. Comparison material

Hoplitomeryx is here compared to three Pleistocene island deer: *Candiacervus* Kuss, 1975 from Crete (Greece); *Cervus astylodon* (Matsumoto, 1926) from the Ryukyu Islands (Japan), and *Megaloceros* Brookes, 1828 from Sardinia–Corsica (Italy–France).

Materials of *Candiacervus* (*C. ropalophorus* De Vos, 1984, spp. II, *C. cretensis* Simonelli (1907); *C. rethymnensis* Kuss, 1975; *C. dorothisensis*; *C. major* Capasso Barbatto and Petronio, 1986, are stored at the Museum of Geology and Palaeontology, National and Kapodistrian University of Athens, Greece. Additional data for *C. ropalophorus* and *C. cretensis* were taken from De Vos (1979); additional data for *C. dorothisensis* and *C. major* come from Kotsakis et al. (1976), who refers to these species as ‘Cervo taglia media’ and ‘Cervo taglia grande’, respectively. For *C. astylodon*, data were taken from Matsumoto and Otsuka (2000) and from (De Vos (2006) appendices 1 and 2); for *M. cazioti*, data were taken from Klein Hofmeijer (1996) and for *Megaloceros sardus*, data were taken from Van der Made and Palombo (2006).

4.4. Measurements

The following measurements are taken, following Heintz (1970): DAPP, antero-posterior diameter of proximal articulation; DTP, transverse (medio-lateral) diameter of proximal articulation; DAPD, antero-posterior diameter of distal articulation; DTD, transverse (medio-lateral) diameter of distal articulation; *L*, length. All measurements

are the maximum values. For the distal humerus, this implies that DTD is measured from the lateral side of the lateral epicondyle to the medial side of the medial epicondyle, and that L is measured from the proximal end of the greater tubercle to the distalmost extension of the condyle.

Measurements are in 0.1 mm, and were taken with a Mitutoyo digital caliper (Absolute Digimatic, model CD-15DC).

5. Results

The massivity index of the distal part (DAPD/DTD) of the humerus shows, practically speaking, a continuous range from 0.61 (San Nazario 4, Pizzicoli 1, Pizzicoli 12) to 1.04 (Pizzicoli 1). No clear size groups can be discerned. The relation between broadness (DTD) and massivity is not clear, since the broadest specimen (DTD 49.0 mm) has an index of 0.76, while the next one in the range (DTD 45.3 mm) has an index of 1.04, and, respectively. Vice versa, two of the narrowest specimens (DTD 25.5 mm and 27.8 mm) have indices of 0.94 and 0.73, respectively.

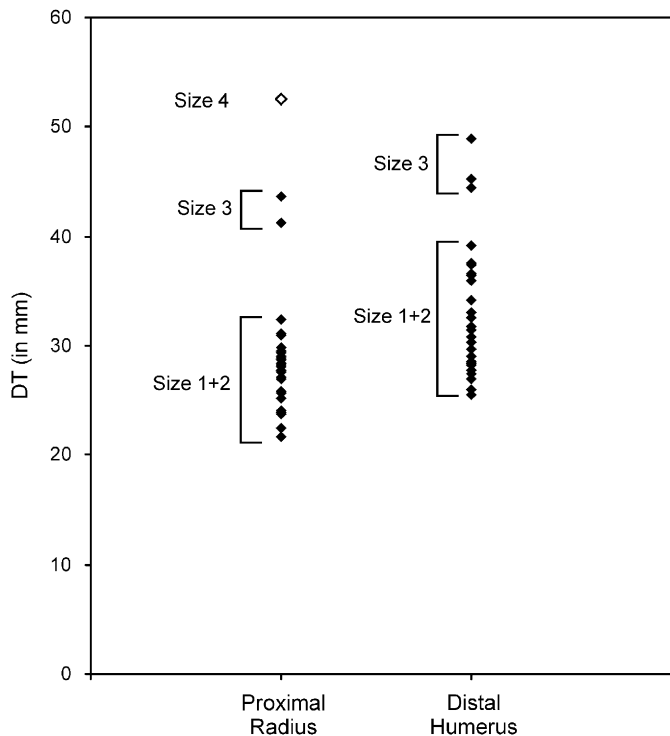


Fig. 4. Diagram of the distal transverse diameter (DTD) of the adult humerus and the proximal transverse diameter (DTP) of the adult radius of *Hoplitomeryx*. The distribution shows three and two size groups, respectively. The largest class is represented by juvenile fragments only, indicated with an open rhomboid; this situation is similar to that with the metapodals (Van der Geer, 2005a). In the case of the humerus, the juvenile fragments cannot be measured, but seem to be slightly larger in DT than size 4 of the radius. The smaller size class (1 and 2) overlap in DT in radius as well as in humerus (see also Fig. 5).

Based upon the distal transverse diameter (DTD) of the humerus, combined with the proximal transverse diameter (DTP) of the radius (Fig. 4), two size groups can be discerned in the adult specimens of humerus as well as of radius. Large juvenile proximal humerus fragments are, however, also present, and they are to be assigned to a larger size class. The DTP/ L scatter for the proximal radius (Fig. 5) indicates that the first size group, at least as far as the radius is concerned, in actual fact consists of two size groups, and that the second size group in the DTD diagram is thus the third size group. Apart from the adult specimens, there are a large juvenile distal epiphysis of the radius and a juvenile olecranon, possibly of the same ontogenetic age, which are both clearly larger than the largest adult specimen. They are to be assigned to a fourth size class.

Since it is not logic that there are four size classes for the proximal radius and only three for the distal humerus, I assume that the largest size class of the humerus coincides with the fourth size class of the radius, based upon comparable size and the fact that they both are represented by juvenile material, as is the case for the metapodals (see Section 3.1). I further assume that the first size group of the humerus corresponds to the first two size groups of the radius, based upon DTD of the humerus and DTP of the radius, which are expected to be similar; needless to say that DTD of the humerus is always somewhat larger than DTP of the radius, due to the additional width of the humeral epicondyles.

The resulting size classes of the humerus are then as follows (from small to large):

- Sizes 1 and 2 (Fig. 6A). Length of the combined and inseparable cluster of sizes 1 and 2 varies between 89 and 140 mm; DTD = 25.5–39.2 mm. This size group includes the complete, but heavily damaged specimen from San Giovannino ($L = 125$ mm, DTD = 34.2 mm), which falls in the upper part of the cluster. The specimens come from the following fissures (in alphabetical order): Chiro 10a, Chiro 20a, Chiro 28a, Chiro D3, Fina H, Fina N, Gervasio 1, Pizzicoli 4, Pizzicoli 12, Posticchia 1B, San Giovannino and San Nazario 4.
- Size 3 (Fig. 6B). Length of the second size group in the diagram varies between 158 and 175 mm; DTD = 44.4–49 mm. Three distal parts and one proximal part can be assigned this size group; they come from the following fissures (in alphabetical order): Chiro E, Pizzicoli 1 and San Giovannino.
- Size 4. The largest specimens are represented by fragments only: a medial epicondyle from Pizzicoli 1, and a greater tubercle from S. Giovannino, which seem similar in size. The size cannot be more than a rough estimation, but seems to be about twice that of size 3 ($L = c.$ 310–350 mm). The fact that the largest metacarpals, metatarsals, radii and cranial

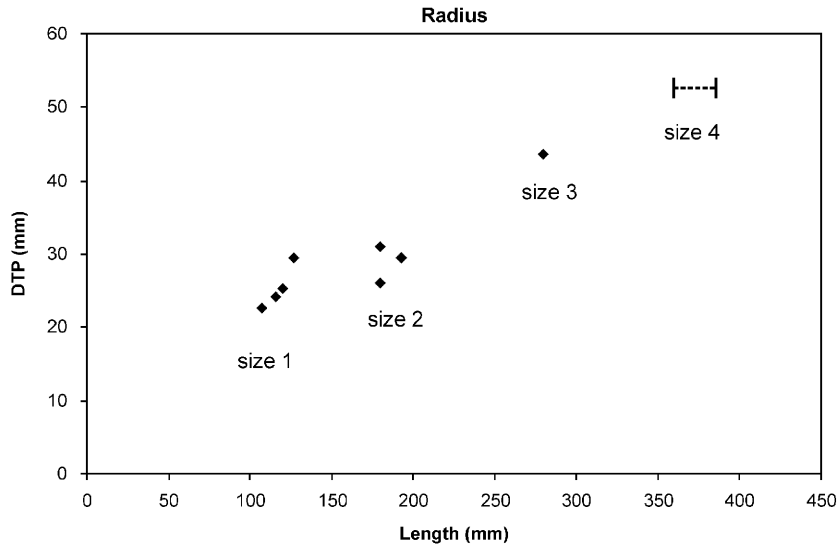


Fig. 5. Bivariate diagram of the proximal transverse diameter (DTP) of the radius against maximal length. The distribution shows three adult size classes, which indicates that the two smaller size classes of Fig. 4 actually consist of two size classes. The fourth class consists of a juvenile specimen; its DTP and length can only be estimated, based on its DTD, and is not meant to represent the actual size of class four when adult.



Fig. 6. Examples of two size classes of the humerus. To the left, size 1, 2 (rgm 425.323 from San Giovannino) and to the right, size 3 (rgm 178.487 from Chiro 20E). Scale bar = 2 cm.

fragments are represented by juvenile fragments strongly indicates that these two fragments, too, belonged to juveniles.

The resulting size classes of the radius are as follows (from small to large) (Fig. 4):

- Size 1. $L = 107.6\text{--}127.1$ mm. The minimal DAPP is 11.6 mm, and the minimal DTP is 22.5 mm. The maximal diameters are impossible to specify with the present data, because they gradually merge with those of the next size group, and the amount of overlap, if any, is not known (see also the large cluster for the DTD of the humerus). For DAPP, the upper limit may be c. 16.3 mm and that for DTP 29.5 mm. $DAPD = 12.3\text{--}18.2$ mm, $DTD = 22.5\text{--}29.1$ mm. The specimens come from the following fissures (in alphabetical order): Aucelli 2, Biancocone 2, Chiro 28a, Chiro D1, F1, Gervasio, San Nazario 4, Pizzicoli 1, Posticchia 1B, Posticchia 4 and San Giovannino.
- Size 2. $L = 180\text{--}192.7$ mm. The maximal DAPP is 17.6 mm, and the maximal DTP is 32.4 mm. The lower limits cannot be separated from the upper limits of size class 1, but may, respectively, be 12.7 and 25.9 mm. $DAPD = 18.8\text{--}21.8$ mm, $DTD = 26.4\text{--}30.4$ mm, with overlap with size 1. The specimens come from the following fissures (in alphabetical order): Gervasio, San Giovannino and San Giovannino Low.
- Size 3. $L = c. 280$ mm, $DAPP = 21.1\text{--}21.7$ mm, $DTP = 41.2\text{--}43.6$ mm. No measurable distal parts are available. The specimens come from the following fissures (in alphabetical order): Fina N, Gervasio, San Giovannino and San Nazario 4.
- Size 4. The largest size class is represented by a juvenile specimen only: a distal epiphysis from San Nazario 4. $DTD = 51.7$ mm, $DAPD = 33.7$ mm. A rough estimation of its $DTP = 52.5$ mm, since DTP is only slightly larger than DTD in *Hoplitomeryx* size classes 1 and 2. The size may be twice that of size 2, which would imply $L = c. 360\text{--}386$ mm. Of comparable size is a juvenile olecranon from Chiro D1.

6. Discussion

6.1. Size classes

In *Hoplitomeryx*, two adult smaller size groups and one large juvenile size group can be recognized in the humerus, whereas one additional adult size group is present in the radius. This implies that there are three (humerus) or four (radius) size groups. For the metacarpal and metatarsal material, three adult sizes and one larger juvenile size were earlier distinguished, which makes four size groups in total. The conclusion seems, therefore, warranted that in the post-cranial material of *Hoplitomeryx*, four size classes are present. There are three ways to explain these size variations: they are the result of either ecological or temporal differences between the fissures, or they are based upon sexual dimorphism acting on two size groups.

This situation is comparable to what is the case in three other extinct island deer: *Candiacervus* from Crete, *C. astylodon* from Ryukyu Islands, Japan and *Megaloceros* from Corsica–Sardinia; all three of Late Pleistocene age. In material of these three deer, different size classes are present. In the case of the first two species, the material seems to come from localities of the same age and come from the same levels, which indicates ecological differences between the localities (De Vos, 1979, 2006; Dermitzakis and De Vos, 1987). In the case of the Sardinian *M. cazioti*, on the other hand, the material belongs to localities of different ages. The material from the geologically older localities is significantly larger (25–40%) than that of the younger localities, and has recently been ascribed to a different species, *M. sardus* Van der Made et Palombo, 2006; an even larger species has been reported from a still older locality (Palombo et al., 2003; Palombo and Melis, 2005). The three species form a lineage with a clear trend towards size decrease (Palombo and Melis, 2005; Van der Made and Palombo, 2006, p. 174).

An interesting parallel between *Hoplitomeryx* and *Candiacervus* is the presence in these two genera of an extremely large morphotype, more or less of the same gigantic size. The Cretan *C. major* had extremely elongated metapodals, relatively and absolutely much longer than any contemporaneous mainland deer, including *Megaloceros giganteus* (Capasso Barbato and Petronio, 1986). Now it appears that *Hoplitomeryx* presents a second example of such ‘giraffid/camelid’ legs.

6.2. Temporal differences

In the case that the various *Hoplitomeryx* morphotypes reflect temporal differences between the fissures, two scenarios can be thought of.

Firstly, the morphotypes are the result of successive invasions from the mainland, e.g. as suggested for *Candiacervus* on Crete (Kuss, 1975; De Vos, 1984, however cf. Capasso Barbato, 1992; Caloi and Palombo, 1996; De Vos, 1996, 2000), and the rodents on the Gargano (De

Giuli et al., 1987), or of successive faunal exchanges between neighboring islands (Freudenthal, 1976, 1985, p. 46; Freudenthal and Martín-Suárez, 2006, p. 21). The Gargano has been considered part of a larger archipelago (Apulo-Dalmatic Realm) to explain the variation and trends observed in the micromammals (De Giuli and Torre, 1984; De Giuli et al., 1985, 1987) and in the ochotonid *Prolagus* (Mazza, 1986). Such an archipelago cannot be confirmed on geological grounds (Abbazzi et al., 1996), but instead a larger, insular paleobioprovince, including the Abruzzo region, is indicated by the presence of a similar fauna at Scontrone. This implies that the Gargano was just part of a very large island, and not a smaller island within an archipelago. For *Hoplitomeryx*, the multiple invasion/faunal exchange option can be excluded for another reason—the high degree of similarity between the different size classes. They all (except maybe for the largest size) share the unique *Hoplitomeryx* features, and since this family has a restricted distribution, it is not likely to assume multiple invasions with a similar bizarre morphology with five horns and sabre-like canines. Scenario one can thus be abandoned.

Secondly, the morphotypes represent a cross-section through history, and the various types (chronomorphs) represent stages in the process of insular evolution, in this case following a trend towards dwarfism. This then implies that the smaller specimens are, geologically speaking, the younger ones, and, vice versa, that the larger specimens are more close to the ancestral species, as is the case with the *M. sardus*–*M. cazioti* lineage. The abundance of remains of the two smaller size groups and the scarcity of those of the two larger size groups seem to confirm the view of chronomorphs. On the other hand, the observation that the different sizes are not neatly distributed over the different fissures, and the fact that the oldest fissure (biostratigraphically dated based on the evolutionary stage of the *Mikrotia* lineages, see Freudenthal, 1976) ‘already’ contain the smallest *Hoplitomeryx*, contradict this option, as well as the coexistence of more than one size group in some fissures, see for example radius size class 1 and 4 in San Nazario 4. The coexistence of two or more size groups per fissure group might also be explained by a mixture of early and later, reworked infillings of the fissures. In that case, the different size groups are chronomorphs as well. The hypothesis of chronomorphs, subject to a trend towards dwarfism, therefore remains open.

6.3. Ecological differences

In the case that the various *Hoplitomeryx* morphotypes reflect ecological differences between the fissures, I can think of only one explanation—that of adaptive intraspecific radiation, in which the various morphotypes are contemporaneous ecomorphs. The main driving force in this case is the urge to occupy new ecological niches, caused by interspecific competition for food and area. Such processes are described for some mainland rodent

communities (Dayan and Simberloff, 1994; Parra et al., 1999), but also for a highly endemic rodent, the murid *Mikrotia* of the same Gargano island (Millien-Parra, 2000), and are suggested for the bovid *Myotragus* of Mallorca (Palombo et al., 2006, p. 160). As a matter of fact, different species of Cervidae occurring in the same mainland habitat under natural conditions are, as a rule, of considerably different size. In the case of exception to this rule, for instance *Rucervus duvauceli* (Cuvier, 1823) and *Rusa unicolor* Kerr, 1792 in some parts of India, the species occupy different ecological niches or in some cases a slightly different habitat (Van Bemmelen, 1973, p. 295). A similar situation seems to exist in *Candiacervus*, because the morphology of its dentition varies between the various size classes (De Vos, 1984), which strongly indicates adaptations to different diets; this is also confirmed by its post-cranials (Van der Geer et al., 2006). Back to the Gargano, a clear example is shown by *Mikrotia*, because in this genus, three lineages are present in fissures Chiro 27 and younger, two lineages in the slightly older Chiro 7 and only one in fissures Fina D and older (Freudenthal, 1976; Millien and Jaeger, 2001). The three *Mikrotia* lineages can be considered ecological variants. They are each subject to gradual size increase (large and medium lineage) or decrease (small lineage) (Freudenthal (1976), based on molars; Millien and Jaeger (2001), based on incisors).

As for *Hoplitomeryx*, different morphologies are in fact seen in the astragalus (Van der Geer, 1999), and in the articulation areas of the distal radius and the proximal metacarpals (unpublished data); the explanation of which is still unclear.

6.4. Sexual dimorphism

Theoretically, the four size groups could alternatively be explained as two size groups displaying a clear sexual dimorphism without overlap between the sexes. The role of sexual dimorphism is not known for *Hoplitomeryx*. The fact that there are many, many isolated horncores and canines indicates that horns were borne by both sexes, but whether they had a different size and/or morphology is not known. Generally, sexual dimorphism does not separate limb bones nicely into two separate clusters, but rather 'elongates' the cloud in bivariate plots. In the case of *Hoplitomeryx*, the plots for all post-cranial elements (unpublished data), all show marginally elongated clusters, nicely separated into size groups. Furthermore, there is no way to explain the incredible size difference between the huge juvenile specimens and the medium-sized adult specimens in terms of sexual dimorphism. Lastly, sexual dimorphism in ruminants decreases with decreasing body weight (Loison et al., 1999). It appears that no ungulate species under 20–30 kg is dimorphic. Precise estimation of body size of the *Hoplitomeryx* groups is beyond the scope of this paper, but an estimation of body mass, based only upon humerus length, yields the following results (based upon Scott, 1990). Size 3 has an estimated body mass

between c. 50 and c. 36 kg. Here, dimorphism might play a modest role, but in any case not in relation to the huge, juvenile size 4. A comparable sized deer is *Axis porcinus*, in which the males weigh c. 40 kg and the females 30 kg (Geist, 1998, table A5). Size dimorphism then is in the magnitude of 25%, not more. The range in size 3 is not in conflict with this, and size 3 thus may very well include males at the right side and females at the left side, but both within one and the same cluster. The largest size 2 specimen has an estimated body mass of c. 23 kg. This is the size of *C. capreolus*, in which males weigh c. 23 kg and females c. 20.6 kg (data from Geist, 1998). The smallest size 1 specimen had a body mass of only c. 5–6 kg. This is the size of *Pudu mephistopheles*, which shows no dimorphism (data from Geist, 1998). The two smallest *Hoplitomeryx* size groups can therefore not be explained by sexual dimorphism.

6.5. Concluding remarks

At present, it seems impossible to exclude either of the two options (chronomorphs versus ecomorphs). In fact, a combination is even possible, more or less comparable to *Mikrotia*, in which several lineages coexist, each subject to gradual change in body size. In all cases, however, the genus *Hoplitomeryx* as found on the Apulia-Abruzzi paleo-island is monophyletic, because the option of successive invasions/ faunal exchanges cannot be confirmed. The smallest *Hoplitomeryx* is therefore either the geographically speaking youngest form (chronomorph), or an extreme adaptation (ecomorph); vice versa for the largest *Hoplitomeryx*. The fact that none of the tenths of fissures contains one morphotype only, and the fact that none of the four morphotypes is restricted to one fissure only, highly complicates the matter. The comparable cases of *Hoplitomeryx*, *Candiacervus* and *C. astylodon* remain unsolved to date. It may be that these species provide exceptions to the general rule, in contrast to other Pleistocene insular artiodactyls, e.g. the *Myotragus* lineage (Mallorca; Bover Arbós, 2004; Bover and Alcover, 2005), and the *Megaloceros* lineage (Sardinia–Corsica; Van der Made and Palombo, 2006), which progressively decrease in size.

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