

ISLAND RUMINANTS AND PARALLEL EVOLUTION OF FUNCTIONAL STRUCTURES

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SUMMARY

Functional structures in island artiodactyls tend to evolve in a parallel way, apart from the well-known dwarfism. These parallelisms are especially known from Plio/Pleistocene Mediterranean true-islands, and are not limited to certain genera. One of the most striking features at first sight is the shape of the skull. The muzzle becomes more massive and short. This implies a reduction in olfactory abilities, but on the other hand, grinding at the molar section is more powerful and economic, and the biting force at the incisor part is increased enormously. As a result, hypsodonty and in some cases an evergrowing rodent-like incisor is observed in insular artiodactyls. Eyes in some islanders face more forward, yielding a better stereoscopy and front view. Another parallelism is seen in the horns. In several species, the horns diverge less than in their mainland relatives, posteriorly they follow the plane of the frontals, and the cross-section at the base is (almost) round. Evolutionary different patterns need to be considered: the horns are newly evolved from a hornless ancestor (neoteny), or the horns are a simplification of the complicated forms of their ancestors (paedomorphosis). Locomotion of many islanders is more characterized by stability than by speed, stimulated by the absence of large mammalian carnivores and inevitably connected with the development of a plump appearance. The increased stability is mainly achieved by fusion of footbones, shortening of limb bones, and by restricting lateral movements in limb joints. The morphology of the stifle and ankle joint can show adaptations needed to correct the posture of the lower limb in connection with the large belly. In fact, the derived characteristics of the higher ruminant astragalus and patella are lost, and a return to the primitive condition is observed. The same accounts for the shortened metapodials.

The parallels are functionally explained by shared adaptational needs, like birds and crocodiles as the only predators, limited availability of resources, a more abrasive and sometimes even toxic diet, and less damaging intra-specific combat. Every functional structure is supposed to evolve as a compromise between advantageous and disadvantageous factors, and if these factors change, as on islands, the new compromise results in a change in functional structure.

The artiodactyls focussed on comprise *Hoplitomeryx* (Pliocene, Italy), *Myotragus* (Pleistocene, Balearics), *Candiacervus* (Pleistocene, Crete), *Anoa* (Holocene to Recent, Sulawesi), *Nesogoral* (Pleistocene, Sardinia).

Key words: insularity, parallel evolution, locomotion, *Hoplitomeryx*, *Myotragus*, Pliocene, Pleistocene.

RÉSUMÉ

LES RUMINANTS DES ÎLES ET L'ÉVOLUTION PARALLÈLE DES STRUCTURES FONCTIONNELLES

Les structures fonctionnelles des Artiodactyles insulaires tendent à évoluer dans une voie parallèle, en plus du célèbre nanisme. Ces parallélismes sont bien connus dans les vraies îles méditerranéennes au Plio/Pléistocène, et ne sont pas limités à quelques genres. L'une des plus importantes caractéristiques à première vue est la forme du crâne. Le museau devient plus massif et court. Ceci implique une réduction des capacités olfactives, mais d'un autre côté, la pression de la molaire est plus puissante et économique, et la force de morsure de la partie incisive augmente énormément. En conséquence, l'hypsodontie et, dans quelques cas, une incisive à croissance continue de type rongeur sont observées chez les Artiodactyles insulaires. Les yeux pour beaucoup d'Artiodactyles insulaires sont orientés vers l'avant, acquérant une meilleure stéréoscopie et une vue frontale. Un autre parallélisme est observé dans les cornes. Chez plusieurs espèces, elles sont moins écartées que celles des formes équivalentes continentales, postérieurement elles sont dans l'axe du frontal, et la section est à la base (presque) ronde. Différents modèles évolutifs peuvent être envisagés : soit les cornes ont évolué récemment à partir d'un ancêtre inerme (néoténie), ou bien elles correspondent à une simplification de formes ancestrales plus complexes (paedomorphose). La locomotion de plusieurs formes insulaires est caractérisée plus par la stabilité que par la vitesse, stimulée par l'absence de gros carnivores mammifères et inévitablement liée avec le développement d'une apparence arrondie. L'augmentation de la stabilité est principalement acquise par la fusion des ossements des pieds, le raccourcissement des ossements des membres, et par la réduction latérale des mouvements des articulations osseuses. Les morphologies du grasset et de la cheville peuvent montrer les adaptations souhaitées pour corriger la posture des membres en connexion avec un gros ventre. En fait, les caractéristiques dérivées de l'astragale et de la rotule des plus grands ruminants sont perdues, et un retour aux conditions primitives est observé. La même explication (stabilité et un retour à l'état primitif) est applicable pour le raccourcissement des métapodes.

Les parallèles sont explicables fonctionnellement par le partage de besoins adaptatifs : oiseaux et crocodiles comme seuls prédateurs, disponibilité des ressources limitées, nourriture plus abrasive et parfois même toxique, faibles dommages corporels lors des combats intra-spécifiques. Chaque structure fonctionnelle est supposée se développer comme un compromis entre les facteurs avantageux et désavantageux, et si ces facteurs changent, comme pour les espèces insulaires, le nouveau compromis entraîne un changement de la structure fonctionnelle.

Les Artiodactyles concernés sont *Hoplitomeryx* (Pliocène, Italie), *Myotragus* (Pléistocène, Baléares), *Candiacervus* (Pléistocène, Crète), *Anoa* (Holocène à actuel, Sulawesi), *Nesogoral* (Pléistocène, Sardaigne).

Mots-clés : insularité, évolution parallèle, locomotion, *Hoplitomeryx*, *Myotragus*, Pliocène, Pléistocène.

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INTRODUCTION

'A dire vrai, il n'y a jamais eu d'éléphant nain ni de mulot géant. C'est l'éléphant normal qui est géant et le mulot de nos bois qui est nain ! Mais il y a quelques milliers d'années, dans des clubs méditerranéens interdits aux grands carnivores, vivaient des mammifères de taille raisonnable'

Louis Thaler, 1973

The observation that endemism occurs world-wide in island megafauna of, in principle, all genera and species, is not new (see for example, Ambrosetti, 1968; Thaler, 1973; Sondaar, 1977; Azzaroli, 1982), and belongs already to the realm of *consensus*. For example, the size reduction, known as dwarfism, has been described for many artiodactyls on Plio/Pleistocene islands: the true deer *Cervus astylodon* (Matsumoto, 1926) from Ryukyu Islands and *Dicrocerus* sp. from Miyako Island, both Japan (Matsumoto, 2000), *Candiacervus* Kuss, 1975 from Crete (Azzaroli, 1961; Kuss, 1965, 1975a; De Vos, 1979), the caprine *Myotragus* Bate, 1909 from the Balearic (Gymnesic) Islands (Andrews, 1915; Adrover & Angel, 1967; Spoor, 1988), the dwarf hippos *Phanourios minor* (Desmarest, 1822) from Cyprus (Boekschoten & Sondaar, 1972; Houtekamer & Sondaar, 1979), *Hippopotamus creutzburgi* Boekschoten and Sondaar, 1966 from Crete (Boekschoten & Sondaar, 1966; Kuss, 1975b; Spaan, 1996), *Hippopotamus pentlandi* (Meyer, 1832) from Sicily and Malta, and the prongdeer *Hoplitomeryx matthei* Leinders, 1983 from Monte Gargano (Freudenthal, 1971) and Abruzzo (Rustioni *et al.*, 1992), both Italy. Till now, the only exception is provided by *Megaloceros cazioti* (Depéret, 1897), which has mainland proportions (Klein Hofmeijer, 1996). In more recent times size reduction is still observed on islands, as seen in the extant reindeer *Rangifer tarandus platyrhynchus* from Spitzbergen (Willemsen, 1983; Geist, 1987) and in the red deer *Cervus elaphus* Linnaeus, 1758 on Jersey, Channel Islands during the last interglacial (Lister, 1989). Dwarfism can be quite substantial: *Myotragus balearicus* reached a shoulder height of only 45-50 cm (Quetglas & Bover, 1998), and one adult specimen is found of only 22 cm shoulder height (Bover & Alcover, 1999a).

As becomes clear from studies on the above mentioned taxa, it is not just an absolute change in size occurs. Apart from the decreased size, an homochronous range in morphologies is present, explained as adaptive radiation (Leinders, 1983; De Vos, 1996, 2000; Van der Geer, 1999; MacPhee & Iturralde-Vinent, 2000), or speciative radiation due to the archipel effect (De Giuli *et al.*, 1985). The common feature, however, of these morphotypes is that they follow a general trend: functional structures evolve in a parallel way. For example, insular artiodactyls have robust and shortened legs, (much) shorter than one would expect in relation to their body size. This is true only for those artiodactyls

that are element of the unbalanced megafauna, characteristic for the so-called true-islands (*sensu* Alcover *et al.*, 1998, who use this term for oceanic and oceanic-like islands, in contrast to continental islands, which are characterized by a mainly harmonic fauna, consisting of a subsample of the continental fauna). The size reduction of the limb bones, especially of the autopodium (Bover & Alcover, 1999a), cannot be explained by the general size reduction of the animal, which implies that standard equations to predict body mass at the basis of long bone lengths and diameters (e.g. Scott, 1983) cannot be used implicitly. The relative proportions of limb elements are drastically changed. Another parallelism is seen in the joints: in general, insular artiodactyls have more stiff, and therefore stable, joints characterised by a decreased range of possible movements, also known as the low-gear system (Leinders & Sondaar, 1974; Sondaar, 1977; Moyà-Solà, 1979; Leinders, 1979, 1983).

Materials used in this study comprise *Hoplitomeryx* (RGM: Rijksmuseum voor Geologie en Mineralogie, Naturalis, Leiden) and *Myotragus* (MNIB: Museu de la Naturalesa de les Iles Balears, Mallorca). Fossil comparison material (AMNH: American Museum for Natural History, New York; F: AM: Frick Collection, American Museum for Natural History; LUSK, S and ESP, stored at the Frick Collection) comprises *Eumeryx*, *Hypertragulus*, *Nanotragulus*, *Hypisodus*, *Archaeomeryx*, *Leptomeryx*, *Longirostromeryx*, all available dromomerycines, *Prodremotherium*, *Dorcatherium*, all available protoceratids. Recent comparison material (Department of Mammology, American Museum for Natural History) finally consists of *Tragulus*, *Hyemoschus*, *Moschus*. Data of other species is taken from the literature, or from personal communication (De Vos for *Candiacervus*).

SHARED ADAPTATIONAL NEEDS

The explanation for the development of parallelism in functional structures should be searched in shared adaptational needs. Stated in a different way, the explanation lies in those ecological needs that are shared by insular artiodactyls. In addition, the combination of these ecological needs has to be restricted to an island environment, and should be lacking as such on the mainland. It is the difference between islands and mainland, in terms of ecology, that is the motor behind the origin of parallelisms observed between the various endemic insular artiodactyls. This ecological difference stimulates the changes in morphology that makes insular artiodactyls differ from their mainland relatives. Several factors can be thought of, such as the absence of large mammalian carnivores (e.g. Thaler, 1973; Sondaar, 1977; and subsequent authors), the presence of birds of prey filling these unoccupied predator niches (Biknevicius *et al.*, 1993; Olson, 1978; Leinders, 1983), limited availability of resources as the main body-size delimiter (MacArthur & Wilson, 1967;

Kurtén, 1972; Cody, 1974; Case, 1978; Anderson, 1994; Alcover *et al.*, 1998), all in relation to island size (Heaney, 1978, 1984). Less obvious, but possibly equally important are factors of an ethological nature, like inter- and/or intraspecific competition. According to Grant (1972) species diverge in body size in competitive situations, and Brown (1975) added that a regular spacing in body size takes place, with increase of mean niche overlap with species richness. The nature and degree of the intra-specific combat plays a role, though difficult to estimate in extinct species. The combined and closely correlated shared factors induce a new equilibrium, reflected in shared morphologies that can be explained in terms of parallel adaptations.

SHARED MORPHOLOGIES

Where do we find those shared, derived morphologies? Shared morphologies are found in the skull as well as in the body skeleton. In the skull we can expect to find morphological changes especially in the dentition, in the shape of the skull, in the position of the eyes, and in the appendages. In the body skeleton we can expect to find changes in locomotory apparatus, but also in the shape of the thorax. In this paper, we will see that such changes in morphology, and therefore in functionality, are evoked by co-operating factors. Functional structures are always a compromise, and when the environment in a broad sense is changed, the factors, or stimuli, are out of balance, and as a result a new compromise evolves, reflected by speciation. The weight of the various selective pressures is changed, and the balance will shift according to the selective pressure that is the most important now.

MUZZLE

Considering the shape of the skull, we can observe that many insular ungulates, for example *Myotragus* (Alcover *et al.*, 1981) and maybe *Nesogoral*, have rather short muzzles. This implies that, seen from ventral, their maxillary tooth row is more arcuate, and less complete. The same might apply to *Hoplitomeryx* as well, but as no skull with preserved anterior part nor a complete hemimandibula has been discovered till now, this cannot be verified at the moment. The fact that P1 and P2 inf are absent in *Hoplitomeryx*, however, is a strong indication for a shortened muzzle: prongbucks, *Palaeomeryx*, *Amphimoschus* have a P2 inf., whereas the insular ungulates *Myotragus*, *Nesogoral*, *Maremmia* lost it. *Maremmia* even lost lower P3 (Hürzeler, 1983).

A reduction in snout length may imply a substantial reduction in olfactory abilities, as the receptors for the sense of smell are located primarily on the ethmoturbinates, which lie in the caudomedial and caudodorsal parts of the nasal cavity. This would lead to the conclusion that the need to detect surrounding predators by their smell has been reduced also

substantially. Artiodactyls use their olfactory functions mainly to perceive danger in the form of predators, and to a much lesser degree in their intra-specific, or social behaviour. The first function, to warn against predators, is not needed so much on an island, as there are no large mammalian carnivores on islands (crocodiles don't smell). For the social communication, especially in the breeding season, it is not the olfactory region that is crucial, but Jacobson's organ, or vomeronasal organ, in the rostral base of the nasal septum. Brain studies of *Myotragus balearicus* through endocasts (Dechaseaux, 1961; Angelelli *et al.*, 1985) reveal that indeed the size of the olfactory bulbs is unusually small, which observation is in accordance with the very small nasal cavity (Alcover, 2000). On the other hand, it should be remarked that snout length is considered to have no influence on the olfactory acuity, but is primarily controlled by requirements of a mechanical nature; increase of olfactory acuity is achieved by tighter folding of the turbinates, not by snout lengthening (Radinsky, 1987).

A long snout has a disadvantage for browsing herbivores, as more muscle action is needed to retain the same level of grinding force at the molar part, needed

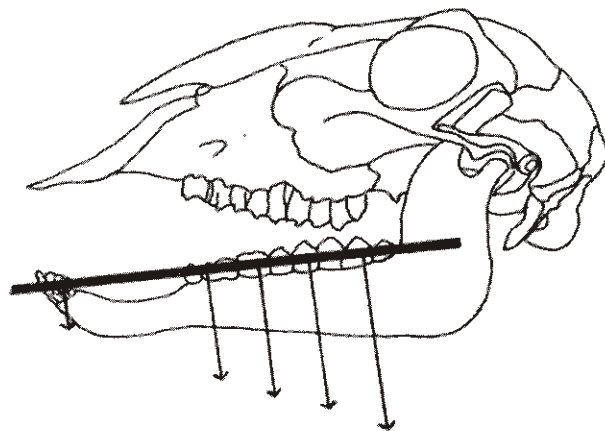


Figure 1: Schematic representation of the forces that apply at the dentition. The total action of the masticatory muscles can be divided into a vertical component (mastication: chewing and biting) and into a horizontal component (stability: pushing the mandible into its joint). The total vertical action can on its turn be divided into separate vertical resultant vectors, one per element, in such a way that the sum of all resultant vectors equals the total vertical muscular force. If we remove some elements and retain the same vertical pressure on the remaining elements, we see that in total less muscular force is needed. Thus, it appears that the shorter the jaw, the less muscular force is needed to retain the same crushing power per retained element, or the other way around, with the same muscular force the crushing power is increased. Another aspect is observed: the shorter the jaw, the more force can be applied at the front teeth. This is due to the smaller distance between the element and the place where the muscular force applies (insertion of the tendon): the vertical resultant vector is now larger, the horizontal smaller, compared to the situation in a normal-sized jaw. To cope with a higher abrasion, hypsodonty or evergrowing elements are necessary.

Figure 1 : Représentation schématique des forces qui s'appliquent à la dentition. La force totale nécessaire à la mastication et la morsure est la somme de tous les vecteurs résultants. Cela signifie que plus la mâchoire est courte, plus la force musculaire est nécessaire pour conserver la même puissance d'écrasement, ou avec la même force musculaire la puissance d'écrasement est augmentée. Un autre aspect est observé: plus la mâchoire est courte, plus la force est appliquée aux dents de devant. C'est particulièrement utile si les incisives sont cruciales. Pour faire face à une abrasion plus forte, l'hypsodontie et des structures en croissance continue sont nécessaires.

HORNS

Another parallelism is seen in some features of the horns (fig. 3). In *Nesogoral melonii*, *Myotragus balearicus*, *M. batei* and *Capricornis sumatrensis*, the position of the horns on the skull is very backwards, as indicated by the percent ratio LF/LFO, where LF is the length of the frontals from the orbits to the horns and LFO is largest width of the skull, measured between the upper edge of the orbits and the occiput, and compared with *Nemorhaedus goral* and *Gallogoral meneghini* (Gliozzi & Malatesta, 1980). As a consequence, the fronto-parietal suture runs just behind the horns. In addition, the frontals in *Nesogoral* are flat, in contrast to other gorals like *Nemorhaedus* and *Gallogoral*, but similar to *Myotragus* (Gliozzi & Malatesta, 1980). In *Hoplitomeryx*, where the pronged horn (or pair of horns) is placed on the supra-orbital process of the frontal bone, the h.c. type II specimen also have a more posteriorly situated insertion, compared to h.c. type I, and the frontal bone medially of the orbita is less convex antero-posteriorly and from side to side than in the type skull (Leinders, 1983). Another positional aspect is the relative distance between the horn-core bases as percentage of the width of the skull at the level of the horn-core bases. It seems that this distance is higher in *Nesogoral melonii* (34%), *Myotragus balearicus* (39%) and *Capricornis sumatrensis* (34%) than in the mainland forms *Rupicapra rupicapra* (28%), *Gallogoral meneghini* (23%) and *Pachygazella grangeri* (19%), with *Nemorhaedus goral* (36%) as an exception (figures

calculated on the basis of the data given by Gliozzi & Malatesta, 1980: 304).

In several species, the horns diverge less than in their mainland relatives. This means that posteriorly they follow the plane of the frontals. At the same time the shape at the base differs, as the cross-section at the base is subcircular. This progressive feature is very clear in *Nesogoral melonii* (Sardinia). On other islands we see these parallel, posteriorly bend horns of subcircular cross section in *Myotragus*, in the recent *Anoa*, and less so in the prongdeer *Hoplitomeryx*. In the latter genus, it seems that the lateral branch or tine of the orbital horn (RGM 260 965, type and RGM 260 944) has a circular cross section, while medial branch is laterally compressed, thus yielding an oval cross-section. As to the direction, the medial branch of the orbital horn, which is clearly the largest branch, points backwards and slightly outwards. However, in type II (RGM 260 945) and type III (RGM 261 097) horncores (Leinders, 1983), we see the almost circular cross-section also in the medial branch, which has an almost straight axis, thus not deviating as in the type specimen. This is more pronounced in type III than in type II. The medial branches of type III even indicate a distal convergence (Leinders, 1983). The type skull seems thus to represent a less developed stage in this sense.

In the case of the parallel changes in the horns, evolutionary different patterns need to be considered. One option is that the horns in the island artiodactyl are newly evolved from a hornless mainland ancestor. These new horns evolve with the characteristics mentioned above. This evolutionary pattern might be true for the cervid *Hoplitomeryx*, as *Amphimoschus*, the supposed sister taxon of *Hoplitomeryx* (according to Leinders, 1983), had no cranial appendages. The same is valid for *Micromeryx*, the other proposed close relative (Moyà-Solà *et al.*, 1999). Within the cervoids, only the antilocaprine and the merycodontines also developed keratine-covered supra-orbital horns, like *Hoplitomeryx*. These cervoids, however, are restricted to North America. Another cervoid taxon, the Palaeomerycidae, including the dromomerycines, too had supra-orbital bony outgrowths (except for *Amphitragulus*), but these were probably skin-covered instead of keratin covered. If the horns of *Hoplitomeryx* are a neotony, it can in a way be considered a return to the more primitive condition, as the orbital position of cranial appendages is considered a primitive configuration in ruminants, because it is typical for the earliest Cervidae (Stehlin, 1937).

Another scenario to explain the changed morphology of the horns in island ruminants can be thought of. The horns are a simplification. This situation seems to be valid for the Pleistocene bovids of Sardinia and Mallorca. Their ancestors had more complicated horns. If the unknown ancestor of *Hoplitomeryx* had more palaeomerycid-like horns, then the horns of *Hoplitomeryx* as well might have become simpler than those of its ancestor. In that case, the parallelism in insular horn evolution is almost perfect. The difference

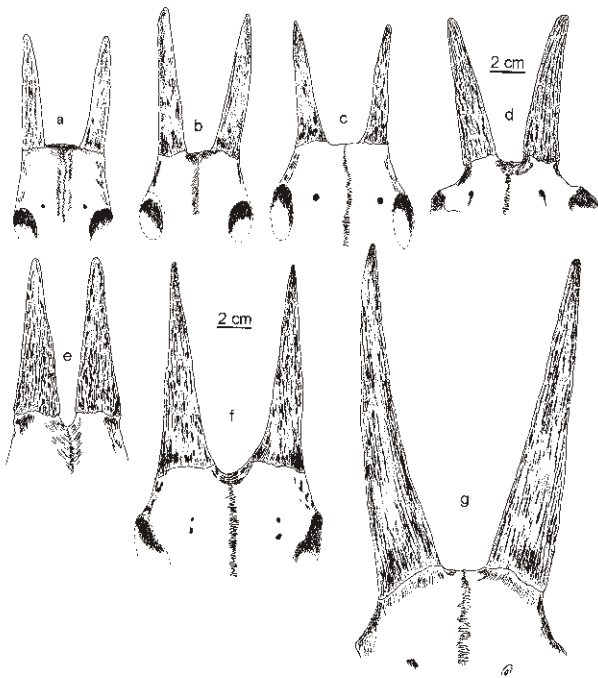


Figure 3: Frontlets of several Caprinae. a: *Myotragus balearicus*; b: *Nesogoral melonii*; c: *Nemorhaedus goral*; d: *Rupicapra rupicapra*; e: *Pachygazella grangeri*; f: *Capra sumatrensis*; g: *Gallogoral meneghini*. After Gliozzi & Malatesta, 1980.

Figure 3: Frontaux de différents Caprinae. a: *Myotragus balearicus*; b: *Nesogoral melonii*; c: *Nemorhaedus goral*; d: *Rupicapra rupicapra*; e: *Pachygazella grangeri*; f: *Capra sumatrensis*; g: *Gallogoral meneghini*. D'après Gliozzi & Malatesta, 1980.

between horncore type I and II, III confirms this evolutionary pathway. A remark should be made here. Though in a way we can speak of a simplification regarding the horns, it is actually an adaptation. It is not a degeneration we are speaking of, but an evolutionary change that made the horns better adapted to the typical insular situation. The same evolutionary change took place several times and in several genera. Selective pressures were the driving force behind the change.

The end result in both types of scenario is a typical configuration of the horns. What kind of shared need can be found on the different islands that gave rise to this shared horn pattern? It cannot be the absence of large mammalian carnivores on itself, as in that case mere reduction or loss of horns would be expected. The remaining factors are a change in intra-specific combat and the increased danger from birds of prey and crocodiles. That birds of prey are an important factor can also be deduced from the bulla tympanica in *Hoplitomeryx*, which is inflated as in the cervid *Axis*, and in most bovids (Leinders, 1983). An inflated bulla cannot be considered just a retention of the primitive condition as originally suggested (Van Kampen, 1905; Van der Klaauw, 1931), as it is small in *Dremotherium* (Sigogneau, 1968), *Dicrocerus* (Ginsburg, pers. comm. to Leinders, 1983), and the recent *Moschus*.

It can be imagined that with more parallel and at the same time less upright horns fighting inflicts less deep wounds in the opponent, while at the same time the more caudally directed horns protect against attacks from the air and the water surface, during grazing and drinking respectively, when the head is bend downwards. It is not likely that the horns developed as defensive weapons against the sabre-like canines of the conspecific rival as is the case in true deer (Grzimek, 1968) for three reasons: the skull roof lacks pneumatized bone tissue, the orbital horns are weakly anchored, and the head was carried higher than is normal in ruminants (Leinders, 1983). It seems that the main need for horns on the mainland, intra-specific combat, has decreased significantly, and that the secondary need, protection against insular predators, is emphasized. At first instance this is strange, as in regions with low predation pressures a relatively greater frequency of aggressive and damaging intraspecific combat is found (Geist, 1974), typical for dispersal phenotypes (sensu Geist, 1987). A plausible reason for a lower frequency of serious damage might be the fact that life on an island is not arcadic at all, and that it was already difficult to stay alive, let alone to progenerate. This difficulty to stay alive promoted the adaptive radiation to fill all possible niches, and the lower rivalry between males. Overpopulation is now ruled by food availability, not by predators, resulting in efficiency selection. An indication that this might be a general rule is given by the assemblage of *Candiacervus* bones in the cave Gerani 4, belonging to one and the same herd, consisting of an approximately equal number of female and male remains (De Vos, 1979). Such situations are typical for genera that do not acculumate a

large harem, thus genera with a mild combat behaviour. It is also typical for maintenance phenotypes, to which the Gerani 4 deer can be reckoned, as it consists of size group 1 (smallest body size, shortened metapodials, high rate of fusions). In recent times, reduction in appendages is also seen in the Spitzbergen reindeer (Geist, 1998).

Thus, here too we see a shift in importance of two factors, combat and protection, in favour of protection, with at the same time a shift in type of protection, as the main danger now comes from the air (birds of prey) and from the water surface (crocodiles) instead of from the same horizon.

LIMB BONES

The locomotion of insular endemics is more characterized by stability than by speed, stimulated by the absence of large mammalian carnivores. This is seen for example in *Phanourios* from Cyprus, in *Myotragus* from Mallorca, in *Candiacervus* from Crete, and in *Hoplitomeryx* from Monte Gargano. Stability has a huge advantage in general, as life expectance for an ungulate is reduced significantly by breaking a leg. This is especially true in a mountaineous area, and the more so if the body is large and heavy. The increase of stability is mainly achieved by shortening of the long bones, most markedly the metapodals. In addition, fusion can sometimes be observed, like the naviculo-cuboid with the cannon bone to form one unit with the loss of an articulation (Leinders & Sondaar, 1974). The degree in which this takes place varies, for example in *Candiacervus* from Gerani 4 it is seen in only 5.9 percent of the specimens (De Vos, 1979), in *Myotragus* in 75 percent, and in *Hoplitomeryx* in 100 percent of the specimens (fig. 4). A third stabilizing factor is provided by the return to a less complete metapodial keels: the distal articulation extends less on the anterior side than in mainland taxa, and the sagittal ridges are less protruding, indicating a substantial reduction of the pogostick-locomotion (Leinders, 1979). Absence of this type of energy-saving locomotion is a characteristic of more primitive ruminants, as the incomplete distal metapodial keels are found in *Amphimoschus* (40693, Langenau, MN 4, observation by Leinders, 1983), *Eumeryx* (AMNH 19147, type, Mongolia, Middle Rupelian), *Hypertragulus* (AMNH 53825), *Nanotragulus* (AMNH 31537, 31538 and 31539, Wyoming, Arikarean), *Hypisodus* (S 602-25500, Nebraska), *Archaeomeryx* (AMNH 20322, Mongolia, Late Eocene), *Leptomeryx* (AMNH 85899, LUSK 0-142-2943, Chadronian), *Prodremotherium* (F: AM 10339, Quercy, Oligocene), *Dorcatherium guntianum* (AMNH 10329, Gunzburg, Upper Miocene), the recent *Tragulus* and *Hyemoschus* and, finally, according to Janis & Scott (1987) *Bachitherium*, *Lophiomeryx*, and *Gelocus*. Thus, in a way loss of the derived condition is seen in endemic island ruminants from unbalanced faunas.

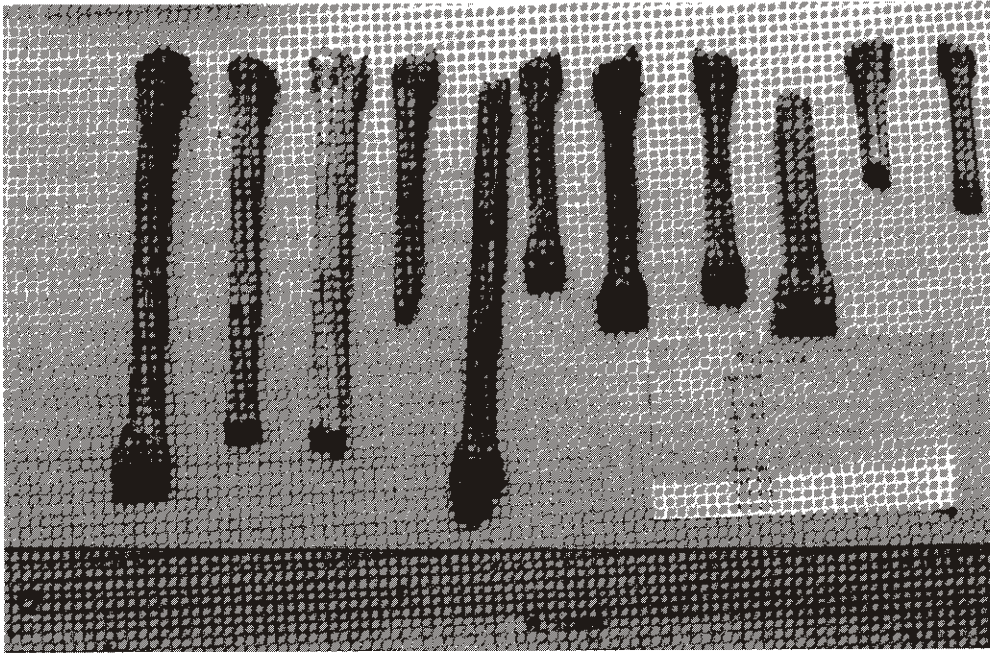


Figure 4: All metatarsals of *Hoplitomeryx* of Monte Gargano (Pliocene, Southern Italy) show fusion with the navico-cuboid, without any exception. Note the closed gully on the anterior side, and the presence of long and slender specimens together with shortened specimens.

Figure 4 : Tous les métapodes postérieurs de *Hoplitomeryx* de Monte Gargano (Pliocène, Italie du Sud) montrent une fusion avec le cubonaviculaire. A noter : la fermeture du canal sur la face dorsale, et la présence de spécimens longs et graciles coexistants avec des spécimens courts.

The increase of stability is accompanied at the same time by a decrease in possible movements and degree of movement. An extreme stable joint permits movement in one direction only, or, in the extreme case of fusion, no movement at all. Obviously, this seemingly disadvantage is no problem anymore on islands, where there are no fast running carnivores chasing the ungulates. Manoeuvrability, too, has lost its significance on islands. The balance of causal factors is disturbed, and a shift towards higher stability and lower manoeuvrability is seen. It is not that short limbs are especially apted for climbing (see the ibex, moufflon etc.), but long legs are apted for running only. So now that this typical mode of locomotion is skipped, only the disadvantages of long limbs remain. The balance has to shift in favour of stability, the more so now that the limbs have to support a plump body: no animal is known to me with a heavy rump and long, ungradate or digitigrade limbs at the same time. A certain degree of manoeuvrability remains, as otherwise walking on non-level substrates is impossible without overloading the mechanical system. The degree, however, of this manoeuvrability varies according to environment, and will therefore differ from island to island.

ASTRAGALUS

A remarkable parallel feature is seen in the astragalus. Normally, in higher ruminants the astragalus has parallel proximal and distal halves. In other words, the axis through the astragalus, from proximal to distal, runs straight. However, in many *Hoplitomeryx* and *Myotragus balearicus* specimens the axes through the proximal and distal part meet each

other at an angle, yielding a bent or twisted appearance, distantly related to the suid shape (Van der Geer, 1999). On itself this shape is not unique for ruminants. The non-parallel sided astragalus is found in the tragulids like the now living *Hyemoschus* and *Tragulus*, in the hypertragulids like *Hypertragulus*, in the leptomerycids like *Leptomeryx* and *Archaeomeryx*, and also in the extinct North American protoceratids. The compact parallel-sided astragalus is considered one of the features found in ruminants above the level of Tragulidae (Janis & Scott, 1987). But why did the endemic bovid *Myotragus* and the endemic deer *Hoplitomeryx* develop an oblique astragalus, a character that is found in pigs and in primitive ruminants before the appearance of bovoids and cervoids? Why got the derived character of a parallel astragalus lost in these island ruminants?

The primitive ruminants are very small, compared to the derived forms. This implies that, due to their higher metabolism, they had a larger abdomen at the same time. Their torso was relatively plumpy and large. This means that the limbs had to deviate slightly. An oblique astragalus corrects for this, thus ensuring a normal foot posture. In pigs the same situation is found: a large belly in relation to the overall shape. Of course such legs are not suitable for running. Such feet are, however, perfectly adapted to a softer substrate, like a forest. The higher bovids and cervids increased enormously in size, and many of them left the forest and entered the plains. They developed long legs and a parallel, compact astragalus, to increase speed.

For the island endemics *Myotragus* and *Hoplitomeryx* this speed had no importance anymore, and the same is valid for a large size. Without being chased by land carnivores, the insular ruminants could afford a smaller

size. With a smaller size, the belly is relatively large, and thus the primitive condition of the tragulids and hypertragulids was attained once again. The heavy belly of *Myotragus balearicus* is established by data: the animal weighted 50-70 kg with a shoulder height of only 45-50 cm (Alcover, 2000). Quite possibly, the belly was even relatively larger than in similar sized tragulids, as many islanders have to feed on less nutritive, or even toxic plants, as is attested by *Myotragus balearicus* (Alcover *et al.*, 1999). This implies an increased digestive effort, and thus a longer intestinal tract.

PATELLA

In *Hoplitomeryx* we find another primitive character. The patella is elongated, with a pointed, snout-like apex, and in some cases a lateral hook (most clear examples: RGM 425.321, RGM 261.547, RGM 425.140, RGM 263.952.). The articular surface does not extend onto the apex, so the function of the elongated apex is to absorb the increased forces in the tendon of the biceps femori. For one reason or another the force exerted on the tendon is much higher than in modern cervids and bovids. In maximal extension there is hardly any lateral mobility, in maximal flexion quite a lot. Two corresponding femoral trochleas show a higher MTR in respect to the LTR (RGM 425.296 and RGM 178.653).

Elongated patellae are found in the *Protoceras celer* (F: AM 1227, Late Oligocene, Dakota), in *Archaeomeryx optatus* (AMNH 20311-8, Late Eocene, Mongolia) and to a lesser extent in *Leptomeryx* (AMNH 85899, Chadronian, North America). In recent ruminants only the chevrotains have an elongated

patella without articular surface on the dorsal facies of the apex, similar to *Hoplitomeryx*.

A straightforward explanation is that the ancestor of *Hoplitomeryx* just retained this primitive character. However, a more likely explanation is that the patella lost its progressive feature and returned to the primitive condition, in parallel with the astragalus. Apparently the need to have a derived patella had disappeared, and quite possibly the derived patella was even disadvantageous. As could already be inferred from the astragalus, a considerable relative increase in body mass took place, and together with the lack of need for speed, and the general advantages of stability, the primitive or less derived constitution turned out to be a better adaptation to the insular environment than the derived mainland constitution. In addition, with the barrel-shaped abdomen, a certain degree of deviating knees cannot be avoided, yielding heavier stress on the medial side of the knee, resulting in a higher MTR of the femoral trochlea.

CONCLUSION

From the many examples of insular endemic artiodactyls, it becomes clear that every functional structure reflects a compromise situation, while every functional structure is adapted to its environment. This means that the island colonizing population is but poorly adapted to its new environment, and the old compromise situation is not useful anymore. As a result, a new compromise situation is needed. Furthermore, similar functional structures in different taxa but in similar environments will evolve in a parallel way to adapt to their environment. These shared parallel evolutions of functional structures are summarized in table 1. Some

structure	change	loss of	gain of	selective pressure	condition
muzzle	short	precision at incisors; large amounts of food	grinding at molars; biting force at incisors	abrasive food	secondarily derived
eyes	anterior position	wide range view	stereoscopy, anterior view	birds of prey, crocodiles	secondarily derived
horns	less diverging	damaging combat	protection if head is bent	birds of prey, crocodiles	secondarily derived
metapodals	short, massive	speed	stability	heavy body	primitive
navicuboid + metatarsus	fusion	mobility	stability	heavy body	secondarily derived
patella	elongated	mobility	stability in max. extension, strong tendon	plump belly, diverging knees; tree-browsing?	primitive
astragalus	non-parallel	speed	posture correction	plump belly	primitive
abdomen	expansion	mobility	digestive abilities	low-nutritious food, toxic plants	primitive

Table 1: Summary of parallelisms in cranial and postcranial features as observed in Plio-Pleistocene artiodactyls, endemic to true-islands. Primitive is the stage before the Pecora, in a cladistic view. Secondarily derived is unique for the island artiodactyls, and is supposed to have derived from the derived condition of the higher ruminants (Pecora).

Tableau 1 : Résumé des parallélismes des caractères du crâne et du squelette post-crânien observés chez les Artiodactyles endémiques des îles vraies du Plio-Pléistocène. L'état primitif est le stade précédant celui de Pecora, d'un point de vue cladistique. L'état dérivé suivant est unique pour les Artiodactyles insulaires. Il est supposé être issu de la condition dérivée de la condition des grands ruminants (Pecora).

structures lose their so-called derived condition, and return to a condition shared with primitive members of the taxon. Thus, in a way, insular artiodactyls can be considered paedomorphic dwarfs, that is, species exhibiting a sharp reversal to ancestral characteristics. This troubles cladistic analyses, as it would group islanders more close to less-derived forms of the same taxon than to their own ancestors. Cladistics without functional analysis, therefore, is a dangerous approach to taxonomy.

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