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REVIEW

Parallel patterns and trends in functional structures in extinct island mammals

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Abstract

Endemic mammalian species on islands are generally known to have followed a different evolutionary pathway than their mainland relatives. General patterns, such as body size trends, have been described regularly. However, most island mammal species are unique and each of them is adapted to a specific local niche as part of an equally specific ecological assemblage. Therefore, comparing island species across taxa, islands and time is inherently dangerous without understanding the adaptational value of the studied feature in the compared taxa and without taking the ecological setting of the taxa into account. In this contribution, general and recurring patterns are described per taxon. Some features, like body mass change and sturdy limbs, are relatively general, whereas most features, like bone fusions and change of orbital axis, occur only in a very few taxa. Some features are even contradictory, such as brain size and degree of hypsodonty, with each taxon having its own particular design. In conclusion, general patterns are more often than not just trends and need to be applied with caution.

Key words: body proportions, fossil record, island rule, paleo-insular mammals, Pleistocene

INTRODUCTION

Body size changes, observed in many extant insular mammalian taxa, are certainly the best known adaptations to insular conditions (e.g. van Valen 1973; Heaney 1978; Lomolino 1985, 2005; Lomolino *et al*. 2012). However, these often spectacular body size changes are not the only modifications of island lineages. Adaptations of island species are also reflected in their craniodental and postcranial anatomy, as first pointed out by Sondaar (1977). Especially in fossil insular mammals, these morphological changes may be so extensive that it is not easy to trace back their direct mainland ancestor. Paleo-insular mammals provide an especially insightful opportunity to assess causality of the variation in morphological structures over much longer time periods. A comprehensive and species-based review of these variations is, however, lacking for the fossil record (general review in van der Geer *et al*. 2010) and often scattered ad-hoc references to general patterns are given without specific details. This may easily lead to misconceptions in cases where a specific feature of a specific insular taxon is taken for a general pattern exhibited by

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many if not all insular mammalian taxa whereas in reality it is a unique feature of just 1 taxon. To infer a more general pattern from local or superficial similarities is prone to error (Donovan 2013). Such is the case, for example, with some studies on *Homo floresiensis* Brown *et al*., 2004 (Brown *et al*. 2004) where this hominid is put in a broader insular perspective: for example, van Heteren and de Vos (2008), Lyras *et al*. (2009) and Meijer *et al*. (2010), who compare the shifts in limb proportions as observed in *H. floresiensis* with those of a few insular artiodactyls, but not with other insular taxa and without paying much attention to the nature of the individual cases. Although I agree with the hypothesis that *H. floresiensis* represents an insular taxon with specific adaptations, I consider it premature to compare totally unrelated endemic taxa with each other in respect to a feature that appears not to be universal. For example, the short limbs of *H. floresiensis* do not necessarily reflect identical evolutionary adaptations as do those of a dwarf hippo, such as *Hippopotamus minor* Desmarest, 1822, especially because the structure of the foot of these 2 taxa is totally different: long and plantigrade in the first, and short and unguligrade in the second (also see below).

This review is the first step towards a better understanding of which patterns are shared by which insular mammals and which are not and why this is the case. Until the developmental, functional and adaptational background of these patterns have been reliably explained per taxon, caution should be taken before comparing unrelated taxa.

MATERIALS AND METHODS

The present study is a review, based on published literature, with the addition of a few personal observations regarding fossil material. Most of the material of the Mediterranean and Indonesian islands cited from the literature was checked by me for control. The cited fossil taxa are given in Table 1, together with their geological age and (paleo-)island.

Observations

Body size trends

Body size variation among various lineages of paleo-insular mammals is generally consistent with the graded trend of the island rule (for a comprehensive overview, see Lomolino *et al*. 2013). Paleo-insular mammals, however, appear to exhibit much more extreme cases of gigantism and dwarfism than living species. Two of the most notorious cases are *Palaeoloxodon falconeri* Busk, 1867, which decreased to just 2% of the body mass of its mainland ancestor (Palombo & Giovinazzo 2005), and *Deinogalerix koenigswaldi* Freudenthal, 1972, which increased to slightly over 200 times the ancestral body mass (Lomolino *et al*. 2013).

The most extreme values occur in final species of geologically old endemic lineages. A slight size reduction is more typical for endemic large mammals that are elements of more balanced faunas or that are geologically very young (i.e. during the early stages of isolation) (e.g. *Cervus elaphus siciliae* Pohlig, 1893, *Cervus elaphus* Linnaeus, 1758 from Jersey, *Bos primigenius siciliae* Pohlig, 1911, and *Bos primigenius bubaloides* Arambourg, 1979) and the earlier species of anagenetic endemic lineages (*Myotragus palomboi* Bover *et al*., 2010, *Myotragus pepgonellae* Moyà-Solà & Pons-Moyà, 1982, *Myotragus antiquus* Pons-Moyà, 1977, and *Praemegaceros sardus* van der Made & Palombo, 2006).

Increased size variation

Some fossil insular species are characterized by an unusually large variation in body size at any given moment in time. Fossils of smaller and larger specimens are found together in the same layer of the same locality without evidence for clear-cut size groups. This has been observed in *Amblyrhiza inundata* Cope, 1868 (McFarlane *et al*. 1998), *Hippopotamus creutzburgi* Boekschoten & Sondaar, 1966 (Kuss 1975), *Palaeoloxodon creutzburgi* (Kuss, 1965) (Kuss 1965), *Mammuthus exilis* (Stock & Furlong, 1928) (Roth 1993), *Mammuthus protomammonteus* (Matsumoto, 1924) (Taruno & Kawamura 2007) and, perhaps, the Maltese *Cervus* Linnaeus, 1758 (figured in van der Geer *et al*. 2010; A. A. E. van der Geer, pers. observ.) (but see remark in Table 1). In these cases, separate species or morphotypes were not recognized.

In a few insular lineages a (much) more pronounced and discontinuous size range is observed and separate species or ‘lineages’ are recognized. This is the case with the murids of Flores, where the giant *Papagomys armandvillei* (Jentink, 1892) and *Papagomys theodorverhoeveni* Musser, 1981 co-occurred with the medium-sized *Komodomys rintjanus* (Sody, 1941) and *Paulamys naso* (Musser, 1981) (Meijer *et al*. 2010; Locatelli 2011), all descendants of *Hooijeromys nusatenggara* Musser, 1981 (van den Bergh *et al*. 2008). Another case is provided by the paleo-island Gargano, where the exact biochronological timing of the start of the murid ra-

Table 1 Fossil insular mammalian taxa discussed in this study. The Maltese deer (*Cervus* sp.) are unresolved. The larger forms may belong to a younger layer, and the smaller forms, with much size variation, might either represent sister species or chronospecies

Species	Island, geological age	Remarks
Proboscidea		
Elephantidae		
Palaeoloxodon falconeri	Sicily, Middle Pleistocene	
Palaeoloxodon '*mnaidriensis*'	Sicily, Late Pleistocene	
Palaeoloxodon creutzburgi	Crete, Late Pleistocene	
Palaeoloxodon tiliensis	Tilos, Late Pleistocene	
Palaeoloxodon cypriotes	Cyprus, Late Pleistocene	
Mammuthus creticus	Crete, Middle Pleistocene	
Mammuthus exilis	Santa Rosa, Late Pleistocene	
Mammuthus protomammonteus	Japan, Early Pleistocene	
Stegoloxodon celebensis	Sulawesi, Middle Pleistocene	
Stegodontidae		
Stegodon florensis florensis, S. florensis insularis	Flores, Late Pleistocene	Chrono(sub)species
Stegodon sondaari	Flores, Middle Pleistocene	
Stegodon aurorae	Japan, Middle Pleistocene	
Stegodon sompoensis	Sulawesi, Middle Pleistocene	
Stegodon hypsilophus	Java, Middle Pleistocene	
Stegodon timorensis	Timor, Pleistocene	
Stegodon mindanensis	Mindanao, Philippines, Pleistocene	
Primates		
Hominidae		
Oreopithecus bamboli	Tuscany, Late Miocene	
Homo floresiensis	Flores, Late Pleistocene	
Homo sapiens	Minatogawa Island, Japan, Late Pleistocene	Known as Minatogawa people
Lagomorpha		
Leporidae		
Nuralagus rex	Menorca, Pliocene	
Ochotonidae		
Gymnesicolagus gelaberti	Mallorca, Middle Miocene	For Menorca: *G.* aff. *G. gelaberti*
Paludotona etruria	Tuscany, Late Miocene	
Prolagus figaro, P. sardus	Sardinia, Early–Late Pleistocene	Chronospecies
Prolagus imperialis	Gargano, Late Miocene	
Rodentia		
Gliridae		
Leithia cartei, L. melitensis	Sicily, Middle–Late Pleistocene	Sister species
Stertomys laticrestatus	Gargano, Late Miocene	At least seven species
Hypnomys waldreni, H. onicensis, H. morpheus	Majorca, Late Pliocene–Holocene	Chronospecies
Cricetidae		
Hattomys beetsi, H. nazarii, H. gargantua	Gargano, Late Miocene	Chronospecies
Muridae		
Papagomys armandvillei, P. theodorverhoeveni	Flores, Late Pleistocene	Sister species
Komodomys rintjanus	Flores, Late Pleistocene	
Paulamys naso	Flores, Late Pleistocene	
Hooijeromys nusatenggara	Flores, Middle Pleistocene	
Kritimys aff. *K. kiridus, K. kiridus, K. catrei*	Crete, Early–Middle Pleistocene	Chronospecies
Mus batei, M. minotaurus	Crete, Late Pleistocene	Chronospecies
Mikrotia magna, 2 other lineages	Gargano, Late Miocene	Sister lineages

Table 1 Continued

Species	Island, geological age	Remarks
Huerzelerimys oreopitheci	Tuscany, Late Miocene	
Anthracomys majori, *A. lorenzi*	Tuscany, Late Miocene	
Heptaxodontidae		
Amblyrhiza inundata	Anguilla and Saint Martin, West Indies, Late Pleistocene	A single island during the Late Pleistocene (Anguilla Bank)
Erinaceamorpha		
Erinaceidae		
Deinogalerix koenigswaldi	Gargano, Late Miocene	Five additional species within 2 lineages
Soricomorpha		
Soricidae		
Nesiotites rafelinensis, N. ponsi, N. aff. *N. ponsi, N. hidalgo*	Majorca, Early Pliocene–Holocene	Chronospecies
Artiodactyla		
Cervidae		
Cervus elaphus siciliae	Sicily, Late Pleistocene	
Cervus elaphus	Jersey, Late Pleistocene	
Cervus sp.	Malta, Late Pleistocene	Sister or chronospecies
Cervus sp.	Masbate, Late Pleistocene	Undescribed species
Cervus astylodon	Ryukyu Islands, Late Pleistocene	
Candiacervus ropalophorus, C. sp. II, *C. cretensis, C. rethymnensis, C. dorothensis, C. major*	Crete, Late Pleistocene	Sister species
‘*Candiacervus*’ *pygadiensis*, ‘*C.*’ *cerigensis*	Karpathos, Kassos, Late Pleistocene	Sister species
Praemegaceros sardus, P. cazioti	Sardinia, Middle–Late Pleistocene	Chronospecies; earliest form unnamed: *P*. sp.
Hoplitomeryx matthei	Gargano, Late Miocene	Three additional morphotypes
Bovidae		
Bos primigenius siciliae	Sicily, Late Pleistocene	
Bos primigenius bubaloides	Pianosa, Late Pleistocene	
Myotragus palomboi, M. pepgonellae, M. antiquus, M. kopperi, M. batei, M. balearicus	Majorca, Early Pliocene–Holocene	
Bubalus cebuensis	Cebu, Philippines, Late Pleistocene	
Dubiosia santeng	Java, Middle Pleistocene	
Nesogoral melonii	Sardinia, Early Pleistocene	Several unnamed sister species
Maremmia lorenzi, M. haupti	Tuscany, Late Miocene	Chronospecies
Turritragus casteanensis	Tuscany, Late Miocene	
Etruria vialli	Tuscany, Late Miocene	
Tyrrhenotragus gracillimus	Tuscany, Late Miocene	
Hippopotamidae		
Hippopotamus creutzburgi	Crete, Middle Pleistocene	
Hippopotamus minor	Cyprus, Late Pleistocene	
Hippopotamus lemerlei, H. madagascariensis	Madagascar, Late Pleistocene–Holocene	Sister species
Suidae		
Sus sondaari	Sardinia, Early Pleistocene	
Carnivora		
Canidae		
Cynotherium sardous	Sardinia, Middle–Late Pleistocene	Earlier chronospecies unnamed: *C*. sp.

diation has not been recorded. Here, after a steady body size increase, the murids (*Mikrotia*) display a sudden radiation into 3 lineages contemporaneous with the last occurrence of the hamsters (*Hattomys gargantua* Freudenthal, 1985). As on Flores, apart from converging on the absent mesoherbivore niche, giant forms exist next to medium and small forms. At the initiation of the murid radiation, the insectivore *Deinogalerix* is also, for the first time, represented by a full range of body sizes (inferred from Fig. 16 in Butler 1980). Radiation is also seen in *Stertomys* Daams & Freudenthal, 1985, with 2 species at any given chronological phase (Rinaldi & Masini 2009), and *Hoplitomeryx* (Leinders 1984) (4 morphotypes for Gargano in van der Geer 2005, 2008), but the start of these radiations are not necessarily contemporaneous with the murid radiation.

Such an increased and discontinuous size variation is also observed in other taxa, sometimes in combination with a variation in morphology, independent of size. Examples are *Candiacervus* (de Vos 1979), *Cervus astylodon* (Matsumoto, 1926) from Kume (Matsumoto & Otsuka 2000), *Cervus* sp. of Masbate (de Vos 2006), subfossil species of lemurs (Mittermeier *et al*. 2008) and nesomyids (Mein *et al*. 2010), in addition to the array of still living species of Madagascar, subfossil hystricomorph rodents and soricomorph insecteaters of the West Indies (cladogenesis on Cuba, Puerto Rico and Hispaniola [Woods & Sergile 2001]), *Leithia* (Bonfiglio *et al*. 2002), Malagasy *Hippopotamus* Linnaeus, 1758 (Weston & Lister 2009) and *Nesogoral* (Palombo *et al*. 2006; Rozzi & Palombo 2014). The species or morphotypes in these cases are all confined within the boundaries of a single island. The presence of various morphotypes within 1 size class seems restricted to cases of adaptive radiation and has been described only for *Nesogoral* (Rozzi & Palombo 2014), *Ce. astylodon* (de Vos 2006) and *Hoplitomeryx* (van der Geer 2005; A. A. E. van der Geer, pers. observ.).

In many cases, however, the increased size variation is progressive; in other words, these species form part of a lineage of anagenetic species (chronospecies), with the next species being either smaller or larger than the previous (depending on the direction of body size evolution). Extended chronoseries befitting this type of increased size variation include *Praemegaceros* of Sardinia (Palombo & Melis 2005; van der Made & Palombo 2006), *Nesiotites* (Rofes *et al*. 2012; van der Geer *et al*. 2013), *Hypnomys* (Bover *et al*. 2010a), *Myotragus* (Bover *et al*. 2010b), *Kritimys* and *Mus* of Crete (Mayhew 1977), *Stegodon florensis* Hooijer, 1957 (van den Bergh *et al*. 2008) and *Cynotherium sardous* Studiati, 1857 (Lyras *et al*. 2010): all of them with at least 2 successive chronospecies. The progressive size increase is not always constant, but may show fluctuations in magnitude through time and even reversals (van der Geer *et al*. 2013).

Changes in postcranial elements

Relative shortening of the distal limb bones, with simultaneous overall dwarfing and increased massivity, is observed in several fossil insular artiodactyls, but also in Minatogawa people (*Homo sapiens* Linnaeus, 1758 [Baba & Endo 1982]). These artiodactyls are *Candiacervus ropalophorus* de Vos, 1984, *Candiacervus cretensis* (Simonelli, 1908) (de Vos 1979), *Candiacervus* spp. II (van der Geer *et al*. 2006), '*Candiacervus*' *pygadiensis* (Kuss, 1975), '*Candiacervus*' *cerigensis* (Kuss, 1975), the smallest *Hoplitomeryx* (van der Geer 2005), *Ce. astylodon* (de Vos 2006), *Bubalus cebuensis* Croft *et al*., 2006 (Croft *et al.* 2006), all species of *Myotragus* (Bover 2004; Bover *et al*. 2010b), *H. minor*, *H. creutzburgi* (Spaan *et al*. 1994), *Stegodon aurorae* (Matsumoto, 1918) (Konishi 2000) and, perhaps, *Maremmia lorenzi* Hürzeler & Engesser, 1976 (Hürzeler 1983) and *Etruria vialli* Abbazzi *et al*., 2008, or *Turritragus casteanensis* Abbazzi *et al*., 2008, but for these latter 3 taxa the ancestor is unknown. Relatively short legs are also typical for *H. floresiensis* (Brown *et al*., 2004). The accompanying exceptionally long feet and arms (Brown *et al*. 2004; Morwood *et al*. 2005) and primitive wrist (Tocheri *et al*. 2007; Orr *et al*. 2013) and foot morphology (Jungers *et al*. 2009), but are unique and find no parallel with other insular taxa. The feet of *H. sapiens* of Minatogawa are robust but not long (Baba & Endo 1982). A number of the abovementioned artiodactyls have shortened phalanges in addition to the shorter distal limb bones, so shorter feet (*Myotragus*, *H. minor*, *H. creutzburgi*), simultaneously with a change in posture towards a more vertical stance (Sondaar 1977). Distal limb length reduction in lineages which underwent adaptive radiation is restricted to the smallest species or morphotypes. Here, the medium and larger species have slender and proportionally normal or even elongated distal limb bones. This is observed in *Candiacervus major* (Capasso Barbato & Petronio 1986) and in the largest *Hoplitomeryx* (size 4 in van der Geer 2008), but also in *Nesogoral* (Palombo *et al*. 2006; Rozzi & Palombo 2014).

The relatively shortened distal limb bones is already present at birth and increases further during postnatal ontogeny due to a relatively slower growth speed of the autopodium, at least in *C. ropalophorus* (van der Geer *et al*. 2006) and the 2 smallest size classes of *Hoplitomeryx* (A. A. E. van der Geer, pers. observ.). The higher massivity of the shortened bones is already observed in neonates of *Myotragus balearicus* Bate, 1909 (Bover & Alcover 1999a), *C. ropalophorus* (van der Geer *et al*. 2006) and the smallest size classes of *Hoplitomeryx* (A. A. E. van der Geer, pers. observ.).

Loss of an articulation is sometimes observed in the form of a complete fusion of the navicocuboid with the cannon bone in insular ruminants (Leinders & Sondaar 1974). This occurs in varying degrees, and is definitely not a universal pattern and not restricted to islands. The percentage of total fusion is 0% in *Praemegaceros cazioti* (Depéret, 1897) (Klein Hofmeijer 1997), 0% in *Ce. astylodon* (Matsumoto & Otsuka 2000) (but 45% according to van der Geer *et al*. [2010]), 6% in *C. ropalophorus* (de Vos 1979), 100% in *Hoplitomeryx* (van der Geer 2005) and 21% in *Cervus* sp. from Malta (A. A. E. van der Geer, unpub. data). In *M. balearicus* this percentage differs according to locality and age, and increases from 40% (Cova de Son Maiol, late Late Pleistocene) to 80% (Cova de Moleta, Holocene) (Moyá-Solá 1979), strongly indicating the progressive nature of this feature in this species at least. In mainland ruminants, this fusion is rarely observed (e.g. less than 5% in *Euprox*/*Heteroprox* [A. A. E. van der Geer, unpub. data]).

An even more rare fusion is that between the distal parts of the fibula (os malleolare) and tibia, observed only in 1 *M. balearicus* (Bover *et al*. 2005) and 1 *Hoplitomeryx* (van der Geer 2005) out of hundreds of specimens. Synostotic fusions between shafts of individual elements are observed as well, such as the fusion of the lateral metapodals with the cannon bone in *Candiacervus* sp. II (van der Geer *et al*. 2006), and more extensive fusion of radius and ulna in *Candiacervus* sp. II (van der Geer *et al*. 2006), *Hoplitomeryx* (A. A. E. van der Geer, unpub. data), *P. falconeri*, *H. minor* and *Stegodon florensis insularis* van den Bergh *et al*. 2008 (van den Bergh 1999; van den Bergh *et al*. 2008), and of the tibia–fibula in *P. falconeri* and *H. minor* (van den Bergh 1999). Synostotic fusions have been observed in juvenile *S. florensis* (van den Bergh 1999) and *P. falconeri* (Palombo 2001), indicating that it has nothing to do with aging. Fusion between the metatarsal and the navicocuboid in *Hoplitomeryx* takes place before the fusion of the distal epiphysis with the shaft (van der Geer 2005) (no information on other ungulates). When the condyles are still separated, the proximal articulation is developed normally, as is the case in mainland deer, e.g. *Dama dama* (Linnaeus, 1758) (A. A. E. van der Geer, unpub. data).

Changes in dentition

A higher degree of hypsodonty, or a relative increase in molar crown height, relative to their ancestor is seen in various insular taxa, such as *S. florensis insularis* (van den Bergh *et al*. 2008), *Stegodon sondaari* van den Bergh, 1999, *Stegodon mindanensis* Naumann, 1890, *Stegodon hypsilophus* Hooijer, 1954, *S. aurorae*, *Stegodon timorensis* Sartono, 1969, and *Stegodon sompoensis* Hooijer, 1964 (e.g. van den Bergh 1999), *Mikrotia* (Freudenthal 1976), *M. balearicus* (e.g. Bover 2004), *Nesogoral melonii* (Dehaut, 1911) (e.g. Palombo *et al*. 2006), *Duboisia santeng* (Dubois, 1891) (Rozzi *et al*. 2013), *C. ropalophorus* (van der Geer *et al*. 2006), *Sus sondaari* van der Made, 1999 (van der Made 1999), *Huerzelerimys oreopitheci* Engesser, 1989, *Anthracomys lorenzi* Engesser, 1989, and *Anthracomys majori* Schaub, 1938 (Casanovas-Vilar *et al*. 2011), and *Kritimys kiridus* (Bate, 1942) (Mayhew 1977). Hypsodont teeth are also present in some taxa for which the mainland ancestor is unknown, which leaves it in the middle whether the degree of hypsodonty increased or not. This is valid for *Ce. astylodon* (Matsumoto 1926), *M. lorenzi* (Huerzeler 1983) and the other Tusco–Sardinian hypsodont bovids such as *Tyrrhenotragus gracillimus* (Weithofer, 1888), and *T. casteanensis* (Abbazzi *et al*. 2008).

The most extreme form of hypsodonty is exhibited by *M. balearicus*, where the roots of the lower first and second molar even distort normal ossification of the base of the mandibular ramus. This lineage also evolved hypselodontincisors (ever-growing and open-rooted) (Alcover *et al*. 1981), a character shared with *M. lorenzi* but because the ancestor of the latter is unknown, it is impossible to determine whether it is an acquired character in *Maremmia* (Hürzeler & Engesser 1976) as well. These incisors were earlier regarded as retained primary teeth like in rodents and lagomorphs in which the secondary incisors never erupt (Bover & Alcover 1999b), but are now considered a modified permanent incisor that erupts at a relatively early ontogenetic stage (Moyà-Solà *et al*. 2007).

Just larger, but non-hypsodont, teeth are observed in *H. floresiensis*, relative to *H. sapiens* and *Homo erectus* (Dubois, 1894), but not to *Homo habilis* Leakey *et* *al*., 1964 (Brown *et al*. 2004; Brown & Maeda 2009), whereas smaller teeth seem to characterize *Oreopithecus bamboli* Gervais, 1872 (Köhler & Moyà-Solà 1997), pending revision on its ancestry.

Increased masticatory stress is inferred for *H. sapiens* from Minatogawa, based on the extraordinarily strong development of the masticatory muscles, the deep temporal fossae with flared zygomatic arches, the wide and high position of the attachment of the masseter muscles in the zygomata, the thick alveolar bones and a high degree of tooth wear (Baba 2000). In addition, *Hypnomys morpheus* Bate, 1918 has a more massive mandible relative to that of related *Eliomys* (Hautier *et al*. 2009).

Loss of premolars is seen in *Hoplitomeryx matthei* Leinders, 1984, *Myotragus batei* Crusafont & Angel, 1966, *M. balearicus* (e.g. Alcover *et al*. 1981), *M. lorenzi* and *M. haupti* (Hürzeler 1983), *T. casteanensis* (Abbazzi *et al*. 2008), *C. sardous* (Lyras *et al*. 2006), *S. sondaari* (van der Made 1999) and *H. minor* (Boekschoten & Sondaar 1972). A reduced and perhaps not-functional p2 is present in *N. melonii* (Palombo *et al*. 2006), *M. palomboi* and *Myotragus pepgonellae* Moyà-Solà & Pons-Moyà, 1982 (Bover *et al*. 2010b). Loss of the fourth antemolar is seen in *Nesiotites hidalgo* Bate, 1944 (Reumer, 1981). Loss of the second and third permanent insicors is seen in *Myotragus kopperi* Moyà-Solà & Pons-Moyà 1981 and its younger chronospecies (Moyà-Solà *et al*. 2007).

More complex enamel patterns are observed in some insular pikas and murids. *Mikrotia* has an increased number of ridges on the first lower and last upper molar (Freudental 1976), in addition to being hypsodont. All species of *Prolagus*, in contrast to *Paludotona etruria* Dawson, 1959, which preserved a plesiomorphic dental morphology, show an increase of enamel complexity of their molars, and an enlargement of the third lower premolars relative to the other lower cheek teeth, without (much) increase in hypsodonty (Angelone 2005). Enamel complexity seems unrelated to hypsodonty: whereas *Prolagus imperialis* Mazza, 1987 and *Prolagus figaro* Lopez-Martinez, 1975 combined a very complex pattern with a low hypsodonty index, *Prolagus sardus* (Wagner, 1832) had a less complex pattern but a higher index.

Cranial and neurological changes

A lack of strong pneumatization of the skull is seen in the dwarf proboscideans *P. falconeri*, *Mammuthus creticus* (Bate, 1907), *Mammuthus exilis* (Agenbroad *et al*., 1994) and *Stegoloxodon celebensis* (Hooijer, 1949). In the most extreme case (*P. falconeri*), the parietal swellings are entirely lost (Palombo 2001; also see below).

Many insular endemics developed rather short muzzles. In these short-snouted endemics, the maxillary tooth row is more arcuate (A. A. E. van der Geer, pers. observ.) and less complete, as evidenced by the loss or reduction of (pre)molars (*H. matthei*, *M. batei*, *M. balearicus*, *M. lorenzi*, *N. melonii*, *C. sardous*, *S. sondaari*, *H. minor*; also see above). A shorter snout in combination with a short diastema is observed (with loss of lower third molar) in *Gymnesicolagus gelaberti* Mein & Adrover, 1982 and *G.* aff. *gelaberti*, and (without such loss) in and *Nuralagus rex* Quintana *et al*., 2011 (Quintana *et al*. 2011), but not in *P. sardus* (Quintana & Agustí 2007) and *Deinogalerix koenigswaldi* Freudenthal, 1972 (Butler 1980), which have an increased diastema length. A marked facial reduction or reduced prognathism (the homonin equivalent of a shorter muzzle) is also seen in *H. floresiensis* (Kaifu *et al*. 2011). In this aspect, *H. floresiensis* is most similar to *H. sapiens*, but in all other characters combined it resembles *H. erectus* most (Baab & McNulty 2009; Lyras *et al.* 2009; Kaifu *et al*. 2011; Orr *et al*. 2013). One of its unique features is the posteriorly positioned caudal border of the palatine (Kaifu *et al*. 2011).

A brain of the same relative size as in their mainland relatives has been documented for *Candiacervus* spp. II, *C. sardous* and *H. minor* (Lyras *et al*. 2009), whereas that of *P. falconeri* is proportionally equally large or perhaps even larger (Palombo 2001). Brain size reduction, in contrast, has been described for *M. balearicus* (Köhler & Moyà-Solà 2004), *Hippopotamus lemerlei* Milne-Edwards, 1868 and *Hippopotamus madagascariensis* Guldberg, 1883 (Weston & Lister 2009). The brain of *M. balearicus* is further characterized by a reduced visual cortex (Köhler & Moyà-Solà 2004), matching the smaller orbits (see below), and unusually small olfactory bulbs (Desachaux 1961), which agrees with the reduced olfactory ability as inferred from the less perforated criba nasalis (Bover & Tolosa 2005). Simultaneously, however, the *Myotragus* brain is remarkably convoluted for its size (Dechaseaux 1961), resulting in a significant increase in cortical surface. *H. floresiensis* has a relative brain size comparable to that of an australopithecine (Brown *et al*. 2004; Falk *et al*. 2005), but anatomical features of the brain resemble those of *H. erectus* most, although with a more pronounced convolution (Falk *et al*. 2005), similar to *M. balearicus*.

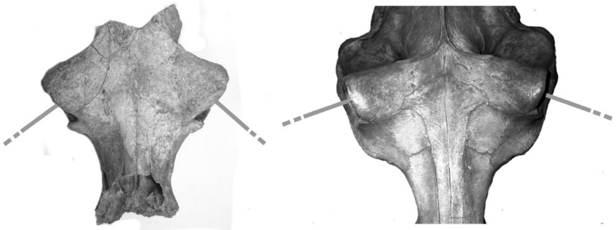

Figure 1 Skulls of *Hippopotamus minor* (right) and *H. amphibius* (left) show a more frontal view of the insular dwarf as compared to that of a mainland hippo. Note that the skulls are not depicted with the same scale. Maximal biorbital breadth is 13.5 cm for *H. minor* and 32 cm for *H. amphibius*.

In *M. balearicus* and less so in *C. ropalophorus*, the orbits are reduced in size relative to body size (Palombo *et al*. 2008). At the same time, the orbits are more frontally orientated in *M. balearicus* (Alcover *et al*. 1981). This is also observed in *H. minor* (Fig. 1).

DISCUSSION

Body size trends

In a comprehensive investigation of causality of the island rule in extant mammals, Lomolino *et al*. (2012) found that body size evolution is influenced by selective forces whose importance and nature of influence (promoting gigantism or dwarfism) varied in a predictable manner with characteristics of the species (in particular, their ancestral body size and diet) and the islands (island size, isolation and climate), and with ecological interactions among mammals.

The existence of a clade-dependent pattern cannot be confirmed for the fossil record, in contradiction to the conclusion of Meiri *et al*. (2008) that heteromyid rodents, carnivores and artiodactyls typically evolve smaller size on islands whereas murid rodents usually grow larger. Lomolino *et al*. (2013) found that proboscideans also grow smaller, and that shrews, gymnures, lagomorphs, glirids and carnivores with aquatic prey grow larger. This contradiction might, in part, stem from a time bias, because most island taxa included in Meiri *et al*. (2008) originate from continental islands that had been connected to the mainland during the last glacial maximum, and, thus, had been isolated for, at most, 10 000 years (Locatelli *et al*. 2012), whereas most taxa included in Lomolino (2013) had been isolated since the onset of the Late Pleistocene. In addition, and this is perhaps the main issue, truly giant and dwarf forms like *Leithia*, *Papagomys* Sody 1941, *Deinogalerix*, *P. falconeri* and *H. minor* were not included in the Meiri *et al*. (2008) analyses because no living mainland conspecific exists (Locatelli *et al*. 2012). Dwarfism is sometimes described as pedomorphism, e.g. Roth (1992), Lister (1996) and Palombo (2001) for dwarf elephants and van Heteren & de Vos (2008) for *H. floresiensis*. I disagree with this hypothesis, because adult insular endemics do not resemble the juveniles of the ancestral species. Especially juvenile artiodactyls, and elephants to a lesser degree, have typically long and slender limbs (not short as van Heteren & de Vos [2008] assume), whereas insular dwarf artiodactyls and proboscideans have short and massive limbs. Dwarfism likely is established by a reduction of growth speed and not by a truncation of growth length as there is no evidence that life history traits would scale allometrically (Clauss *et al*. 2014). Maximum lifespan and gestation period in island dwarfs tend to reflect those of their larger relatives (Clauss *et al*. 2014; see further below). A slower growth speed is also attested for molar formation in a dwarf elephant species (Dirks *et al*. 2012), whereas Bromage *et al*. (2002) calculated a similar growth speed between *Palaeoloxodon cypriotes* (Bate, 1903) and the mainland *Palaeoloxodon recki* (Dietrich, 1915), based on the number of cross-striations and striae of Retzius in molars (see further below under Dentition). However, *P. recki* is phylogenetically distinct from *Palaeoloxodon antiquus* (Falconer & Cautley, 1847) (the ancestor of *P. cypriotes*), whose growth speed is unknown. Studies of extant insular taxa also indicate a slower, not a faster, life. Lower basal metabolic rates have been found in fruit pigeons on small islands in the South Pacific and for *Capromys pilorides* (Say, 1822), *Geocapromys browni* Fischer, 1830 and *Geocapromys ingrahami* (Allen, 1891) of the West Indies (McNab 2000), and small nectar-eating flying foxes (*Macroglossus*, *Syconycteris*) of Australia and New Guinea and on large and small islands from the Moluccas to the Solomons readily enter torpor (Bonacorso & McNab 1997).

Increased size variation

A very interesting effect of release from competition on body size evolution is the increased size and morphological variation. The most typical cases are referred to as adaptive radiation or multispecies assemblages. Body size evolution in these cases is likely directed towards niche partitioning, resulting in the filling of all usual (mainland) roles, with much morphological convergence. Living examples are the tenrecs of Madagascar (Tenrecidae). The Tenrecidae are a widely diverse family with species ranging from approximately 5 g to just over 1 kg and occupying niches convergent to those of shrews, desmans, hedgehogs and opossums in diverse environments (aquatic, terrestrial, arboreal and fossorial). The insular fossil record contains quite a number of sympatric multispecies assemblages, including herbivores, rodents and insect eaters. Even very large herbivores might be able to diverge morphologically and evolve into 2 different species when the area is large enough, as is the case with *H. madagascariensis* and *H. lemerlei* on Madagascar. Radiations sometimes were more extensive in the past than today: for example, the Malagasy lemurs were further represented by 15 now extinct species before the Holocene, including the gorilla-sized giant *Megaladapis* Forsyth Major, 1894 (Mittermeier *et al*. 2008), and the diversity of most lineages of the West Indies was larger during the Pleistocene than it is today (Woods & Sergile 2001).

Changes in postcranial elements

Change in body proportions is perhaps best explained in terms of niche expansion. Large herbivores might need to enhance their climbing abilities and improve stability to be able to expand their niche to otherwise inaccessible mountainous areas (Sondaar 1977). This is the most common explanation behind the observed shortening and thickening of the long bones, most markedly the metapodials in ungulates and the femur and humerus in proboscideans and hippos. Increased stability is, in a few cases, further achieved by a restriction of directions of movements and the degree thereof through bone fusions. The inherent loss of speed and manoeuvrability ('low-gear system' in Sondaar [1977]) pose no problem when terrestrial mammalian predators are lacking. Short, robust limbs in *H. floresiensis*, in contrast, need not necessarily have the same adaptational background. Long limbs in humans did not evolve to outrun predators as is the case in ungulates but are in all likelihood better explained in terms of locomotor efficiency and endurance (Polk 2004). On Flores, the loss of migratorial habits may have driven the reversion of morphology instead. Another scenario could be that *H. floresiensis* simply returned to the (rain) forest and was no longer adapted to open environments. The proportionally long arms and feet of *H. floresiensis* fit an arboreal adaptation very well.

In a few cases, the short, robust limbs form a plesiomorph feature. Niche expansion is not the case here but was earlier a conservative trait that managed to survive under reduced ecological pressure. This might be partly the case for *Myotragus*, as it has been suggested that its ancestor already had short, robust metapodials (i.e. Palombo *et al*. [2013] suggest *Norbertia* or *Aragoral* as potential candidates). In the case of *H. floresiensis*, this might indicate a pre-*erectus* ancestry, as is currently the consensus opinion of the discovery team (see Morwood & Jungers 2009). However, Neanderthals also have proportionally shorter limbs (Polk 2004).

The changes in body proportions relative to the ancestor are likely the result of changes in relative growth speed of the various body parts (heterochrony) during ontogeny (van Heteren & de Vos 2008). This, however, does not explain the fusion of the cannon bone with the navicocuboid. Because this fusion takes place in an early developmental stage, and not in adulthood, it might be related to a local inhibition of the expression of articular surfaces to enable fusion. Bone fusions are difficult to explain in terms such as heterochrony and are certainly not to be considered pedomorphism. Information on synostotic fusions and how and at what age they occur is even scantier, but there is an indication that this starts at a young age (see above for *S. florensis insularis*) In any case, fusions are extremely rare, also in insular taxa, with as the only exception that of the metatarsal with the tarsal bone in *Myotragus* and *Hoplitomeryx*.

Dentition, diet and longevity

A higher degree of hypsodonty in insular mammals is often explained as an adaptation towards more abrasive food (Schüle 1993). This is evidenced by *M. balearicus*, which fed on less nutritive or even toxic plants like *Buxus balearica* Lamarck, 1785 (Alcover *et al*. 1999; Winkler 2010), implying an increased digestive effort, perhaps combined with a longer intestinal tract, resulting in a relatively large belly or a change in intestinal bacterial fauna (Bover 2004).

Another hypothesis is a response to increased food intake, in line with an increased metabolic rate in dwarf forms due to a shift in volume–surface ratio, and, correspondingly, a 'fast' life (Raia *et al*. 2003). This increase would result in more rapid tooth wear, which is compensated for by an increase in hypsodonty. The 'fast' life was originally forwarded for *P. falconeri*, based upon the lack of tusks in the females and a high percentage of juveniles (Raia *et al*. 2003), but has also been suggested for other insular proboscideans (Palombo 2007), *M. balearicus* (Meiri & Raia [2010] *contra* Köhler & Moyà-Solà [2010]; also see below) and *H. floresiensis* (van Heteren & de Vos 2008). However, this hypothesis fails to explain similar strategies to reduce tooth wear in insular giant taxa, where metabolic rate, if changed, would be lower compared to their normal-sized ancestors, due to the same volume–surface ratio shift, resulting in a 'slower' life. The anoa [*Bubalus depressicornis* (Hamilton-Smith, 1827)], an extant island dwarf buffalo, has a surprisingly high longevity and an extremely long gestation time for its body size, which stands in sharp contrast to a 'faster' life. Likely, its maximum lifespan and gestation period reflect those of its larger relatives (Clauss *et al*. 2014), as is also the case for domestic breeds: dwarf breeds of horses, dogs, rabbits, goats and cattle have the same values as large-sized and normal-sized breeds (overview in Clauss *et al*. 2014). There is no evidence that life history traits would scale allometrically (Clauss *et al*. 2014).

A 'slower' life, in contrast, has been suggested for *M. balearicus* based on lines of arrested growth in bones (Köhler & Moyà-Solà 2010) and the number of cementum layers of its teeth (Jordana *et al*. 2012), which imply a higher maximum lifespan for *Myotragus* than for similar-sized extant bovids. Without predators around, investment in K-strategy pays off and longevity is a means to achieve this. In line with this is the observation that tooth growth appears to be slow in a small fossil insular elephant species (*P. cypriotes*) but fast in a large fossil mainland species (*Mammuthus columbi* Falconer, 1857) (Dirks *et al*. 2012). Jordana *et al*. (2012) go a step further and maintain that the coexistence of hypsodonty and longevity in *M. balearicus* is entirely interlinked and of a causal nature, with diet playing no role at all. However, the incisors of *Myotragus* are ever-growing while the molars are just (extremely) hypsodont, implying that the prolonged tooth wear did not affect all positions equally and that the attrition–abrasion gradient varied along the tooth row. The ever-growing incisors show that incisal preparation was significantly more demanding, which is unexpected for a browser. It is more likely that the incisors evolved their ever-growing capability in response to something other than just longevity. As far as the molar crowns are considered, their hypsodonty may, indeed, have evolved partly in response to the demands of an extended lifespan.

The response to diet-induced abrasion, resulting in hypsodonty and complex enamel patterns, could also be a reaction to a change in eating methods, including rooting, overgrazing and near-surface browsing, resulting in a significant soil particle intake (Damuth & Janis 2011). This latter factor should not be underestimated. There is evidence of high tooth wear in sheep that graze among the highly mobile and windswept sandy beaches and dunes on the west side of New Zealand's North Island (Healy & Ludwig 1965). Soil mineral particles are very mobile in beach environments, and onshore or littoral winds are always strongest right at the beach. Islands are, in general, more windy than mainlands of the same latitude. A higher intake of mineral particles could, therefore, form an important factor to explain hypsodonty in insular taxa.

An alternative strategy to cope with a higher degree of abrasion seems to have been implemented by *H. sapiens* of Minatogawa, where the skull architecture indicates heavy action of the masticatory muscles, but where the teeth had not responded adequately, as shown by a high degree of wear (Baba 2000). In this case, it is unlikely to assume either a fast life or increased longevity. The same seems to apply to *H. morpheus* with its more massive mandible relative to that of related *Eliomys* but without having evolved particular hypsodont or complex dentition (Hautier *et al*. 2009). This, in combination with microwear patterns, is explained as an adaptation towards a more abrasive and generalized diet, and not as a longevity strategy. This seems contrary to the case of other insular murids; namely, *Huerzelerimys* and *Anthracomys*. The increased wear-resistancy observed here as well as in the contemporaneous bovids of the same insular bioprovince is in conflict with paleobotanical evidence that shows that grasses formed only a minor component of the vegetation (Casanovas-Vilar *et al*. 2011). Increased particle intake is, however, not considered here, whereas it could be a logic explanation for the high degree of hypsodonty seen in most members of this fauna.

Cranial changes

Usually, the lack of strong pneumatization of the skull in insular dwarf proboscideans is explained as a response to size reduction because a smaller and, thus, lighter skull relaxes the need for strong neck musculature (Accordi & Palombo 1971; Sondaar 1977).

The relatively short muzzles may be an adaptation to a higher degree of tooth wear (in herbivores) or towards a higher degree of hypercarnivory (in carnivores). However, not all cases of relatively short snouts are an insular adaptation. For example, the short diastema in insular lagomorphs represents a retained plesiomorphic character (Quintana & Agusti 2007).

Relative shortening of the muzzle might result in a relative increase in power exerted at the molariforms (Reilly *et al*. 2001). In hypercarnivorous carnivores (e.g. *Lycaon pictus* (Temminck, 1820*)*, felids), snout length and number of molariforms are reduced. This model fits *C. sardous* best (Lyras *et al*. 2006). In contrast, the facial reduction observed in *H. floresiensis* is attributed to reduced masticatory stresses (Kaifu *et al*. 2011) instead. This would oppose *H. floresiensis* to carnivores, although there is evidence that the teeth of *H. floresiensis* are large relatively to *H. sapiens* and *H. erectus* (Brown *et al*. 2004), perhaps implying an increased masticatory stress. At the same time, the more caudally positioned caudal palatine border of *H. floresiensis* is found without exception in short-faced wild and fossil canids relative to their long-faced relatives (Lyras 2009). Morphogenetic factors that affect the shortening of the facial region seem also to affect the position of the posterior palatine border, independent of changes in masticatory function.

Neurological changes

Brain size is sometimes reduced with a simultaneous increase in complexity (convolution), retaining in this way a larger surface area. This is the case in *M. balearicus* and perhaps in *H. floresiensis* as well. Future studies on the brain of insular taxa should not take only brain mass into account but measure surface area as well. In that respect, effective brain size may appear to be similar to that of the ancestor.

Decrease in olfactory and/or visual functions may be promoted by a shift in predator pressure.

CONCLUSION

Putting all observations together, it appears that some parallel phenomena exist among insular taxa, but none of them is shown by all and most of them are shown by just a few or even only 2. The most widespread phenomena are those concerning body size and body proportions, the rarest bone fusions. Some phenomena are even contradictory, such as limb length and brain size, which can be either reduced or enlarged.

The parallel patterns and trends that are present are functionally best explained by shared adaptational needs (adaptations to ecologically similar environments and assemblages) in response to a deviation from the ancestral (mainland) situation, such as more rugose terrain, higher abrasiveness of the food items, increased intraspecific competition and change in predator spectrum. Caution should be taken when comparing parallel adaptations in unrelated taxa: short limbs in an ungulate may indicate rugose terrain but in a hominid perhaps an arboreal habitat. Such comparisons can even be inopportune between related taxa. See, for example, Rozzi & Palombo (2014), who found that different habitats triggered similar adaptations within a genus of insular bovids (*Nesogoral*).

As a result of restructuring of anatomical units, some characters may depart from their apomorphic condition, and may even secondarily return to a condition shared with geologically earlier members of the taxon. This is sometimes referred to as a return to a primitive condition (e.g. van der Geer 2005) but that phrase is misleading as it gives the impression that the entire anatomical structure lost its apomorphic morphology and, as a whole, returns to a plesiomorphic stage. This is, however, explicitly not the case. The brain may be smaller in size in insular endemics (‘pseudo-primitive’), but, at the same time, its fissuration can be significantly stronger (apomorphic). To complicate the matter even more, a seemingly apomorphic feature, increased longevity (and gestation period) in insular large mammals relative to similar-sized mammals, is probably unrelated to body mass but likely merely reflects the values of the ancestor and is, thus, rather, a plesiomorphic feature. Developmental speed is then necessarily slower in secondary dwarfs (because gestation length is fixed) and this may be indirectly advantageous in an environment with more pronounced fluctuations in resource availability, resulting in decreased size.

This confusion between apomorphic and plesiomorphic conditions may drastically complicate phylogenetic and taxonomical analyses. The immediate danger of this is that arrival time may be calculated far too much in the past and time in isolation may be hugely overestimated.

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