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Dinosaurs and the island rule: The dwarfed dinosaurs from Haţeg Island

Michael J. Benton [a,*], Zoltan Csiki [b], Dan Grigorescu [b], Ragna Redelstorff [c], P. Martin Sander [d], Koen Stein [d], David B. Weishampel [e]

[a] Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK
[b] Department of Geology and Geophysics, University of Bucharest, Bd. N. Bălcescu 1, RO-010041 Bucharest, Romania
[c] School of Geological Sciences, University College Dublin, Belfield, Dublin 4, Ireland
[d] Institut für Palaontologie, Universität Bonn, Nussallee 8, 53115 Bonn, Germany
[e] Center for Functional Anatomy and Evolution, Johns Hopkins University—School of Medicine, 1830 East Monument St., Baltimore, MD 21205, USA

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ABSTRACT

Islands are fascinating natural laboratories of evolution. One much debated theme among evolutionary ecologists is whether there is an 'island rule', the observation that large animals tend to become smaller and small animals larger. Franz Nopcsa was the first, in 1914, to suggest that the latest Cretaceous dinosaurs from Haţeg, Romania were an island fauna, based on its low diversity and apparently unbalanced composition, and the basal position ("primitiveness") of many of the included taxa within their respective clades. In turn, the small size of the taxa compared to their relatives from other landmasses in conjunction with the proposed island setting were used to support the presence of the island rule and size reduction (dwarfing; nanism) among the Haţeg dinosaurs. In Nopcsa's day, palaeontologists had seen the same phenomenon many times in the Pliocene, Pleistocene, and Holocene mammals of the Mediterranean islands. Although often quoted as a key Mesozoic example of the island rule, the supposedly dwarfed Haţeg dinosaurs have never been investigated thoroughly. Here we review a wealth of new data, from tectonics and regional geology to limb proportions and dinosaur bone histology, which support Nopcsa's original claim of insularity of the Haţeg fauna. Current evolutionary studies confirm that the island rule applies in many, if not all, modern cases, as well as to the Mediterranean island mammals. Geological evidence confirms that Haţeg was probably an island in the Late Cretaceous, and phylogenetic, ecological, and bone histological evidence shows that at least two of the Haţeg dinosaurs, the sauropod *Magyarosaurus* and the ornithopod *Telmatosaurus*, as well as possibly the ornithopod *Zalmoxes*, were dwarfs by progenesis, a form of paedomorphosis.

1. Introduction

The Haţeg dinosaurian faunas from the latest Cretaceous of Romania have achieved widespread recognition as dwarfed island faunas. The suggestion was made first by Baron Franz Nopcsa (1877–1933) at a meeting in Vienna in November 1912 (published as Nopcsa, 1914b). Nopcsa (1914b) wrote that "while the turtles, crocodilians and similar animals of the Late Cretaceous reached their normal size, the dinosaurs almost always remain below their normal size." He observed that most of the Transylvanian dinosaurs hardly reached 4 m in length and, for the largest (what was to become *Magyarosaurus dacus*), it was a puny 6 m long compared to a more representative 15–20 m for other sauropods. During the discussion following his paper, Othenio Abel (1875–1945) agreed, and pointed to dwarfing of Mediterranean Pleistocene elephants, hippopotamus, and deer, as well as to island giantism among smaller animals. Nopcsa and Abel referred to earlier work by Forsyth Major (1843–1923) on Malta and the then-current discoveries by Dorothea Bate (1878–1951) on Cyprus and Crete.

The idea of dwarfing in the Haţeg dinosaurs has been suggested many times, on the basis of morphometrics (Weishampel et al., 1991, 1993, 2003; Jianu and Weishampel, 1999; Grigorescu, 2005), and yet additional testing is required. In sequence, these points must be established: the 'island rule' is confirmed from observations of modern and Pleistocene examples, the Haţeg fauna lived on an island, the dinosaurs (or some of them) are on average smaller than their nearest relatives from elsewhere, and the putative dwarfed dinosaurs really are small-sized adults, and not juveniles. We shall explore these points in this paper.

Museum abbreviations used in this paper are: BMNH, Natural History Museum, London; DFMMh, Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Germany; FGGUB, Facultatea de Geologie şi Geofizică, Universitatea Bucureşti, Bucharest, Romania; MAFI, Magyar Állami Földtani Intézet, Budapest (Hungarian Geological Survey, Budapest, Hungary).

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* Corresponding author. Tel.: +44 954 5400; fax: +44 925 3385.
E-mail address: mike.benton@bristol.ac.uk (M.J. Benton).

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2. Nopcsa's contribution, and later work in Romania

The famous story is told that in 1895 Nopcsa's younger sister Ilona discovered dinosaur bones at Sânpetru (or Szentpéterfalva) near the family estate at Săcel (also called Szacsal) in Transylvania, then part of the Austro-Hungarian Empire, now in western Romania. Nopcsa was enrolled at the University of Vienna and he undertook to study the fossilized bones. He advanced quickly in his studies, and at the age of twenty Nopcsa (1897) first reported dinosaur remains from Haţeg. He continued to do field work in the area, to collect new fossils, and to publish on them until the outbreak of the First World War. The family estate was seized by the Romanian government in 1920, and Nopcsa never came back, although he continued to publish on the Haţeg faunas until his untimely suicide.

Grigorescu (2005, this volume) outlined Nopcsa's key contributions to knowledge of the Haţeg fauna as:

(1) Systematic palaeontology. Nopcsa described nine species of dinosaurs and other fossil reptiles, of which six are still regarded as valid taxa.
(2) Chronostratigraphy and mapping. Nopcsa dated the Haţeg deposits as terminal Cretaceous in age, and he produced the first detailed geological map of the region. Through this work, he correlated several continental deposits in different neighbouring basins as the Sânpetru Formation.
(3) Evolution. Nopcsa recognized that most of the Haţeg taxa were primitive, and they showed, he felt, most similarity with Late Jurassic and Early Cretaceous forms from elsewhere.
(4) Palaeobiology. Nopcsa interpreted the apparently primitive nature of the Haţeg reptiles as a result of isolation on an island. He also noted that most of the Haţeg species were smaller than their relatives elsewhere, and he attributed this to the phenomenon of ‘island dwarfing’.

After Nopcsa's death, only limited work was done in the Haţeg area for the next seventy years. For example, studies of regional geology led to the discovery of some interesting bones (Mamulea, 1953a,b) and fossil plants (Mărgărit and Mărgărit, 1967), but also opened a controversy regarding the age of the continental deposits with dinosaur remains. Following Mamulea (1953a,b), a large part of Nopcsa's Danian deposits were assigned to different stages of the Palaeogene, and the dinosaur bones were interpreted as reworked from older beds. However, the latest Cretaceous age of the deposits from the western part of the Haţeg Basin and all of Nopcsa's list of fauna was confirmed by Dincă et al. (1972) who also adjusted this age to Maastrichtian, after the Danian became the first stage of the Palaeogene.

Grigorescu initiated systematic palaeontological searches after this long gap. From 1977 onwards, he organized summer camps every year for geology students whose main aims were to find ‘fossiliferous pockets’ and to excavate them. The first years were focused on the Sibisel valley, where Nopcsa's classic fossiliferous sites are located, and soon after the searches were extended to other areas of the basin. An important contribution to expanding the bone collection came from Ioan Groza of the Museum in Deva (capital of Hunedoara county, in which Haţeg is located); being closer to the fossiliferous deposits, Groza was able to continue the excavations during the autumn, after Grigorescu and his student team from Bucharest had left the camp. These excavations were supplemented by micropalaeontological studies, which led to a great increase in the number and variety of vertebrate taxa.

These field-based studies attracted more geologists and palaeontologists, from Romania and from overseas, and new studies were initiated in sedimentology, taphonomy, clay-mineralogy, stable isotopes, and palaeomagnetic analysis, all contributing to more accurate reconstructions of the Haţeg Basin palaeoenvironments. Among the new palaeontological discoveries dinosaur eggs (Grigorescu et al., 1990; Codrea et al., 2002), a wide range of microvertebrates (Grigorescu et al., 1999), including lissamphibians and squamates (Folie and Codrea, 2005), small theropods (Csiki and Grigorescu, 1998), pterosaurs (Jianu et al., 1997; Buffetaut et al., 2002), and mammals (Grigorescu et al., 1985; Csiki and Grigorescu, 2000) should be mentioned.

3. Size change on islands

3.1. Principles, and debate over validity of the island rule

Nopcsa's (1914b, 1923) proposal of insular dwarfing was not an original concept, and it derived from former and then-current discussions of the Pleistocene mammals of the Mediterranean islands (e.g., Forsyth Major, 1902; Bate, 1903, 1906). It is interesting then that modern reviews of the subject (e.g. Foster, 1964; Van Valen, 1973; Case, 1978; Lomolino, 1985; Damuth, 1993; Lomolino, 2005; Lomolino et al., 2006; Raia and Meiri, 2006; Welch, 2009) make little reference to these Victorian and early twentieth century publications by Forsyth Major, Bate, Nopcsa, and others on Pleistocene mammals and Cretaceous dinosaurs. The principle of size change in mammals on islands was established by Foster (1964), who noted that small taxa generally become larger and large animals smaller. This phenomenon was termed the *island rule* by Van Valen (1973), the commonest term, although it has been called ‘Foster's island rule’ (e.g., Palombo, 2007), or simply ‘Foster's rule’ (e.g., Welch, 2009). The island rule has been identified among mammals (Foster, 1964), birds (Clegg and Owens, 2002), and snakes (Boback and Guyer, 2003), but its occurrence in lizards and other groups is equivocal (Case, 1978; Lomolino, 2005). Meiri (2007) was clear that lizards do not follow the island rule, and indeed Meiri et al. (2004, 2006, 2008) have argued that there are so many exceptions that the term ‘island rule’ should be abandoned.

It is important to establish some aspects of terminology. We use the terms ‘dwarf’ and ‘giant’ to mean forms that are, respectively, smaller and larger than expected, in this case, smaller or larger than sister taxa, and than the mean size of members of the wider clade. There is no formal understanding of the degree to which a dwarf or giant differs from the norm, but in most modern cases, and indeed in the case of the Haţeg dinosaurs, they are often one half or one-third, or twice or three times, the ‘normal’ size. The phenomenon of small size on islands has been termed ‘island dwarfing’ or ‘insular dwarfism’, and other variants, whereas large size is often termed ‘gigantism’. Gould and MacFadden (2004) argued that the terms dwarf, dwarfing, dwarfism, and gigantism generally refer to medical abnormalities within species, and yet the terms have been widely extended to indicate size changes between races or species. They recommend the term *nanism* for phyletic size reduction and *giantism* for phyletic increase in size. We follow their use of ‘giantism’, but we continue to use the term ‘dwarfing’ because it is so widely used in the context of discussions of the island rule.

Foster (1964) reported the common occurrence of giantism among smaller island taxa (rodents) and dwarfing among others (lagomorphs, carnivores, artiodactyls), with mixed results indicated by the rather small samples of marsupials and insectivores. Case (1978) agreed broadly with these data, except for the carnivores: he suggests that these show a mixture of responses when a wider census of island taxa is taken. In his overview, Case (1978) found that lagomorphs, bats, artiodactyls, elephants, foxes, raccoons, snakes, and teiid and lacertid lizards often show reduced size on islands, whereas cricetid rodents, iguanid lizards, tortoises, and bears often show larger size on islands.

More recent comprehensive overviews have offered conflicting viewpoints, with Lomolino (1985, 2005) presenting a strong case for the island rule among mammals and other groups, and Meiri et al. (2004, 2006, 2008) expressing considerable uncertainty. In these studies, ‘islands’ are in the range from 1 to well over 100,000 km^2, so from tiny

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patches of land to islands no larger than Cuba (Lomolino 2005). Lomolino (1985, 2005) confirmed Foster's earlier findings (Table 1), with significant tendencies for small mammals (?lagomorphs, rodents) to become larger on islands (size ratio >1.00), and for large mammals (carnivores, artiodactyls) to become smaller (size ratio <1.00). Marsupials and insectivores showed no clear pattern, but mammals as a whole showed a highly significant correlation ($p<0.0001$).

When Meiri et al. (2008) re-analysed the data, they found significant support for the island rule in only limited cases: artiodactyls and carnivores (in particular herpestids and viverrids) tend to become smaller on island, and rodents (especially murids) tend to become larger, but there were no significant trends for other groups, nor for mammals as a whole. Meiri et al. (2008) also found that there was a substantial phylogenetic signal in all subsets of the data; such a signal could lead to pseudo-replication and apparently more significant correlations if, for example, several closely related taxa showed parallel responses. So, they argue, an apparently significant relationship could arise if rodents, say (rather than all small mammals) become larger on islands whereas artiodactyls (but not all large mammals) become smaller. When the phylogenetic signal is removed (Table 1, last two columns), surprisingly the all-mammal sample shows a significant (but weak) negative relationship, but the constituent clades do not. So, overall, after phylogenetic correction, it remains true, as Foster (1964) had said, that small mammals tend to become larger, and large mammals smaller on islands. Meiri et al. (2008) argued that this weak relationship could rest entirely on those clades that do show size changes in line with the island rule: giantism in murid rodents, and dwarfing in artiodactyls, heteromyids, and some carnivores.

Why did two analyses of essentially the same data set lead to such opposite interpretations? First, both authors were assessing different proposals, or null models, as Welch (2009) pointed out:

(1) Lomolino (1985, 2005) and others were testing whether or not there is a size difference between pairs of island and mainland species, with assumptions that size changes on islands do not depend on the ancestral state, and that the mainland relatives remain close to the ancestral state.
(2) Meiri et al. (2008) were testing whether there is a heritable tendency to change body size in a particular way after island colonization, assuming that this tendency evolves independently of current body size.

Both models may lead to biased results. In the first, any size evolution of the mainland population could suggest that the island population has changed in size, when it need not have. Further, the use of a regression as the basis of the test (Lomolino, 1985, 2005) may be inappropriate because this is a parametric approach and assumes equal variances for all data points, which is unlikely, not least because the island colonizations are scattered widely through time and so each pair-wise comparison involves different amounts of evolutionary change (Welch, 2009). A nonparametric test would be more appropriate (Meiri et al., 2004; Bromham and Cardillo, 2007). The second test is also problematic: Meiri et al. (2008) argued that previous studies involved pseudo-replication because phylogeny was not taken into account. However, this is only a requirement in the context of null model (2), and is not true of null model (1), in which no example of body size evolution was counted more than once because all island–mainland pairs of taxa were phylogenetically independent. Welch (2009) showed that many tests used so far in the context of model (1) may falsely detect the island rule when island and mainland evolution are indistinguishable. Further, tests that account for phylogeny in the context of model (2) may lack power to detect the island rule under certain conditions. In his study of primate data, Welch (2009) found, frustratingly, that the island rule held for some measures of body size (skull length; body mass), but not for others (head–body length).

Table 1
Results from a census of 365 island races, subspecies, or species of mammals, from Lomolino (1985, 2005) and Meiri et al. (2008). Size ratio is the sum of insular weights divided by mainland weights for each group, and slope is based on a regression of island/ mainland comparisons for all 71 species (365 subspecies/races), where slopes less than one indicate a trend from giantism in the smaller species to dwarfing in the larger species. The *t*-test assesses whether the distribution of size ratios is significantly different from one; * significant difference from ratio of 1.00, at $p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$; [1] from Lomolino (1985); [2] from Meiri et al. (2008), non-phylogenetic values for whole sample (marsupial data for Diprotodontia only).

	Smaller	Same	Larger	Size ratio[1]	Slope[1]	Size ratio[2]	*t* test[2]
All mammals	131	44	190	1.01^{***}	0.95^{***}	1.00	-2.98^{**}
Marsupials	3	0	5	1.08	0.88^{***}	[1.07]	[0.77]
Insectivores	15	8	15	1.07	1.01	1.00	−1.05
Lagomorphs	12	3	5	1.03^{*}	0.81^{**}	1.03	−1.73
Rodents	53	26	151	1.10^{**}	0.91^{***}	1.08	−1.09
Chiroptera	–	–	–	–	–	0.99	0.77
Primates	–	–	–	–	–	0.92	−0.72
Scandentia	–	–	–	–	–	0.94	−0.62
Carnivores	33	7	14	0.90^{*}	0.88^{**}	0.94	1.14
Artiodactyls	15	0	0	0.71^{**}	0.84^{*}	0.88	−1.66

The debate continues, and yet it seems there will not be a clear-cut demonstration of the ubiquity of the island rule for large sets of examples. All seem to agree that certain clades of mammals, for example, show giantism or dwarfing, and so for those clades at least the island rule holds. The problem may lie in the term ‘rule’, which some might interpret to mean a regular law-like principle that always applies, whereas others might see a ‘rule’ as something that happens in many cases, but may be overwhelmed by other processes as well. In the latter ‘soft’ interpretation, the island rule is a useful generalization, analogous to others in biology, such as Cope's rule, the observation of a trend to larger body size, or Dollo's law or rule, that evolution is not reversible.

3.2. Hypotheses for size change on islands

There have been many explanations for the island rule, and these seek to explain either why large animals become smaller, why small animals become larger, why both relative size changes occur, and sometimes why the rule seems to be best expressed in warm-blooded animals such as mammals and birds.

Several of the hypotheses have been rejected, whether outright, or partially, and these are listed first.

(1) The *relict population* viewpoint (Hinton, 1926; Cowan, 1935) is that giant rodents on islands may be relicts of once more widespread populations. Tougher selection on the mainland perhaps led to the extinction of the majority of the larger species or morph, leaving only relict population on islands. Foster (1964) rejected the relict population model using several arguments: there are differences among the island giant forms of rodents (relicts of a formerly more widespread population ought to be more similar), there is limited evidence that the smaller mice had displaced the putative larger mainland forms, the size changes may be seen in many unrelated mammals, birds and lizards, and it is not clear that the large size of insular rodents is a conservative character.
(2) A further suggestion is that *reduced prey size on islands* could induce dwarfing among predators. This idea stems from the observation of a general correlation between predator and prey size. With few competitors, small-sized prey is abundant, and predators therefore might scale down in size in order to exploit it. Case (1978) rejected this idea because of limited evidence that island giants or island dwarfs are matched by either giant or dwarfed prey. Further, this hypothesis cannot explain the

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dwarfing of herbivores because they do not match their size to the size of the plants they eat.

(3) *Sexual selection* on islands could foster increases in body size where other selective pressures present on the mainland have been removed (Carlquist, 1965). This might be a contributing factor for some mammals, where sexual selection favours large size, but clear examples have not been demonstrated.

(4) Island dwellers might show a tendency to move towards an *optimal body size* (Brown et al., 1993; Damuth, 1993; Lomolino, 2005; Palombo, 2007) when competition and other pressures are relaxed. This optimum is the size at which energy capture from the environment is maximized, and for mammals this might be 0.1 kg (Brown et al., 1993) or 1 kg (Damuth, 1993). Meiri et al. (2004) found less predictable results among carnivores than had been expected, and they were concerned that the predictions of optimal body size for mammals varied so much. Further, Raia and Meiri (2006) showed that related island species tend to different body sizes depending on local conditions, and so there is no tendency towards a single optimal body size. This is part of the wider observation that the body mass of the largest animals in a region depends on the maximum area available, which relates to the size of the required home range, which in turn reflects food requirements (Burness et al., 2001).

(5) Some examples of giantism may stem from *selection of immigrants for large size* (Lomolino, 2005). The idea is that, in some cases, immigrants swam to the islands they colonize, and so the larger and stronger animals could swim farther, or more successfully, based on size-related metabolic demand (Roth, 1992). The founding population then might consist of larger species, at least in the early stages of colonization. A criticism is that this might apply in some cases, but not all, and in any case would be hard to demonstrate.

Among the hypotheses for the island rule that still have currency are ecological release, niche expansion, resource limitation, and optimization of life-history traits.

(1) *Ecological release* has been a key suggestion, that island species are freed from normal pressures from competitors, predators, and parasites on the mainland, and so may change body size as a result (Foster, 1964; Carlquist, 1965; Van Valen, 1973; Azzaroli, 1982; Lomolino, 1985, 2005; Raia and Meiri, 2006). Islands typically have fewer species than equivalent mainlands, an example of the species-area effect (Williams, 1943; Connor and McCoy 1979). Those species that on the mainland are typically present at low abundance, such as large herbivores and top predators, are the most likely to be absent from an island, but this depends on dispersal ability (so dear and proboscidenas are good island colonizers). Absence of larger mammals or birds means there is generally less competition for food and shelter, and less predation, and tiny, furtive mammals can become larger and bolder. Birds on islands often become flightless perhaps for the same reasons, as well as to conserve energy (McNab, 1994). For large animals that become smaller on islands, the absence of predators removes one of the benefits of large size (escaping predation by being big), and so animals can become smaller without risking being picked off from the herd by a predator (Van Valen, 1973; Lomolino 1985). In their study of Pleistocene and modern mammals, Raia and Meiri (2006) found strong evidence for size decreases among island herbivores in the absence of competitors and predators.

(2) A linked explanation may be *niche expansion* (Grant, 1965; Van Valen, 1973; Heaney, 1978), where the lower numbers of species on islands open possibilities for the expansion of normal niches to take in new diets and opportunities. So, animals constrained to small size on the mainland can allow their overall size range to expand, and in certain cases take over the roles of absent middle-sized animals.

(3) *Resource limitation* on islands has often been suggested (Foster, 1964; Case, 1978; Lomolino, 1985; Burness et al., 2001; Lomolino, 2005; Raia and Meiri, 2006) as a selective pressure on larger mammals and birds. Large herbivores, such as elephants, rhinoceroses, deer, or cattle often require large foraging areas, and they may traverse hundreds or thousands of kilometres in order to find appropriate food supplies at different seasons of the year. Such long treks are impossible on islands, and so a large herbivore might either become reduced in size so as to accommodate itself to the size of the island, or go extinct. Raia and Meiri (2006) found that body sizes of island carnivores are influenced by resource limitation, and little else.

(4) Other models suggest that size changes depend on *optimization of life-history traits* such as metabolic rate, gestation time, size at birth, age and size at maturity, birth and death rates, trophic level, home range size, and population density (Palkovacs, 2003; Palombo, 2007). It is likely that in certain cases, r-selected animals, through their earlier sexual maturity, and hence smaller size, could simply make better island colonizers. Island mammals then change their size according to their *Bauplan*, the most appropriate empty niches, and presence or absence of potential competitors or predators. This relates to views expressed by Case (1978), Meiri et al. (2004, 2006) and others, that size change may be contingent on circumstances, and so regular predictable patterns of the island rule may not always be found.

In summary, Lomolino (2005) argued that dwarfing on islands may be maintained by ecological release from predators, resource limitation, and escape from parasites, whereas giantism on islands may be promoted by ecological release from large competitors and predators and immigrant selection (Fig. 1). In both cases, intensified natural selection promotes the directional shifts in mean body size.

3.3. Dwarfing in Pleistocene and Holocene mammals

Island faunas of mammals, most studied from the Pliocene, Pleistocene, and Holocene of the Mediterranean islands (Boekschoten and Sondaar, 1966; Azzaroli, 1982; Lister, 1996; Marra, 2005; Raia and Meiri, 2006; De Vos et al., 2007; Palombo, 2007, 2008), show low diversity. The Pleistocene mammalian faunas of Mallorca and Menorca include only three genera of mammals, the bovid *Myotragus*, the glirid rodent *Hypnomys*, and the shrew *Nesiotites*. The faunas of the same age

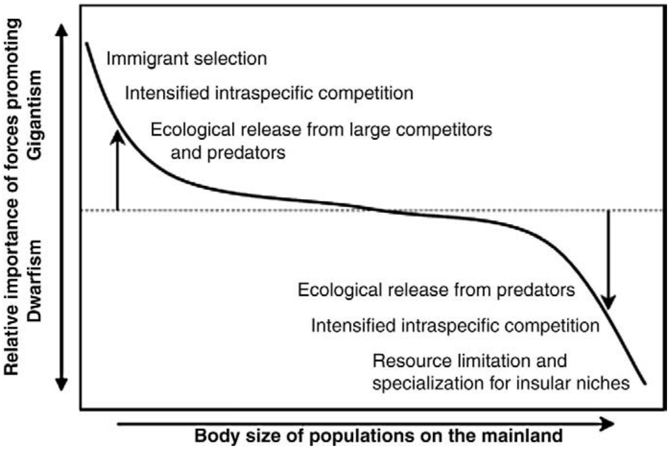

Fig. 1. The island rule is an emergent pattern resulting from a combination of selective pressures whose importance and influence on insular populations change in a predictable manner along a gradient from relatively small to relatively large species. Based on Lomolino, 2005.

from Malta include pigmy elephants, pigmy hippo, pigmy deer, and the giant dormouse *Leithia*. Sicily shows a similar fauna, and other Mediterranean islands, including Cyprus, Corsica, Capri, and many Aegean islands yield similarly depauperate faunas.

Two larger Mediterranean islands, Crete and Sardinia, have yielded slightly more diverse mammalian faunas. Crete was populated by pigmy elephant, pigmy hippo, and pigmy deer, as well as two genera of giant rodents and giant insectivores. The Pleistocene faunas of Sardinia were most diverse of all, but still less so than those of the mainland, with pigmy elephant, pigmy hippo, and pigmy deer, as well as large rodents and shrews, as on the other islands. In addition, Sardinia was populated by moles, rabbits (*Prolagus*), carnivores (the dog *Cynotherium* and the weasel *Enhydrictis*), a pig, and a macaque.

Islands elsewhere show similar patterns. The late-surviving dwarf mammoths of Wrangel Island, lying offshore from the north of Russia, are well known, but there were some even smaller, and younger, mammoths on islands in the North Pacific that existed 7900 years ago. These tiny mammoths became larger and smaller as sea level fell and rose, suggesting a direct connection between body size and resource use (Guthrie, 2004). In a further example, the Greater Antilles in the Caribbean were home to dwarfed ground sloths. The Pleistocene of the Channel Islands off the California coast (Johnson, 1978) has yielded specimens of dwarfed elephant (*Mammuthus*) and over-sized species of the rodent *Peromyscus*. Low diversity of dwarfs and giants are seen on larger islands, such as Java and Borneo, where pigmy elephants and large rodents are known from the Pleistocene, and the pigmy buffalo *Bubalus depressicornis* survives today in Sulawesi (e.g. De Vos et al., 2007). The pigmy human species, *Homo floresiensis* from Flores Island, Indonesia, is a remarkable example of possible Pleistocene dwarfing of humans on an island (Bromham and Cardillo, 2007). Madagascar, an even larger island, still had less diverse faunas than in neighbouring parts of Africa, and these included in the Pleistocene and Holocene giant lemurs, giant insectivores, a pigmy hippo, and the giant flightless bird *Aepyornis* (Tyson, 2000).

Size may reduce in line with the expectations of allometry. Azzarolli (1982) showed an example of *Megaceros giganticus*, the great Irish deer, up to 2.1 m tall at the shoulder. The smaller species *M. algarensis* from Sardinia is 0.8–1 m at the shoulder, while the tiny *M. cretensis* from Crete is 55–65 cm at the shoulder (Fig. 2). In tracking back through these dwarfs, the antlers become smaller and simplify in a negatively allometric manner. So the smallest deer has relatively tiny and simple antlers with only a couple of points, and barely as long as the skull, whereas *M. giganteus* has antlers with up to ten points and four times the length of the skull. The middle-sized *M. algarensis* shows intermediate antlers, three times the length of the skull and with four or five points. Other deer show similar negative allometry in the reduction of limb length: a dwarf deer from Pianosa in the Tyrrhenian Sea has relatively short legs in comparison to its full-sized relatives.

Pleistocene island mammals are generally said to show paedomorphosis. Size reduction through dwarfing implies a process of heterochrony, or size change during development, and in particular paedomorphosis (retention of juvenile conditions in the adult). Paedomorphosis can occur by one of three processes: an overall reduced rate of development (neoteny), a postponed onset of development (post-displacement), or achievement of sexual maturity early (progenesis). The first two can lead to adults of the same size as the unaffected relatives, whereas progenesis usually leads to adults of reduced size (Gould, 1977; Alberch et al., 1979). Indeed, selection for small body size is likely the driver, and morphological change through progenesis the consequence.

In their study of the dwarfed elephant *Elephas falconeri* (Fig. 3) on Sicily, Raia et al. (2003) argued for paedomorphosis by progenesis. They also presented an ecological model based on the preponderance of juveniles, nearly 60% of the 104 specimens studied. From this they argued that food supplies were good for such a small elephant (weighing 100 kg rather than 5 tonnes), and that reproductive rates may have increased, but that calf mortality was also high — together a rather more r-selected strategy than seen in modern elephants. Perhaps this was a response to a highly seasonal environment, as experienced by elephants today, but without the space to migrate when climate and food supply become harsh. Their measurements of tibiae suggest (Fig. 4) distinct size classes and highest numbers of the smallest size category. This they interpret as evidence that *E. falconeri* bred at discrete times of the year, instead of all year round as modern elephants do, and that juvenile mortality was high perhaps during seasonal droughts.

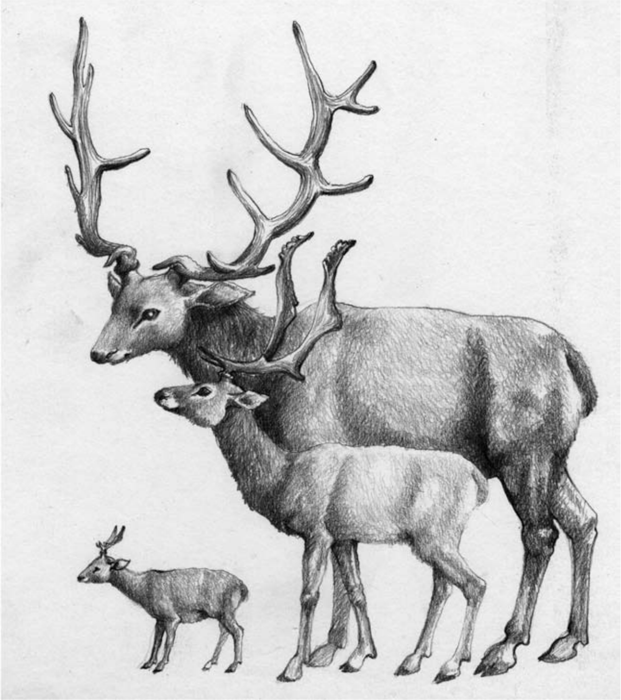

Fig. 2. Artist's reconstruction of the dwarfed Mediterranean island deer from the Pleistocene, *Megaceros cretensis* from Crete (shoulder height 55–65 cm) and *Megaceros algarensis* from Sardinia (shoulder height 80–100 cm), compared to their presumed ancestor *Megaceros verticornis* from continental Europe. Drawing by Cristina Andreani.

In other cases, the dwarfed mammals have become adapted morphologically to their new size and changed habits. The pigmy *Hippopotamus creutzburgi* from the late Pleistocene Crete has longer legs than its larger relatives from Africa, presumably an adaptation to getting around on a rugged island where there were no large rivers or lakes (Boekschoten and Sondaar, 1966). The bovid *Myotragus balearicus* from the Balearic Islands has evolved modified teeth and eyes: the lower incisors are reduced to one pair and these grow continuously, as in rodents, and the orbits have shifted forward to give the animal improved stereoscopic vision. Further, as the animal became dwarfed, its limbs became relatively very short and stocky, and these changes may all be followed through successions of fossils through the Pliocene, Pleistocene and Holocene (Moyà-Solà and Pons-Moyà, 1980). All these changes suited the unusual *Myotragus* to a life in rugged, hilly terrain, leaping from rock to rock (need for stereoscopic vision), and without fear of predators (less need for lateral vision).

Studies of dwarfed Pleistocene and Holocene mammals have shown peculiar anatomical features. For example, Azzarolli (1982) noted that dwarfed mammals often retain over-sized dentition because the teeth sometimes do not reduce in proportion to the rest of the body or skull, and he noted as an example a small macaque from Sardinia in which the cheek teeth are relatively large in comparison to those of related species of normal size.

Two well-known 'fossil islands' are southern Calabria and the Gargano promontory (Azzarolli, 1982; De Vos et al., 2007), the toe and

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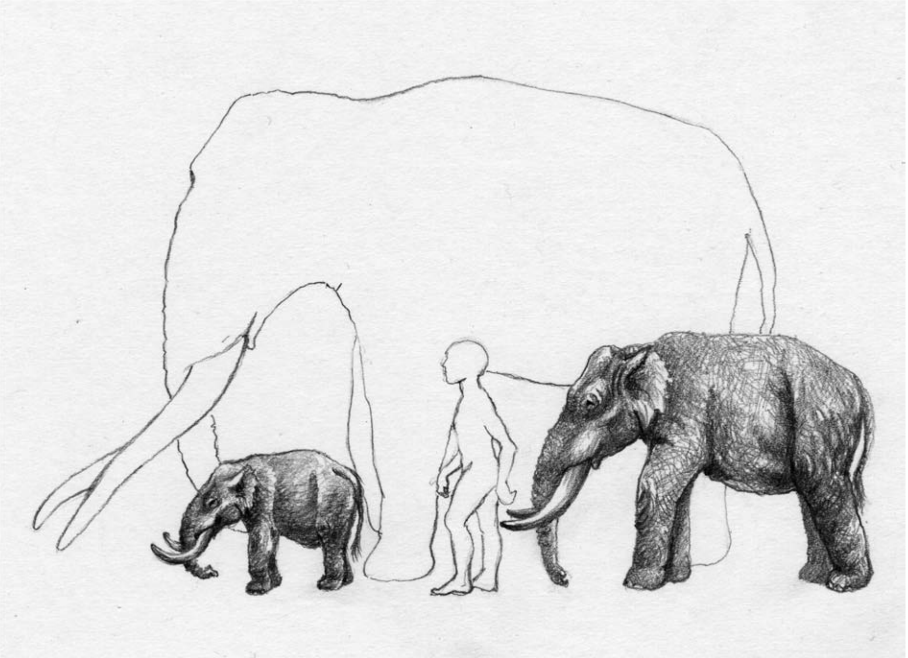

Fig. 3. Artist's reconstruction of the extinct dwarf elephant, *Elephas falconeri* (left), from the late Pleistocene of Sicily and Malta (height at shoulder, 0.9–1.0 m), *Elephas mnaidriensis* (right) from the middle and late Pleistocene of Sicily and Malta (height at shoulder, 1.6–1.8 m), and *Elephas antiquus* (behind) from the middle and late Pleistocene of continental Europe, the supposed ancestor of the two dwarfed forms (height at shoulder, 3.0–3.5 m). Drawing by Cristina Andreani.

heel of the boot of Italy, which were surrounded by seawater when sea levels were higher before the Pleistocene ice ages began. The southern Calabrian island was home to a small elephant and a small deer, *Megaceros*, in the Pleistocene. The Gargano island in the Miocene was populated by the gigantic hedgehog *Deinoglaerix* and large mice, among other mammals, and these were preyed on by giant owl, *Tyto gigantea*, and a giant eagle, *Garganoaetus freudenthali*, which were twice the size of their nearest relatives.

The ages of the various islands in the Mediterranean may be determined with some precision, and so the likely rates of size change among the mammals and birds may be estimated. Mammals in particular can have reached the various islands only when the sea retreated and left a land bridge. Likely dates when the endemic faunas reached the islands are: Sardinia (0.9–1.0 Ma), Crete (0.7 Ma) Sicily (0.4 or 0.23 Ma). The dwarfs and giants largely became extinct from the end of the Pleistocene and beginning of the Holocene (0.01 Ma), so dwarfing or giant size must have happened in hundreds of thousands of years (Azzarolli, 1982; Guthrie, 2004; De Vos et al., 2007); indeed, fast morphological evolution of mammal faunas seems to be a common phenomenon (Millien, 2006).

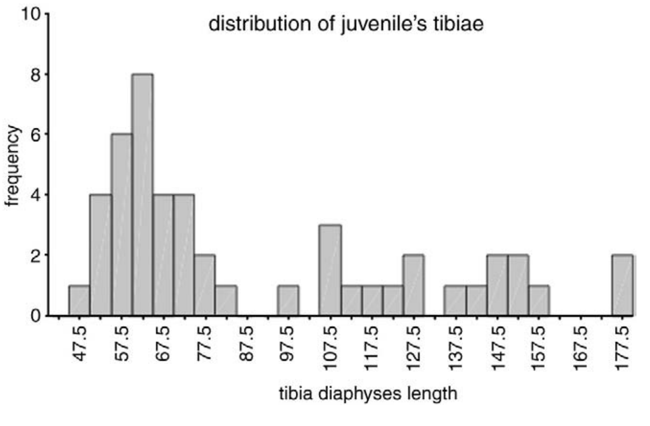

Fig. 4. Frequency histogram of tibia lengths in a sample of 104 specimens of *Elephas falconeri*, the island dwarf form from Sicily, showing the occurrence of three size classes, and highest numbers in the most juvenile. This is possible evidence of year classes and seasonal breeding and/ or seasonal mortality.
From Raia et al., 2003.

Advantages of dwarfing for elephants and other large taxa on islands might include the reduction in food requirement and so of the time spent searching for and processing food, and the reduction in size of home range and so of competition with other populations (Palombo, 2007). Size reduction among Mediterranean island elephants was achieved by paedomorphosic processes, and probably a shorter period of pregnancy (Palombo, 2007). Life cycles may have been generally shortened and fecundity increased, both features associated with size reduction.

4. Was Haţeg an island?

Nopcsa (1914b, 1923) was the first to suggest that the Haţeg dinosaurs lived on an island, but his reasoning was that the animals had undergone island dwarfism and so must have lived on an island. Further, in his dissertation on the geology of the Haţeg region, Nopcsa (1905) included discussion of geological evidence for insularity, but little further independent geological evidence was adduced until late in the twentieth century (Grigorescu, 2005).

Modern tectonic and palaeogeographic studies (Săndulescu 1990; Dercourt et al., 1993, 2000; Csontos and Vörös, 2004) have shown an archipelago of islands over much of southern Europe in the Late Cretaceous (Fig. 5). The Haţeg Island has been estimated to have had an area varying from 7500[1] to as much as 200,000 km^2 (based on Dercourt et al., 1993, 2000). Obviously, the Haţeg Island was more extensive than the Haţeg Basin itself, and included the Transylvanian Basin and surrounding areas with preserved Maastrichtian continental deposits (Codrea and Dica, 2005; Codrea and Godefroit, 2008) as well as uplifted segments of the Carpathian chain with no net deposition (e.g., Bojar et al., 1998; Willingshofer et al., 2001). According to this, more reliable estimates show an area of

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[1] Weishampel et al. (1991) gave a figure for the area of the island of 7500 km^2, but this was an error (DBW) and represents the strict size of the Haţeg Basin today, some 45 km long (E–W) and 15 km wide (N–S), rather than island area.

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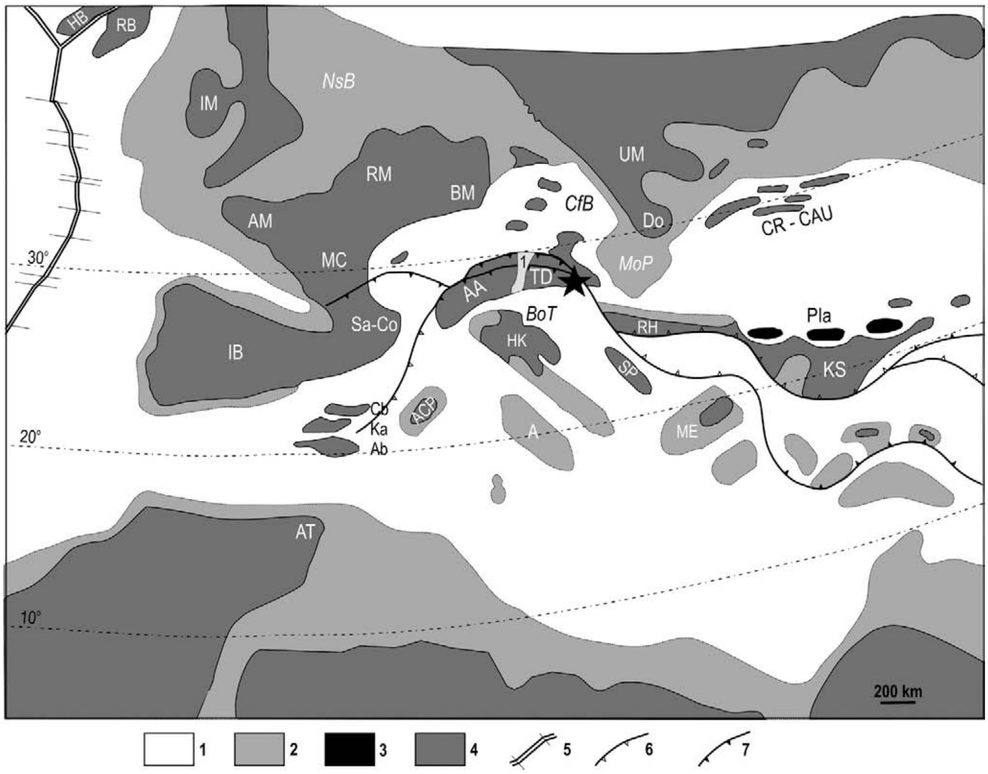

Fig. 5. Palaeogeographic map of the Mediterranean sector of Tethys during the Maastrichtian, showing the location of Haţeg (after Camoin et al., 1993). Palaeolatitude revised based on Panaiotu and Panaiotu (this issue). Abbreviations: A, Apulia; AA, Austro-Alpine Domain; Ab, Alboran Block; ACP, Apennine Carbonate Platform; AM, Armorican Massif; AT, Atlas; BM, Bohemian Massif; BoT, Bosnian Trough; Cb, Calabrian Block; CfB, Carpathian Flysch Basin; CR–CAU, Crimea–Caucasus; Do, Dobrogea; HB, Hatton Bank; HK, High Karst (Dinaric Carbonate Platform); IB, Iberia; IM, Irish Massif; Ka, Kabylia; KS, Kirshehir; MC, Massif Central; ME, Menderes; MoP, Moesian Platform; NsB, North Sea Basin; Pla, Pontides Island arc; RB, Rockall Bank; RH, Rhodope Massif; RM, Rhenish Massif; Sa–Co, Sardinian–Corsican Block; SP, Serbo–Pelagonian Massif; TD, Tisia–Dacia Block (the position of "Haţeg Island" is marked by a black star); UM, Ukrainian Massif; 1, the western boundary of Tisia–Dacia, as marked by the Maramureş–Szolnok Trough and the Mid-Hungarian Line. Legend: 1, deep-marine basins (pelagic carbonates, flysch); 2, shallow-marine basins (mainly siliciclastic and carbonate shelf deposits); 3, island arc; 4, emergent land; 5, active speading ridge; 6, thrust; 7, subduction.

approximately 80,000 km^2, corresponding to an island of about the size of Hispaniola (Csiki, 2005). Palaeogeographic reconstructions also suggest that the Haţeg Island was located at least some 200–300 km from the nearest landmasses in all directions, the Franco-Iberian land to the west, the Bohemian Massif to the northwest, and the Balkan–Rhodope Massif to the southeast; probably the closest continental areas were the emerged segments of the ALCAPA block (Austro-Alpine domain) to the west and those of the Adriatic–Dinaric Carbonate Platform to the south. The surrounding marine areas were represented by mainly deep-marine basins with flysch sedimentation, eventually passing into shallower epicontinental seas covering the nearby Moesian and East-European platforms (e g. Săndulescu, 1984, 1990; Pamic, 1998; Willingshofer et al., 1999). Based on palaeomagnetic studies, Haţeg lay at a latitude of about 27°N (Grigorescu, 2005; Panaiotu and Panaiotu, this issue), so just within the equatorial belt.

Jianu and Boekschoten (1999) suggested that Haţeg had not been an island based on tectonic, sedimentological, and palaeontological evidence. They argued that some palaeogeographic reconstructions show continuity from the proto-Carpathians to other European landmasses, and that the alluvial sediments on Haţeg are too extensive and too thick (up to 2.5 km thick) to have been deposited on an isolated volcanic island. Such a thickness of sediment points rather to a large-scale subsiding basin as part of a mainland. Finally, with dozens of species, the fauna would have been much too diverse, especially for an island only 7500 km^2 in dimensions. Jianu and Boekschoten (1999) then preferred to regard Haţeg as an outpost, a remote tip of the mainland, rather than an island.

However, when considering the larger dimensions of the island, as outlined above, most of the arguments presented by Jianu and Boekschoten (1999) are significantly weakened. The emergent area of Haţeg was only part of a larger tectonic block with continental crust (the Tisia–Dacia Block; Săndulescu, 1990; Sanders, 1998; Csontos and Vörös, 2004) assembled during the late Early to latest Cretaceous orogenic phases affecting the Carpathian areas (Willingshofer, 2000; Willingshofer et al., 2001). Large parts of this block were actively uplifting during the latest Cretaceous, synchronously with the deposition of the Sânpetru and Densuş–Ciula formations (Bojar et al., 1998; Willingshofer, 2000) and this coincidence between strong uplift, marked subsidence within an extensional basin and subtropical, seasonally variable climate represents probably the explanation for the deposition of thick sequences of continental deposits. The estimated size of the emergent Haţeg area was also probably large enough to support a relatively diverse palaeofauna. Palaeogeographic evidence still strongly indicates the existence of an archipelago of islands bordering the northern margin of Tethys. Although, admittedly, the changing palaeogeography of this archipelago was influenced by tectonic events such as extension within oceanic basins, continental convergence and collision, as well as eustatic sea-level changes (see e.g. Dercourt et al., 2000), possibly leading to formation of occasional land bridges or shallow-marine dispersal corridors to the European mainland or other emergent landmasses of southern Europe, the presence of a larger Haţeg Island seems relatively well supported.

A final question should address how long the Haţeg Island existed. Evolving within the dynamic framework of the Mediterranean Sill (Dercourt et al., 2000), besides the continuously changing geographic extent of the Haţeg Island, its evolution was circumscribed by its duration. It is noteworthy, that an emergent landmass corresponding to the position of the Haţeg Island can be followed continuously from

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the latest Early Cretaceous onward on the palaeogeographic maps of Dercourt et al. (1993, 2000).

As noted above, coalescence of former continental blocks (pre-Apulian, Rhodope — in the area of modern Greece and the Aegean) to form the Tisia–Dacia Block took place during the late Early to earliest Late Cretaceous (Săndulescu, 1984; Sanders, 1998; Willingshofer et al., 1999; Willingshofer, 2000), and during this time there are continental sediments in the Haţeg area (Stilla, 1985; Grigorescu, 1992) and other Carpathian areas (Grigorescu, 1992). The presence of an earliest Late Cretaceous emergent area can thus be suggested, representing the earliest identifiable occurrence of the Haţeg Island.

Subsequent collisional events during the late Turonian (pre-Gosau or Subhercynian tectogenetic phase) was followed by enlargement of the continental area, and deposition of continental or littoral deposits in several areas of the Apuseni Mountains and Southern Carpathians during the Coniacian and Santonian (Dragoş, 1971; Petrescu and Huică, 1972). Tree trunks found in marine deposits of Campanian age in southwestern Transylvania (Iamandei et al., 2005) also suggest the proximity of emergent areas. Nopcsa (1902) reported an isolated theropod tooth from Coniacian to early Santonian littoral deposits (Csiki and Grigorescu, 1998) of the Borod Basin, northern Apuseni Mountains, northwestern Romania, as '*Megalosaurus hungaricus*' (now a nomen nudum, as the specimen lacks diagnostic characters, and in any case seems to be lost from the MAFI collections, Budapest). This theropod tooth suggests that colonization of the Haţeg Island had already occurred by the Coniacian.

Based on this evidence, the continuity of an emergent landmass can be suggested from the Cenomanian to the Maastrichtian, this landmass occupying more or less the same area as the larger surroundings of the present-day Haţeg Basin.

5. Sedimentary setting, palaeoclimate, and fauna

While Nopcsa (1914a) interpreted the Haţeg deposits as fluvial–lacustrine, but representing mainly lakes and swamps subject to periodic inundations, more recent work (e.g. Grigorescu, 1983; Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005, 2006; Therrien et al., 2009) has identified a wider range of sedimentary settings. Further, the stratigraphy has been clarified since Nopcsa's day. There are two Maastrichtian successions, the Densuş–Ciula and Sânpetru formations, both representing molasse-type deposits (Grigorescu, 1992); whether these include also the lower Palaeogene is yet to be substantiated. The Densuş–Ciula Formation occurs in the northwestern part of the Haţeg Basin, and it has a total thickness of some 4 km. The Sânpetru Formation crops out mainly along the Râul Mare and Sibisel valleys, and it is up to 2.5 km thick.

The Densuş–Ciula Formation is divided into three members. The lower member consists of volcano–sedimentary sequences interlayered with lacustrine marls. The thick middle portion consists of matrix-supported conglomerates, massive and cross-bedded sandstones, and massive red, brown, and green–grey mudstones. These deposits have yielded diverse microvertebrates (Grigorescu et al., 1999; Csiki et al., 2008) including multituberculates (Csiki and Grigorescu, 2000), dinosaur bones and eggs (Grigorescu et al., 1990), as well as mollusc shells and plants (Antonescu et al., 1983). The upper part of the formation, possibly Palaeogene in age, lacks volcaniclastic sediments and dinosaur remains.

The Sânpetru Formation is almost devoid of volcaniclastic sediments, but dinosaur and other vertebrate bones are common at certain levels. The sedimentology is primarily alluvial, including coarse, unsorted debris flows, channels, and overbank deposits (Grigorescu, 1992). Stream types were mainly braided, yielding gravel and sandy channel infills, gravel and sandy bars, sandy and silty levees and crevasse splays, and silty and clayey overbank deposits. Meandering streams are rarer, in association with well-drained and poorly drained floodplain deposits, the first associated with calcrete palaeosols, and the second with hydromorphic palaeosols (Therrien, 2005). Vertebrate fossils are found mainly in the lower part of the Sânpetru Formation, and their rarity in the upper part of the formation led some previous workers to mistakenly place the Cretaceous–Tertiary boundary at the transition between the lower and upper Sânpetru Formation (Therrien, 2006). In the upper Sânpetru Formation, the sediments indicate an episode of rapid uplift of the sediment source area and the creation of extensive wetlands, not conducive to preservation of large-scale bone accumulations (Therrien et al., 2009; Csiki et al., this issue).

Climates were subtropical, with rainy and dry seasons, as indicated by study of palaeosols (Van Itterbeeck et al., 2004; Therrien, 2005), the mixed floras of ferns and *Normapolles–Postnormapolles* angiosperms (Antonescu et al., 1983), and stable isotopes. Carbon isotopes indicate 'dry woodland' conditions (Bojar et al., 2005), and oxygen isotopes suggest a mean annual temperature of about 20–25 °C. Rainfall estimates differ between evidence from plants and from palaeosols. The palaeosols indicate a climate characterized by seasonal precipitation in which evapotranspiration exceeded precipitation, and where the water table fluctuated during the year (Therrien, 2005). Geochemistry of the palaeosols indicates that palaeoprecipitation was less than 1000 mm/year, significantly lower than estimates from the tropical palaeoflora of the region (1300–2500 mm/year — Pop and Petrescu, 1983). The difference in estimates may be explained by the fact that tropical plants can live in warm, monsoonal climates if they have access to sufficient water during the dry seasons to satisfy their metabolic needs, and so the palaeobotanical value was perhaps an overestimate (Therrien, 2005).

Over 70 vertebrate taxa make up the Haţeg faunal assemblage, divided into aquatic (rare fishes), semi-aquatic (frogs, albanerpetontids, turtles, crocodilians), aerial (pterosaurs, birds), and terrestrial (lizards, snakes, dinosaurs, mammals) forms (e.g. Grigorescu et al., 1985; Weishampel et al., 1991; Grigorescu et al., 1999Folie and Codrea, 2005; Grigorescu, 2005; Therrien, 2005). The fauna shows general connections with the Euramerican fauna of the Early Cretaceous (Weishampel et al., this issue). Intermittent connections with surrounding landmasses were probably established during low sea levels, and species may have passed between the Ibero-Armorican landmass and Haţeg, as suggested for the second part of the Campanian by Csiki and Grigorescu (1998).

6. Dwarfed dinosaurs on islands

6.1. Background

The large size of dinosaurs has posed intriguing questions about their growth rates: did they have low metabolic rates and take decades or centuries to reach adult size, or did they have high metabolic rates and growth to full size very fast? Current work on bone histology suggests the latter (Horner et al., 1999; Sander, 2000; Erickson et al., 2001; Padian et al., 2001), and that growth followed a sigmoid curve, with a relatively slow growth rate in their first 1–5 years, an accelerated rate for 2–6 years, and then a levelling-off when sexual maturity and adult size were attained. Sexual maturity might have been achieved at 40–70% adult size in sauropods (Sander, 2000). Estimates of the time to achieve maximum size for the largest dinosaurs range from ten (Erickson et al., 2001) to 26 (Sander, 2000) years, and the lower estimate would imply maximum growth rates of more than 5 tonnes per year during the juvenile growth spurt. Estimates of how long dinosaurs lived include 8–18 years and 13–14 years for the medium-sized theropods *Oviraptor* and *Deinonychus* (Erickson et al., 2007), up to 28 years for *Tyrannosaurus* (Erickson et al., 2004), and 38 years for the sauropod *Janenschia* (Sander, 2000). The estimates of age are made by counting lines of arrested growth (LAGs, sometimes called 'growth lines') that are best seen in fibrolamellar primary bone, indicating fast growth. As growth slowed in adult individuals, lamellar-zonal bone was laid down in the outer

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cortex, followed by denser bone with narrowly spaced LAGs in the outermost cortex.

An island dwarf should be smaller than its closest mainland relative and show demonstrable evidence that it is a small adult and not a small juvenile. Such evidence includes morphological indicators of adulthood (fusion of the suture between the centrum and neural arch in vertebrae; firm junction or fusion of cranial sutures, especially of the braincase; long bones of adults should also have a surface of smooth lamellar bone (Callison and Quimby, 1984), well developed surface structures for muscle and ligament attachment (Coombs, 1986), well ossified articular ends, sharp and well developed processes, as well as bone histological indicators of slowing growth (transition to lamellar-zonal bone, and outer cortical bone with many closely spaced LAGs)).

The best reported example of an insular dwarfed dinosaur analysed in detail is *Europasaurus* from the Kimmeridgian of northern Germany (Sander et al., 2006). Individuals ranging in body length from 1.7 to 6.2 m show bone histological characteristics of juveniles to adults (Fig. 6). The 6.2 m long adult is one-third the length of its close relative *Camarasaurus* (18 m long). The largest *Europasaurus* shows these histological characters of adulthood:

(1) the inner cortical fibrolamellar bone is extensively remodelled by secondary osteons that nearly obliterate the primary bone;
(2) the outer cortex has closely spaced LAGs indicating radical slow-down in growth rate;
(3) and the outer zone shows characteristics of being an external fundamental system (outer cortex is avascular and consists of lamellar bone).

Palaeogeographic maps show that there were islands across northern Germany less than 200,000 km^2 in area, and these could have been large enough to support populations of dinosaurs, but small enough to induce dwarfing. The growth marks in the bones of *Europasaurus* suggest it achieved small size by a slowing of its growth rate, in contrast to the accelerated growth of giant sauropods (Padian et al., 2001; Sander et al., 2004).

Further evidence for dinosaur dwarfing has also been reported for the ornithopods of the lowermost Cretaceous fissure fillings of Cornet, near Oradea, northwestern Romania (Benton et al., 1997, 2006). First, the Cornet dinosaur fauna is more depauperate than a typical Wealden assemblage from England or continental western Europe, consisting of only four or five species, instead of ten or more, and the ornithopods are smaller on average than their European and North American counterparts. Insular adaptations are shown in the Romanian *Camptosaurus* sp., the iguanodontids, and dryosaurids, which are smaller than their west European and North American counterparts. The dryosaurid is at the lower end of the size ranges of *Dryosaurus* and *Valdosaurus*, the camptosaurid is two-thirds the size of its American and British relatives, and the iguanodontid is one-quarter to one-third the size of western European *Iguanodon*. Scaling to weight, an animal that is half the overall length of another of identical shape and proportions, weighs one-eighth as much ($0.5 \times 0.5 \times 0.5 = 0.125$). So, if a large American *Camptosaurus* weighed 700 kg (Peczkis, 1994), then the Cornet camptosaurid weighed only 87.5 kg. Likewise, if the range of body masses for different species of *Iguanodon* was 4–7 tonnes (Peczkis, 1994), the Cornet iguanodontid, at say one-third the length, weighed only one-twenty seventh (0.037) as much, a mere 150–260 kg. Dwarfing in the Cornet ornithopods may have occurred via progenetic paedomorphosis, i.e. retention of ancestral juvenile characteristics by earlier maturation in the descendant (Benton et al., 2006), but skeletochronological study is still required.

Several other ancient island faunas have been identified. One postulated example comes from the Late Triassic and Early Jurassic fissure faunas of Bristol and South Wales (Whiteside and Marshall, 2008). Palaeogeographic reconstructions show numerous small islands in the area, most only a few km across, and these were populated by small faunas, ranging from 2 to 16 species, of basal reptiles, dinosaurs, and early

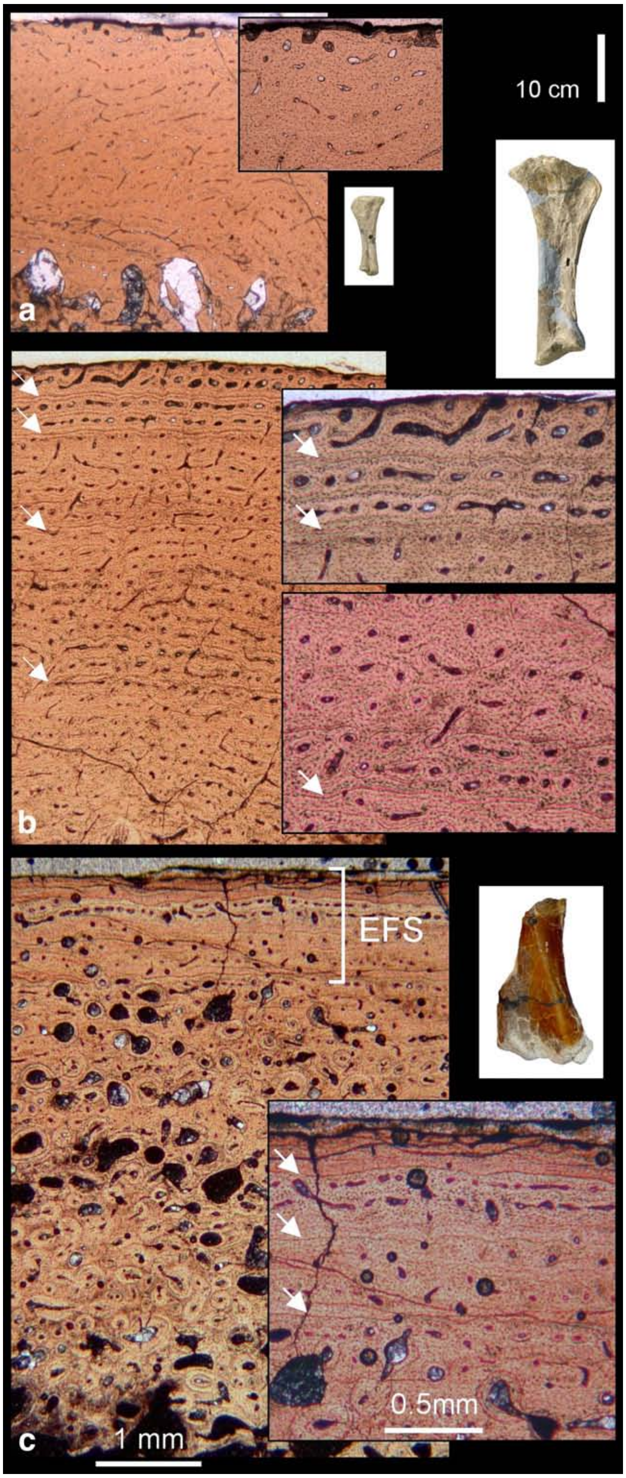

Fig. 6. Histological growth series and sampled bones of *Europasaurus holgeri* Mateus, Laven, and Knötsche, 2006: (a) Tibia from the smallest individual (DFMMh/FV009; body length 1.75 m). The reticular fibrolamellar tissue, which grades into laminar fibrolamellar tissue (inset), and the absence of growth marks indicate its juvenile status. (b) Tibia from a mid-sized individual (DFMMh/FV 459.5; body length 3.7 m). The cortex consists of laminar fibrolamellar bone interrupted by growth marks (arrows). Wide vascular canals opening to the outer bone surface (inset) indicate that this animal was still actively growing. (c) Distal femur from the largest individual (DFMMh/FV 415; body length 6.2 m). The external fundamental system (ESF; inset) indicates that it was fully grown. Bone surface is at the top of all photomicrographs. Black arrows indicate sample locations; white arrows indicate growth marks.

mammals. Body sizes were small, normally less than 30 cm body length, and including rarely the 1.5 m-long prosauropod dinosaur *Thecodontosaurus*, which might be a dwarfed relative of larger, 7-m long prosauropods such as *Plateosaurus* and *Lufengosaurus*. This case requires further evidence, however, because other basal sauropodomorphs, such as *Panphagia*, *Saturnalia* and *Efraasia* are also small, and so small size is a basal character of the clade, and later relatives became larger as the clade diversified (Galton and Upchurch, 2004). Dalla Vecchia (2002) has reported a further example from the mid Cretaceous Adriatic Carbonate Platform, where he found a sauropod half the length of close relatives from North America, and postulated that this was a dwarfing phenomenon brought about by a rise in sea levels and temporary formation of islands. Dinosaurs from the Early and Late Cretaceous of the area were of more normal size, linked with more extensive landmasses at those times, and suggesting a temporary dwarfing phenomenon. In another example, Antunes and Sigogneau-Russell (1996) also claimed dwarfism in the Campanian–Maastrichtian dinosaurs of Portugal. Island-dwelling dinosaurs have also been reported from the Late Cretaceous of New Zealand (Molnar and Wiffen, 1994) and the Chatham Islands nearby (Stilwell et al., 2006). The area consisted of small islands at the time, and some of these taxa may also represent dwarfed dinosaurs, although more specimens and histological studies are required to be sure.

6.2. Impoverishment of the Haţeg dinosaur faunas

Nopcsa (1914a) and others have suggested that the Haţeg dinosaurian faunas were impoverished, and this has been used as key evidence that they lived on an island. The low diversity Nopcsa detected was partly a result of limited collecting, and totals of dinosaurian species from Haţeg are much higher now: 13 (Sânpetru Formation) and 10 (Densuş–Ciula Formation), some of them as yet unnamed (Weishampel et al., 2004; Table 2 here). It turns out that the Haţeg dinosaurian fauna is impoverished on a global scale, but that all European faunas of the age are similarly impoverished.

Latest Cretaceous (Campanian, Maastrichtian) dinosaurian faunas from North America and Asia frequently exceed 30 or 40 taxa (e.g. Hell Creek Formation of South Dakota, Wyoming, and Montana, Lance Formation of Wyoming, Scollard and Horseshoe Canyon formations of Alberta, Djadokhta and Nemegt formations of Mongolia). Within Europe, the Sânpetru Formation yields the richest Late Cretaceous dinosaurian fauna, somewhat more diverse than French and Spanish dinosaur sites of similar age. The nearest contenders are the Grès à Reptiles Formation of Bouches-du-Rhône and Var in France, with ten taxa, the Aren Formation in Lleida, Spain, with eight, and the Grès de Saint-Chinian in Hérault, France, with seven, and others have as few as two or three reported taxa (Weishampel et al., 2004). Some of these western European dinosaurian faunas may be particularly limited because they have not been so thoroughly collected as those from Romania, and some are sampled from only one site.

Table 2
The dinosaurs of the two stratigraphic units, of equivalent age that comprise the Haţeg faunas.

Sânpetru Formation	Densuş–Ciula Formation
1. *Bradycneme draculae* (?troodontid)	1. Dromaeosauridae indet.
2. *Elopteryx nopcsai* (?troodontid or alvarezsaurid?)	2. Unnamed theropod
3. *Heptasteornis andrewsi* (?troodontid)	3. Oviraptorosauria indet.
4. cf. *Saurornitholestes* sp.	
5. cf. *Euronychodon* sp. (?troodontid)	4. cf. *Euronychodon* sp.
6. cf. *Paronychodon* sp.	
7. cf. *Richardoestesia* sp.	5. cf. *Richardoestesia* sp.
8. *Magyarosaurus dacus* (titanosaurid)	6. *Magyarosaurus dacus*
9. Titanosauria n. gen et sp.	7. Titanosauria n. gen et sp.
10. *Struthiosaurus transylvanicus* (nodosaurid)	
11. *Zalmoxes robustus* (euornithopod)	8. *Zalmoxes robustus*
12. *Zalmoxes shqiperorum* (euornithopod)	9. *Zalmoxes shqiperorum*
13. *Telmatosaurus transsylvanicus* (hadrosaurid)	10. *Telmatosaurus transsylvanicus*

European latest Cretaceous dinosaurian faunas are all impoverished in numbers, but also in ecological types and major clades. Missing groups throughout Europe include large tetanuran theropods, ankylosaurids, pachycephalosaurs, and ceratopsians (but see Godefroit and Lambert, 2007; Lindgren et al., 2007). The Haţeg faunas show closest similarities to Late Cretaceous faunas from Gosau in Austria, southern France, and Spain (Holtz et al., 2004) as well as Hungary (Ösi and Rabi, 2006), all of which share rhabdodontid ornithopods and basal nodosaurids (*Struthiosaurus*, *Hungarosaurus*) (Weishampel et al., 1991). However, other taxa such as the sauropods *Ampelosaurus* and *Lirainosaurus*, the ?dromaeosaurid *Variraptor*, abelisaurs, and the bird *Gargantuavis*, known from the western European faunas, are absent from Haţeg, possibly indicating the need for more collecting, but not really showing that Haţeg Island was depauperate in comparison to other European faunas. All these dinosaurian faunas throughout Romania, southern France, and Spain are depauperate on a global scale, and all apparently occupied islands.

6.3. Primitiveness of the taxa

The Haţeg dinosaurs generally occupy basal positions in cladograms. *Magyarosaurus* requires anatomical revision, but has been identified as a titanosaur, ranking basally within a poorly supported '*Rapetosaurus* clade' that includes *Rapetosaurus* from Madagascar, *Nemegtosaurus* from Mongolia, *Malawisaurus* from Malawi, *Agustinia* from Argentina, and *Trigonosaurus* from Brazil (Curry Rogers, 2005). The clade includes a mix of Early and Late Cretaceous taxa; if *Magyarosaurus* is basal within the clade, then it postdates many older relatives. *Telmatosaurus* is the basalmost hadrosaur, sister taxon to Euhadrosauria (Weishampel et al., 1993). This position so low in the phylogeny is unexpected for a Maastrichtian hadrosaur, and it places *Telmatosaurus* phylogenetically below hadrosaurids from the Santonian and Campanian of North America and Asia, so introducing a minimum ghost lineage of some 15 My. If *Trachodon cantabrigiensis* is considered a *nomen dubium* hadrosaurid, then the ghost lineage goes back to the late Albian.

Zalmoxes is even more of a 'living fossil' in the Haţeg fauna. In their cladistic analysis, Weishampel et al. (2003) found that the two species of *Zalmoxes* pair with *Rhabdodon*, known from the Campanian and Maastrichtian of France and Spain, as the new family Rhabdodontidae, sister clade of Iguanodontia, confirming a long-held assumption. Iguanodontians are primarily from the Early Cretaceous, and this implies a ghost lineage of 73 My, connecting the latest Cretaceous rhabdodontids with their closest, Early Cretaceous, relatives. In this case, *Zalmoxes* is not uniquely primitive to Haţeg Island, but the whole ornithopod fauna of Europe in the Late Cretaceous appears to be relictual, consisting of derived non-iguanodontian ornithopods, with rare hadrosaurids, rather than dominated by the hadrosaurids as seen elsewhere in the Northern Hemisphere.

Finally, *Struthiosaurus* shows the same kind of low phylogenetic position, interpreted either as a basal nodosaurid (e.g. Ősi, 2005) or as a basal ankylosaurian (Vickaryous et al., 2001). The basal position of *Struthiosaurus* would result in a similarly long (about 55 My) ghost lineage in the first case, or even a more extended one (at least 85 My) as its sister taxa are Late Jurassic (possibly even Middle Jurassic) in age. The relictual status of *Struthiosaurus* appears similar to that of *Zalmoxes*.

The common occurrence of relictual taxa across Europe in the latest Cretaceous suggests that there must have been communication earlier than the late Campanian and Maastrichtian: dinosaurian genera have durations estimated at typically 5–10 My (Dodson, 1990). Whether these genera were formerly ubiquitous and their range was split by the division of a larger landmass into islands, so stimulating vicariant phylogenetic events, or whether the Haţeg dinosaurs dispersed from the mainland by island hopping, as first suggested by Nopcsa (1923), is not clear (Weishampel et al., 1991).

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6.4. Dwarfing in the Haţeg dinosaurs

Dwarfing has been suggested in *Magyarosaurus*, *Zalmoxes*, and *Telmatosaurus* from Haţeg, but not in the other taxa. The ankylosaur *Struthiosaurus* and the unnamed pterosaur (Jianu et al., 1997) are smaller than expected compared to their close relatives, but it has yet to be shown that the specimens come from mature adults or subadults. In contrast, the dromaeosaurid and troodontid theropods from Haţeg, although small, appear to be no smaller than are their close relatives in Asia and North America. Only the pterosaur *Hatzegopteryx* (Buffetaut et al., 2002) is large, with an estimated wingspan of 12 m, in the range of the largest members of the azhdarchid clade. The crocodilians, turtles, and mammals are no smaller or larger than their relatives elsewhere.

The titanosaurian sauropod *Magyarosaurus*, with an estimated body length of 5–6 m, was much smaller than its relatives, which ranged from the 7 m long *Saltasaurus* to the 25–20-m long *Argentinosaurus* (Jianu and Weishampel, 1999). From a study of humeri, these authors found that *Magyarosaurus* was the smallest of the adult neosauropods they studied, that the humeri appear to be more similar to those of subadults than to adults of other taxa, that the dwarfing is apomorphic, and that the scaling suggests *Magyarosaurus* achieved small size as an adult by paedomorphosis.

The hadrosaurid *Telmatosaurus* was about 4 m long, which contrasts with mean body lengths for other hadrosaurids of 7–10 m. To understand ontogenetic trends in *Telmatosaurus*, we compared it to one of the best known ontogenetic series among "higher" iguanodontian ornithopods, the hadrosaurid *Maiasaura* (Dilkes, 2001; Fig. 7). Based on humeral and femoral robustness (midshaft circumferences plotted against length), these regressions indicate that the smallest individuals of *Telmatosaurus* (Grigorescu and Csiki, 2006) are smaller than those thought to be very young nesting *Maiasaura* (data for *Maiasaura* from David Dilkes pers. comm.). In addition, adults of *Telmatosaurus* are slightly more robust than *Maiasaura* of comparable size. However, these latter are thought to be relatively young subadults, indicating that adult *Telmatosaurus* were downsized relative to the ontogenetic trend represented by *Maiasaura*.

The two species of *Zalmoxes* achieved different estimated lengths, up to 3 m (*Z. robustus*), and 4.0–4.5 m (*Z. shqiperorum*), larger than some basal relatives, such as *Hypsilophodon* from the Early Cretaceous (2.3 m long), similar in length to others, such as *Thescelosaurus* from the Late Cretaceous (3–4 m), but smaller than other relatives, such as *Camptosaurus* from the Late Jurassic (5–7 m) and *Tenontosaurus* from the mid Cretaceous (7–8 m). Weishampel et al. (2003) presented an analysis of growth and heterochrony, based on measurements of femoral length and midshaft width in ontogenetic samples of *Zalmoxes robustus*, *Z. shqiperorum*, *Rhabdodon priscus*, *Tenontosaurus tilletti*, *Hypsilophodon foxii* and *Orodromeus makelai*. Pair-wise comparisons of the growth series of these euornithopods (e.g. between *Zalmoxes* and *Orodromeus*, between *Zalmoxes* and *Tenontosaurus*, etc.) revealed that the relative ontogenetic change in femoral shape is statistically indistinguishable between taxa ($P>0.2$), except between *T. tilletti* and *Z. robustus* ($P=0.03$). In other words, femoral proportions changed in the same fashion in ontogenetic series of *Hypsilophodon*, *Thescelosaurus*, *Rhabdodon*, and *Zalmoxes*.

Weishampel et al. (2003) went on to evaluate heterochrony in *Zalmoxes* by plotting maximal (adult?) femoral length of terminal taxa on their cladogram of basal euornithopods and comparing each node from the base of the tree to *Tenontosaurus*. The femora of both *Orodromeus* and *Hypsilophodon* reached a length of 17 cm. At the other extreme, the largest femora (54–58 cm) belong to *Tenontosaurus* and *Rhabdodon*. The femora of *Zalmoxes shqiperorum* and *Z. robustus* are intermediate in length (47 cm and 36 cm, respectively). Through optimization of maximal femur length onto the cladogram, Weishampel et al. (2003) identified a peramorphic trend (peramorphocline) from basal euornithopods such as *Orodromeus* through more highly positioned taxa such as *Hypsilophodon*, *Rhabdodon* and *Tenontosaurus*. However, downsizing occurred in *Z. shqiperorum* and more so in *Z. robustus* (a 36% decrease in length), compared to their closest relatives.

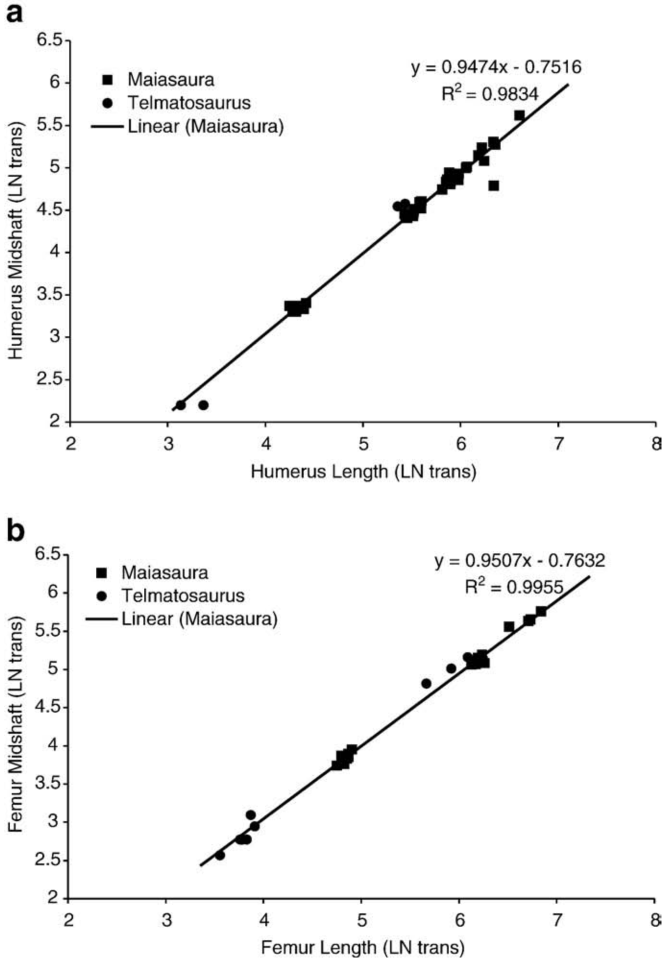

Fig. 7. Heterochrony in the ornithopod *Telmatosaurus*, in comparison to its close relative *Maiasaura* from North America. Measurements of element length and midshaft diameter for humeri (a) and femora (b), showing that *Telmatosaurus* specimens plot in the lower part of the size range, but closely follow the growth trajectory (equations of the lines, and correlation coefficients at $p<0.001$, are given) of the undwarfed relative *Maiasaura*. All measurements are natural logarithm-transformed (LN trans).

As adults, the sauropod *Magyarosaurus* and the ornithopod *Telmatosaurus* seem to have been about one half the length of their close relatives from elsewhere, and a linear reduction of one half, corresponds to much reduced body masses, about one-eighth ($0.5^3=0.125$). Downsizing in *Zalmoxes robustus* to 64% corresponds to a reduction in mass to 26% (0.64^3), about one-quarter. These reduced body masses are more meaningful biologically speaking in terms of metabolism and the amount of food required by the insular Haţeg dinosaurs.

6.5. Juvenile characters in the Haţeg dinosaurs

The Haţeg hadrosaurid *Telmatosaurus* is smaller than more basal iguanodontians like *Ouranosaurus* and *Iguanodon bernissartensis*, and its teeth retain features found in juveniles of these last-mentioned taxa (Weishampel et al., 1993). The maxillary teeth of *Telmatosaurus* are narrow, diamond-shaped, and equipped with a single centrally placed ridge, most like the juvenile condition seen in non-hadrosaurid iguanodontians, but also similar to the typical maxillary teeth of more derived hadrosaurids. Its dentary teeth, in contrast, are wider,

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asymmetrical, and bear several low ridges, making them intermediate between those of other hadrosaurids and more primitive iguanodontians. They too were small, but most resemble the shape of adults of non-hadrosaurid iguanodontians. Weishampel et al. (1993) regarded this juvenilization of the teeth in *Telmatosaurus* as marking an important step in the evolution of hadrosaurid dentitions from those of ancestral iguanodontians, but also as auxiliary evidence of dwarfing by paedomorphosis in this taxon.

The small adult size of most of the better-known Haţeg dinosaurs is also supported by osteological correlatives of growth cessation. Complete fusion of neurocentral sutures in vertebrae (Galton, 1981, 1982; Coombs, 1982; Britt and Naylor, 1994; Chure et al., 1994) is a commonly observed phenomenon in small ornithopod dorsal vertebrae, around 30 mm in length, from the Haţeg Basin. Even in a juvenile specimen of *Zalmoxes shqiperorum* (FGGUB R.1087–1133 and R.1355–1357; Weishampel et al., 2003), the neurocentral suture is not fused only in the anterior dorsals (15 mm in length), while it is fused, although still visible, in the more posterior ones. Some of the smallest known titanosaur dorsals from Haţeg (such as BMNH R.4896; centrum length about 80 mm) show the neurocentral suture completely obliterated, suggesting a post-juvenile developmental stage.

Specimens of *Zalmoxes* show changes in certain osteological features and in relative proportions with growth that match findings in other taxa, such as *Tenontosaurus*, and so confirm that the larger examples of the Haţeg taxon are indeed probably adults. For example, Weishampel et al. (2003) note several changes seen in an ontogenetic series of some 12 *Zalmoxes* individuals whose femora range from 0.3 to 0.5 m long: increase in the number of tooth positions in the dentary from 8 to 10, change in dentary shape from markedly convex ventrally in small individuals to more or less parallel-sided in adults, lengthening and increasing angularity of the deltopectoral crest, increasing prominence of the anterior trochanter and a slight distal shift in the position of the fourth trochanter in the femur, increasing robustness of the tibia, with a larger cnemial crest, and changes in hindlimb proportions from a relatively short femur in juveniles to one that equals or exceeds the length of the tibia in adults.

Of the three heterochronic processes that can produce paedomorphosis, neoteny and post-displacement can lead to adults of the same size as the unaffected relatives, whereas progenesis usually leads to adults of reduced size (Gould, 1977; Alberch et al., 1979). In many, or most, cases of dwarfing in Pleistocene mammals, as noted above, selection for small body size was likely the driver, and morphological change through progenesis the consequence. Additional evidence for progenesis is the retention of anatomically juvenile characters in adult *Telmatosaurus*: this suggests that development of the dentition finished early by comparison with larger close relatives, and so this points to progenesis (early offset) as the heterochronic process.

6.6. Bone histological evidence for dwarfing in the Haţeg dinosaurs

We investigated the bone histology of all Haţeg dinosaur species for which long bone material from different-sized individuals is available. Two of the species, actually some of the largest members of the fauna, show unequivocal evidence that they were fully grown at a small body size compared to their sister taxon (*Telmatosaurus transsylvanicus*, cf. Euhadrosauria), or closely related titanosaurs (*Magyarosaurus dacus*). The rhabdodontids *Zalmoxes robustus* and *Z. shqiperorum* cannot unequivocally be interpreted as being fully grown, although they are certainly not juveniles.

Stein et al. (submitted for publication) sampled an ontogenetic series of *Magyarosaurus dacus* long bones (Fig. 8) and found that they show a histology that is only seen in very large and senescent individuals of other sauropod species. The cortex of even the smallest specimen in the *Magyarosaurus dacus* growth series (45% maximum size) is dominated by secondary osteons, with only a few islands of remnant laminar primary fibrolamellar bone with a strong lamellar component in the bone matrix (Fig. 9a–d). Although the only unequivocal sign of a fully grown specimen is the presence of an external fundamental system (EFS) in the outermost bone cortex, none was observed in the entire sample set. However, the advanced secondary remodelling is typical of the oldest histological ontogenetic stages (HOS) (stages 12–13) of large-sized sauropods, when even the EFS has been remodelled (Klein and Sander, 2008). In addition, an EFS is easily destroyed by rough mechanical cleaning of the bone surface. In the many other sauropod taxa studied so far (Sander, 2000; Klein and Sander, 2008), a completely remodelled long bone cortex occurs only in the largest and fully grown specimens of *Apatosaurus* (femur length 1800 mm) and *Supersaurus* (ulna length 1250 mm). The largest *Magyarosaurus* long bones are only a fraction of that size (femur length 550 mm, humerus length 490 mm).

The secondary bone remodelling has continually and progressively obliterated the primary growth record in *Magyarosaurus dacus* long bones, and thus any growth marks or other indicators of the growth rate. Therefore, it is difficult to say how fast *Magyarosaurus* really grew. However, the strong lamellar component of the remnant primary bone suggests a slower growth rate than in similar-sized bones of large sauropods (Fig. 9e), but still faster than ectothermic reptiles, which have a lamellar-zonal bone dominated cortex (Fig. 9f). The extensive remodelling and remnant primary bone indicate that the largest *M. dacus* specimens had attained full size, and that the

Fig. 8. Photographs of some of the sampled titanosaur bones from the Maastrichtian of Romania. (a–d) *Magyarosaurus dacus* humeri, specimens: (a) MAFI Ob. 3092 (the smallest recorded body size, 45% maximum size); (b) FGGUB R.1246 (65% maximum size); (c) MAFI v.13492 (76% maximum size); (d) FGGUB R.1048 (largest known specimen). (e) Titanosaur indet., MAFI Ob.3104. Scale bar equals 100 mm.

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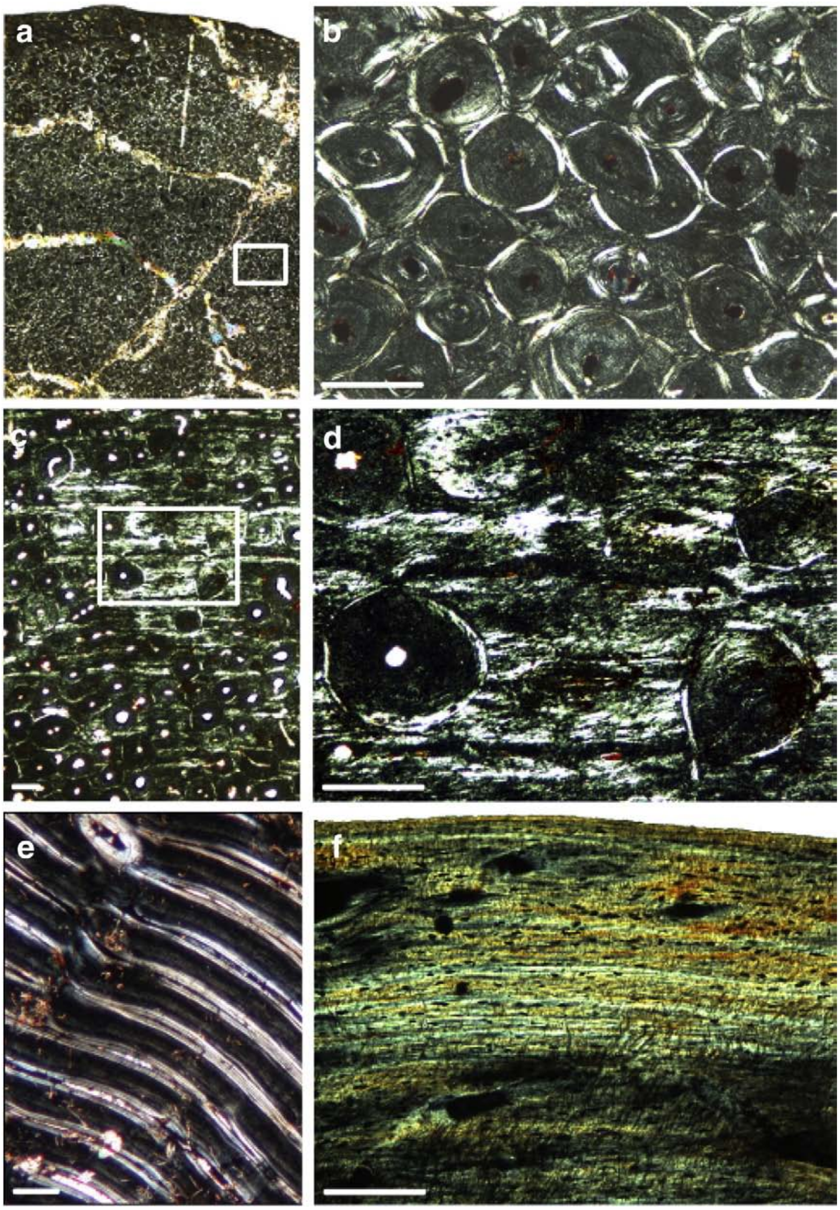

Fig. 9. Long bone histology of *Magyarosaurus dacus* compared with other vertebrates. (a) overview of cross section (specimen MAFI V.13492, 76% max size); (b) close-up of (a): cortex dominated by secondary remodelling. (c) Close-up of largely interstitial laminar primary bone in outermost cortex of the smallest available specimen of *M. dacus* (MAFI Ob.3092, 46% max size). The vascular canals are oriented circumferentially as in laminar fibrolamellar bone, but the bone matrix between the vascular canals consists largely of parallel-fibered and lamellar bone, with only a minute fraction of fibrous (or woven) bone tissue. (d) Close-up of (c). (e) Laminar fibrolamellar bone of *Apatosaurus*. (f) Alligator long bone histology showing lamellar-zonal bone. All scale bars equal 200 µm.

species achieved its small size by a slowing of the growth rate, analogous to *Europasaurus* (Stein et al., submitted for publication).

Le Loeuff (2005) questioned the dwarfing of *Magyarosaurus dacus*, based on the presence of large long bones in the collection of the BMNH and the MAFI. However, bone histological features (larger size, but earlier HOS than the largest *M. dacus* specimen) suggest that these bones belong to a different taxon (Stein et al., submitted for publication) and are listed in Table 2 as "titanosaurid indet." The presence of a larger sauropod species together with *M. dacus* is an interesting exception to the general dwarfing of other dinosaurs on Haţeg Island. The presence of several individuals of a larger titanosaurian species might relate to a time of lower sea level, for example, when the effective island size increased, or a chance observation of an immigrant population before it reduced in size or went extinct. However, this exception to the 'rule' of dwarfing seen in all other Haţeg dinosaurs may simply indicate that, while dwarfing is common and is related to isolation on a small island, it is not an absolute rule to which all species adhere, a case that has been made forcefully for modern mammals and lizards (Meiri et al., 2004, 2006; Meiri, 2007; and see above). Examples of sympatric occurrences of closely related, but differently sized taxa within isolated island environments have been cited from the Plio-Pleistocene of the Mediterranean and Indonesian areas as well (e.g. Marra, 2005; Palombo et al., 2008), including even the largest components of the local assemblages such as the Late Pliocene–Early Pleistocene proboscideans of Sulawesi (e.g., De Vos et al., 2007), so comparable co-occurrences in the Cretaceous are not unexpected. In this latter case (Sulawesi), the presence of a larger-sized *Stegodon* species along with the dwarf taxa *Stegodon sompoensis* and '*Elephas*' *celebensis* is explained as a consequence of a later immigration event.

Long bones of the hadrosaurid *Telmatosaurus transsylvanicus* were sampled from a wide range of ontogenetic stages, from hatchlings to fully grown specimens (Weishampel et al., 1993; Grigorescu and Csiki, 2006). The primary bone tissue consists of fibrolamellar bone with reticular primary osteon organization in hatchlings and laminar

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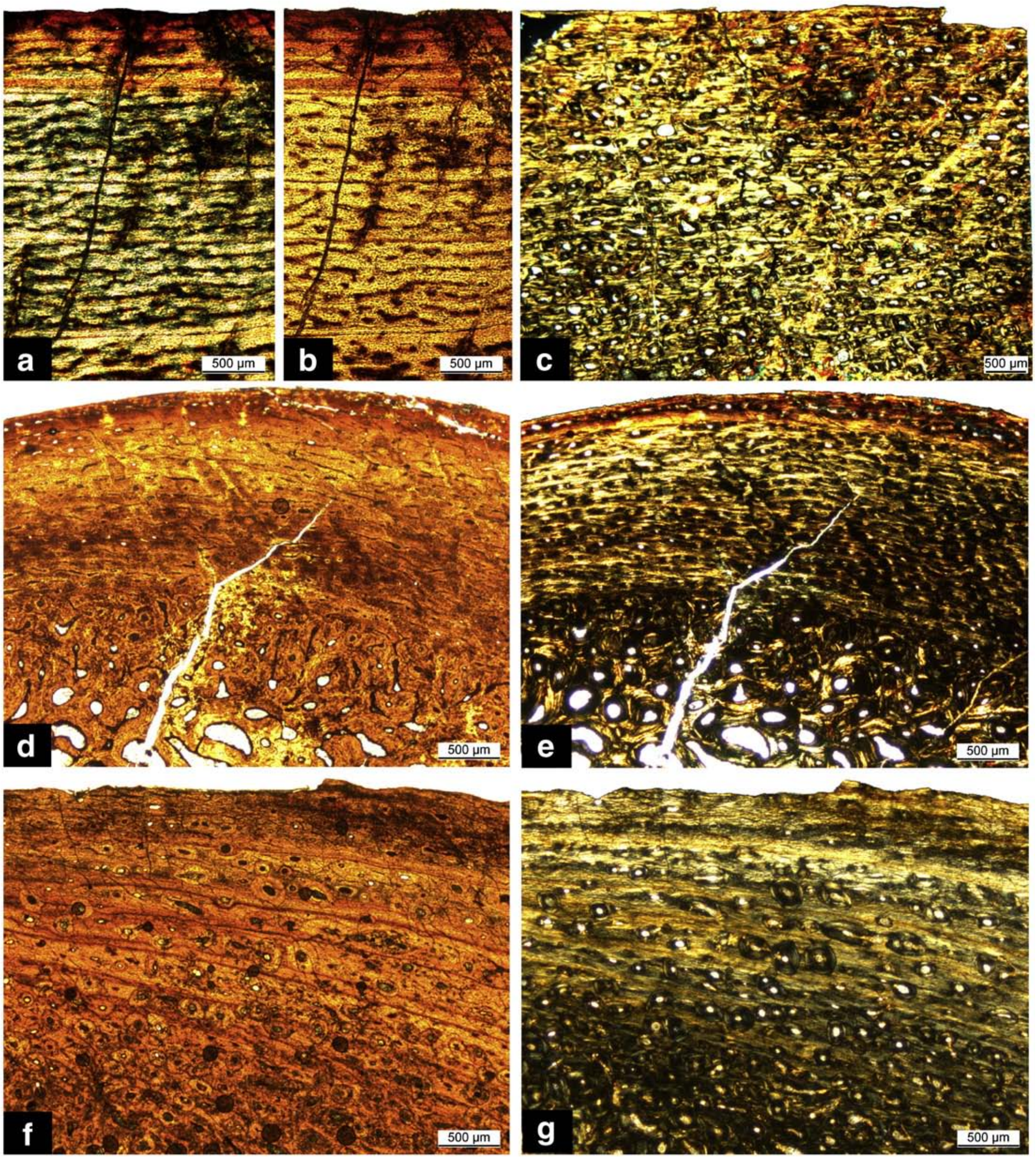

Fig. 10. Histology of the long bones of the ornithopods *Telmatosaurus trannsylvanicus* (a–c), *Zalmoxes shqiperorum* (d–e), and *Z. robustus* (f–g). (a–b) Overview of the bone histology of the femur of subadult specimen FGGUB R.1362 (femur length 25 cm). No secondary remodelling has altered the primary bone of the middle and outer cortex yet. Primary bone consists of fibrolamellar bone tissue with reticular organization of the primary osteons. Growth marks occurr regularly spaced throughout the cortex. (b) Same view in polarized light. (c) The femur of the oldest adult specimen MAFI Ob.3130 (estimate of femur length around 46 cm = max. size) reveals secondary remodelling of the primary bone up to the outer cortex. The bone surface is missing and thus no EFS was observed. View in polarized light. (d–e) Long bone histology of *Z. shqiperorum*. The femur (length 16.4 cm) of the subadult specimen FGGUB R.1088 shows that secondary remodelling is restricted to the inner cortex indicating a late onset of remodelling. Primary osteons occur in longitudinal and reticular organization. Vascular canals open to the bone surface indicating active growth at the time of death. (e) Same view in polarized light. (f–g) Bone histology in the femur of *Zalmoxes robustus* FGGUB R.1382 (estimate of femur length 28 cm). The high number of growth marks (11; only 7 seen in this view) indicates an adult stage of this specimen. Remodelling is dense in the inner cortex and scattered in the middle cortex. (g) Same view in polarized light.

organization in subadults (Fig. 10a, b) and adults (Fig. 10c). The fibrolamellar bone matrix has a strong lamellar component, analogous to *Magyarosaurus dacus*, suggesting a slow growth rate. Open vascular canals at and near the bone surface were only found in the subadult specimen and the hatchlings. These are an unequivocal sign of active growth at the time of death.

The largest long bones (Fig. 10c) show dense secondary remodelling in the inner cortex, but secondary osteons become more scattered closer to the surface of the bone, similar to remodelling of adult specimens of the hadrosaur *Maiasaura peeblesorum* (Horner et al., 2000). The largest specimens also preserve a high number of growth marks (eight in total). This supports the suggestion that the animal was fully grown. An EFS could not be observed due to abrasion of bone surfaces. The largest *Telmatosaurus* specimens (femur length, 460 mm) were thus most likely adult and significantly smaller than other adult hadrosaurs (*M. peeblesorum*: 1000 mm, Horner et al., 2000).

The ornithopod *Zalmoxes* was sampled from subadult (Fig. 10d, e) and adult (Fig. 10f, g) femora and humeri. *Zalmoxes* has a remarkable histology in terms of a late onset of the secondary remodelling in the subadult stage (Fig. 10d, e). In the oldest specimens, dense remodelling is restricted to the inner cortex. Isolated to scattered secondary osteons occur in the middle cortex, and are absent in the outermost cortex (Fig. 10f, g). In addition, vascular canals opening to the bone surface in all sampled specimens indicate that a fully grown stage had not been reached yet. Nevertheless, from the high number of growth marks (up to 13 in *Z. robustus* and 7 in *Z. shqiperorum*), a juvenile stage can be excluded for these bones. Bone histology also shows that *Z. robustus* is smaller than *Z. shqiperorum* at the same ontogenetic

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stage, as has been suggested before by bone morphology (Weishampel et al., 2003). Femur lengths between 250 and 320 mm were estimated for *Z. robustus*, and between 333 and 355 mm for *Z. shqiperorum*. The high number of growth marks compared to the femur lengths suggests a slow growth rate for *Z. shqiperorum* and very slow for *Z. robustus*. Although the sampled specimens had probably not reached their maximal size yet, femur lengths of fully grown *Z. shqiperorum* and *Z. robustus* would still be significantly smaller than those of other euornithopods: 557 mm in *Tenontosaurus dossi* (Winkler et al., 1997), 400 mm in *Tenontosaurus tilletti* (Forster, 1990), 544 mm in the small iguanodontid *Camptosaurus dispar* (Paul, 2008), and 600 mm in *Rhabdodon priscus* (Garcia et al., 1999). Dwarfing may therefore be suggested for *Zalmoxes* but cannot be confirmed by bone histology.

7. Conclusions

The island rule is hotly debated among evolutionary biologists, with some finding it is a general principle that applies to island-living mammals, birds, and some other groups, whereas others reject the rule, saying it is an artefact of poor statistical analysis. Both sides agree, however, that many large animals on islands have become small, while many small animals have become larger.

Many reasons for the size changes on islands have been proposed. The commonest explanation for size reduction (dwarfing) is shortage of resources, whereas size increase is explained most commonly as a response to the absence of larger competitors, the absence of predation, and perhaps the absence of parasites.

Island dwarfing among Pliocene, Pleistocene, and Holocene mammals of the Mediterranean was noted first by Victorian palaeontologists, and many examples of dwarfing among elephants, deer, hippos, and other herbivores were reported. These studies of dwarfed elephants and giant dormice on Malta have entered school textbooks. Franz Nopcsa was first in 1914 to suggest that the dinosaurs from the latest Cretaceous of Haţeg had lived on an island, and had undergone dwarfing by comparison with the nearest relatives on larger landmasses, particularly in the area of France–Spain and in North America.

Our studies confirm that Haţeg was probably an island, and that at least two of the herbivorous dinosaurs, the sauropod *Magyarosaurus* and the ornithopod *Telmatosaurus*, and possibly also the ornithopod *Zalmoxes*, are indeed reduced in size as adults, and their dwarfing arose through paedomorphosis, and possibly progenesis. The evidence comes from measurements of relative limb lengths and evidence for allometric shape change in the small-sized adults, as well as bone histology.

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