Dwarf dinosaurs in the latest Cretaceous of Europe?

¿Dinosaurios enanos en el Cretácico terminal de Europa?

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Abstract

The remarkable small body size of the latest Cretaceous dinosaurs of Transylvania has long been regarded as an example of dwarfing on islands. Adult individuals of the ornithopods *Zalmoxes* and *Telmatosaurus*, the ankylosaur *Struthiosaurus* and the sauropod *Magyarosaurus* are smaller than their closest relatives (estimated body length approximately 2.5-3 m in *Zalmoxes robustus* and *Struthiosaurus transylvanicus*, about 5 m in *Telmatosaurus transsylvanicus* and no more than 6 m in *Magyarosaurus dacus*) from elsewhere. This downsizing may have involved heterochronic alterations of growth processes, but alternative explanations (e.g., taphonomic and sampling biases) have also been suggested. A review of the arguments used for and against the hypothesis of insular dwarfism in latest Cretaceous dinosaurs of Europe indicates that the available data are not conclusive enough to support the suggestion that the above mentioned taxa (with the possible exception of *Zalmoxes*) are true heterochronic dwarfs in the paedomorphic sense. The discovery of additional fossil material, in particular complete ontogenetic series, and the development of osteohistological studies may help to solve the problem.

Key words: Dinosaurs, Late Cretaceous, Europe, dwarfing, insularity.

Resumen

El remarcable pequeño tamaño corporal de los dinosaurios del Cretácico terminal de Transilvania ha sido considerado desde hace tiempo un ejemplo de enanismo insular. Los individuos adultos de los ornitópodos *Zalmoxes* y *Telmatosaurus*, del anquilosaurio *Struthiosaurus* y del saurópodo *Magyarosaurus* son menores en tamaño (con una longitud total estimada de 2,5-3 m para *Zalmoxes robustus* y *Struthiosaurus transylvanicus*, unos 5 m para *Telmatosaurus transsylvanicus* y no más de 6 m para *Magyarosaurus dacus*) que sus parientes filogenéticamente más próximos. Esta reducción de tamaño podría ser debida a cambios heterocrónicos durante el desarrollo. No obstante, también se han propuesto hipótesis alternativas (por ejemplo, sesgos tafonómicos y de muestreo). Una revisión de los argumentos utilizados a favor y en contra de la hipótesis del enanismo insular de los dinosaurios finicretácicos de Europa indica que los datos conocidos actualmente no son suficientemente concluyentes para afirmar que los taxones antes mencionados (con la posible excepción de *Zalmoxes*) son

verdaderos enanos heterocrónicos (pedomórficos). El descubrimiento de material fósil adicional, principalmente series ontogenéticas completas, y el desarrollo de estudios de tipo osteohistológico pueden ayudar a resolver la cuestión.

Palabras clave: Dinosaurios, Cretácico superior, Europa, enanismo, insularidad.

INTRODUCTION

Dinosaurs include the largest animals that have ever walked on land, with some gigantic forms (all sauropods) whose body lengths exceed 30 m and a corporal mass superior to 40-50 metric tons (Upchurch *et al*., 2004; Royo-Torres *et al*., 2006). On the other hand, dwarfed species of dinosaurs are rare in the fossil record (Sander *et al*., 2006).

Early last century, Nopcsa (1914, 1923) noted the remarkable small size of the latest Cretaceous dinosaurs of Transylvania, "the biggest not exceeding 18 feet (6 m) in length, tail included". These dinosaurs consist mainly of the ornithopods *Telmatosaurus* and *Zalmoxes* (Nopcsa, 1900, 1904, 1928; Weishampel *et al*., 1993, 2003), the sauropod *Magyarosaurus* (Huene, 1932; Le Loeuff, 1993), and the ankylosaur *Struthiosaurus* (Nopcsa, 1929; Pereda Suberbiola and Galton, 1997). Nopcsa (1914, 1923) regarded the small body size of the Transylvanian dinosaurs as an example of dwarfing on islands. This topic is currently controversial: some authors have supported Nopcsa's original claim (Jianu and Weishampel, 1999; Weishampel *et al*., 1993, 2003; Pereda Suberbiola and Galton, 2001), but others have challenged it (Le Loeuff, 2005).

The aim of this paper is to review the arguments used in favour and against the hypothesis of the insular dwarfism (or "autapomorphic nanism" according to Gould and MacFadden, 2004) of Late Cretaceous dinosaurs of Europe and to discuss the role that heterochrony may have played in the evolution of these animals.

HETEROCHRONIES IN DINOSAUR EVOLUTION

Heterochronies are evolutionary changes in timing or rate of development relative to the same events in the ancestor (McNamara, 1990). These changes may have played a significant role in dinosaur evolution (Weishampel and Horner, 1994; McNamara and Long, 1998). Until recently, examples of heterochrony in dinosaur evolution were sparsely documented in the literature. The upsurge in interest in the developmental history of dinosaurs, together with recent discoveries of embryonic and juvenile specimens (Carpenter and Currie, 1990; Carpenter *et al*., 1994; Carpenter, 1999), is noteworthy as it has largely improved the situation.

Long and McNamara (1995) provided documentation of heterochronic changes within major groups of dinosaurs. Heterochrony is expressed in two ways: as *paedomorphosis* (ancestral juvenile characters are retained by the descendant adult species) and as *peramorphosis* (descendant adults have additional character modifications relative to the ancestral species, or new features) (McNamara, 1990). Peramorphic processes (e.g., acceleration) appear to have been a major factor in the evolution of several dinosaur lineages, but examples of paedomorphosis (such as progenesis) are less obvious (Long and McNamara, 1995). According to these authors, peramorphosis has been a principal factor underlying ceratopsian evolution in terms of both skull size enlargement and of increase in the complexity and extent of cranial structures, i.e., horns and frill ornaments (Long and McNamara, 1997). The massive increase in size of sauropods and the elongation of neck and tails from that of prosauropods points again to longer growth periods and accelerating rates of development (Sander *et al*., 2004). On the other hand, the evolution of birds from theropod dinosaurs exemplifies the dissociated nature of the heterochronic processes. The evolutionary changes that led to the success of the birds include the retention of small body size and paedomorphic skull features (McNamara and Long, 1998).

LATE CRETACEOUS DINOSAURS OF EUROPE AS POSSIBLE EXAMPLES OF ISLAND DWARFS

As originally noted by Nopcsa (1923), adult dinosaur individuals from the Maastrichtian of Transylvania (now Romania) are comparatively smaller than their closest relatives from elsewhere in the world. The nodosaurid ankylosaur *Struthiosaurus transylvanicus* and the rhabdodontid ornithopod *Zalmoxes robustus* were approximately 3 m long (Pereda Suberbiola and Galton, 2001; Weishampel *et al*., 2003), the basal hadrosaurid *Telmatosaurus transsylvanicus* was about 5 m long (Weishampel *et al*., 1993), and the titanosaurian sauropod *Magyarosaurus dacus* possibly did not exceed 6 m in length (Nopcsa, 1915). Dwarfing in these dinosaurs may have involved heterochronic alterations of growth processes (Jianu and Weishampel, 1999; Pereda Suberbiola and Galton, 2001; Weishampel *et al*., 2003), but alternative arguments have also been suggested. A review of the taxa is presented below.

Telmatosaurus (Ornithopoda, Hadrosauridae)

Telmatosaurus (formerly *Limnosaurus*; see Nopcsa, 1900, 1903) is represented by material from several Maastrichtian sites of the Hateg and Transylvanian basins of Romania (Weishampel *et al*., 1993; Dalla Vecchia, 2006). The remains are not abundant and a number of fossils previously assigned to *Telmatosaurus* are in fact referable to the non-hadrosaurid *Zalmoxes* (Weishampel *et al*., 2003). *T. transsylvanicus* is regarded phylogenetically as the most basal of known hadrosaurids (Weishampel *et al*., 1993; Horner *et al*., 2004). It was probably no more than approximately 5 m in length and weighed in excess of half a ton, which is at most 10% of an average adult of other hadrosaurid species (sensu Weishampel *et al*., 1993). According to these authors, the miniaturization of the maxillary teeth and the evolution of a dental battery in *T. transsylvanicus* (and perhaps in all hadrosaurids) may owe their development to a progenetic paedomorphosis. It should be noted that derived non-hadrosaurid members of Hadrosauroidea, such as *Bactrosaurus* and *Probactrosaurus*, probably have a body length comparable to that of *Telmatosaurus* (femoral length: *Bactrosaurus*, 781 mm; *Probactrosaurus*, 565 mm; *Telmatosaurus*: 731 mm; data from Carrano, 2006). This casts doubt about the assertion of Weishampel *et al*. (1993) that adults of *Telmatosaurus* are at most 10% smaller compared to their closest relatives. Additional measurements and comparisons are necessary to support the dwarf condition of *Telmatosaurus* among hadrosauroids.

Zalmoxes (Ornithopoda, Rhabdodontidae)

Zalmoxes (originally named *Mochlodon*, later referred to *Rhabdodon*; see Nopcsa, 1902, 1904, 1915, 1928) consists of abundant material from the Hateg Basin and the southwestern Transylvanian Depression (Weishampel *et al*., 2003; Codrea and Godefroit, 2008)). There, fossils of *Zalmoxes* are known from more than 25 localities. They occur mainly as isolated remains, but some specimens were apparently found in reasonably close association. *Zalmoxes* was a robust, small to medium-sized ornithopod. Weishampel *et al*. (2003) distinguished two species: *Z. robustus* (type-species) and *Z. shqiperorum*. *Zalmoxes* and *Rhabdodon* are united in the clade Rhabdodontidae, which constitutes the most basal members of Iguanodontia (Norman, 2004). Size estimates of *Zalmoxes* are based on partial ontogenetic series: *Z. robustus* is probably 3 m in length (but note that the skeletal reconstruction of Weishampel *et al*., 2003: fig. 36 is no longer than 2.1 m), whereas *Z. shqiperorum* is approximately 4.0 to 4.5 m long (Weishampel *et al*., 2003). In order to evaluate patterns of heterochrony in *Zalmoxes*, Weishampel *et al*. (2003) plotted maximal (presumably adult) femoral length of several taxa on a cladogram of basal euor-nithopods, including the rhabdodontids *Zalmoxes* and *Rhabdodon*. They recognized a peramorphocline from the most basal euornithopods through more highly positioned taxa, such as *Tenontosaurus*. However, *Zalmoxes*, and more especially *Z. robustus*, reverses the peramorphic trend and offers support for a possible paedomorphic dwarfing (with a 36% decrease in length in *Z. robustus*; see Weishampel *et al*., 2003: figs. 37, 38A). These authors concluded that dwarfing did not occur apomorphically in Rhabdodontidae, and that insular dwarfing (whether related to an acceleration of the timing of sexual maduration, or another cause) is only modestly supported in *Zalmoxes*.

Magyarosaurus (Sauropoda, Titanosauria)

Nopcsa (1915) described titanosaurian remains from the Haţeg Basin of Transylvania as *Titanosaurus dacus*. The body size of *T. dacus* was estimated to be less than 6 m in length (Nopcsa, 1923). More material added to Nopcsa's original collection was studied and revised by Huene (1932), who renamed it *Magyarosaurus* and recognized three species: *M. dacus* (type species), *M. transsylvanicus* and *M. hungaricus*. McIntosh (1990) and Le Loeuff (1993) regarded only one species, *M. dacus*, as valid, but it seems that *Magyarosaurus* requires further revision (Wilson and Upchurch, 2003; Csiki *et al*., 2007). Jianu and Weishampel (1999) studied the ontogeny of *Magyarosaurus* and other titanosauriform sauropods on the basis of two approaches: a) a linear regression analysis of humeral data as a means of establishing patterns in body size, and b) an optimization analysis of the data onto titanosaurian phylogeny to evaluate evolutionary trends. They showed that *Magyarosaurus* exhibits an apomorphic shift to small, "juvenilised" morphology. Thus, *Magyarosaurus* humeri appear to be more similar to those of subadults than to adults of other taxa (Jianu and Weishampel, 1999). Consequently, these authors concluded that this "juvenile" morphology may constitute dwarfing in *M. dacus* by paedomorphosis. Mussell and Weishampel (2000), who continued the work of Jianu and Weishampel (1999), took additional measurements of the humerus and femur in several sauropod clades, including titanosaurians. Using regression analyses and non-parametric statistical tests, *Magyarosaurus* indeed appears to be a dwarf sauropod, but the data does not support progenesis (paedomorphosis) as the cause of this condition (Mussell and Weishampel, 2000).

In a recent paper, Le Loeuff (2005) noted that a few large limb bones (i.e., humerus, ulna, femora) assigned to *Magyarosaurus* indicate the existence of some large individuals (estimated to be 10-15 m long) among the titanosaurian assemblage of Transylvania. According to this hypothesis, taphonomical and sampling biases are responsible for this apparent dwarfism. Thus, the abundance of small sauropod bones (which probably represent juvenile

individuals) in the Haţeg Basin may be an artefact and reflects the existence of age-classed communities among dinosaur populations (Le Loeuff, 2005). In answer to the doubts about the dwarf status of *Magyarosaurus*, Csiki *et al.* (2007) have suggested that, as originally expressed by Huene (1932), "*M*." *hungaricus* is different from the type species of *Magyarosaurus* and probably represents a distinct, still unnamed, large-sized titanosaurian genus.

Struthiosaurus (Ankylosauria, Nodosauridae)

In contrast to the above mentioned taxa, *Struthiosaurus* is not exclusive to the Hateg Basin of Transylvania as its fossil remains have also been found in other latest Cretaceous sites of central and southwestern Europe. Several species of *Struthiosaurus* have been recognized: *S. austriacus* (type species) from the Early Campanian of Lower Austria (Bunzel, 1871; Seeley, 1881; Nopcsa, 1929; Pereda Suberbiola and Galton, 1994, 2001), *S. transylvanicus* from the Early Maastrichtian to early Late Maastrichtian of Transylvania (Nopcsa, 1915, 1929; Pereda Suberbiola and Galton, 1997; see Dalla Vecchia, 2006 for a discussion of the age), *S. languedocensis* from the Early Campanian of Languedoc (Garcia and Pereda Suberbiola, 2003), and *Struthiosaurus* sp. indet. from the Late Campanian-Early Maastrichtian of the Iberian Peninsula (Pereda Suberbiola *et al.*, 1995; Pereda Suberbiola, 1999). Most of the material is incomplete and represents isolated mature individuals, but different growth stages are known in the Austrian assemblage. *Struthiosaurus* was a small ankylosaur, with adults having a body length of about 2.5-3 m and an estimated body weight of probably less than 300 kg (Pereda Suberbiola, 1992; Fig. 1). *Struthiosaurus* is regarded as conservative within the Nodosauridae in retaining several symplesiomorphies (Pereda Suberbiola and Galton, 2001). On the basis of a few immature-like features (i.e., lack of fusion between quadratojugal and jugal, shortness of the dentary) present in presumed adult individuals of *S. austriacus*, these authors preliminarily interpreted it as a paedomorphic dwarf. The conclusion that *S. austriacus* is both primitive and paedomorphic with regard to its larger relatives is considered to be somewhat incongruous by Makovicky (2002) because heterochronic characters showing transformations to states that are seen in juveniles of outgroup taxa were not presented by us. Ontogenetic growth series are not well known among thyreophorans to test the occurrence of the observed immature-like features of *Struthiosaurus*, but at least the basal thyreophorans *Scelidosaurus* and *Emausaurus* have a quadratojugal that is not fused to the quadrate (Norman *et al.*, 2004). In a recent paper on ankylosaurian phylogeny, *Struthiosaurus* appears to be one of the most basal nodosaurids and tentatively less derived than *Hungarosaurus* from the Santonian of Hungary (Ösi, 2005). Adults of *Struthiosaurus* are considerably smaller than those of *Hungarosaurus* (4.5-5 m; Ösi, 2005) and other nodosaurids, as well as most ankylosaurids and all stegosaurs. *Struthiosaurus* retains a small body size, which is the plesiomorphic condition for Thyreophora; increases of body size occur independently in Stegosauria, Ankylosauridae and Nodosauridae (Fig. 2). In this phylogenetic context, *Struthiosaurus* is not paedomorphic, but rather a primitive component of the nodosaurid morphocline. Its small body size may be explained by simple natural selection of small non-paedomorphic individuals.
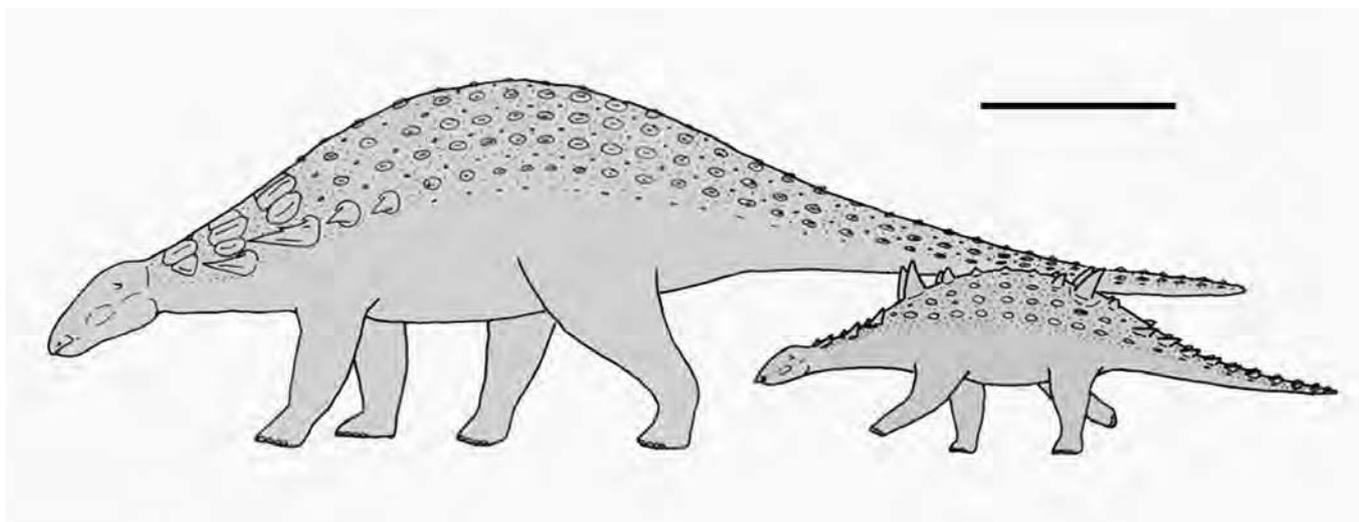

FIGURE 1. Hypothetical life restorations of the nodosaurid ankylosaur *Struthiosaurus* from the latest Cretaceous of Europe and of its contemporary relative *Edmontonia* from North America (modified from Pereda Suberbiola, 1992: fig. 5). Adult individuals of species of *Struthiosaurus* had a body length of approximately 2.5-3 m and an estimated body weight probably less than 300 kg as against 6-7 m and about 2000-2500 kg for *Edmontonia*. Scale bar: 1 m.
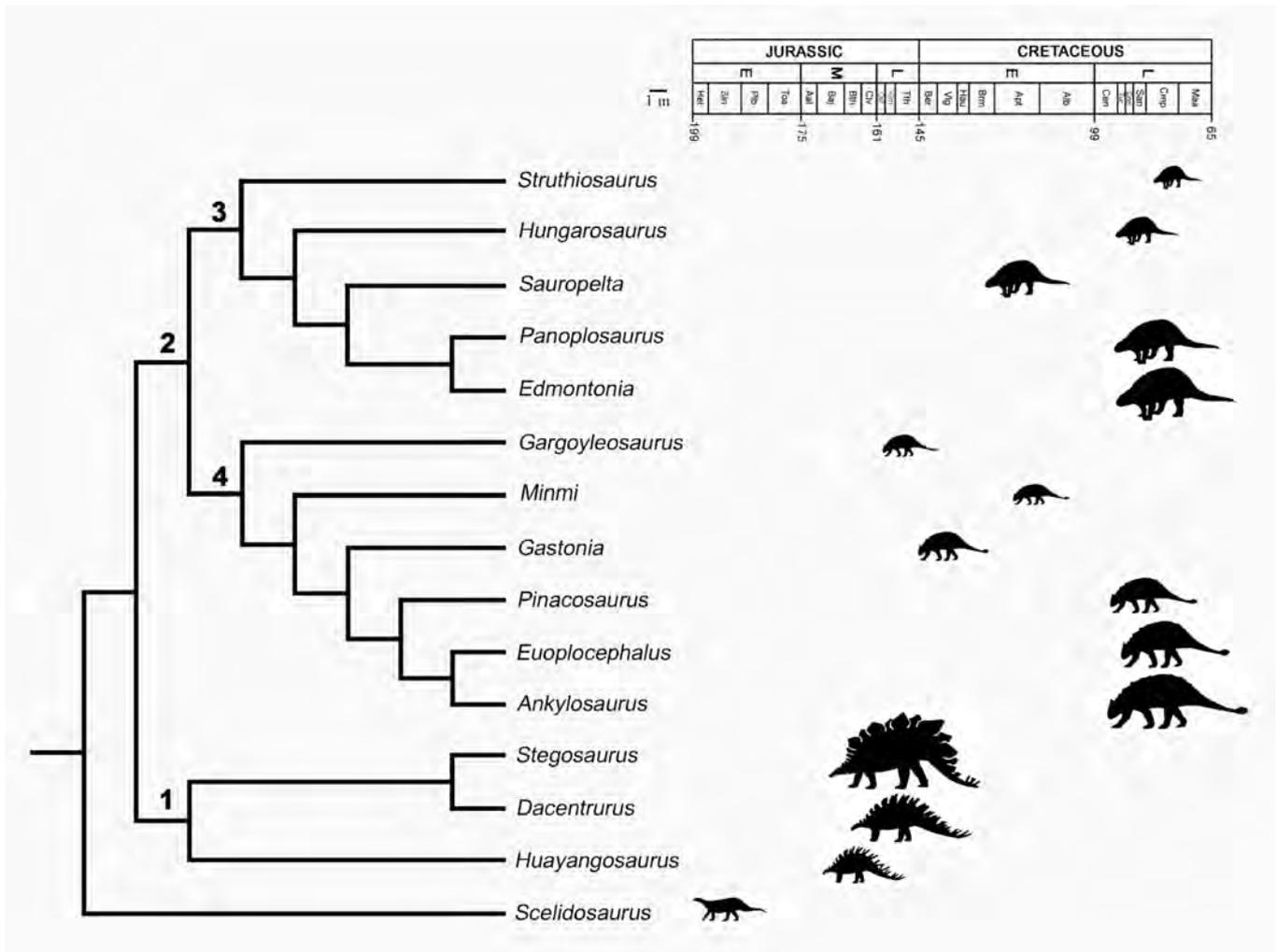
FIGURE 2. Left, simplified phylogeny of thyreophoran dinosaurs, with emphasis on the ankylosaurs. Explanation of nodes: (1) Stegosauria, (2) Ankylosauria; (3) Nodosauridae; (4) Ankylosauridae. Right, temporal distribution of the thyreophoran taxa with relative size indicated by body length in outline. Data from Galton and Upchurch (2004), Norman *et al*. (2004), Vickaryous *et al*. (2004), and Ösi (2005). The primitive condition for Thyreophora (retained by *Struthiosaurus*) is a relatively small body size; independent body increases occur in Stegosauria, Ankylosauridae and Nodosauridae.

DISCUSSION

According to Weishampel *et al*. (1993, 2003) and Jianu and Weishampel (1999), the adult individuals of the Transylvanian dinosaurs *Magyarosaurus dacus* (sauropod), *Telmatosaurus transsylvanicus* (hadrosaurid) and *Zalmoxes robustus* (basal iguanodontian) are smaller than their closest relatives and look like the juveniles of their putative ancestors. Therefore, they have been regarded as paedomorphic dwarfs. However, these results should be treated cautiously as: a) the statistical data does not support paedomorphosis as the cause of the dwarf condition of *Magyarosaurus* (Mussell and Weishampel, 2000); b) hadrosauroids closely related to *Telmatosaurus* have a similar adult body size to it (measurements of Carrano, 2006). Only the rhabdodontid *Zalmoxes* possibly undergoes paedomorphic dwarfing, more extremely in *Z.*

robustus, within the context of its immediate clades (Weishampel *et al*., 2003). With regard to the ankylosaur *Struthiosaurus*, another component of the dinosaur fauna of Transylvania (but also known in other areas of the European archipelago), whose small body size was previously interpreted in terms of heterochronic trends (Pereda Suberbiola and Galton, 2001), it may simply retain the plesiomorphic condition for Thyreophora.

The paucity of detailed ontogenies limits the interpretation of dwarf dinosaurs in the Late Cretaceous of Transylvania and of the European Archipelago in general. Only the rhabdodontid *Zalmoxes robustus* is known from a partial ontogenetic series, which provides the opportunity to analyze intraspecific growth and to discuss the potential for heterochronic changes in skeletal features (Weishampel *et al*., 2003). Other presumed dwarf dinosaurs, such as *Telmatosaurus*, *Magyarosaurus* and

Struthiosaurus, are known mainly from fragmentary or incomplete remains. The discovery of additional, more complete fossil material can help to test the dwarfing hypothesis and in interpreting possible heterochronic trends.

The emergent field of osteohistology, i.e. the study of bone microstructure, is a useful tool to assess dinosaur life-history parameters such as growth rates and timing of developmental events (Erickson, 2005). Palaeohistologic research is one of the most exciting avenues to help gain a comprehensive understanding of dinosaur evolutionary biology (Erickson *et al*., 2004). For example, Sander *et al*. (2006) described *Europasaurus holgeri* as a diminutive macronarian sauropod (body length up to 6.2 m in adults) from the Late Jurassic of Germany; bony histology suggests that this dwarf species evolved on islands around the Lower Saxony Basin through a decrease in growth rate from its larger ancestor. Sander *et al*. (2006) noted that previous hypotheses about island dwarfs among dinosaurs have focused on the Cretaceous of Europe, in particular on the dinosaurs from the Maastrichtian Haţeg Basin of Romania (also the mid-Cretaceous dinosaurs from the peri-Adriatic carbonate platform; see Dalla Vecchia, 2005; and the basal Cretaceous dinosaurs from the Cornet Basin of Romania; Benton *et al*., 2006), but the ontogenetic growth patterns of these dinosaurs remain uncertain in the absence of bone histological studies.

Nopcsa (1923) linked the downsizing of Transylvanian dinosaurs to insular evolution, which apparently has ecological counterparts in the Pleistocene-Holocene faunas of dwarfed mammals on various Mediterranean islands (Crete, Cyprus, Sicily, Malta, Sardinia, etc.). These islands were populated by endemic terrestrial mammals with highly specialized features, such as dwarf elephants, hippopotami and deer (Sondaar, 1977; Azzaroli, 1982). In comparison with the faunas of the mainland, insular mammals share a number of peculiar features, as follows: limited diversity; lack of large carnivores; reduction in size of large herbivore mammals; increase of size of small mammals (e.g., rodents and insectivores); low individual variability within populations; high evolutionary rates; vulnerability (leading to a rapid extinction in the event of arrival of continental species) and, lastly, each island has its own fauna, different from the assemblages of other islands (Thaler, 1973; Sondaar, 1977; Azzaroli, 1982). Dinosaurs and their habitats are not comparable to mammals and theirs; at best, they can be regarded as analogues. Anyhow, several of the above mentioned typical insular mammalian features do not apply to the European dinosaurs. For example, predators are present, including several kinds of small to medium-sized theropods (dromaeosaurs, other maniraptoriforms, ceratosaurians, etc.; Csiki and Grigorescu, 1998; Allain and Pereda Suberbiola, 2003). Moreover, some dinosaurs (at the generic level) are not endemic to

an island: besides Transylvania, *Zalmoxes* sp. (with possible affinities to *Z. shqiperorum*; Sachs and Hornung, 2006) and *Struthiosaurus austriacus* are known from the Early Campanian of the Austroalpine Island (Pereda Suberbiola and Galton, 2001), whereas other small-sized species of *Struthiosaurus* are represented in the Campanian-Maastrichtian sites of the Ibero-Armorican Island (Garcia and Pereda Suberbiola, 2003). Occurrences of gigantism have not been reported so far from the Late Cretaceous of Europe, with the possible exception of the very large flightness bird *Gargantuavis* from southern France, which reached approximately the size of an ostrich (Buffetaut and Le Loeuff, 1998). Finally, some of the insular features mentioned above, such as the degree of variability within populations, vulnerability, and evolution rates, cannot be tested because of the incompleteness of the fossil record.

The Haţeg Basin and the surrounding regions has long been regarded as representing a Late Cretaceous island (Nopcsa, 1923), but its exact surface area is imprecisely known and represents a matter of controversy due to its complex palaeogeography (Le Loeuff, 2005; Dalla Vecchia, 2006). Weishampel *et al*. (1991) suggested that the surface of the Haţeg Island was of only 7500 km^2 and that it was separated from neighboring islands of central Europe by at least 200 km of shallow sea. This is consistent with Nopcsa's (1923) interpretation about the restriction of the size of the territory as the explanation of the small size of Transylvanian dinosaurs. However, subsequent interpretations showed that this region was part of a tectonically-dynamic mainland and argued rather for an isolated outpost (Jianu and Boekschoten, 1999). In fact, the Haţeg Basin occurred in the zone of collision of three microcontinental plates: Apulia, Rhodope and Moesia, as a postorogenic, extensional basin within the southern Carpathian Orogen (Therrien, 2005). Recent palaeogeographical reconstructions of the European Tethys during the latest Cretaceous (see maps in Dalla Vecchia, 2006) show that the Haţeg Basin was a long strip of emerged land separated from the Australpine Island; it was either a peninsula of the Ukranian Shield (Philip *et al*., 2000) or a narrow island (Odin and Lamaurelle, 2001). This landmass could have reached at the very least 50000 km^2 in area, and probably as much as 100000 km^2 (Le Loeuff, 2005; based on Csiki and Grigorescu, 2001). Other European islands, presumably also inhabited by dwarf dinosaurs (such as the ankylosaur *Struthiosaurus*), were even much larger: up to 250000 km^2 for the Austroalpine Island, and about 1000000 km^2 for the Ibero-Armorican Island, the largest of the European islands (surface area estimations based on Philip and Floquet, 2000).

After studying the main latest Cretaceous vertebrate localities of Beira Litoral in Portugal, Antunes and Sigogneau-Russell (1992, 1996) concluded in favour of a faunal impoverishment and dwarfing in this area as a result of the reduction of the land surface and posteriorly

of climatic changes. Only fossils of small to very small vertebrates have been collected in the Aveiro, Taveiro and Viso sites; middle-sized forms are rare and large ones are absent. According to Antunes and Sigogneau-Russell (1992, 1996), the complete absence of large dinosaurs (e.g., sauropods), "which were frequent in Portugal as late as the upper Cenomanian", leads one to conclude that their extinction occurred well before the end of the Cretaceous, probably following the major regression that progressively restricted the Lusitanian Gulf during most of the Late Cretaceous and part of the Paleogene. The severe modifications of the environment would have spared the small dinosaurs, which survived up to the latest Cretaceous. However, the absence of fossils of large vertebrates in the Beira Litoral assemblages may be explained as well by taphonomic (and even palaeoecological) biases. As admited by Antunes and Sigogneau-Russell (1996), there is a gap in the fossil vertebrate record of the Iberian Peninsula from the Turonian to the Campanian. Moreover, the Lusitanian area was in contact with other lands of the Ibero-Armorican Island during the Late Cretaceous (see palaeogeographical maps in Dercourt *et al*., 2000), where large dinosaurs have been recorded. This does not support the interpretation of the Beira Litoral dinosaurs as dwarfs forms.

CONCLUSIONS

Since Nopcsa's time, the dinosaurs from the latest Cretaceous of Transylvania, including the ornithopods *Zalmoxes* and *Telmatosaurus*, the ankylosaur *Struthiosaurus* and the sauropod *Magyarosaurus*, have been considered as possible dwarfs because they are smaller in size than their closest relatives elsewhere. This pattern does not seem to be exclusive to the Transylvania fauna because small-sized species of *Struthiosaurus* are also known from other sites in the European Archipelago (Austria, southern France, Iberian Peninsula). Recent works have suggested that the heterochronic changes might be the reason for the reduction in size of European dinosaurs, but alternative hypothesis (e.g., taphonomic biases) have questioned this interpretation. Fossils belonging to medium to large-sized dinosaurs (such as sauropods and theropods) have been recovered, together with the remains of the presumably dwarfs forms, in Transylvania and in other European outcrops. Arguments used in favour of the hypothesis of heterochronic dwarfism in latest Cretaceous dinosaurs of Europe are so far tentative; the available information is not conclusive in confirming (but it does not invalidate) the occurrence of true paedomorphic dwarfs. Only the rhabdodontid *Zalmoxes* appears to be a good candidate. Additional fossil material, preferably consisting of complete growth series, is needed to solve the problem. Osteohistological studies can be of great help for a better understanding of the evolution of insular dinosaurs.

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Late Cretaceous vertebrate assemblages of Romania and elsewhere in Europe are classic examples of island faunas in the fossil record, and are characterized by dwarfed herbivorous dinosaurs and other endemic taxa that are noticeably primitive relative to their mainland contemporaries. Fossils of the predators inhabiting the European paleoislands, however, are exceptionally rare and fragmentary. We describe a new dromaeosaurid theropod, based on an articulated skeleton from the Maastrichtian of Romania, which represents the most complete predatory dinosaur from the middle to Late Cretaceous of E... Cretaceous period dinosaurs list with pictures, information & facts. Discover the dinosaurs that lived in the Cretaceous Period. T Rex, Spinosaurus & more. Â The specimen was found in the Anacleto Formation â€" a Late Cretaceous rock formation located in Argentina. You can find out more about this dinosaur here: Abelisaurus Facts. Albertosaurus. Characterization of macroecological patterns for latest Cretaceous dinosaur communities is essential to understand how those faunas were changing during the run-up to the Cretaceous-Paleogene extinction event, and thus the cause of the more. Characterization of macroecological patterns for latest Cretaceous dinosaur communities is essential to understand how those faunas were changing during the run-up to the Cretaceous-Paleogene extinction event, and thus the cause of the extinction. Â Diversity and faunal changes in the latest Cretaceous dinosaur communities of southwestern Europe.