

THE "DINOSAUR ISLAND" – NEW INTERPRETATION OF THE HAȚEG BASIN VERTEBRATE FAUNA AFTER 110 YEARS

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Rezumat

“Insula Dinozaurilor” - Noi interpretări asupra faunei de vertebrate din Bazinul Hațegului după 110 ani

Fauna de vertebrate maastrichtiane din Bazinul Hațegului, România, a fost descrisă de către F. Nopcsa drept una insulară, datorită numeroaselor caracteristici paleobiologice ieșite din comun, cum ar fi: endemicitatea ridicată și diversitatea scăzută a faunei, precum și caracterul primitiv și dimensiunile reduse (considerate a fi rezultatul unui fenomen de nanism insular) ale taxonilor componenți. Totuși, această ipoteză nu a fost serios re-investigată în lumina cantității apreciabile de noi date și descoperiri care s-au acumulat între timp. Prezenta contribuție sintetizează corpul de noi evidențe acumulate, pro sau contra ipotezei de faună insulară, și ajunge la concluzia că fauna de vertebrate din Bazinul Hațegului reprezintă o faună insulară; însă originea și istoria evolutivă a acestei faune a fost complexă, implicând mai multe valuri de migrații ce au avut istorii evolutive diferențiate. "Insula Hațeg" a fost nu numai o fundătură evolutivă, după cum a sugerat Nopcsa, dar și un leagăn ce a dat naștere unor noutăți evolutive.

INTRODUCTION

Beginning with the early years of the 20th century, when the first Late Cretaceous continental vertebrate remains were discovered by NOPCSA (1900, 1902, 1905) in the Hațeg Basin (and surrounding areas of Transylvania), several peculiar features of this assemblage were noted. One of the most outstanding aspects of this mostly reptilian fauna was represented by its presumed insular habit. Nopcsa, a promoter and early supporter of the

theory of plate tectonics (WEISHAMPEL & REIF 1984), suggested that this fauna (made up, in his best knowledge, mainly of dinosaurs, besides turtles, crocodilians and pterosaurs) lived on an island within the realm of the Tethys Ocean (NOPCSA 1923 a). And this restrictive, insular habitat markedly influenced the composition and evolution of the assemblage, leading to the development of peculiar features, seen rarely in the case of fossil assemblages, especially from the Mesozoic (see below). Until recently, this paradigmatic conclusion of Nopcsa was largely accepted, but was never analysed in detail and supported by independent data.

The present contribution seeks to discuss the hypothesis of the insular nature of the Late Cretaceous fauna from the Hațeg Basin in the light of the newest discoveries and developments, made both locally and worldwide, to establish whether the data accumulated during the 110 years that went on from its first discovery supports or contradicts the insular hypothesis.

GEOLOGICAL BACKGROUND

The Hațeg Basin, situated in the northwestern part of the Southern Carpathians, and surrounded by the Retezat, Șureanu and Poiana Ruscă Mountains, represents a post-tectonic depression formed subsequently to the Latest Cretaceous Laramian tectogenetic phase that built up the major structural framework of the Southern Carpathians (SĂNDULESCU 1984). The formation of the basin took part concomitantly with the uplift of the nappe structure of the Carpathians, as a consequence of local post-orogenic collapse of the new orogen, along major faults (WILLINGSHOFER 2000). The temporal overlap between the raise of the surrounding areas and marked subsidence within the basin led to the accumulation of a thick pile of siliciclastic continental deposits, preserved especially in the central and northwestern areas of the basin.

The molasse-type detritic sequences, varying from conglomerates and breccias to sandstones, silts and mudstones, were grouped in two major lithostratigraphic units, considered as being largely synchronous: the Sânpetru and Densuș-Ciula formations, the first one outcropping in the central part of the basin, around Pui and in the Sânpetru-Totești-Nălaț-Vad area, the second one in the western part, in the Densuș-Vălioara-Tuștea-Fărcădin area (GRIGORESCU 1992). The lithology of the two units is slightly different, mainly due to the presence of the pyroclastic sediments and volcanoclasts in the lower part of the Densuș-Ciula Formation; however, the known faunal and palynological assemblages from the two units are comparable and supports their synchronicity. The age of these deposits were first considered as Danian (in the sense of Latest Cretaceous, NOPCSA 1905), then as Late Maastrichtian

(DINCĂ & all. 1972; ANTONESCU & all. 1983). Recently, the age of the deposits was established to be Maastrichtian, based on palaeomagnetism (PANAIOTU & PANAIOTU 2002) and palynology (VAN ITTERBECK & all. 2005); biostratigraphic studies in the underlying marine deposits, based on foraminifera (e. g. NEAGU 2006) and calcareous nannoplankton (e. g. GRIGORESCU & MELINTE 2002; MELINTE & BOJAR 2006) also support this age assignment.

Lithological, sedimentological and geochemical features of the Maastrichtian deposits (BOJAR & all. 2005; THERRIEN 2005, 2006; VAN ITTERBECK & all. 2004) allowed the reconstruction of the environmental conditions in which the Hațeg vertebrate assemblage lived. The sediments accumulated within a setting dominated by fluvial processes, placed at the foothills of the surrounding uplifted metamorphic massifs; the rapid, anastomosed river channels, the well or poorly drained floodplains, small lakes and swamps created a mosaic of microhabitats populated by a diverse invertebrate and vertebrate fauna. Vegetation was similarly diverse, varying from savannah-like plains with a groundcover of ferns and early angiosperms and disperse trees, swamps with a dense vegetation of ferns and angiosperms or gallery forests developed along the rivers, to mangrove forests (PETRESCU & DUȘA 1982).

The presence of a subtropical, seasonally variable, but dominantly semiarid climate is independently supported by paleobotany and palynology (PETRESCU & DUȘA 1982, VAN ITTERBEECK & all. 2005), sedimentology and geochemistry (BOJAR & all. 2005; THERRIEN, 2005), clay mineralogy (S. RĂDAN, unpublished data), taphonomie (CSIKI 2006) and palaeomagnetism (PANAIOTU & PANAIOTU 2002). According to the paleomagnetic studies, the present area of the Hațeg Basin was situated at a more southerly position, of about 28-30⁰N, which is in agreement with the independent geological data.

NOPCSA AND THE DINOSAURS OF THE "HAȚEG ISLAND"

The discoverer and first student with important contribution to the understanding of the Late Cretaceous vertebrate faunas of the Hațeg Basin and surrounding areas was F. Nopcsa. Nopcsa, a local nobleman, had dedicated a large part of his prodigious scientific activity to the study of these fossil vertebrates, first reported by him in 1897 (2007 marking thus the 110th anniversary of the Hațeg Basin dinosaurs). Nopcsa published several monographical descriptions of the different reptilian taxa (mainly dinosaurs, but also turtles and crocodylians) from Hațeg (e. g. NOPCSA 1900, 1902, 1923 b, 1928), as well as a few synthetic overviews of the assemblage, discussing its relationships to faunas from Europe or other continents, and trying to decipher its origin and evolution (NOPCSA 1915, 1923 a).

In these contributions, Nopcsa drew attention to several peculiar features of the Hațeg reptilian fauna, features that in his opinion made this assemblage a particular one. These features included in the first place

(1) the **primitive character** of the assemblage in overall, as well as that of most of the included taxa. Nopcsa demonstrated that many of the Hațeg Basin dinosaurs were anachronistic relative to their late chronostratigraphic position, at the end of the Cretaceous. Thus, the hadrosaur "*Orthomerus*" (*Telmatosaurus*) *transsylvanicus* was considered as closely related to the primitive "trachodontids", while "*Rhabdodon*", another ornithopod taxon, was representing the even more ancestral group of "kallodontids", known mainly from the Late Jurassic. Nopcsa identified the same primitiveness also in the case of the sauropod "*Titanosaurus*" and in that of the ankylosaurian *Struthiosaurus*, as well as in the cases of the turtles (*Kallokibotion*) or pterosaurs ("*Ornithodesmus*"). Moreover, the assemblage itself had an archaic composition, being dominated by taxa considered by Nopcsa typical for the Late Jurassic – Early Cretaceous (sauropods, "kallodontids"), but lacking or occurring rarely in the contemporaneous faunas of North America.

Besides the archaism of the fauna, Nopcsa noted several other outstanding features, such as:

(2) the **markedly endemic nature** of the assemblage. In different stages of his work on the Hațeg fauna Nopcsa changed his views about the taxonomy and systematic position of the different taxa, proposing 3 different names for the hadrosaur *Telmatosaurus* (WEISHAMPEL & all. 1993): *Limnosaurus*, *Telmatosaurus* and *Orthomerus*, and as much as 4 for the basal euornithopod *Zalmoxes* (WEISHAMPEL & all. 2003): *Camptosaurus*, *Onychosaurus*, *Mochlodon* and *Rhabdodon*. However, regardless of these different understandings of the taxa, it was obvious to him that most of them represented endemics, either with a distribution strictly restricted to the Transylvanian area, or having a somewhat wider, European range. The names Nopcsa gave to the newly described species (*transsylvanicus*, *dacus*, *bajazidi* – after the name of his Albanian secretary, D. E. Bajazid) also illustrates this opinion, and even many of the genera he described were considered at least in different stages of his studies as being unknown from other areas (*Telmatosaurus*, *Kallokibotion* or the crocodylian *Allodapouschus*).

(3) the **small size** of many of the dinosaurian taxa was considered by Nopcsa as being one of the most important arguments supporting his idea of the Hațeg fauna as an insular one, by comparison to those from the Neogene Mediterranean islands (NOPCSA 1923 a). By comparing the different dinosaur taxa from the Hațeg Basin with their close relatives from other areas, Nopcsa noticed that those from Hațeg were significantly smaller than their

western European, North American, African or South American counterparts. The size of the Hațeg individuals of "*Rhabdodon*" was only half that of the individuals of the same genus discovered in southern France, that of the *Telmatosaurus* individuals only one-third or less than those of other hadrosaurs (especially from North America, the only ones known to Nopcsa outside Europe), while the size of the titanosaurs from Hațeg, illustrating the most important case of dwarfing, not exceeded one-fourth of the size of the large Late Jurassic neosauropods from North America or Africa. Nopcsa explained these observations as examples of "island dwarfism" (size reduction due to the insular habit of taxa that are represented in continental areas by large-sized individuals: elephants, hyppopotames etc.; Roth, 1990, 1992). The scientific community received the interpretation put forward by Nopcsa positively and since then it is cited as a classic example (and, for long time, the only one known from the Mesozoic) of insular dwarfism (e. g. DALLA VECCHIA 2003; WEISHAMPEL & all. 1991).

(4) the **low diversity** of the Hațeg fauna was also noticed early by Nopcsa (NOPCSA 1915), who underlined that it (and the Late Cretaceous European faunas in general, considered by Nopcsa as having a similar, almost identical composition with that from Hațeg) included a small number of taxa – not more than 6 dinosaurs (including the purported bird *Elopteryx nopcsai* – ANDREWS 1913), as well as one turtle (or at most two congeneric species, cf. Nopcsa, 1923b), one crocodylian and one pterosaur. This composition was in neat contrast with that of the Late Cretaceous faunas of North America that included, in Nopcsa's times, at least 25 dinosaur taxa.

To explain all these peculiarities of the Hațeg vertebrate fauna, Nopcsa made appeal to a simple and attractive hypothesis, namely that this fauna lived in an insular environment (NOPCSA 1923 a). Nopcsa, a promoter of the ideas grouped subsequently under the name of "plate tectonics" (WEISHAMPEL & REIF 1984), had no difficulties in imaging the habitat of the Cretaceous Hațeg vertebrates as an island placed in the middle of the Tethys Ocean, even in the lack of much supporting geological, tectonical and palaeogeographical evidence. And, once the idea of the insular habitat was accepted, the particular palaeobiological features observed by Nopcsa were easy to explain, these reproducing those observed in several instances of Neogene or Recent island faunas. This working hypothesis, similarly to that of the existence of the insular dwarfism in the case of the Hațeg dinosaurs, achieved widescale acceptance, and the dinosaur fauna of the Hațeg Basin was frequently cited as a classical example of Mesozoic insular faunas, one of the few ones known, without critically reviewing the arguments put forward by Nopcsa in the light of the subsequent new discoveries, both locally or worldwide.

However, there are several recent attempts to question either the validity of Nopcsa's most important argument for an insular habitat – that of the existence of insular dwarfs in the Hațeg Basin (LE LOEUFF 2005), as well as the insular character of the fauna in overall (JIANU CORALIA MARIA & BOEKSCHOTEN 1999).

This contribution is an essay to critically review the original Nopcsa hypothesis, that of the Cretaceous vertebrate fauna from the Hațeg Basin seen as an island fauna, in the light of the new geological and paleontological data acquired from the Hațeg Basin, on one hand, as well as taking into account the most recent developments in the fields of Mesozoic vertebrate Paleontology and phylogeny, paleobiogeography and paleogeography - tectonics, on the other.

NEW DISCOVERIES AND NEW INTERPRETATIONS

1. New discoveries in the Maastrichtian of the Hațeg Basin

Following the tragical death of Nopcsa, the studies concerning the reptilian fauna from the Hațeg Basin were interrupted for over a half century, a period marked only by isolated paleontological discoveries made during geological mapping or exploration activities, or by small-scale studies on different components of the local fauna and flora (CSIKI 2005, for a review). It was only beginning with 1977, that the geological and paleontological research activities were renewed, first by the Paleontology Laboratory of the University of Bucharest (under the supervision of dr. Dan Grigorescu) in collaboration with the Hunedoara County Museum (to become later the Muzeul Civilizației Dacice și Romane) from Deva (Ion Groza, Coralia-Maria Jianu). Since then, the researches continued without major interruptions, with contributions from other researchers from Romania (the Babeș-Bolyai University, Cluj-Napoca, under the supervision of dr. Vlad Codrea, in collaboration with researchers of the Royal Belgian Institute of Natural Sciences, Bruxelles, Belgium) or from abroad (SUA, United Kingdom, France, Germany, the Netherlands, Spain) (CSIKI 2005). These ongoing researches led to the accumulation of a wealth of new data concerning the vertebrate fauna (as well as the invertebrates and floras) from the Maastrichtian of Hațeg Basin and surrounding areas, as well as the paleogeographic – paleotectonic context in which it lived. The most important new developments are:

- discovery of several new taxa of vertebrates, widening the faunal list from 10 taxa (known to Nopcsa) to over 60 taxa (GRIGORESCU 2005), including members of all major vertebrate groups: fishes, amphibians (anurans, albanerpetontids), sauropsid (turtles, lizards,

snakes, crocodylians, pterosaurs, ornithischian and saurischian dinosaurs including birds) and synapsid (multituberculate and possibly therian mammals) amniotes;

- revision of the anteriorly discovered taxa, either by Nopcsa or others, leading to the clarification of their taxonomy and systematic-phylogenetic position; these revisions showed that almost all taxa are new: the name *Magyarosaurus* was erected instead of *Titanosaurus* (HUENE 1932) or that of *Zalmoxes*, instead of *Rhabdodon*, with two different species (WEISHAMPEL & all. 2003), while *Telmatosaurus* was resurrected to replace *Orthomerus* (WEISHAMPEL & all. 1993). Besides these, several new, yet undescribed taxa of sauropods and theropods were also reported (CSIKI & GRIGORESCU 2004, 2005);

- discovery of important assemblages of invertebrates (PANĂ & all. 2002; CSIKI 2006) and plants, represented by macrofloral remains (e. g. MĂRGĂRIT & MĂRGĂRIT 1967) or palynomorphs (ANTONESCU et al. 1983; VAN ITTERBECK et al. 2005), allowing a better understanding of the Maastrichtian paleocommunity of the Hațeg Basin, reconstruction of the local vegetation and a more complete picture of the trophic relationships within the ecosystem;

- methodological diversification and in-depth analysis in the domains of sedimentology and geochemistry (e. g. VAN ITTERBECK & all. 2004; THERRIEN 2005, 2006; BOJAR et al. 2005) as well as regional geology and tectono-sedimentary evolution (e. g. SANDERS 1998; STILLA 1985; WILLINGSHOFFER 2000), allowing a more detailed understanding of the existing sedimentary environments and that of the geographical, climatic and sedimentological parameters controlling the accumulation of the Maastrichtian deposits, and, implicitly, the characteristics of the physico-geographical context of the environment of the Hațeg Basin paleocommunity.

2. New discoveries and interpretations in the vertebrate palaeontology, palaeogeography and paleobiogeography

After the completion of the scientific work of Nopcsa, a large number of new discoveries and conceptual advancements were made, allowing a reassessment of the explanatory framework he put forward to explain the peculiarities of the Hațeg paleocommunity.

One of the most important subsequent developments concerns the theoretical and methodological advancements made in the field of "insular biogeography" especially by MCARTHUR & WILSON (1967). The Insular Biogeography represents a field of the biogeography that defines and explains the factors controlling the specific diversity found in

an insular habitat (under this term being included all types of isolated communities, living on islands but also in oases, mountain tops or lakes).

According to the theory of island biogeography, the number of species existing on an island is controlled by several factors that influence directly the two parameters controlling local diversity: immigration rate (the rate at which new taxa are introduced) and extinction rate (the rate at which already present taxa are eliminated). The interconnected fluctuations of these two parameters lead to the establishment of a dynamic equilibrium state (the *equilibrium state* of the insular ecosystem), represented by the total number of taxa that can inhabit the island (the *equilibrium number*). The most important factors influencing these parameters, and respectively the equilibrium state, are: the dimension of the island (through the species-area effect, a larger area being capable of hosting a larger diversity), distance from the closest mainland (controlling the degree of isolation of the island, in the one and, and the taxonomic composition of the immigration, a function of the types of isolating barriers and of the dispersive potential of the different taxa, on the other hand) and the age of the island (controlling the degree to which the state of dynamic equilibrium was achieved).

Moreover, the island biogeography also identifies several of the biological blueprints that characterize an insular fauna such as the taxonomic bias in the composition of the island faunas (due to a severe filtering of the possible immigrants), presence of wide-scale intraclade adaptative radiations and that of evolutionary-adaptative phenomena such as insular gigantism or dwarfism, linked to the absence of the threatening predators or due to the shortage in the available resources or the relict and endemic character of the island faunas.

Besides the theory of insular biogeography, another important contribution is represented by the theory of vicariance biogeography, resulted from the synthesis of two paradigmatic theories (a geological one, represented by global tectonics, and a biological one, represented by the phylogenetic systematics; this theory is especially important in the evaluation of the different competing models of historical-biogeographical evolution of different paleofaunas (e. g. WEISHAMPEL & JIANU CORALIA MARIA 1997).

A second important advancement was made in the knowledge about the taxonomic composition of the different Late Cretaceous (and Mesozoic, in general) continental vertebrate faunas, from Europe and worldwide (see a synthesis of these in Csiki, 2002, unpublished, with more recent data from KIELAN-JAWOROWSKA et al. 2004; WEISHAMPEL & all. 2004 a). During the last century, Cretaceous continental vertebrate assemblages were discovered in all continents, sometimes covering the complete chronostratigraphic scale for this period; the dating of the different fossil assemblages became more precise, including absolute ages; using new procedures of investigation and fossil recovery led to the discovery

of previously ignored components of the paleocommunities, especially the small-sized ones; the accumulation of a large quantity of fossil material permitted the detailed taxonomical-systematic study of the different taxa, thus leading to a better understanding of the composition, abundance and taxonomic diversity of the different faunas; and, finally, the development of new analytical techniques for mapping the phyletic and evolutionary relationships between the different taxa (especially the methods of phylogenetic analysis, based on the concepts of the phylogenetic systematics) allowed a clearer and more detailed understanding of these relationships, the only ones that can reliably be used in the evolutionary and paleobiogeographic analysis of a certain area.

Finally, a third important theoretical contribution to the reassessment of the insularity of the Hațeg fauna is represented by the new studies and syntheses of paleogeography, paleotectonic and palinspastic reconstructions of the Tethys and surrounding areas. According to these syntheses (e. g. DERCOURT & all. 1993, 2000; ZIEGLER 1987), during the Cretaceous, the Tethys Ocean covered the southern part of present-day Europe and epicontinental seas connected it, while the emergent areas were restricted to islands of different sizes. The extension, limits of and relationships between these different continental areas fluctuated during the Cretaceous, depending on the sea-level changes, tectonical and orogenetic events taking place, and by mapping these fluctuations one can reconstruct the individuality and spatio-temporal continuity of any selected landmass along this period.

In the palinspastic reconstructions cited, the area of the present-day Hațeg Basin and surrounding areas was an emergent area during the Latest Cretaceous, having a considerable spatial extension: this emergent area can be conventionally designated as the "Hațeg island" (or the "Transylvanian Island"). Moreover, this emergent area shows a remarkable temporal continuity (although with considerable modifications in size and position, both in absolute terms and relative to other emergent landmasses) along the Cretaceous. The presence of an emergent area in this position suggests that the Maastrichtian vertebrate fauna of Hațeg can be considered as an island fauna.

3. Synthesis of the new data and the new model of the "Hațeg Island"

The new discoveries and theoretical advancements outlined above allow a critical reassessment of the paleobiological features considered by Nopcsa while outlining the hypothesis of the "Hațeg island fauna", from two viewpoints: (1) whether these features are still valid, and (2) whether they support the insular model of the Hațeg fauna. The 4 paleobiological features listed above will be rediscussed here, according the new arguments pro and contra.

(1) the **primitive character** of the assemblage itself, as well as that of the included taxa

For Nopcsa, the identification of the primitive status of the different taxa relied on the inherently restricted comparisons with the taxa known at his time, without a well-established systematic-phylogenetic background. Subsequently, through the discovery of supplementary skeletal material in the Hațeg Basin, or referred to closely related taxa from other areas, as well as development of phylogenetic analyses concerning these taxa, allowed the compared phylogenetic study of the Hațeg taxa within a much broader and sounder framework. The phylogenetic analysis of the better-known taxa: *Kallokibotion* (GAFFNEY & MEYLAN 1992), *Allodaposuchus* (BUSCALIONI & all. 2001), *Telmatosaurus* (WEISHAMPEL & all. 1993), *Zalmoxes* (WEISHAMPEL & all. 2003) and *Struthiosaurus* (PEREDA-SUBERBIOLA & GALTON 2001) revealed that these are basal, primitive members within their respective clades. This basal phylogenetic position contrasts with their late chronostratigraphic position, suggesting the presence of extended *ghost-lineages* (evolutionary lines suggested by phylogenetic analyses, but not yet supported by paleontological evidence; NOVACEK & NORELL 1992; WEISHAMPEL 1996), some of them descending into the later part of the Early Cretaceous. In overall, the identified ghost-lineages suggest the presence of long evolutionary lines evolving in geographical areas that lack fossil record during long time spans, thus "hidden" from a paleontological viewpoint – and the insular areas represent such regions, due to their fluctuating areal extension and their low potential of continental sediment accumulation and preservation. Mesozoic insular faunas with late chronostratigraphic appearance in the fossil record, relative to their moment of individualisation (faunas which we can call *resurgent faunas*), were cited from other parts of the world as well (e. g. MOLNAR & WIFE 1994; STILWELL & all. 2005).

Not only the individual taxa, but also the composition of the fauna (both overall taxonomic composition and relative abundance of the taxa) shows a pronounced archaic character, especially in the dominance of the rhabdodontid-type basal euornithopods and that of the titanosaur sauropods, this composition being more reminiscent of those of the Early Cretaceous faunas of Europe and North America, than of those from the Late Cretaceous of North America or Asia (e. g. HOLTZ et al. 2004). This similarity suggests the survival of a certain type of community structure characterising the Early Cretaceous, in isolation up into the Maastrichtian.

As a conclusion, both the basal position of many of the vertebrate taxa, and the community structure of the assemblage suggests a relict fauna, a conclusion that supports (although not exclusively) the hypothesis of insular fauna.

(2) the **endemic character** of the assemblage.

The monographic review of many of the taxa described by Nopcsa (WEISHAMPEL & all. 1993, 2003; BUSCALIONI & all. 2001), besides the discovery of a large number of new taxa redraw the conclusions reached by Nopcsa regarding the endemism of the fauna, but, *surprisingly*, in the sense of better supporting its endemic nature.

A partial faunal analysis, considering only the dinosaurian component of the assemblage, compared to the overall reptilian diversity (in order to keep it comparable with a similar analysis, for Nopcsa's period) allows the following observations. From the taxa described by Nopcsa, between 10% (pessimistic view, minimizing the degree of endemism) and 80% (optimistic view, with maximized endemism) of the described species (from a total of 11) represented endemic taxa, with the mention that Nopcsa himself, in his later syntheses, favored a more pessimistic viewpoint. Presently, from the about 50 reptilian taxa known, between 30% (pessimistic; 40% representing, however, uncertain taxa with regard to their endemic nature, due to lack of low-level taxonomic resolution) and 60% (optimistic; 38% uncertain) represent probably endemic elements. Further detailed studies of the less well known groups would lead to a degree of endemism varying from 35% to over 90% (!!), in this last, hyper-optimistic evaluation virtually the complete reptile assemblage would prove itself endemic at a specific or even at a generic level. From this viewpoint it is probably noteworthy that from the better-known and described reptile taxa only one (*Allodaposuchus precedens*) is reported to occur also in western Europe (France, Spain; BUSCALIONI & all. 2001).

The degree of endemism at the level of the whole fauna is probably comparable or even greater, taking into account that the anurans (VENCZEL & CSIKI 2002), lizards (FOLIE & CODREA 2005) and mammals (de ex. KIELAN-JAWOROWSKA & all. 2004) are represented almost exclusively by taxa known only from the Hațeg Basin.

As a conclusion, the endemic nature of the fauna, as noted by Nopcsa, remains significant even after considering the latest discoveries. Moreover, if Nopcsa considered that the endemic nature of the Hațeg fauna is representative at the level the Late Cretaceous of Europe, the new discoveries suggest that it is highly endemic even compared to other Late Cretaceous European faunas.

The marked endemism of the Hațeg assemblage also supports (although not exclusively) the hypothesis of insular fauna.

(3) the **small size** of the included taxa.

Recent phylogenetic analyses concerning dinosaur taxa (WEISHAMPEL & all. 1993, 2003) or other studies (JIANU & WEISHAMPEL 1999) demonstrated what Nopcsa had only suggested (based on coarse size comparisons between not closely related taxa), namely that at

least some of the taxa populating the Hațeg area (*Telmatosaurus transsylvanicus*, *Magyarosaurus dacus*, *Zalmoxes robustus*) represent possibly cases of autapomorphic dwarfing (a size reduction that affects only the respective taxa, not being characteristic of a whole phyletic line). In all these cases, the autapomorphic size reduction was explained by insular dwarfisms and considered to be linked to the insular habitat of the respective taxa, as suggested already by Nopcsa. However, recent studies also showed that autapomorphic size reduction is not the general rule even in the case of dinosaurs (it was not yet documented in any other vertebrate group). Thus, in the case of *Zalmoxes*, the description of a second species, *Z. shqiperorum* (WEISHAMPEL & all. 2003) as being larger than *Z. robustus* and attaining sizes comparable to those of the closest relatives of the genus (individuals of the genus *Rhabdodon*, known from France and Spain), shows that size reduction apparently affected these two congeneric and sympatric species differently (e. g. JIANU & WEISHAMPEL 2001; WEISHAMPEL & all. 2003). Possible explanations to this pattern can be sought probably in ecological differentiation between the two species (each of them exploiting different food resources, at least partially, to avoid direct competition), differentiation that probably promoted reproductive isolation within the ancestral *Zalmoxes* stock, followed by subsequent taxonomic diversification.

On the other hand, the case for insular dwarfism in the Hațeg sauropods was contested by LE LOEUFF (2005) based on the identification of several large-sized specimens, considered conspecific with the smaller individuals. The review of the sauropod material from the Hațeg Basin revealed, however, the existence of a larger taxonomic diversity in the case of the sauropods than considered before, the large-sized specimens being referred to another titanosaur taxon, different from *Magyarosaurus dacus* (e. g. CSIKI & GRIGORESCU 2006 a, CSIKI et al. 2007). The identification of the presence of a large-sized sauropod (reaching about 12-14 m in length) shows that, similarly to the case of *Zalmoxes*, dwarfing did not affect all sauropods in a uniform way.

In conclusion, even the presence of the small-sized taxa documents possible cases of insular dwarfism in the Hațeg fauna, this included large-sized taxa as well, comparable in dimensions to their close relatives in the mainland. This observation suggests that the answer of the different dinosaur taxa to a potentially restrictive habitat and resource shortage was differential, probably depending also on the ecological requirements and the particular evolutionary-paleobiogeographic history of each taxon as well.

(4) **low diversity** of the Hațeg fauna.

The most important reassessments of the original Nopcsa arguments for an insular theory occurred probably in the case of the faunal diversity. The discovery of a large number

of vertebrate taxa, including dinosaurs, in the Hațeg Basin showed that the local biodiversity was significantly higher than that known a century ago. The total count of 69 vertebrate taxa represents a much higher figure than anything reported from other Late Cretaceous European faunas. To preserve the terms of comparison mentioned above, only the reptilian component was considered in the different Late Cretaceous faunas, with a specific regard to the dinosaurs. This analysis suggests that the diversity of the Hațeg reptilian assemblage (17 taxa of dinosaurs, 41 of reptiles) matches that seen in much better studied faunas occupying larger continental areas, such as those from the Hell Creek or the Kirtland formations from North America, and the Djadochta or Nemegt formations from Mongolia, being surpassed only by the exceptionally fossil-rich fauna of the Judith River Group of North America or, marginally, by that from the Barun Goyot Formation of Mongolia (WEISHAMPEL & all. 2004 b, CSIKI 2002, unpublished). Moreover, the well-balanced faunal composition, including representatives of all major vertebrate groups and trophic levels and guilds (herbivores, insectivores, omnivores, predators, scavengers) from different size categories and habitat types (aquatic, terrestrial, arboricole, flying), suggests an old, stabilized fauna instead of a recent one established accidentally and by chance on an insular area.

Some features of the fauna are still remarkable:

- the lack of a large-sized predator in the top of the food chain. Although several discoveries of theropods were published (e. g. CODREA & all. 2002, CSIKI & GRIGORESCU 2003, KESSLER & all. 2005), suggesting a high diversity of them, large-sized theropods, usually representing the top predators in Mesozoic ecosystems, are missing. The recent report of one isolated remain of a middle-sized theropod (SMITH & all. 2002) does not change this picture in its essence. Most Hațeg Basin theropods have small sizes. The situation is reminiscent of those from the Early Cretaceous of China (the Yixian fauna) or the Late Cretaceous of Mongolia (the Barun Goyot and Djadochta faunas) (WEISHAMPEL & all. 2004 b), all of these being dominated by a diverse assemblage of small theropods, including representatives of trophically specialized, omnivorous-herbivorous taxa, that are also present in the Hațeg fauna (e. g. CSIKI & GRIGORESCU 2005; KESSLER & all. 2005). It is remarkable, however, that both the Chinese and the Mongolian faunas, although coming from continental settings occupying large areas, represent ecosystems developed under severe environmental stress: the presence of a habitat dominated by intense volcanic eruptions (Yixian) or by an arid, desertic climate (Mongolia). By comparison, it is thus conceivable that the special faunal composition of the Hațeg assemblage is similarly indicating a stressed environment – which supports, although not directly suggests, the idea of an insular fauna, with severe control on the resources (food, space).

- a low-diversity large-sized herbivore assemblage, which, together with the absence of the large-sized predators, might be indicative a restrictive, possibly insular, habitat.

- the presence of several groups of small, invertivorous/omnivorous, possibly opportunistic organisms showing high levels of diversity (lizards, multituberculates). Especially interesting is the case of the multituberculate mammals, represented by an endemic clade known only from the Hațeg Basin in the European Late Cretaceous, but which underwent here an important intra-clade radiation (e. g. CSIKI & GRIGORESCU 2006 b), suggestive of an adaptative radiation leading to diversification and to filling in of several ecological niches left empty by the isolated nature and filtered immigration pattern of a presumed insular habitat.

All these paleoecological features supports, although not directly and exclusively, the idea of an insular fauna; on the other hand, the balanced structure of the fauna suggests that it resulted from a long-term evolution that allowed reaching a state of dynamic equilibrium characterizing the mature island faunas.

CONCLUSIONS

The hypothesis of NOPCSA (1923 a) concerning the insular character of the Cretaceous vertebrate assemblage from the Hațeg Basin represented an innovative solution to explain a number of outstanding paleobiological features observed within this fauna. The hypothesis was afterward retaken by most of the researchers, being cited as a standard exemplification of Cretaceous insular faunas (e. g. MOLNAR & WIFFEN 1994) or representing the general explanatory background for the origin and evolution of the Hațeg fauna (e. g. WEISHAMPEL et al. 1991). However, the hypothesis itself was never reinvestigated, in order to assess to what measure the new discoveries and theoretical advancements support or contradict the original idea. Moreover, recent studies put into question arguments used by Nopcsa to support the insular status of the fauna (e. g. JIANU & BOEKSCHOTEN 1999; LE LOEUFF 2005). For these reasons, the reassessment of this hypothesis was considered necessary, looking especially at the paleobiological characteristics used to lay the foundations of the idea of " Hațeg Island", in the light of the newest discoveries and progresses made in fields such as Mesozoic continental vertebrate paleontology, systematics, phylogeny, stratigraphic and paleobiogeographic distribution of the taxa, as well as in the paleogeography and regional tectonics of the Central Tethyan region.

Analyzing the paleobiological arguments given by Nopcsa to support the idea of the Hațeg fauna as an insular one (*primitiveness of the taxa, highly endemic composition, small*

size of many dinosaurs, low diversity of the fauna), it is not less than remarkable that these are still valid, even if the accent put on the different arguments changed over the time due to the newest discoveries (locally, in Europe or worldwide), and especially due to the new concepts and methods of phylogenetic and paleobiogeographic analysis.

Thus, the argument of the primitiveness of the taxa, in the case of most of the better known ones (turtles, crocodylians, dinosaurs, multituberculates), is still upheld; actually, the primitive character is even better argued in many of these cases by placing the respective taxa into comprehensive phylogenetic analyses (dinosaurs, turtles), or was even only recently demonstrated in the case of others (*Allodaposuchus*). The overall assemblage has an atavistic, primitive aspect compared to other contemporaneous faunas from outside Europe, especially taking into account its late chronostratigraphic setting; it is more reminiscent of the late Early Cretaceous Euramerican faunas. The relict character of the fauna suggests that the Hațeg area functioned as a sort of evolutionary refugium.

The degree of endemism of the fauna is even greater than was known to Nopcsa, being underscored by the discovery of numerous new vertebrate taxa. Within the framework of the Late Cretaceous European faunas, it shows a degree of endemism of at least 35-40% (depending on the taxonomic resolution), but this can be as much as 90%. In a larger, global context, the endemism of the fauna is even more pronounced. This feature of the Hațeg fauna suggests the presence of a long hidden evolutionary history (not yet documented by fossils).

The small size of several of the dinosaurian taxa (*Telmatosaurus*, *Zalmoxes*, *Struthiosaurus*, *Magyarosaurus*), compared to that of their close relatives, represent probably cases of dwarfism (and possibly autapomorphic, insular dwarfism), even if these hypotheses were not yet supported by independent evidence (bone histology, e. g. SANDER et al. 2006). On the other hand, apparently not all dinosaurian taxa were affected by dwarfism, at least *Zalmoxes shqiperorum* (WEISHAMPEL & all. 2003) and "*Magyarosaurus*" *hungaricus* (CSIKI & GRIGORESCU 2006 a) reaching larger sizes, comparable to those of their relatives from the French-Iberian Landmass (*Rhabdodon*, *Ampelosaurus*) or other continents. This observation suggests that the evolution of the fauna was not a simple, linear one, with a single moment of immigration followed by the adaptation to the insular environment, but instead a complex one in which some taxa avoided to be influenced by the reduction in the available resources, either due to the lack of time necessary to achieve these adaptations (i. e. reaching the island later than other taxa, and not having time to reduce their size, or, alternatively, arriving at a moment when the size of the island augmented by accretion or continental collision, thus rendering unnecessary this adaptation – a possible case being that of "*M.*" *hungaricus*), or by

adopting a different lifestyle and feeding habit, thus avoiding direct competition with their sympatric relatives (*Zalmoxes*).

Finally, the diversity, considered low by Nopcsa, proved itself to be much higher than previously thought, several other groups of vertebrates being added to the already known dinosaurs, pterosaurs, crocodylians and turtles. The comparative analysis of the Hațeg fauna shows that is more similar to the relatively rich ones from the Late Cretaceous Asia or North America, but somewhat greater than those contemporaneous from Europe. However, even if the overall diversity is not low, it shows several distinctive features such as lack of a top predator, low diversity of the mega- and mezoherbivores, high diversity of the small-sized theropods and that of the trophic specialists (lizards, multituberculates – among these, the significant adaptative radiation of the latter is especially noteworthy). All these observations are compatible, although not exclusively, with the "insular fauna" hypothesis.

The synthesis of the known paleontological – paleoecological data shows that the Maastrichtian fauna from Hațeg presents several features that characterize modern (Recent or Plio-Pleistocene) insular faunas. Even if these characters do not prove definitively the insular character of the Hațeg fauna, they are supporting it and, along with the paleogeographic-paleotectonic arguments, represent support for the hypothesis put forward by Nopcsa a century ago – that of the insular character of the Maastrichtian vertebrate fauna from the Hațeg Basin.

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REFERENCES

ANDREWS C. W. 1913. On some bird remains from the Upper Cretaceous of Transylvania. Geological Magazine. **10**: 193-196.

- ANTONESCU E., LUPU D. & LUPU M. 1983. Correlation palinologique du Crétacé terminal du sud-est des Monts Metaliferi et des Depressions de Hațeg et de Rusca Montană. *An. Inst. Géol. Géophys.*, **59**: 71-77.
- BOJAR A.-V., GRIGORESCU D., OTTNER F. & CSIKI Z. 2005. Palaeoenvironmental interpretation of dinosaur - and mammal-bearing continental Maastrichtian deposits, Hațeg basin, Romania. *Geological Quarterly*, **49** (2): 205-222.
- BUSCALIONI A. D., ORTEGA F., WEISHAMPEL D. B. & JIANU CORALIA. MARIA. 2001. A revision of the crocodyliform *Allodaposuchus precedens* from the Upper Cretaceous of the Hațeg Basin, Romania. Its relevance in the phylogeny of Eusuchia. *J. Vert. Paleontology*, **21**, (1): 74-86.
- CODREA V., SMITH T., DICA P., FOLIE A., GARCIA G., GODEFROIT P. & VAN ITTERBEECK J. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Hațeg Basin (Romania). *C. R. Palevol.*, **1**(3) : 173-180.
- CSIKI Z., 2002. unpubl. Paleobiogeografia faunelor continentale cretacice. Univ. Bucharest.
- CSIKI Z., 2005. unpubl. Sistematica și tafonomia microvertebratelor și dinosaurilor saurischieni din Maastrichtianul Bazinului Hațeg. Ph. D. thesis, Univ. Bucharest.
- CSIKI Z. 2006. Insect borings in dinosaur bones from the Maastrichtian of the Hațeg Basin, Romania - paleoecological and paleoclimatic implications. In: Z. Csiki (ed.) *Mesozoic and Cenozoic Vertebrates and Palaeoenvironments. Tributes to the career of Dan Grigorescu*, Ed. Ars Docendi, 95-104
- CSIKI Z. & GRIGORESCU D. 2003. Theropod dinosaurs of the Hațeg Basin – are they more diverse than thought?. Abstracts volume. Fourth National Symposium of Paleontology, Cluj-Napoca, 17.
- CSIKI Z. & GRIGORESCU D. 2004. Maastrichtian sauropods of the Hațeg Basin, Romania. Abstracts, 2nd Symposium of the European Association of Vertebrate Paleontologists, Brno, 10.
- CSIKI Z. & GRIGORESCU D. 2005. A new theropod from Tustea: are there oviraptorosaurs in the Upper Cretaceous of Europe? Abstracts volume, 3rd Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP), Darmstadt.
- CSIKI Z. & GRIGORESCU D. 2006 a. The revision of „*Magyarosaurus*” *hungaricus* Huene (Dinosauria: Sauropoda) from the Hațeg Basin. Extended Abstracts, 8th Mining, Metallurgy and Geology Conference, EMT, **65-70** (In Hungarian).
- CSIKI Z. & GRIGORESCU D. 2006 b. Maastrichtian multituberculates of the Hațeg Basin, Romania – implications for multituberculate phylogeny, evolution and paleobiogeography. In Barrett, P. M. & Evans, S. E. (eds.), 9th International

Symposium on Mesozoic Terrestrial Ecosystems and Biota, Abstracts and Proceedings, **29-32**.

- CSIKI Z., GRIGORESCU D. & WEISHAMPEL D. B. 2007. A new titanosaur sauropod (Dinosauria: Saurischia) from the Upper Cretaceous of the Hațeg Basin (Romania). Abstracts Volume, 5th Annual Meeting of the European Association of Vertebrate Palaeontologists, Carcassone, Franța.
- DALLA VECCHIA F., 2003. Observations on the presence of plant-eating dinosaurs in an oceanic carbonate platform. *Natura Nascosta*, **27**: 14-27.
- DERCOURT J., RICOU L. E. & VRIELYNCK B. (eds.), 1993. Atlas Tethys Paleoenvironmental Maps. Gauthier-Villars, Paris
- DERCOURT J., GAETANI M., VRIELYNCK B., BARRIER E., BIJU-DUVAL B., BRUNET M., CADET J. P., CRASQUIN S. & SANDULESCU M. 2000. Atlas Peri-Tethys, Palaeogeographical Maps. CCGM/CGMW, Paris, 269 pp., 24 hărți.
- DINCĂ A., TOCORJESCU M. & STILLA A. 1972. Despre vârsta depozitelor continentale cu dinozaurieni din Bazinele Hațeg și Rusca Montană. *D. S. Inst. Geol.*, **58**: 83-94.
- FOLIE A. & CODREA V., 2005. New lissamphibians and squamates from the Maastrichtian of Hațeg Basin, Romania. *Acta Palaeontologica Polonica*, **50**(1): 57–71.
- GAFFNEY E. S. & MEYLAN P. A. 1992. The Transylvanian Turtle, *Kallokibotion*, a primitive cryptodire of Cretaceous Age. *American Museum Novitates*, **3040**: 1-37.
- GRIGORESCU D. 1992. Nonmarine Cretaceous Formations of Romania. In: Matter N.J. & Pei-Ji C. (eds.) *Aspects of Nonmarine Cretaceous Geology*. China Ocean Press, Beijing, 142-164.
- GRIGORESCU D. 2005. Rediscovery of a “forgotten land”. The last three decades of research on the dinosaur-bearing deposits from the Hațeg Basin, *Acta Palaeont. Romaniae*, **5**, Ars Docendi, Bucharest, 191-204.
- GRIGORESCU D. & MELINTE M. C. 2002. The stratigraphy of the Upper Cretaceous marine sediments from the NW Hațeg area (South Carpathians, Romania). *Acta Pal. Romaniae*, **3**: 153-160.
- HOLTZ T. R., CHAPMAN R. E. & LAMANNA M. C. 2004. Mesozoic Biogeography of Dinosauria. In: Weishampel, D. B., Dodson, P. & Osmólska, H. (eds.) *The Dinosauria*, 2nd edition, University of California Press, Berkeley, Los Angeles and London, 627-642.
- HUENE F. 1932. Die fossile Reptile-Ordnung Saurischia ihre Entwicklung und Geschichte. *Monogr. Geol. Palaeontol.*, **1**(4): 1-361.

- JIANU CORALIA-MARIA & BOEKSCHOTEN G. J. 1999. The Hațeg area: island or outpost? In: Reumer, J.W.F. & de Vos, J. (eds.), *Elephants Have a Snorkel*. pp. 195-199. *Deinsea Special Volume*.
- JIANU CORALIA-MARIA & WEISHAMPEL D. B. 1999. The smallest of the largest: a new look at possible dwarfing in sauropod dinosaurs. *Geologie en Mijnbouw*, **78**: 335-343.
- JIANU CORALIA-MARIA & WEISHAMPEL D. B. 2001. The dinosaurs of Transylvania. *Actas de las II Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*, Salas de los Infantes, Burgos, Spain, 31-46.
- KESSLER E., GRIGORESCU D. & CSIKI Z. 2005. *Elopteryx* revisited - A new bird-like specimen from the Maastrichtian of the Hațeg Basin (Romania). *Acta Palaeontologica Romaniae*, **5**: 249-258.
- KIELAN-JAWOROWSKA Z., CIEFELLI R. L. & LUO Z.-X. 2004. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. Columbia University Press, New York. 630 pp.
- LE LOEUFF J. 2005. Romanian Late Cretaceous dinosaurs: Big dwarfs or small giants?, *Hist. Biol.*, **17**: 15–17.
- MACARTHUR R. H. & WILSON E. O. 1967. *The Theory of Island Biogeography*. Princeton, N. J.: Princeton University Press. 203 pp.
- MĂRGĂRIT G. & MĂRGĂRIT M. 1967. Asupra prezenței unor resturi de plante fosile în împrejurimile localității Demsuș (Hațeg Basin). *St. cerc. geol. geofiz. geogr., Geologie*, **12** (2): 471-476.
- MELINTE M. C. & BOJAR A.-V. 2006. Upper Cretaceous marine red beds in the Hațeg area (SW Romania). In: Z. Csiki (ed.), *Mesozoic and Cenozoic Vertebrates and Paleoenvironments. Tributes to the career of Dan Grigorescu*, Ed. Ars Docendi, 167-174
- MOLNAR R. E. & WIFFEN J. 1994. A Late Cretaceous polar dinosaur fauna from New Zealand. *Cretaceous Research*, **15**: 689-707.
- NEAGU T. 2006. Turonian- Lower Senonian planktonic foraminifera from the Ohaba-Pui-Ponor area – Hațeg, Romania. In: Z. Csiki (ed.), *Mesozoic and Cenozoic Vertebrates and Paleoenvironments. Tributes to the career of Dan Grigorescu*, Ed. Ars Docendi, 175-195
- NOPCSA F. 1900. Dinosaurierreste aus Siebenbürgen I. Schädel von *Limnosaurus transsylvanicus* nov. gen. et nov. spec. *Denkschriften der königlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftlichen Klasse*, **68**: 555-591.

- NOPCSA F. 1902. Dinosaurierreste aus Siebenbürgen II. (Schädelreste von *Mochlodon*). Mit einem Anhang: zur Phylogenie der Ornithopodiden. Denkschriften der königlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftlichen Klasse, **72**: 149-175.
- NOPCSA F. 1905. Zur Geologie der Gegend zwischen Gyulafehérvár, Déva, Ruszabánya und der Rumänischen Landesgrenze. Mitteilungen aus dem Jahrbuche der königlich ungarischen geologischen Reichsanstalt, Budapest, **14**: 93-279.
- NOPCSA F. 1915. Erdély dinoszauruszai. Magyar Állami Földtani Intézet Évkönyve, **23**: 1-23.
- NOPCSA F. 1923 a. On the geological importance of the primitive reptilian fauna of the uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallokibotium*). Quarterly Journal of the Geological Society of London, **79**: 100-116.
- NOPCSA F. 1923 b. *Kallokibotium*, a primitive amphichelydean tortoise from the Upper Cretaceous of Hungary. Palaeontologica Hungarica, **1**: 1-34.
- NOPCSA F. 1928. Paleontological notes on Reptilia 7. Classification of the Crocodilia. Geologica Hungarica, Ser. Palaeontologica, **1**(1): 75-84.
- NOVACEK M. J. & NORELL M. A. 1992. Fossils, phylogeny and taxonomic rates of evolution. Systematic Zoology, **31**: 366-375.
- PANAIOTU C. & PANAIOTU C. 2002. Paleomagnetic studies. In: GRIGORESCU D. & CSIKI Z. (eds.), 7th European Workshop on Vertebrate Palaeontology, Abstracts volume and excursions field guide, 59, Sibiu.
- PANĂ I., GRIGORESCU D., CSIKI Z., & COSTEA C. 2002. Paleo-ecological significance of the continental gastropod assemblages from the Maastrichtian dinosaur beds of the Hațeg Basin. Acta. Pal. Romaniae, **3**: 337-343.
- PEREDA-SUBERBIOLA X. & GALTON P. M. 2001. Reappraisal of the nodosaurid ankylosaur *Struthiosaurus austriacus* Bunzel from the Upper Cretaceous Gosau Beds of Austria, In: CARPENTER K. (ed.), The Armored Dinosaurs. The Indiana University Press, Bloomington, 173-210.
- PETRESCU I. & DUSA A. 1982. Paleoflora din Senonianul bazinului Rusca Montană. *D. S. Inst. Geol. Geofiz.*, **69** (3): 107-124.
- ROTH V. L. 1990. Insular dwarf elephants: a case study in body mass estimation and ecological inference. In: DAMUTH, J. & MACFADDEN, B. J. (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications, Cambridge University Press, 151-179.

- ROTH V. L. 1992. Inferences from allometry and fossils: dwarfing of elephants on islands. *Oxford Survey in Evolutionary Biology*, **8**: 259-288.
- SANDER P. M., MATEUS O., LAVEN T. & KNÖTSCHKE N. 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature*, **441**: 739-741
- SANDERS C. 1998. Tectonics and erosion; a fission-track study of the Romanian Carpathians. Unpublished PhD dissertation, Free University, Amsterdam, 204 pp.
- SĂNDULESCU M., 1984. Geotectonica României. Ed. Tehnică, 329 p., Bucharest.
- SMITH T., CODREA V., SĂSĂRAN E., VAN ITTERBECK J., BULTYNCK P., CSIKI Z., DICA P., FĂRCAȘ C., FOLIE A., GARCIA G. & GODEFROIT P., 2002. A new exceptional vertebrate site from the Late Cretaceous of the Hațeg Basin (Romania). *Studia Universitatis Babeș-Bolyai, Geologia, Special issue 1*: 321-330.
- STILLA A. 1985. Géologie de la région de Hațeg-Cioclovina-Pui-Bănița (Carpathes Meridionales). *An. Inst. Geol. Geofiz.*, **66**: 91-179.
- STILWELL J. D., CONSOLI C. P., SUTHERLAND R., SALISBURY S., RICH T. H., VICKERS-RICH P. A., CURRIE P. J. & WILSON G. J., 2006. Dinosaur sanctuary on the Chatham Islands, Southwest Pacific: First record of theropods from the K–T boundary Takatika Grit. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **230** (3-4): 243-250.
- THERRIEN F. 2005. Paleoenvironments of the Late Cretaceous (Maastrichtian) dinosaurs of Romania: insights from fluvial deposits and paleosols of the Transylvanian and Hațeg basins. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **218** (1-2): 15-56.
- THERRIEN F., 2006. Depositional environments and fluvial system changes in the dinosaur-bearing Sânpetru Formation (Late Cretaceous, Romania): Post-orogenic sedimentation in an active extensional basin. *Sedimentary Geology*, **192**: 183–205.
- VAN ITTERBEECK J., SĂSĂRAN E., CODREA V., SĂSĂRAN L. & BULTYNCK P. 2004. Sedimentology of the Upper Cretaceous mammal- and dinosaur-bearing sites along the Râul Mare and Bărbat rivers, Hațeg Basin, Romania. *Cretaceous Research*, **25** (3): 517-530.
- VAN ITTERBEECK J., MARKEVICH V. S. & CODREA V. 2005. Palynostratigraphy of the Maastrichtian dinosaur- and mammal sites of the Râul Mare and Bărbat Valleys (Hațeg Basin, Romania). *Geologica Carpathica*, **56** (2): 137-147.
- VENCZEL M. & CSIKI Z., 2003. New discoglossid frogs from the Latest Cretaceous of Hațeg Basin (Romania). *Acta Palaeontologica Polonica*, **48** (4): 599-606.
- WEISHAMPEL, D. B. 1996. Fossils, phylogeny and discovery: a cladistic study of the history of tree topologies and ghost lineage durations. *Journal of Vertebrate Paleontology*, **16**: 191–197.

- WEISHAMPEL D. B. & REIF W.-E. 1984. The work of Franz Baron Nopcsa (1877–1933): dinosaurs, evolution and theoretical tectonics. *Jahrbuch der Geologischen Bundesanstalt*, 127–203.
- WEISHAMPEL D.B., GRIGORESCU D. & NORMAN D.B. 1991. The Dinosaurs of Transylvania. *National Geographic Research & Exploration*, 7: (2): 196- 215.
- WEISHAMPEL D. B. & JIANU CORALIA-MARIA 1997. The importance of phylogeny in paleobiogeographic analyses, with examples from the North American hadrosaurids and European titanosaurids. *Sargetia*, 17: 261-278.
- WEISHAMPEL D. B., JIANU C.-M., CSIKI Z., AND NORMAN D. B. 2003. Osteology and phylogeny of *Zalmoxes* (n.g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. *Journal of Systematic Palaeontology*, 1(2): 65-123.
- WEISHAMPEL D. B., NORMAN D. B. & GRIGORESCU D. 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. *Palaeontology*, 36 (2): 361- 385.
- WEISHAMPEL D. B., DODSON P., AND OSMÓLSKA H. (eds.). 2004 a. The Dinosauria. 2nd edition. Univ. California Press, Berkeley. 833 pp.
- WEISHAMPEL D. B., BARRETT P. M., CORIA R. A., LE LOEUFF J., XU X. ZHAO X. J., SAHNI A., GOMANI E. M. P., NOTO C. R., 2004 b. Dinosaur distribution. In: Weishampel D. B., Dodson P. & Osmólska H. (eds.) The Dinosauria., 2nd edition, University of California Press, Berkeley, Los Angeles and London, 517-606.
- WILLINGSHOFER E. 2000. Extension in collisional orogenic belts: the Late Cretaceous evolution of the Alps and Carpathians. Ph.D. dissertation, Free University, Amsterdam. 146 pp.
- ZIEGLER P. A., 1987. Evolution of the Arctic - North Atlantic and the Western Tethys. AAPG Memoir 43, 198 pp.

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