



Preface

An island of dwarfs – Reconstructing the Late Cretaceous Hațeg palaeoecosystem

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ABSTRACT

The Cretaceous was a special time in the evolution of terrestrial ecosystems, and yet the record from Europe in particular is patchy. This special issue brings together results of multidisciplinary investigations on the Late Cretaceous Hațeg area in southwestern Romania, and its continental fossil assemblage, with the aim of exploring an exceptional palaeoecosystem from the European Late Cretaceous. The Hațeg dinosaurs, which seem unusually small, have become especially well known as some of the few latest Cretaceous dinosaurs from Europe, comparable with faunas from the south of France and Spain, and preserved at a time when most of Europe was under the Chalk Seas. Eastern Europe then, at a time of exceptionally high sea level, was an archipelago of islands, some of them inhabited, but none so extraordinary as Hațeg. If Hațeg truly was an island (and this is debated), the apparently small dinosaurs might well be dwarfs, as enunciated over 100 years ago by the colourful Baron Franz Nopcsa, discoverer of the faunas. The dwarfing of dinosaurs, and other taxa, is explored in this volume. The Hațeg dinosaurs appear to be very latest Cretaceous (Maastrichtian) in age, and they provide unique evidence, at a time when there are few dinosaurs known from Europe, about some of the last faunas before the KT mass extinction. Further, the flora and fauna (ostracods, fishes, frogs, turtles, lizards, crocodylians, pterosaurs, dinosaurs, and mammals) have never been reviewed comprehensively, and we provide here the current best evidence of what was there, and how the taxa fit in a global context.

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1. Islands and dwarfs

The unusual nature and composition of island faunas, as well as the causes underlying these oddities, have been a matter of scrutiny since Darwin's (1859) and Wallace's (1860, 1876) revolutionary contributions to the biological sciences. Islands are remarkable in the ways they control (and, by consequence, allow for tracking and understanding) evolutionary phenomena such as speciation (e.g., Mayr, 1942), survival of dwindling evolutionary lineages within refugia (e.g., Vartanyan et al., 1993; Guthrie, 2004; Vargas, 2007) or, conversely, extinction of such lineages restricted to over-shrunken habitats (e.g., O'Regan et al., 2002), development of significant within-clade evolutionary divergence (adaptive radiations sensu Simpson, 1953; e.g., Fritts, 1984; Schluter, 2000; Grant and Grant, 2002; Glor et al., 2004; Baker et al., 2005; Parent et al., 2008) often occurring at a fast pace (e.g., Kapralov and Filatov, 2006; Millien, 2006; Herrel et al., 2008), as well as phyletic size changes ("dwarfing" and "giantism"; e.g., Foster, 1964; Sondaar, 1977; Vartanyan et al., 1993).

Of these special evolutionary features of island biotas, size changes by island colonists has received wide attention, beginning with early reports of oversized birds (Owen, 1843) and tortoises (Harlan, 1827),

as well as those of miniaturized mammals (Busk, 1867; Adams, 1874; Bate, 1903). This pattern of certain (usually large-sized) animals becoming smaller, while others became larger after colonizing an island habitat, was identified as one of Nature's recurrent phenomena ("rules") by Foster (1964), and named as such ("island rule") by Van Valen (1973). The processes of phylogenetic size changes (dwarfing/giantism) that occur on islands (the "island rule") became one of the hallmark aspects of the theory of island biogeography (MacArthur and Wilson, 1967; Whittaker, 1999; Cox and Moore, 2005), despite ongoing controversy on its generality, patterns and underlying causes (for a review, see Benton et al., 2010–this issue).

Examples of insular dwarfism in the fossil record are not uncommon; however, these have mainly been described from the Pliocene–Pleistocene (see, e.g., de Vos et al., 2007 and references therein), while far fewer cases have been documented from earlier time periods (e.g., Dalla Vecchia, 2002; Sander et al., 2006; Benton et al., 2006). This rarity is at odds with the fact that one of the earliest documented examples of a fossil assemblage with putative insular dwarfs was the latest Cretaceous reptilian fauna of the Hațeg Basin (southern Carpathians, western Romania). This fauna was suggested to have inhabited an island at the eastern margin of a palaeo-archipelago stretching across Tethyan Europe during most of the Cretaceous, with the particularly small size of its dinosaurs a direct consequence of their restrictive habitat (Nopcsa, 1914). Although the Hațeg dinosaurian assemblage was subsequently often cited as a

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classical example of an island dwarf palaeofauna, this claim has not been investigated in detail up to now; moreover, the dwarf status of some of the dinosaurian components was questioned recently by [Le Loeuff \(2005\)](#) and [Pereda-Suberbiola and Galton \(2009\)](#).

2. The European Late Cretaceous ecosystems: islands of palaeodiversity

The Late Cretaceous continental assemblages of Europe are somewhat overshadowed by the much better studied ones from North America and Asia, as well as by those described recently from South America. This is largely because of the more extensive outcrops of continental units in all these areas compared to those in Europe, correlated with the larger number of fossiliferous localities (see, e.g., the reviews of [Weishampel et al., 2004](#); and [Kielan-Jaworowska et al., 2004](#) for dinosaurs and mammals, respectively), as well as the higher diversity of local faunal assemblages relative to those described from Europe. Starting as early as 1915 ([Nopcsa, 1915](#)), the different European Late Cretaceous faunas were often interpreted as depauperate compared to those known from other continental landmasses (low alpha diversity, i.e., raw local species richness; see [Whittaker, 1972](#)) both at the level of the major clades present, and of the number of individual taxa represented; moreover, the overall composition of the European Late Cretaceous palaeobiocoenosis was considered to be comparatively less diverse (gamma diversity, i.e., total diversity across a larger geographical area; [Whittaker, 1972](#)). This low-level diversity was considered to be complemented by several other unusual features, such as the survival of several basal tetrapod lineages up to the terminal Cretaceous, giving these faunas a “primitive” aspect (e.g.; [Nopcsa, 1915, 1923](#); [Weishampel et al., 1991](#); [Gaffney and Meylan, 1992](#)), the relative uniformity of the faunas across the different parts of Europe (see, e.g., [Nopcsa, 1915](#); [Le Loeuff, 1991](#)) supporting relatively low beta diversity (i.e., degree of differentiation of local assemblages along habitat gradients or simply between different part of a larger area; [Whittaker, 1972](#)), and the ambiguous palaeobiogeographic affinities of this Late Cretaceous ecosystem, in which the mixture of taxa of either southern (Gondwanan) or northern (Laurasian) origin blurred its biogeographic individuality ([Le Loeuff, 1991](#); [Le Loeuff and Buffetaut, 1995](#); [Le Loeuff, 1997](#)). These special palaeobiological features of the European Late Cretaceous assemblages were paralleled by their particular palaeogeographic–tectonic setting, inhabiting an archipelago with a geography undergoing large-scale temporal and spatial fluctuations (e.g., [Tyson and Funnell, 1987](#); [Smith et al., 1994](#); [Dercourt et al., 2000](#); [Csontos and Vörös, 2004](#)), quite unlike the larger, spatially continuous continental landmasses of North America and Asia (e.g., [Smith et al., 1994](#)).

Recent advances in the study of Late Cretaceous European ecosystems appear to support the emergence of a significantly different picture for this part of the world, as foreshadowed by [Rage \(2002\)](#). Discovery of rich and diverse fossil assemblages ranging from the Cenomanian of France (e.g., [Vullo and Néraudeau, 2008](#)) to the Santonian of Hungary ([Makádi et al., 2006](#); [Ősi and Rabi, 2006](#)) and to the Campanian–Maastrichtian of the Ibero–Armorican landmass (e.g., [Barroso-Barcenilla et al., 2009](#); [Company Rodriguez et al., 2009](#)) have revealed much greater alpha and gamma diversity within Late Cretaceous European ecosystems than had been thought before, while also pointing to a greater beta diversity than previously acknowledged. A recent review of the palaeobiogeographical affinities of these faunas ([Pereda-Suberbiola, 2009](#)) has presented a rather complex picture of their inter- and intra-province relationships. In view of these recent additions to our knowledge of Late Cretaceous European ecosystems, an update on the Hațeg palaeobiota and its environment appears necessary in order to better understand its position and relationships within a European palaeobioprovince.

3. The Late Cretaceous Hațeg Island – current research and prospectus

The Hațeg area became a focus of geological and palaeontological interest after the discovery of remains of fossil vertebrates in continental beds ([Nopcsa, 1897](#)) referred subsequently to the uppermost Cretaceous as equivalents of the “Rognacian” or “Garumnian” of Western Europe ([Nopcsa, 1905, 1915, 1923](#)). Subsequently, through the efforts of Nopcsa and, after him, of several other researchers, a large amount of data has been amassed on the Upper Cretaceous deposits and their biotas from the Hațeg Basin (see a synthesis of this research in [Grigorescu, 2010-this issue](#)). While early work was mainly concerned with establishing the age and geological context of the deposits, as well as description of the most conspicuous members of the macrofauna, more recent research activity has been more multidisciplinary, bringing together specialists working in different fields of geosciences, from palaeozoology and palynology to stable isotope geochemistry and palaeomagnetism. The main aim of this activity (although not always stated) was to achieve as complete as possible a reconstruction of this latest Cretaceous island ecosystem and to better understand its relationships with other contemporaneous ecosystems from Europe and abroad (e.g., [Csiki and Grigorescu, 2007](#)). Documenting research efforts on the Hațeg localities and faunas over the past 111 years since they were discovered reveals an all-time peak in the number of scientific papers in the past 15 years (see [Csiki, 2005](#); [Csiki and Grigorescu, 2007](#); [Grigorescu, 2010-this issue](#)).

Several results of this increased recent research activity on Hațeg have already been published, most notably on the vertebrate palaeontology, sedimentology, and distribution of the Maastrichtian vertebrate-bearing beds, but other topics are less well represented. This volume brings together 14 contributions that address previously less well represented research topics, from igneous petrography and stable isotope analyses to ichnology (dinosaur eggs) and taphonomy; the institutional affiliations and research interests of the 27 researchers co-authoring these contributions reflect well the breadth of international cooperation involved in this research project.

The introductory chapter of the issue ([Grigorescu, 2010-this issue](#)) offers an overview of the previous research done on the Upper Cretaceous deposits of the Hațeg area and their palaeontological content, focusing mainly on the early years and the seminal and prodigious activity of Baron Franz Nopcsa. The data synthesized in this overview are supplemented by the historical information offered by the other contributions to this issue.

Although not directly concerned with the Late Cretaceous Hațeg Island and its continental ecosystem, the next two contributions to this volume, focusing on the marine deposits directly beneath the vertebrate-bearing beds, are nevertheless integral parts of the ongoing multidisciplinary research in the area. They are critical in establishing the age of the Hațeg continental deposits, which do not contain such age-diagnostic fossils as the better-dated underlying marine deposits. This information is here updated and supplemented by [Melinte-Dobrinescu's \(2010-this issue\)](#) contribution on calcareous nannoplankton biostratigraphy, which suggests that, despite earlier reports (e.g., [Stilla, 1985](#); [Pop, 1990](#)), marine deposition in the area continued only as late as the latest Campanian, thus allowing continental deposition to start in the earliest Maastrichtian. These age constraints are confirmed by stable isotope studies reported by [Melinte-Dobrinescu and Bojar \(2010-this issue\)](#) through the identification of several time-significant isotope excursions in these marine deposits. Moreover, climatic trends identified in the late Late Cretaceous (as recorded by the marine deposits) are hypothesized to continue into the Maastrichtian as well, thus contributing to our understanding of the dominant palaeoclimate in the Hațeg area after its emergence.

The age constraints offered by the study of the underlying marine deposits are supported by palaeomagnetic studies on the continental

deposits themselves, reported here by [Panaiotu and Panaiotu \(2010-this issue\)](#). Based on their magnetostratigraphic data, the authors suggest that continental deposition started at the beginning of the Maastrichtian at the latest, but possibly even as early as the end of the Campanian. Moreover, the recorded palaeomagnetic data also constrain the palaeogeographic position of the emergent Hațeg Island and thus offer independent control for the previous palaeoclimatic reconstructions based on palynology (e.g., [Van Itterbeek et al., 2005](#)) and paleosol sedimentology (e.g., [Therrien, 2005](#)).

Volcaniclastic deposits associated with the vertebrate-bearing continental deposits of the Hațeg Basin (e.g., [Grigorescu, 1992](#)) were often overlooked in previous palaeoenvironmental reconstructions, despite the major impact the explosive volcanic events might have had upon the environments and biotas (e.g., [Goldberg and Garcia, 2000](#); [Guo et al., 2003](#); [Fürsich et al., 2007](#); [Zhao et al., 2007](#)). The study of [Bârzoi and Șeclăman \(2010-this issue\)](#) offers new petrographical and geochemical data for the interpretation of the palaeogeotectonic context of the volcanoclastics. According to these authors, volcanic activity responsible for generating these deposits must have taken place in an island arc setting, relatively far from the geotectonic settings within which the dinosaur-bearing beds were deposited; accordingly, it can be hypothesized that these eruptions might have had a reduced impact upon the development of the terrestrial biotas.

Closing in on the Maastrichtian continental deposits, the contribution of [Bojar et al. \(2010a – this issue\)](#) analyses their heavy mineral spectra in order to reconstruct possible source areas. The data derived from their study allow a better understanding of the tectonic context within which the Hațeg area evolved; according to the identification of distinct northern and southern source areas that operated during the Maastrichtian, it can be reconstructed reliably as an intramontane basin fed by the uplifted marginal areas. Moreover, the tectonic evolution of the surrounding mountainous areas appears to have had significant impact upon the palaeoenvironmental evolution of the basin itself, promoting a shift towards wetter, more mesic environments during the later part of the Maastrichtian.

The palaeoclimatic conditions of Hațeg Island were also investigated using stable isotopes derived from sediments and organic remains ([Bojar et al., 2010b – this issue](#)). According to this investigation, reconstructed palaeotemperature values suggest a rather low-latitude palaeogeographic setting, in accordance with the conclusions of [Panaiotu and Panaiotu \(2010-this issue\)](#) discussed above. The most important results of this stable isotope investigation appear to concern, however, the ethology and physiology of several archosaurian taxa (*Zalmoxes*, *Telmatosaurus*, *Allodaposuchus*), part of a wider debate about dinosaurian metabolism and the use of isotopic measurements to investigate environmental water composition. These results open up the possibility of wider comparisons with Late Cretaceous vertebrates from other areas (e.g., [Amiot et al., 2006](#); [Fricke and Pearson, 2008](#); [Fricke et al., 2008](#)).

Plant remains are rare in the continental deposits of the Hațeg Basin, being represented mainly by spores and pollen (e.g., [Van Itterbeek et al., 2005](#); [Csiki et al., 2008](#)), while rare leaf impressions ([Mărgărit and Mărgărit, 1967](#)) make up the only known macrofloral remains. Similarly, plant remains, except for palynomorphs, are exceedingly rare in other Upper Cretaceous vertebrate-bearing continental units of Western Europe (see, e.g., [Nichols and Johnson, 2008](#)), unlike the contemporaneous deposits of North America (e.g., [Johnson, 2002](#)). Consequently, the mesofloristic remains (seeds and fructifications) reported by [May Lindfors et al. \(2010-this issue\)](#) represent an important addition to our knowledge of the Maastrichtian floras of Hațeg Island. These are even more significant in that they are associated with palynomorphs and microvertebrate remains at the same site, thus allowing a detailed reconstruction of the local palaeoenvironment. The morphotypes and size compositions of the preserved Hațeg mesoflora suggests a semi-arid, seasonally variable climate, so providing a further independent palaeoclimatic signal in

agreement with those based on palaeomagnetism, paleosol sedimentology and palynology (see above).

The Hațeg Basin is also well known as the source of the only documented field association between dinosaur eggs and hatchling remains from the Upper Cretaceous of Europe (e.g., [Grigorescu, 1993](#)). Somewhat ironically, this co-occurrence, usually held up as a good opportunity to identify the egg-laying animals, has involved controversy (see, e.g., [Grigorescu, 2003](#)) over whether the eggs were laid by titanosaur sauropods or by hadrosaurids. [Grigorescu et al. \(2010-this issue\)](#) review the main stratigraphic, sedimentological, and taphonomic features of the different nesting sites from the Maastrichtian of the Hațeg Basin, and their work further supports the originally suggested association between megaloolithid eggs and the hadrosaurid *Telmatosaurus*.

[Csiki et al. \(2010-this issue\)](#) present a thorough overview of taphonomic modes of the Hațeg vertebrates, a theme that has been touched on by many authors since [Nopcsa's \(1902, 1914\)](#) original suggestion that most of the vertebrate accumulations had been produced by crocodylians gathering together carcasses of dead and dying animals. In fact, as recent work has shown, the Hațeg deposits represent a wide range of taphonomic modes within the prevailing fluvial-dominated upland setting that experienced seasonal semi-arid conditions. The major sedimentary settings are channel lags and fills, crevasse splays and channels, well-drained floodplains, mature non-calcareous paleosols, hydromorphic paleosols, abandoned channels and ponds, and marshy ponds. Most of the Hațeg vertebrates occur in fine-grained floodplain deposits, rather than in channels, the opposite of the situation in many other dinosaur-bearing formations. Skeletons show evidence of disturbance, breakage, and weathering, and bonebeds, whether of larger or smaller elements, show remarkable mixing of materials from many sources, some relatively fresh and others much abraded. Further, although the smaller vertebrates show evidence of habitat preferences (amphibians and lizards in ponds; crocodiles, turtles, and mammals in less marshy areas), the dinosaurs are found randomly across all sedimentary settings.

Equating the Hațeg Basin with the Hațeg Island might seem legitimate, and certainly has been done (see, e.g., [Weishampel et al., 1991](#)). However, this could be misleading, since island area is one of the main controlling factors of island ecosystems (e.g., [MacArthur and Wilson, 1967](#); [Whittaker, 1999](#); see [Lomolino, 2001](#)) and thus inferences concerning expected alpha diversity or distance from surrounding landmasses could be seriously flawed. Consequently, establishing the extent of the emergent Hațeg area is key for any attempt to understand this island palaeoecosystem. Hațeg Island must have been significantly larger than the Hațeg Basin itself, as already suggested by [Nopcsa \(1905\)](#). The contribution of [Codrea et al. \(2010-this issue\)](#) attempts to estimate the area of emergent land by mapping the wider outcrop of continental deposits that preserve vertebrate remains reminiscent of those from the Hațeg Basin itself. According to their data, Hațeg-type assemblages can be recognized all over the southwestern, western and northwestern margin of the Transylvanian Basin, thus significantly increasing the mappable area of this former island. Preliminary work suggests some taxonomic and palaeoecological differences between these local assemblages (e.g., between the Hațeg local fauna and those from outside the Hațeg Basin), pointing to the need for further study to determine whether these outlying assemblages really pertain to the same island as represented by the Hațeg Basin itself.

The larger palaeobiogeographic significance and relationships of the Hațeg ecosystem are addressed by two contributions. [Martin and Delfino \(2010-this issue\)](#) survey the stratigraphic and geographic distribution of Cretaceous European eusuchians (represented on Hațeg Island by the apparently endemic *Allodaposuchus precedens*; e.g., [Delfino et al., 2008](#) and references therein) in order to identify patterns of their evolution. Their analysis allows the reconstruction of a Late Cretaceous European archipelago supporting widely divergent

(eusuchian) assemblages on the different landmasses, a point also upheld by the palaeobiogeographic analysis of Weishampel et al. (2010-this issue). Building on two different approaches (overall faunal comparison and phylogenetic analyses of biogeographic relationships), they conclude that the Late Cretaceous European bioprovince was far from being uniform (see also Pereda-Suberbiola, 2009). Within this province, the faunal assemblage of Hațeg Island is characterized by both the presence of late-surviving “relict” members of phylogenetic lineages that can be traced back to the Early Cretaceous, and endemic taxa that speciated on the island itself. Patterns of differences among the local assemblages inhabiting the different landmasses suggest a clear-cut palaeobiogeographic divide inside the European bioprovince, a hypothesis that requires further testing.

The concluding chapter of this volume synthesises palaeobiological data on the Hațeg faunal assemblage and its environment, and especially how convincing it is to interpret Hațeg Island and its vertebrate faunas using concepts from modern island biogeography, especially in the context of the “island rule”. By drawing together information from such different fields as geotectonics and palaeogeography, bone histology and heterochrony, the contribution of Benton et al. (2010-this issue) builds up a rationale to support the dwarf status of several of the Hațeg dinosaurs, thus suggesting that the validity of an “island rule” can be extended back to the Mesozoic and resurrecting the century-old claim of Nopcsa, that “dwarf island dinosaurs” inhabited “Hațeg Island” within the Tethys Ocean. This chapter provides a wider overview of the current state of understanding of the “island rule” among modern ecologists, some of whom dispute the very concept, and the context of fossil data, especially the heavily studied Pleistocene and Holocene mammals of Mediterranean, and other, coastal islands.

The contributions in this volume highlight at least five areas in which the Late Cretaceous (Maastrichtian) Hațeg biota and environments will repay further study. First, the Hațeg fauna represents a microcosm, perhaps including island dwarfs, and their study widens the crossover in applying modern ecological-evolutionary models to ancient examples. Second, as one of the latest Cretaceous continental ecosystem of Europe, the Hațeg island fauna opens up the potential for new insights into latitudinal and geographic variations in the last dinosaur faunas, and aspects of their changes before the KT event. Third, as relicts, or island isolates, many of the plants and animals are also important in the phylogenies of their particular groups often extending global stratigraphic ranges of clades to include these ‘late survivors’. Fourth, the ecosystem as a whole is important as one of many examples that are close to the origin of modern terrestrial ecosystems, following their remarkable transformation during the so-called Cretaceous Terrestrial Revolution (Lloyd et al., 2008), through the radiation of angiosperms from the late Early Cretaceous onwards, and consequent diversifications of pollinating, leaf-eating, and social insects, and their predators such as lizards, birds, and mammals. Fifth, clarification of the temporal and spatial relationships between the volcanoclastic and vertebrate-bearing sedimentary deposits on and around Hațeg Island, will clarify the extent, origin, and history of this extraordinary Late Cretaceous archipelago.

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