Palaeogeography, Palaeoclimatology, Palaeoecology 293 (2010) 419–437

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Palaeobiogeographic relationships of the Haţeg biota — Between isolation and innovation

David B. Weishampel [a,*], Zoltán Csiki [b], Michael J. Benton [c], Dan Grigorescu [b], Vlad Codrea [d]

[a] Center for Functional Anatomy and Evolution, Johns Hopkins University—School of Medicine, 1830 East Monument St., Baltimore, Maryland 21205, USA
[b] Department of Geology and Geophysics, University of Bucharest, 1 N. Bălcescu Blvd., RO-010041 Bucharest, Romania
[c] Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK
[d] Department of Biology and Geology, Babeş-Bolyai University, 1 Kogălniceanu St., RO-400084 Cluj-Napoca, Romania

ARTICLE INFO

Article history:
Received 1 May 2009
Received in revised form 15 December 2009
Accepted 10 March 2010
Available online 16 March 2010

Keywords:
Haţeg Basin
Vertebrate fauna
Late Cretaceous
Palaeobiogeography
Evolution

ABSTRACT

The biogeographic significance of the Late Cretaceous Haţeg fauna is assessed using both faunal and phylogenetic analyses. Although extremely endemic at the species level, the Haţeg fauna is part of a larger European palaeobioprovince compared to roughly contemporary (Campanian–Maastrichtian) terrestrial faunas elsewhere in Europe. Phylogenetic analyses of five Haţeg taxa, calibrated by biostratigraphic occurrences provide evidence of long ghost lineages. The geographic distributions of kogaionids, *Kallokibotion*, *Allodaposuchus*, and *Zalmoxes* (together with their European sister taxa) may have arisen from vicariant events between western Europe and North America, while the distribution of *Telmatosaurus* is an example of European endemism of Asiamerican origin.

While Haţeg seems to have acted as a dead-end refugium for *Kallokibotion* and *Telmatosaurus*, other faunal members (and their immediate sister taxa) are not restricted to Transylvania, but known otherwise from localities across southern Europe. In addition, Transylvania may have acted as an evolutionary cradle for kogaionids.

Transylvania and the other southern faunas of Europe may represent a distinct division of the Late Cretaceous European palaeobioprovince. A boundary between this Tethyan Europe and the more western and northern cratonic Europe suggests something like the Wallace Line in the Malay Archipelago, in which two distinct faunal provinces with separate histories within a much larger, seemingly uniform geographic region are separated by a narrow boundary.

1. Introduction

Understanding the history of any particular extant or extinct ecosystem represents one of the major topics of evolutionary studies. It concerns establishing the relationships of that particular assemblage with its contemporaries from other areas (i.e., its palaeogeographic ties), as well as those between the same assemblage and those preceding it (i.e., its origin as a complex system of interacting organisms).

In particular, the biogeographic relationships of a given fauna are the results of the combined effects of changing palaeogeography and organismal evolution. Continental breakup and assembly, eustatic sea-level changes, tectonic cycles, and climate shifts all influence the geographic context within which the development of the particular palaeobiotic unit took place. On the other hand, individual evolutionary histories of the organisms making up that ecosystem depend on their phylogenetic relationships, biological characteristics (such as dispersal potential, ecological requirements, reproductive strategies), and opportunity (i.e., being in the right place at the right moment).

In the case of the Maastrichtian Haţeg ecosystem, its palaeobiogeographic relationships were probably controlled by its insular setting within an archipelago-like southern Europe (Nopcsa, 1923a; Weishampel et al., 1991; Dercourt et al., 2000; Benton et al., 2010-this issue) and the typically continental composition of the fauna (see reviews in Grigorescu, 2005; Benton et al., 2010-this issue), dominated by exclusively terrestrial taxa. The peculiar composition of the fauna and its palaeobiologic characteristics (Nopcsa, 1923a; Weishampel et al., 1991, 1993, 2003; Csiki and Grigorescu, 2007; Benton et al., 2010-this issue) represent a continuous challenge to our understanding of its palaeobiogeographic relationships.

Like organisms everywhere, the Haţeg vertebrates were the products of their individual histories. One aspect of these histories is their arrival in this region of what is now western Romania. Nopcsa's approach to where the dinosaurs (and the remainder of the Haţeg fauna) originated was to look solely within Europe. For example, he compared his Transylvanian hadrosaurid with *Iguanodon* from the rich Early Cretaceous Wealden faunas of England, Belgium, and France (Nopcsa, 1923a), for the simple reason that both *Telmatosaurus* and

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* Corresponding author. Tel.: +1 410 955 7145; fax: +1 410 614 9030.
E-mail address: dweisham@jhmi.edu (D.B. Weishampel).

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doi:10.1016/j.palaeo.2010.03.024

Table 1
Overview of the palaeobiogeographic affinities of the Maastrichtian Haţeg Basin vertebrate assemblage.

Taxon	Least-inclusive clade	Selected references	Species[a]	Europe[b]	World	Genus	Europe	World	Clade	Europe	World
Acipenseriform indet.	Acipenseriformes	Grigorescu et al., 1985	**0**	x	x	**0**	x	x	**1**	Y; Cz	N
Lepisosteus sp.	Lepisosteidae	Grigorescu et al., 1999	**0**	x	x	**1**	N	N	**1**	N	N
Atractosteus sp.	Lepisosteidae	unpublished	**0**	x	x	**1**	N	N	**1**	N	N
Characidae indet.	Characidae	Grigorescu et al., 1985	**0**	x	x	**0**	x	x	**1**	Y; Pg	N
Hatzegobatrachus grigorescui	Anura	Venczel and Csiki, 2003	**1**	Y	Y	**1**	Y	Y	**1**	N	N
Paralatonia transylvanica	Discoglossidae	Venczel and Csiki, 2003	**1**	Y	Y	**1**	Y	Y	**1**	N	N
Cf. *Eodiscoglossus*	Discoglossidae	Folie and Codrea, 2005	**0**	x	x	**1**	Y; EK	Y	**1**	N	N
Cf. *Paradiscoglossus*	Discoglossidae	Folie and Codrea, 2005	**0**	x	x	**1**	Y	N	**1**	N	N
Anura indet. 1	Anura	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Albanerpeton sp.	Albanerpetontidae	Grigorescu et al., 1999; Folie and Codrea, 2005	**0**	x	x	**1**	N	N	**1**	N	N
Kallokibotion bajazidi	Kallokibotionidae	Nopcsa, 1923b	**1**	Y	Y	**1**	Y	Y	**1**	N ?	Y
Pleurosternon or *Polysternon* (Pleurodira indet) - large sized	? Bothremydidae	Vremir, 2004	**0**	x	x	**0**	x	x	**1**	N	N
Solemydidae indet. (aff. *Helocheydra*)	? Solemydidae	Vremir and Codrea, 2009	**0**	x	x	**1**	Y; EK	N	**1**	N	Y, LJ
Dortokidae n. gen. et sp.	Dortokidae	Vremir and Codrea, 2009	**1**	Y	Y	**1**	Y	Y	**1**	N	Y
Bicuspidon hatzegiensis	Polyglyphanodontinae	Folie and Codrea, 2005	**1**	N	Y	**1**	N	Y; EK	**1**	N	Y; EK
?*Becklesius* or ?*Paracontogenys*	Paramacellodidae	Folie and Codrea, 2005; unpublished	**0**	x	x	**1**	Y; EK	Y; EK	**1**	Y; EK	Y.; EK
?*Beckesius cf. hoffstetteri*	Paramacellodidae	Folie and Codrea, 2005	**0**	x	x	**1**	Y; EK	Y; EK	**1**	Y; EK	Y.; EK
?*Contogenys*	Scincidae	Smith et al., 2002; unpublished	**0**	x	x	**1**	Y	N	**1**	N	N
?*Slavoia*	Scincomorpha	unpublished	**0**	x	x	**1**	Y	N	**1**	N	N
Sauria indet. 1	Sauria	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 1	Scincomorpha	Grigorescu et al., 1999	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 2	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 3	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 4	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 5	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 6	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 7	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 8	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 9	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 10	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 11	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Scincomorpha indet. 12	Scincomorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Anguimorpha indet. 1	Anguimorpha	Grigorescu et al., 1999	**0**	x	x	**0**	x	x	**1**	N	N
Anguimorpha indet. 2	Anguimorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Anguimorpha indet. 3 (cf. *Paraderma* sp.)	Anguimorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Anguimorpha indet. 4 (cf. ?*Paraderma* sp.)	Anguimorpha	unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Madtsoiidae sp.	Madtsoiidae	Folie and Codrea, 2005	**0**	x	x	**0**	x	x	**1**	N	N
Doratodon sp.	Ziphosuchia	Grigorescu et al., 1999	**0**	x	x	**1**	N	Y	**1**	N	N
Allodaposuchus precedens	basal Eusuchia	Nopcsa, 1928a; Buscalioni et al., 2001	**1**	Y	Y	**1**	N	Y	**1**	N	N
Acynodon n. sp.	Alligatoroidea	Jianu and Boekschoten, 1999; Martin et al., 2006	**1**	Y	Y	**1**	N	Y	**1**	N	N
Musturzabalsuchus sp.	Alligatoroidea	Jianu and Boekschoten, 1999	**0**	x	x	**1**	N	Y	**1**	N	N
Ziphosuchia gen et sp. indet.	Ziphosuchia	Martin et al., 2006	**1**	Y	Y	**1**	Y	Y	**1**	Y	N
Mesoeucrocodylia gen et sp. nov.	Mesoeucrocodylia	Martin et al., in prep.	**1**	Y	Y	**1**	Y	Y	**1**	N	N
Pteranodontidae indet.	Pteranodontidae	Jianu et al., 1997	**0**	x	x	**0**	x	x	**1**	Y	N
Hatzegopteryx thambema	Azhdarchidae	Buffetaut et al., 2002	**1**	Y	Y	**1**	Y	Y	**1**	N	N
Magyarosaurus dacus	Titanosauria	Nopcsa, 1915; von Huene, 1932	**1**	Y	Y	**1**	Y	Y	**1**	N	N
Titanosauria gen et sp. nov.	Titanosauria	Csiki et al., in press	**1**	Y	Y	**1**	Y	Y	**1**	N	N
"*Magyarosaurus*" *hungaricus*	Titanosauria	Csiki et al., 2007	**1**	Y	Y	**1**	Y	Y	**1**	N	N
Dromaeosauridae (cf. *Saurornitholestes*)	Dromaeosauridae	Weishampel and Jianu, 1996	**0**	x	x	**1**	Y	N	**1**	N	N
Elopteryx nopcsai	Alvarezsauridae	Naish and Dyke, 2004; Kessler et al., 2005	**1**	Y	Y	**1**	Y	Y	**1**	Y; EK	N
Euronychodon sp.	Troodontidae or Dromaeosauridae	Grigorescu et al., 1999; Codrea et al., 2002	**0**	x	x	**1**	N	N	**1**	N	N
Troodontidae indet.	Troodontidae	Codrea et al., 2002; Smith et al., 2002	**0**	x	x	**0**	x	x	**1**	Y; EK	N
Paronychodon sp.	Troodontidae	Codrea et al., 2002; Smith et al., 2002	**0**	x	x	**1**	Y; EK	N	**1**	Y; EK	N
Richardoestesia sp.	Basal Tetanurae or Coelurosauria	Codrea et al., 2002	**0**	x	x	**1**	Y; EK	N	**1**	N	N
Caenagnathidae indet. (cf. *Chirostenotes*)	Caenagnathidae	Csiki and Grigorescu, 2005	**0**	x	x	**0**	x	x	**1**	N	N
Theropoda 1	Theropoda	Unpublished	**0**	x	x	**0**	x	x	**1**	N	N
Theropoda 2 (Nălaţ)	Theropoda	Smith et al., 2002	**0**	x	x	**0**	x	x	**1**	N	N
Aves	Aves	Unpublished	**0**	x	x	**0**	x	x	**1**	N	N

Table 1 (*continued*)

Taxon	Least-inclusive clade	Selected references	Species[a]	Europe[b]	World	Genus	Europe	World	Clade	Europe	World
Zalmoxes robustus	Rhabdodontidae	Weishampel et al., 2003	**1**	Y	Y	**1**	N	Y	**1**	N	Y
Zalmoxes shqiperorum	Rhabdodontidae	Weishampel et al., 2003	**1**	Y	Y	**1**	N	Y	**1**	N	Y
Telmatosaurus transsylvanicus	Hadrosauridae	Weishampel et al., 1993	**1**	Y	Y	**1**	Y	Y	**1**	N	N
Struthiosaurus transylvanicus	Nodosauridae	Nopcsa, 1929	**1**	Y	Y	**1**	N	Y	**1**	N	N
Barbatodon transylvanicum	Kogaionidae	Rădulescu and Samson, 1986; Csiki et al., 2005	**1**	Y	Y	**1**	Y	Y	**1**	Y; Pc	Y
Barbatodon sp. (Nălaţ)	Kogaionidae	Smith et al., 2002	**0**	x	x	**1**	Y	Y	**1**	Y; Pc	Y
Kogaionon ungureanui	Kogaionidae	Rădulescu and Samson, 1996	**1**	Y	Y	**1**	Y	Y	**1**	Y; Pc	Y
Kogaionon sp. (Nălaţ)	Kogaionidae	Smith et al., 2002	**0**	x	x	**1**	Y	Y	**1**	Y; Pc	Y
Kogaionon sp. (Toteşti)	Kogaionidae	Codrea et al., 2002	**0**	x	x	**1**	Y	Y	**1**	Y; Pc	Y
Kogaionon sp. (Pui)	Kogaionidae	Smith and Codrea, 2003	**0**	x	x	**1**	Y	Y	**1**	Y; Pc	Y
Hainina sp. A	Kogaionidae	Csiki and Grigorescu, 2000	**0**	x	x	**1**	Y; Pc	Y	**1**	Y; Pc	Y
Kogaionidae gen. et sp. nov.	Kogaionidae	Csiki and Grigorescu, 2000	**1**	Y	Y	**1**	Y	Y	**1**	Y; Pc	Y
Theria indet.	Theria	Csiki and Grigorescu, 2001	**0**	x	x	**0**	x	x	**1**	N	N

[a] Abbreviations used in taxonomic columns: 0 — indeterminate at the given taxonomic level; 1 — determinate at the given taxonomic level.

[b] Abbreviations used in distribution columns: Y — endemic; N — present in other areas; x — not applicable. Cz — Cenozoic, EK — Early Cretaceous, LJ — Late Jurassic, Pc — Palaeocene, and Pg — Palaeogene.

Iguanodon, although separated by 50 M.y. and representing phylogenetically distinct taxa, were European members of Ornithopoda. Likewise, Nopcsa directly compared the other members of the Transylvanian fauna with their European relatives from the Early Cretaceous as he attempted to understand how his peculiar dinosaurs arose. Nopcsa's was a good and logical beginning to our understanding of these taxa, but his comparison to other European taxa only explores the possibility of within-continent biogeographic relationships, while ignoring those with other continents. In other words, to understand where the Haţeg taxa fit in the global biogeographic history of their clades, it is not enough to consider only *Iguanodon*, *Hypsilophodon*, *Hylaeosaurus*, and *Pelorosaurus* (and other vertebrates) from Europe, but the net should be spread to include a great many more from other continents (as synthesized recently by, e.g., Kielan-Jaworowska et al., 2004; Weishampel et al., 2004).

Interestingly, one of Nopcsa's lasting contributions to palaeontology represents an early attempt to understand the evolution of life in the context of changing palaeogeography (Nopcsa, 1934). This contribution, foreshadowing the ascent of cladistic palaeobiogeography (Nelson and Platnick, 1981; Wiley, 1988; Grande, 1990), was a surprisingly modern in approach (see Le Loeuff, 1997), but was largely overlooked by subsequent authors. Unfortunately, Nopcsa never applied his palaeobiogeographic ideas specifically to the Haţeg vertebrate fauna because his life was cut short by suicide.

2. Haţeg palaeobiogeography today

A large amount of new palaeontological and palaeogeographical data has been gathered since Nopcsa's original work, both for the Haţeg Basin (see contributions in this issue) and globally. Palaeogeographic reconstructions of the Cretaceous of Europe (e.g., Ziegler, 1987; Dercourt et al., 2000; Stampfli and Borel, 2002; Csontos and Vörös, 2004; Schmid et al., 2008) and the globe (e.g., Smith et al., 1994; Hay et al., 1999; Scotese, 2004) provide a better understanding of the palaeogeographic context within which the Haţeg fauna evolved. Discovery of a large number of taxa related to the major groups represented in the Haţeg assemblage on most important continental landmasses (e.g., Weishampel et al., 2004; Kielan-Jaworowska et al., 2004) has significantly improved our knowledge of the stratigraphic and geographic distribution of the relatives of the Haţeg taxa. Meanwhile, phylogenetic analyses have led to increased accuracy in understanding of the phylogenetic relationships of Haţeg taxa. Numerous palaeobiogeographic studies of the Mesozoic (and more specifically the Cretaceous) continental vertebrates have been published (e.g., Le Loeuff, 1991, 1997; Russell, 1993; Forster, 1999; Sereno, 1999, 2000; Hirayama et al., 2000; Cifelli, 2000; Upchurch et al., 2002; Holtz et al., 2004; Turner, 2004), and the evolution of faunal provinciality during the Cretaceous is relatively well established.

3. Materials and methods

Currently, the Maastrichtian vertebrate assemblage from Haţeg includes over 70 taxa (Grigorescu, 2005, 2010-this issue; Benton et al., 2010-this issue; see Table 1), ranging from fishes to mammals and dinosaurs. There is a wide variation in taxonomic and especially phylogenetic information available for these taxa: while many dinosaurs, turtles, crocodilians and multituberculates are relatively well understood phylogenetically (Gaffney and Meylan, 1992; Weishampel et al., 1993, 2003; Hirayama et al., 2000; Buscalioni et al., 2001; Pereda-Suberbiola and Galton, 2001; Curry Rogers, 2005; Csiki and Grigorescu, 2006; Delfino et al., 2008), such information is at best limited for other groups. This places a constraint on the utility of these less well understood taxa in palaeobiogeographic analyses: better-known ones are well suited for detailed phylogenetics-based analysis, while the others allow only similarity-based faunal comparisons.

Several palaeobiogeographic analytical techniques have been developed to analyze distribution patterns of fossil organisms. These can be divided roughly into two approaches — faunal similarity-based and phylogeny-based techniques (Newton, 1990; see Holtz et al., 2004, for a review of these techniques as applied to dinosaurs). Analyses based on faunal similarities employ comparisons of faunal lists, without regard for the phylogenetic relationships of the taxa represented. Some of these techniques rely on simple comparisons of the faunas based on overall similarity (e.g., Molnar, 1980; Russell, 1993). Other techniques, however, imply a more analytical approach (Le Loeuff, 1991; Holtz et al., 2004), using taxon-occurrence data matrices to build dendrograms clustering together faunas showing close biogeographic affinities.

Phylogeny-based approaches develop from the idea that geographic distribution patterns of related taxa should be correlated, among other factors, with their phylogenetic relationships, as the temporal succession of cladogenetic events must reflect that of the barrier-forming events that disrupted the unity of once-continuous taxon distributions. However, barrier formation is one way in which palaeobiogeographic units also originate (vicariance), and thus the observed patterns of cladogenetic events should match to a certain extent the patterns of palaeobiogeographic unit individualization. Events that might blur this direct relationship (regional extinctions, dispersals) can be identified by comparing deduced ages of barrier formation and clade divergence, respectively (e.g., Sereno, 2000). In this study, *a posteriori* optimization analysis of clade origin (e.g., Weishampel and Jianu, 1997) was used to establish areas of origin for the most important taxa from the Haţeg Basin for which resolved cladograms are available.

This palaeobiogeographic analysis concentrates on the Maastrichtian mammals, turtles, crocodilians, and dinosaurs of the Haţeg Basin,

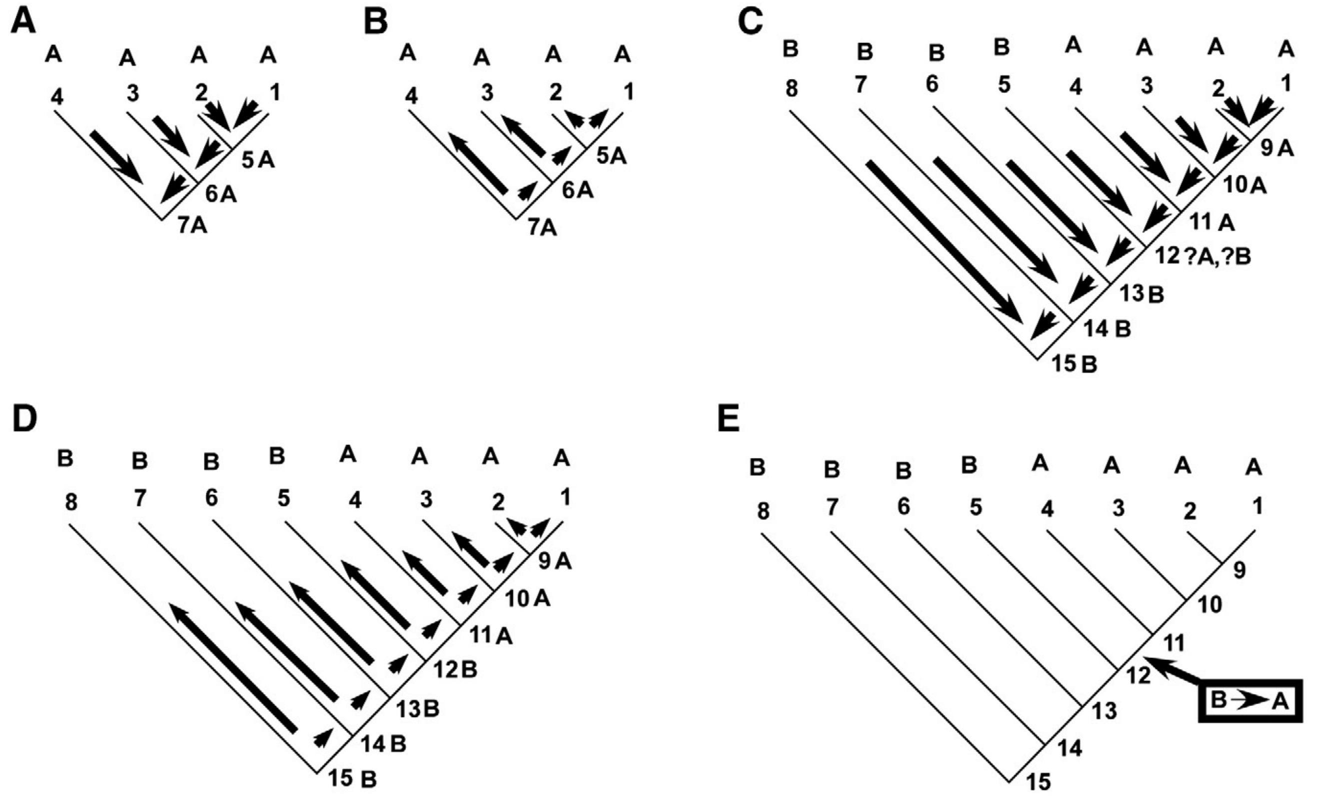

Fig. 1. *A posteriori* character optimization A. Assignment of geographic data (Area A) to the terminal taxa (1–4) on a cladogram. The ancestral area of origin for taxa 1 and 2 (Node 5) is most parsimoniously interpreted as Area A, shared with its two descendants. Furher down the tree, taxon 3 and 4 also come from Area A, thus their ancestors (Nodes 6 and 7) are inferred to have come from the same area. This down-pass is called character generalization. B. Optimization double-checks characters back up the tree to resolve any ambiguities that may be left (none in this case). C. Hypothetical example with a clade, half of which (taxa 1–4) come from Area A, while the others (taxa 5–8) from Area B. Generalizing down the tree, the ancestors reconstructed at Nodes 9–11 would also have been found in Area A. The ancestral area at Node 12 could be either Area A or B, so it is registered as "?A/?B. Generalization proceeds to Node 13, where Area B is held in common with Node 12, so the ancestral area at Node 13 is inferred to be Area B. Thereafter down the tree, Area B is inferred as the ancestral area at Nodes 14 and 15. D. Characters are optimized back up the tree. The ancestral area at Nodes 15, 14, and 13 is clearly Area B. Node 13 is then compared with Taxon 5 to resolve the ambiguity encountered at Node 12. As Area B is held in common between Node 13 and Taxon 5, the ancestral area at Node 12 is inferred to be Area B. E. With all remaining ancestral areas already identified as A, the shift from Area B to Area A (dispersal) occurred between Node 12 and 11 (E).

by combining cladistic analysis of these taxa with the global geographic occurrences of the clades in which they occur. *A posteriori* optimization (Fig. 1) of the geographic occurrences of the Haţeg taxa and close relatives onto their phylogeny requires an explicit, well-supported cladogram. This cladogram is then used to determine the most parsimonious distribution and transformation of the geographic occurrences (Farris, 1970; Wiley et al., 1991; Brooks and McLennan, 1991; Weishampel and Jianu, 1997). Simple and direct *a posteriori* analyses can be done by hand, but character optimization on a tree is more easily accomplished using a numerical cladistic algorithm, such as PAUP, MacClade, and Winclada.

In this search for the source areas of clades, we rely not only on the palaeogeographic reconstructions of this part of Europe through the Cretaceous, but also those of other relevant landforms. This certainly means the palaeogeographic conditions and proximity of parts of Asia, South America, North America, Africa, Antarctica, and Australia. However, inferences about global biogeographic histories can be only as good as the fossil record will allow and the biases inherent in this record should be admitted at the start: this is best exemplified by the skewed geographic sampling of dinosaurs throughout the world. For example, Asia and Europe contribute about 30% of the world's number of dinosaur localities for the Early Cretaceous, followed by North America at 13% (data from Weishampel et al., 2004). The remaining continents — South America, Africa, and Australia — each contribute no more than 7%, (not surprisingly, Antarctica has so far contributed nothing). In the Late Cretaceous, North America dominates at 36%, followed by Asia at 28%, and South America at 16%; Africa, Australia, and Antarctica together comprise a paltry 7%. Even though knowledge of dinosaur distribution around the world is always on the increase, it is also dominated at present by the three continents — North America, Europe, and Asia — which constitute Laurasia.

Consequently, any search for the area of origin of any of the Haţeg dinosaurs and their immediate clade (as well as those of the other Haţeg vertebrates) is possibly biased in favour of Laurasia and away from Gondwana, based on the number of fossiliferous locations rather than real biogeographic history. Nothing can be done about this problem except to extend fieldwork in the southern continents to equalize sampling.

4. Results

4.1. Faunistics

A first approach taken in this study was to compare the Maastrichtian Haţeg vertebrate fauna to other faunas from Europe and worldwide to get a first-hand insight into its possible relationships.

A recent review of the biogeographic relationships of the Late Cretaceous continental vertebrates of Europe (Pereda-Suberbiola, 2009) synthesized the large-scale biogeographic affinities of these taxa, including those from the Haţeg Basin. According to this review, most Haţeg taxa can be identified as showing either Palaeolaurasian (*sensu* Russell, 1993, representing North America and Asia, eventually Europe: albanerpetontids, discoglossid frogs, paramacellodid and polyglyphanodontine lizards, basal crocodylians, hadrosaurids, oviraptorosaurs) or Euramerican (covering North America and Europe: alligatoroids, nodosaurids) affinities, while several others (*Kallokibotion*, dortokids, rhabdodontids, kogaionids) are European endemics. Finally, a few other taxa are considered to point to southern, Gondwanan relationships of the fauna, such as madtsoiid snakes and sebecosuchian crocodyliforms (*Doratodon*); the same claim is, however, dismissed in the case of the titanosaurians, frequently cited to support Gondwanan affinities of the Late Cretaceous southern European assemblages (e.g., Le Loeuff, 1991). This biogeographic partitioning of the Late Cretaceous European continental vertebrates falls short, however, in accommodating all the palaeobiogeographic partitions that can actually be recognized during the Cretaceous. For instance, Palaeolaurasia was defined by Russell (1993) as a biogeographic entity covering all northern continents from the Early to the latest Cretaceous; however, subsequent studies revealed a different pattern of biogeographic subdivisions during the same time interval (see below; Fig. 2). Moreover, lumping together Santonian to Maastrichtian vertebrate assemblages from all over Europe to assign them to a hypothetical European bioprovince does not recognize the fundamental differences in taxic composition between the different sectors of the European Late Cretaceous archipelago (e.g., Buffetaut and Le Loeuff, 1991; Le Loeuff and Buffetaut, 1995; Rage, 2002). Consequently, the present faunistic analysis focuses specifically on the Haţeg faunal assemblage, without mingling it into a composite European bioprovince.

Geographic resources for our study include the evolving framework of biogeographic provinces (Fig. 2) derived from the studies of Bonaparte and Kielan-Jaworowska (1987), Le Loeuff (1991, 1997), Russell (1993), Apesteguía (2002), Upchurch et al. (2002), Krause et al. (2006), and Upchurch (2008) in conjunction with published palaeogeographic and plate tectonic reconstructions (e.g., Smith et al., 1994; Hay et al., 1999; Dercourt et al., 2000; Golonka, 2004; Scotese, 2004; Schmid et al., 2008). According to the proposed reconstruction, most of the Jurassic is characterized by the presence of two major continental bioprovinces: Central Asia and Neopangea, the last including most major continental landmasses except Asia (Russell, 1993). Beginning with the Late Jurassic (Fig. 2A), minor differentiation within Neopangea points to the development of a distinct Euramerican bioprovince that had intermittent links to the southern, Gondwanan bioprovince through Africa. Whether differentiation was present during this time within Gondwana is still a matter of debate, but was probably already underway (Rauhut and López-Arbarello, 2008 and references cited therein).

During the Early Cretaceous (Fig. 2B), separation of Africa from Euramerica was completed, and differentiation also began within Euramerica starting in the Aptian, leading to the individualization of a North American and a European bioprovince (Kirkland et al., 1997).

Fig. 2. Schematic continental palaeobiogeography of the Cretaceous, outlining the main palaeobioprovinces (M — Madagascar); continental landmasses shown in their approximate present-day position, drift is not accounted for. A. Late Jurassic: 1 — Neopangea, 2 — Central Asia; B. Early Cretaceous (Neocomian–Barremian): 2 — Asia, 3 — Euramerica, 4 — Gondwana; *a* — intermittent and selective inter-province exchange route between Asia and Euramerica (e.g., Barrett and Wang, 2007; Barrett et al., 2002; Canudo et al., 2002; Cuenca-Bescós and Canudo, 2003); C. Early–Late Cretaceous boundary (Albian–earliest Cenomanian): 5 — Asiamerica, 6 — Greater Gondwana (Apesteguía, 2002); intermittent and selective inter-province exchange routes: *b* — between North America and Europe (Weishampel and Jianu, 1997), *c* — between Europe and Asia (Milner and Norman, 1984), *d* — between North America and Asia (Beringia; e.g., Kirkland et al., 1997), *e* — between Europe and Africa (Canudo et al., 2009 and references therein), *f* — between Africa and South America (e.g., Buffetaut and Rage, 1993); D. Late Cretaceous (latest Campanian–Maastrichtian); intermittent and selective inter-province exchange routes: *g* — between North America and Europe (Martin et al., 2005), *h* — between North America and Asia (Sullivan, 1999; Sereno, 1999, 2000), *i* — between North and South America (Bonaparte, 1984; Gayet et al., 1992), *j* — between Europe and Africa (e.g., Buffetaut, 1989; Gheerbrant and Rage, 2006; Pereda-Suberbiola, 2009), *k* — between Asia and India–Madagascar (e.g., Prasad and Rage, 1991; Rage, 2003).

Meanwhile, intermittent connections of Europe with Asia allowed limited faunal exchanges between the two provinces (e.g., Barrett and Wang, 2007, and references therein) after a long period of Central Asian endemism, although the two palaeobiogeographic units preserved their identity. Despite the suggestion of the existence of an Eastern (including India, Madagascar and Australia) and a Western Gondwanan (Africa and South America) province, as hypothesized by, e.g., Le Loeuff (1997), the patchy fossil record of the southern continents far from convincingly supports this separation. Instead, Australia at least seems to have been connected to South America as suggested by the presence of closely related taxa during the Aptian–Albian (Smith et al., 2008). Intermittent faunal connections between Europe and Africa apparently continued during the Early Cretaceous (Gheerbrant and Rage, 2006), but were probably restricted only to post-Barremian times (Canudo et al., 2009).

The Early–Late Cretaceous boundary is marked by important palaeogeographic events (Fig. 2C). The ongoing opening of the North Atlantic led to the complete severing of the connections between America and Europe (thus the end of the Euramerican province). To the west, North America became connected to Asia through the rise of Beringia in the latest Early Cretaceous, leading to a large Asiamerican bioprovince (Kirkland et al., 1997) that lasted into the latest Cretaceous (Sereno, 1999, 2000; Sullivan, 1999; Cifelli, 2000), although regional differences have been recognized within this province (e.g., Godefroit et al., 2003, 2004). Transgression of the epicontinental Western Interior Seaway resulted in the fragmentation of this province and the individualization of an Eastern North American biogeographic unit (Appalachia), although faunal support for this unit is still weak (Schwimmer, 1997; Carr et al., 2005). To the south, opening of the South Atlantic and Indian Oceans disrupted the continuity of Gondwana. The detailed timing and succession of fragmentation of this palaeogeographic province is controversial (see Sereno et al., 2004; Turner, 2004; Krause et al., 2006), but apparently by the early Late Cretaceous Africa became isolated from other Gondwanan landmasses, while some degree of connection was probably still present between South America and Antarctica–Australia, and India and Madagascar, respectively.

The latest Cretaceous (Fig. 2D) was a time of increased faunal exchanges between different southern and northern landmasses. Such exchanges were hypothesized to occur between South and North America (e.g., Bonaparte, 1984; Bonaparte and Kielan-Jaworowska, 1987; Gayet et al., 1992), Europe and Africa (e.g., Buffetaut, 1989; Gheerbrant and Rage, 2006), and Asia and India (Prasad and Rage, 1991; Rage, 2003), respectively, but the exact timing, magnitude, direction of the dispersal, and taxa involved are still matters of debate. Dispersal between Europe and North America along a high-latitude corridor was also suggested by Martin et al. (2005).

Within a global framework, the Haţeg fauna was obviously part of a larger European bioprovince, based on the presence of a typical rhabdodontid–titanosaur–basal nodosaurid assemblage (Le Loeuff, 1997; Holtz et al., 2004). However, within Europe, it must be emphasized that the Haţeg fauna is markedly endemic and by no means a “typical” European Late Cretaceous fauna (whether such an entity can really be defined — see below, Section 5.2).

Although the presence of the Haţeg turtle *Kallokibotion bajazid* (or closely related forms) was suggested in western European sites (see Gaffney and Meylan, 1992), none of these occurrences was substantiated by more recent studies (Lapparent de Broin and Murelaga, 1999). The basal eusuchian *Allodaposuchus precedens* from Romania was also reported to occur in the Late Cretaceous of southern France and northern Spain (Buscalioni et al., 1999, 2001); these claims are not supported by new studies (Martin and Buffetaut, 2005; Delfino et al., 2008; but see Martin and Delfino, 2010–this issue). The presence of the hadrosaurid *Telmatosaurus transsylvanicus* was cited from sites in southern France and northern Spain by Le Loeuff et al. (1993), but these claims were not substantiated more recently (Laurent et al., 1997). Finally, basal euornithopod material from Haţeg was referred customarily to *Rhabdodon priscus* (Nopcsa, 1915; Weishampel et al., 1991), but recently was re-interpreted as representing the closely related rhabdodontids *Zalmoxes robustus* and *Zalmoxes shqiperorum* (Weishampel et al., 2003).

An overall endemicity analysis was conducted to assess the nature and magnitude of endemicity of the Haţeg fauna (Fig. 3). From the 70+ vertebrate taxa listed from the Haţeg Basin (Csiki, 2005; Grigorescu, 2005; Therrien, 2005 and references cited therein; see Table 1), fewer than two-thirds (42) are sufficiently well known taxonomically to offer a meaningful palaeobiogeographic signal. Of these, three taxa are flying animals (pterosaurs and birds) whose superior dispersal capabilities over potential geographic barriers make them less useful in palaeobiogeographic analysis.

The palaeobiogeographic significance of better-known taxa was evaluated on their known palaeobiogeographic distribution at European and global scale. Three comparisons were made — at species level, at genus level, and at the least-inclusive clade level, in order to avoid biasing the analysis only towards the clades represented by well-known taxa. Moreover, the dataset was analyzed using two assumptions, regardless of the taxonomic level involved: first, all taxa present in Haţeg, but missing from the Late Cretaceous of Europe, and world, respectively, were counted as endemic (*conservative approach*); second, taxa that are represented in Haţeg and not in other areas in the Late Cretaceous, but occur either in older or younger beds of Europe, and the world, respectively (called *non-coextensive endemic taxa*), were excluded from the list of possible endemisms (*relaxed approach*). This second assumption identifies the presence of a non-coextensive endemism as resulting either from regional extinction (if the respective taxa occur in older beds of other areas), or from the appearance of local evolutionary novelties through speciation (if the respective taxa occur in younger beds of other areas). In the first case, the respective taxa can be considered as late-occurring terminal taxa of declining clades (Lazarus taxa; Jablonski, 1986) or local survivors of a regional extinction event (named here Masada taxa), while in the second case the early-occurring members of a clade (what might be called Noah taxa) point to possible centres of origin for that respective clade.

This approach provides an idea about the level of endemism in the Haţeg vertebrate fauna, as well as gives hints about its potential palaeobiogeographic ties and evolutionary history. It should be underlined that although, admittedly, this analysis might include certain flaws (such as those produced by incorrect taxonomic identification or mistaken stratigraphic and geographic distribution patterns of the individual clades, resulting from missing data), it can yield a general background for the understanding of the palaeobiogeographic affinities of the fauna.

The analysis revealed a high level of endemism in the Haţeg fauna (Fig. 3). It appears that from the Haţeg taxa known to species level (21 taxa, including one aerial taxon — *Hatzegopteryx thambema*; Buffetaut et al., 2002), regardless of the assumption used, none is present in any other fauna worldwide, except one (*Bicuspidon hatzegiensis*; Makádi, 2006) reported elsewhere in the Late Cretaceous of Europe. Turning to generic-level taxa (42, including 1 aerial — *Hatzegopteryx*), using the conservative approach almost three-quarters (30 taxa; 71.4%) of the taxa are still endemic at a European level, while slightly more (31 taxa; 73.8%) are endemic at the global level. Using the relaxed approach, the level of endemism is, as expected, somewhat lower, but still considerable: 57.1% (24 taxa) at the level of Europe, and 66.7% (28 taxa) globally. In this case, the list of potential endemisms excludes possible Lazarus taxa with earlier occurrences in Europe (*Eodiscoglossus*, Estes and Sanchíz, 1982), possible local survivors of a regional extinction (Masada taxa such as *Richardoestesia*, *Paronychodon*, known from the Lower Cretaceous of Europe [Rauhut, 2002], but still present in the Upper Cretaceous of North America [e.g., Sankey et al., 2002]), as well as Noah taxa (*Hainina*, known from the Palaeocene of Europe [Vianey-Liaud, 1979]). The shared presence of

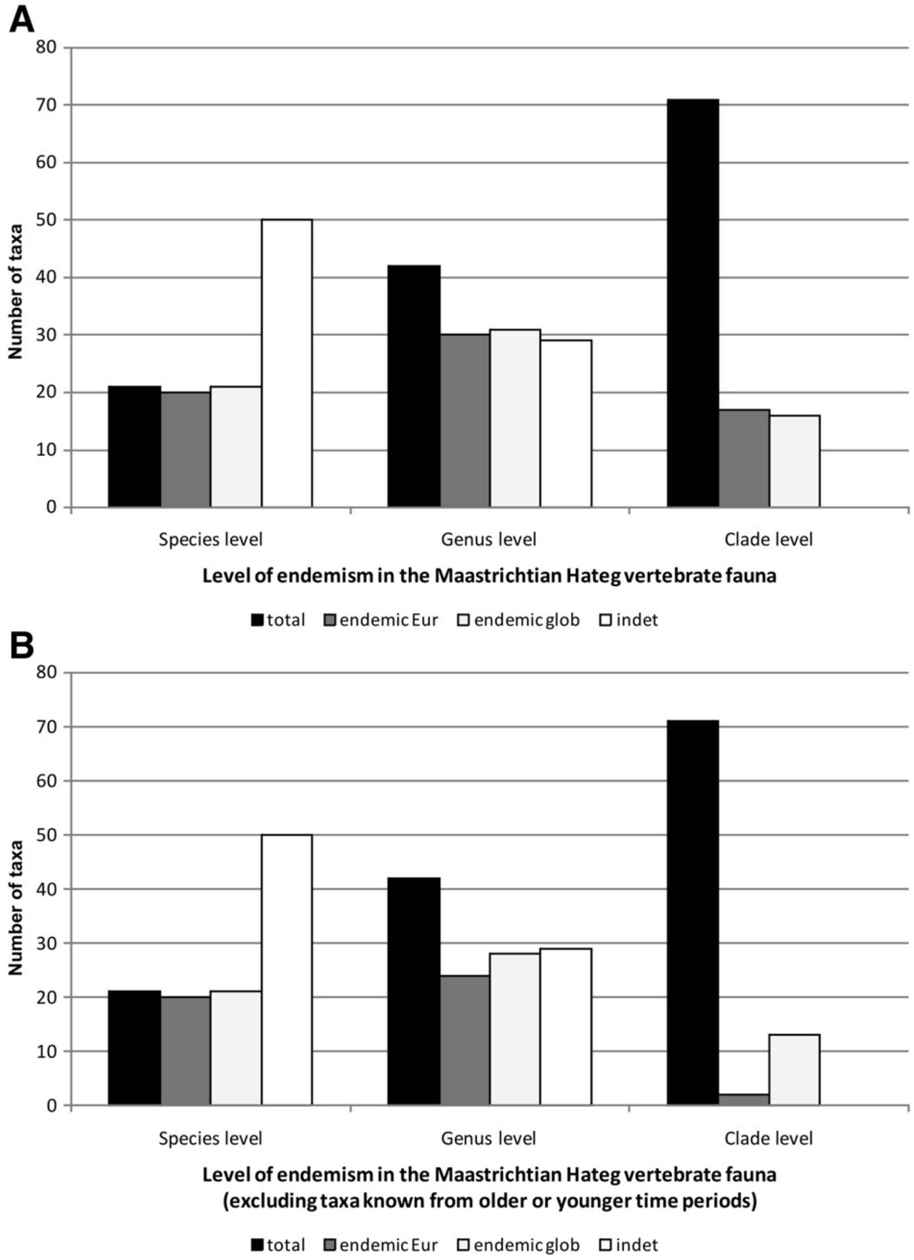

Fig. 3. Histogram showing the degree of endemism of the Haţeg vertebrate fauna at species-, genus- and least-inclusive clade level, at European and global scale, respectively. A. Conservative estimate of endemism, considering only the Late Cretaceous presence–absence data of the taxa; B. relaxed estimate of endemism, excluding taxa that are present in Haţeg and absent in Europe/worldwide in the Late Cretaceous, but are represented either in older (Early Cretaceous) or younger (Palaeogene) time slices. Legend: total — total number of taxa from the Haţeg fauna known at the considered hierarchical taxonomic level; endemic Eur — Haţeg taxa endemic at European scale; endemic glob — Haţeg taxa endemic at global scale; indet — indeterminate Haţeg taxa at the respective taxonomic level.

these taxa between the Maastrichtian Haţeg assemblage and older (or younger) assemblages in Europe or worldwide suggests palaeobiogeographic connections between Haţeg and other parts of Europe and/or the world before (and after) the Maastrichtian.

Finally, the clade-level analysis still shows a certain amount of endemism, which is relatively high under the conservative approach (23.9% – 17 taxa – compared to European faunas, 22.5% – 16 taxa – globally), but drops significantly under the relaxed approach and relative to Europe (only 2.82% – 2 taxa). This is due to the fact that many higher-level taxa from Haţeg occur either in older or younger deposits of Europe, showing that the origin of these taxa should be sought in the Early Cretaceous faunas of Europe (Euramerica), or else that certain European Palaeocene taxa might have originated in Haţeg and spread subsequently throughout the continent (see e.g., Csiki and Grigorescu, 2002). Clade-level endemism compared to areas other than Europe is still considerably high even under relaxed assumption (18.3% – 13 taxa), which might lend support to the idea that the Haţeg fauna was part of a distinct Late Cretaceous European palaeobioprovince.

To explain this high level of endemism, especially when compared to late Late Cretaceous (Santonian–Maastrichtian) continental assemblages from Europe, a high amount of divergent evolution in isolation, producing markedly different local faunas, must be hypothesized. Splitting of the former Euramerican palaeobiogeographic province, followed by extreme fragmentation in southern Europe as a consequence of a complex interaction between plate tectonic processes and eustatic sea-level changes (e.g., Tyson and Funnell, 1987; Dercourt et al., 2000; Golonka, 2004) were probably the driving factors behind this divergent evolution. In order to gain more insight into the temporal and spatial framework of this process, selected taxa were analyzed in their phylogenetic context.

4.2. Phylogenetic analyses

Implementation of the *a posteriori* optimization method presented in the Materials and methods section requires the existence of a well-supported phylogenetic hypothesis that includes the taxon under scrutiny. This prerequisite sets the limits of the following survey, as only few taxa from the Haţeg vertebrate assemblage have so far been included in phylogenetic analyses. Accordingly, despite the fact that a large number of endemics can be identified in the Haţeg fauna (see Table 1), and the potentially important palaeobiogeographic signal these might offer, taxa such as *Paralatonia*, *Hatzegobatrachus*, *Elopteryx*, or *Bicuspidon* cannot be discussed within the *a posteriori* optimization method. On the other hand, poor skeletal representation of, and taxonomic uncertainty surrounding, taxa such as *Acynodon*, *Doratodon* or several small theropods (*Paronychodon*, *Euronychodon*, and *Richardoestesia*) hinder their utility in the same endeavour. Accordingly, only better-known taxa fitted previously into a detailed phylogenetic framework will be considered here; these include the kogaionid multituberculates, kallokibotionid turtles (*Kallokibotion*), basal eusuchians (*Allodaposuchus*), and several herbivorous dinosaurs (*Zalmoxes*, *Telmatosaurus*, *Struthiosaurus*, and *Magyarosaurus*).

4.2.1. Mammals

The mammals of the Haţeg fauna are almost exclusively referable to the peculiar multituberculate clade Kogaionidae (Rădulescu and Samson, 1996; Csiki and Grigorescu, 2000, 2002, 2006; Codrea et al., 2002; Smith et al., 2002; Kielan-Jaworowska et al., 2004; Csiki et al., 2005); one isolated and fragmentary premolar possibly belongs to an undetermined therian (Csiki and Grigorescu, 2001).

Kogaionids are currently restricted to the Late Cretaceous and Palaeocene of Europe; they occurred exclusively in the Haţeg Basin (and surrounding areas; Codrea et al., 2009a, 2010-this issue) during the Maastrichtian, but achieved a larger distribution (France, Spain, Belgium, and Romania) during the Palaeocene (Vianey-Liaud, 1979, 1986; Gheerbrant et al., 1999; Peláez-Campomanes et al., 2000; see also Csiki and Grigorescu, 2002). The presence of *Hainina* was cited from Late Cretaceous deposits of eastern North America by Denton et al. (1996), but more details on this discovery are unavailable and a possible North American occurrence of the kogaionids was not listed by Kielan-Jaworowska et al. (2004). Kogaionids have been included in several phylogenetic analyses, but each analysis places them in different positions (compare e.g. Kielan-Jaworowska and Hurum, 2001, and Rougier et al., 1997, respectively), mainly resulting from the incomplete data sets used by these authors. Only one preliminary phylogenetic analysis including most members of Kogaionidae and a more complete data set is available (Csiki and Grigorescu, 2006: Fig. 1) which recovered an unresolved Kogaionidae with other cimolodontans (Fig. 4). The distinctiveness of this clade, however, is generally accepted (Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004).

Almost all Late Cretaceous kogaionids are clustered as basal taxa relative to the more derived Palaeocene representatives of the clade, suggesting a good concordance between their stratigraphic and phylogenetic positions. Moreover, kogaionids are basal to all other cimolodontan multituberculates, but are more derived than Eobaataridae, considered to represent one of the most derived clade of plagiaulacidans, closely related to the ancestry of Cimolodonta (Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004). Eobaatarids are known from the Early to late Early Cretaceous deposits of Europe (England, Spain – Hahn and Hahn, 2002; Kielan-Jaworowska et al., 2004; Badiola et al., 2008), and Asia (China, Mongolia, Japan – Kielan-Jaworowska et al., 1987; Hu and Wang, 2002; Kusuhashi, 2008), where they postdate the earliest moments of faunal interchanges between Europe and Asia (Barrett and Wang,

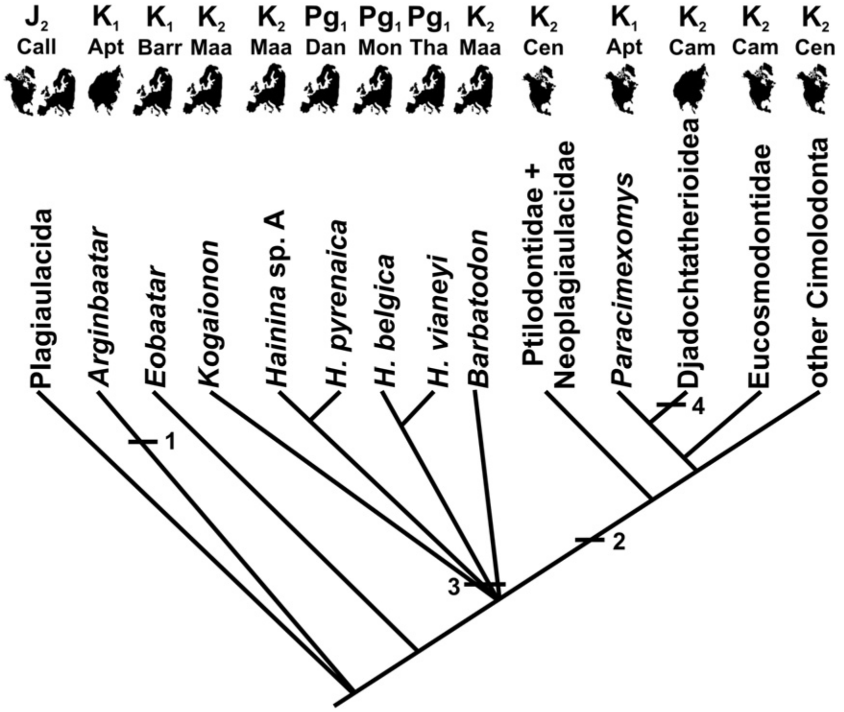

Fig. 4. Phylogenetic relationships of derived Multituberculata (= Cimolodonta) with the position of Kogaionidae (modified from Csiki and Grigorescu, 2006). Events: 1 — dispersal of the ancestors of *Arginbaatar* from Europe (Euramerica) to Asia (pre-Aptian), 2 — isolation of basal cimolodontans in North America, with the fragmentation of Euramerica (before the Aptian), 3 — isolation of ancestral kogaionids in Europe, with the fragmentation of Euramerica (before the Aptian), 4 — dispersal of djadochtatherioidean ancestors from North America to Asia (before the Aptian — the older of the two sistergroups). Abbreviations (used in Figs. 4–10): periods: J — Jurassic, K — Cretaceous, T — Triassic, subscript numbers: 1 — Early, 2 — Middle, 3 — Late; stages: Alb — Albian, Apt — Aptian, Barr — Barremian, Ber — Berriasian, Cam — Campanian, Call — Callovian, Cen — Cenomanian, Dan — Danian, Haut — Hauterivian, Kimm — Kimmeridgian, Maa — Maastrichtian, Mon — Montian, Neo — "Neocomian" (undivided early Early Cretaceous), Nor — Norian, Pg — Palaeogene, San — Santonian, Sin — Sinemurian, Tha — Thanetian, Tith — Tithonian, Val — Valanginian, and Was — Wasatchian. For each terminal taxon, the biogeographic distribution (black figures) and chronostratigraphic position of the oldest member is indicated.

2007). The oldest occurrence of the group is Valanginian (the eobaatarid *Loxaulax*, Kielan-Jaworowska et al., 2004). The earliest record of cimolodontans more derived than the kogaionids is in the Aptian–Albian (oldest occurrence of the paracimexomyid ?*Paracimexomys crossi*, Cifelli, 1997). If kogaionids are indeed the sister group to other Cimolodonta, the minimal time of origin of Kogaionidae must be the Aptian (the age of *Paracimexomys*).

The place of origin of Kogaionidae is constrained by the distribution of cimolodontans, their immediate sister taxon (eobaatarids), and plagiaulacids (their outgroup after eobaatarids). Most plagiaulacids are distributed in the Late Jurassic and Early Cretaceous of Europe and North America, appearing in the earliest Cretaceous of Asia and northern Africa (Morocco), while eobaatarids are restricted to Europe and Asia (Kielan-Jaworowska et al., 2004). According to this distribution, plagiaulacids are typical Euramerican taxa with a geographic range extension into Asia and northern Africa during the earliest Cretaceous; a similar scenario is probably applicable to Eobaataridae, except they seem to have been restricted to the European part of Euramerica. On the other hand, almost all the Cretaceous derived cimolodontans (with the exception of the Asian endemic Djadochtatherioidea; Kielan-Jaworowska and Hurum, 1997) have a distribution restricted to North America during the latest Early to latest Cretaceous, suggesting they evolved here in isolation beginning in the Aptian. This date is coincident with the interruption of the connections between Europe and North America during the Aptian–Albian (Kirkland et al., 1997) and the end of a contiguous Euramerican palaeobioprovince. Optimization of these distribution patterns onto the cladogram of Csiki and Grigorescu (2006) (Fig. 4) reveals that Cimolodonta had a Euramerican origin sometime during the Early Cretaceous, followed by a vicariant event leading to the divergence between kogaionids (in Europe) and other cimolodontans (in North America). According to this evolutionary scenario, Kogaionidae represents an example of European endemism of Euramerican origin.

Be that as it may, the long time gap between the proposed time of origin of kogaionids during the Early Cretaceous and their late appearance in the fossil record, in the Maastrichtian, implies an extended ghost lineage (Norell, 1992; Weishampel, 1996) with a duration of about 45–50 M.y. This long ghost lineage is similar to that reported for many other taxa from the Haţeg Basin (see Weishampel et al., 1993, 2003), suggesting a common underlying evolutionary history.

4.2.2. *Kallokibotion bajazidi*

When described by Nopcsa (1923a,b), *K. bajazidi* was considered a primitive turtle. Apparently restricted to the Transylvanian landmass, *Kallokibotion* is known only from the Haţeg Basin and the neighbouring Transylvanian Basin (Codrea and Dica, 2005; Codrea et al., 2010-this issue). *Kallokibotion*-like turtles were reported from the Maastrichtian of European Russia by Averianov and Yarkov (2004), but this referral needs more material to be substantiated.

The first phylogenetic analysis of the taxon (Gaffney and Meylan, 1992) underscored the primitiveness of the taxon by proposing that it represents the sister taxon of Selmacryptodira (all cryptodires more derived than *Kayentachelys* from the Early Jurassic of North America). Further, more inclusive phylogenetic analyses considering *Kallokibotion* (Hirayama et al., 2000; Joyce, 2007) recovered this taxon at the base of the cryptodiran radiation, in a more basal position than Pleurosternidae. The analysis by Hirayama et al. (2000) found a sister-taxon relationship between *Kallokibotion* and *Tretosternon*, a basal cryptodiran considered by them to include, as synonyms, several other taxa from the earliest Early to Late Cretaceous (Berriasian–Campanian) of Europe, as well as the Aptian–Albian and Campanian of North America. Based on Buffetaut et al. (1999), *Tretosternon*-like taxa (*Solemys*) from the Upper Campanian–Lower Maastrichtian of southern France seem to have been present in Europe up to the Maastrichtian.

Optimising the distribution of age and geographic data for basal cryptodirans onto the cladogram of Hirayama et al. (2000) (Fig. 5) suggests that the lineage leading to *Kallokibotion* must have had its origin by the earliest Cretaceous (Berriasian), the age of the oldest occurrence of the *Tretosternon*-group turtles. Moreover, this *Kallokibotion*–*Tretosternon* clade must have had its origin much earlier, since the more derived Xinjiangchelyidae (a subclade of higher crtyptodires) is known from the Middle–Late Jurassic of Central and Eastern Asia (Peng and Brinkman, 1993; Sukhanov, 2001; Matzke et al., 2005). Hirayama et al. (2000) suggested that, based on the presence of basal cryptodirans in the Early Cretaceous of Australia (*Otwayemys*), distribution of these basal

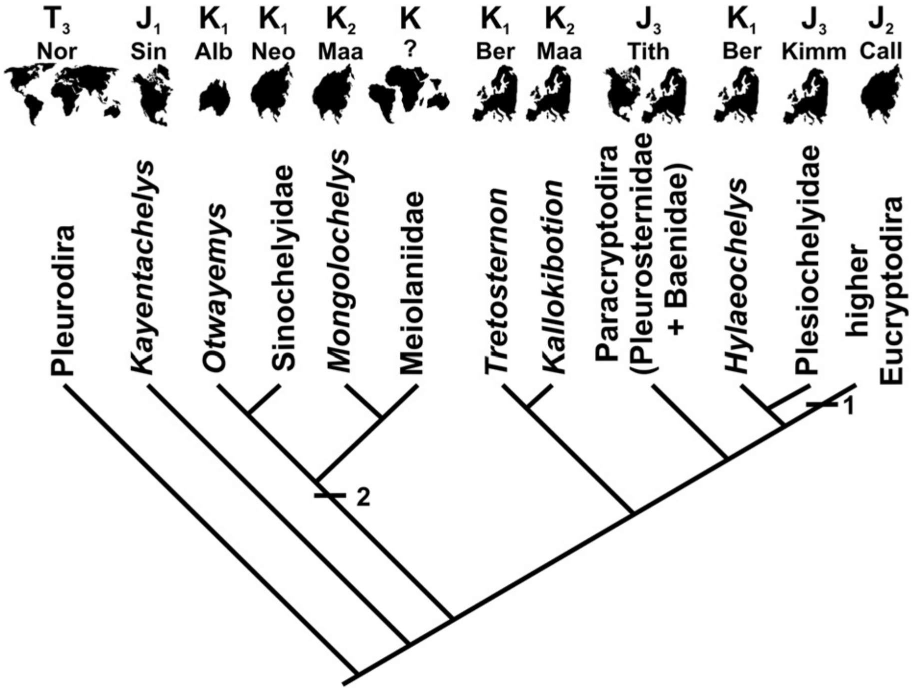

Fig. 5. Phylogenetic relationships of basal Cryptodira, with the position of *Kallokibotion* (based on Hirayama et al., 2000). Events: 1 — isolation of the ancestors of derived Eucryptodira in Asia (before the end of the Middle Jurassic), and 2 — paradoxical apparent close biogeographic relationships between Central Asia and Gondwana during the Cretaceous suggested by basal cryptodiran distribution (not represented in Fig. 2).

cryptodirans must have been nearly global as early as the Middle–Late Jurassic.

As noted above, the cladogenetic event separating the *Kallokibotion* lineage from its sister-taxon *Tretosternon* must be placed no later than the earliest Cretaceous (Berriasian, approx. 142 M.y.). This timing, together with the geographic distributions of its successive outgroups, suggests that *Kallokibotion* represents the terminus of a very old phylogenetic lineage of Euramerican distribution, a relict in the Late Cretaceous European fauna (palaeo-endemism); as Hirayama et al. (2000, p. 192) put it, "…Europe seems have functioned primarily as a biogeographical "Jurassic Park" or protected area for primitive cryptodires such as pleurosternids, *Tretosternon*, *Kallokibotion*, plesiochelyids, and xinjiangchelyids during the Cretaceous."

Occurrence of *Kallokibotion* late in the stratigraphic record (Maastrichtian, approx. 70–68 M.y.) implies the existence of an extended ghost lineage of about 70 M.y., apparently much longer than in the case of any other taxon from the Haţeg Basin. Despite such a long hidden history, *Kallokibotion* seems to have undergone only minor evolutionary change, and its restricted geographic range (Transylvanian landmass and perhaps southwestern Russia) suggests that this might have been driven by vicariance processes after the separation from the *Tretosternon* lineage that was distributed in western Europe and North America.

On the other hand, the analyses of Joyce (2007) and Danilov and Parham (2008) found *Kallokibotion* to lie outside crown-group Testudines, as a relatively derived stem testudinate. Considering this alternative, more basal position of *Kallokibotion* does not alter the palaeobiogeographic scenario outlined above. Instead, shifting *Kallokibotion* into a more basal position within Testudinata only underlines the antiquity of the evolutionary lineage leading to it, since its sister-taxon (Paracryptodira + crown-group testudines) is already known from the Middle Jurassic (Danilov and Parham, 2008). Accordingly, the ghost lineage leading to *Kallokibotion* extends from the Middle Jurassic (probably Bathonian–Callovian; see Weishampel et al., 2004 and references therein) to the Maastrichtian, spanning an even more impressive time interval of about 90–95 M.y. According to these authors, the replacement of stem testudines with stem cryptodires and even crown-group Cryptodira in Europe was already under way by the Late Jurassic, and thus survival of a basal testudinate lineage into the latest Cretaceous is even more remarkable.

4.2.3. *A. precedens*

Nopcsa (1928a) proposed the name *A. precedens* for crocodilian remains he described from the Maastrichtian of the Haţeg Basin (Nopcsa, 1915), invoking the possibility that in the future a specific difference should be established with the crocodilian remains from Fuveau, southern France, known at that time as *Crocodylus affuvelensis* (see Martin and Buffetaut, 2008). Specimens referred to *Allodaposuchus* were described from the Upper Cretaceous of southern France and northern Spain (Buscalioni et al., 1999, 2001), but these identifications were questioned (Martin and Buffetaut, 2005; Delfino et al., 2008). Currently, the taxon is known only from Transylvania, although other species of *Allodaposuchus* might have been present in western Europe (Delfino et al., 2008; Martin, in press).

The first phylogenetic analysis to include *Allodaposuchus* (Buscalioni et al., 2001) suggested that it occupies a basal position within Eusuchia, representing the sister taxon of crown-group Crocodylia. More recent analyses, based on larger character-taxon matrices (Salisbury et al., 2006; Ősi et al., 2007) and more complete referred material of *Allodaposuchus* (Delfino et al., 2008) group *Allodaposuchus* with *Hylaeochampsa* from the Early Cretaceous (Barremian) of Europe (Clark and Norell, 1992), in an unresolved tritomy with Hylaeochampsidae and the crown-group, or even into moving it into a slightly more basal position as the sister group of (*Hylaeochampsa* + crown-group). Despite this uncertainty regarding the exact phylogenetic position of *Allodaposuchus*, its phylogenetic proximity to Hylaeochampsidae at the base of Eusuchia seems well established.

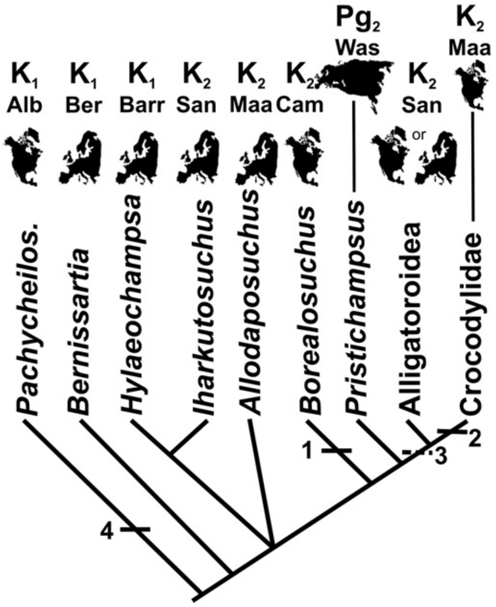

Fig. 6. Phylogenetic relationships of basal eusuchians, with the position of *Allodaposuchus* (simplified after Ősi et al., 2007). Events: 1 — dispersal of *Borealosuchus* from Europe to North America (during or prior to the Santonian), 2 — dispersal of the ancestors of Crocodylidae from Europe to North America (before the Maastrichtian), based on the hypothesis of the European origin of Alligatoroidea (e.g., Rabi, 2005), 3 — alternative hypothesis, placing the origin of Alligatoroidea + Crocodylidae in North America, after a dispersal of their common ancestor from Europe to North America (before the Santonian), 4 — isolation of the ancestors of the derived mesoeucrocodylian *Pachycheilosuchus* in North America, with the fragmentation of Euramerica (after the Barremian).

Based on this phylogenetic position (Fig. 6), the age and place of origin of the *Allodaposuchus* lineage can be estimated by optimising the stratigraphic and geographic distribution of eusuchians and their closest relatives onto the cladogram of Delfino et al. (2008). A sister-group relationship between *Hylaeochampsa* and *Allodaposuchus* suggests that divergence between the two lineages occurred at least by the Barremian (at approx. 130 M.y.). During the Mesozoic, crown-group crocodylians are restricted to the Late Cretaceous, and the dominantly North American distribution of the oldest members of the clade (e.g. Brochu, 1999; Salisbury et al., 2006) was used to suggest a North American origin. However, the presence of basal alligatoroids in the Santonian–Campanian of Europe challenges this view (Rabi, 2005; Martin, 2007; Martin and Buffetaut, 2008) and, together with the European distribution of the hylaeochampsid sister group (Clark and Norell, 1992; Ősi et al., 2007) to the crown-group, suggests a possible European origin of the ancestral crown-group crocodylians. Most of the successive advanced neosuchian outgroups to the *Hylaeochampsa*–*Allodaposuchus*–*Crocodylia* group (e.g., *Bernissartia*, *Goniopholis*, and *Theriosuchus*) have a Euramerican distribution during the Late Jurassic–Early Cretaceous, and suggest a Euramerican origin of the derived neosuchians. Recent discoveries of Gondwanan late Early Cretaceous non-crocodylian eusuchians (Salisbury et al., 2003, 2006) were cited as arguments for a possible southern location of the Neosuchia–Eusuchia transition. However, their late stratigraphic occurrence, compared to that of the next outgroup taxa of Eusuchia (Late Jurassic) predating the definitive fragmentation of Neopangea, suggests that the Gondwanan presence of mesoeucrocodylians of neosuchian-basal eusuchian grade can be probably explained by vicariant processes fragmenting an already wide Neopangean distribution. Choosing between these palaeobiogeographic scenarios might rest ultimately on the relative phylogenetic positions of *Susisuchus* and *Isisfordia*, recovered as a polytomy with *Goniopholis* and *Bernissartia* at the base of Eusuchia by Delfino et al. (2008), but as a clade more basal than *Hylaeochampsa* by Martin and Buffetaut (2008). New discoveries, especially from the more poorly sampled southern continents might shed more light on the exact timing and location of the events leading to the origin of Eusuchia, but it is unlikely that these will challenge the ideas of a Neopangean origin of the Neosuchia, nor of a Euramerican origin of the advanced Eusuchia during the Early Cretaceous, before the Barremian.

Allodaposuchus, as a result, is recognized here as an endemic taxon, descending from a Euramerican common ancestor shared with *Hylaeochampsa*. Evolution of Hylaeochampsidae continued in the European area after the post-Barremian fragmentation of Euramerica, leading to *Iharkutosuchus* in the Santonian of Hungary (Ősi et al., 2007), while another closely related lineage peaked in *Allodaposuchus* from the Maastrichtian of Romania The late stratigraphic occurrence of *Allodaposuchus* suggests the presence of a long ghost lineage of about 55–60 M.y., similar to other vertebrates known from the Haţeg Basin, thus a long period of hidden history. (An alternative evolutionary scenario would be required if *Allodaposuchus* shifts to a more derived position within basal alligatoroids, according to Martin (in press). However, this scenario will not be further explored here, pending the studies of Martin on a possible new species of *Allodaposuchus* in southern France).

4.2.4. *Zalmoxes* species

Until recently, nearly all basal ornithopods from the Late Cretaceous of Europe were assigned to *Rhabdodon* (Matheron, 1869; Nopcsa, 1902, 1915, 1928b; Weishampel et al., 2003). Of modest size and robust build, these dinosaurs are known from present-day France, Spain, Austria, Romania, and Hungary. In 2003, Weishampel et al. revised the basal ornithopod material from Haţeg referred previously to *Rhabdodon* and analyzed its phylogenetic significance, noting that the Transylvanian material was different from that elsewhere in Europe. Called *Zalmoxes*, two species were recognized: *Z. robustus* and *Z. shqiperorum*. Both share the same stratigraphic distribution and geographic provenance — the Late Cretaceous of present-day western Romania; subsequently, the genus was also reported from the early Campanian of Austria (Sachs and Hornung, 2006). Its closest relative, *R. priscus* from southern France and northern Spain, appears roughly contemporaneous with the two *Zalmoxes* species from Transylvania (Weishampel et al., 2003). From this, it can be concluded that there was a negligible ghost lineage in this clade of rhabdodontids (which did not include the new material from Hungary) and that this clade originated in Europe (Fig. 7).

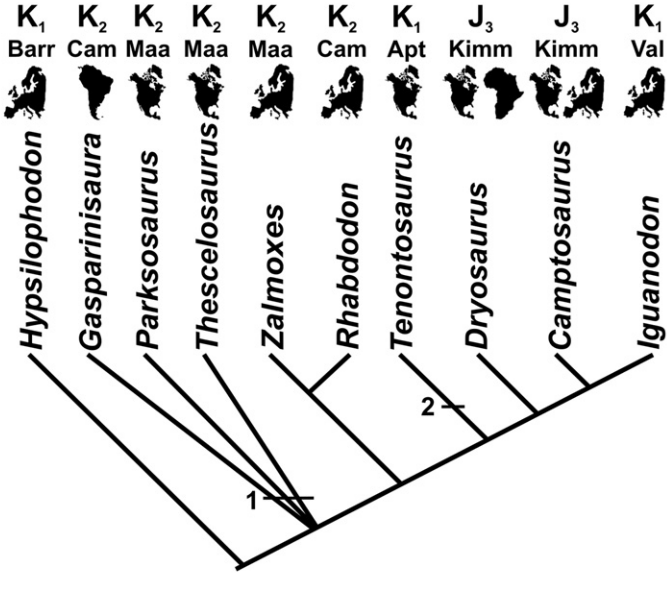

Fig. 7. Phylogenetic relationships of basal Ornithopoda, with the position of *Zalmoxes* and Rhabdodontidae (based on Weishampel et al., 2003; Butler et al., 2006, 2008). Events: 1 — dispersal of the ancestors of Late Cretaceous American basal ornithopods (*Thescelosaurus*, *Parksosaurus*, and *Gasparinisaurus*) from Europe to the New World (during or prior to the Kimmeridgian), 2 — isolation of the ancestors of *Tenontosaurus* in North America, with the fragmentation of Euramerica (after the Barremian).

The sister-group of Rhabdodontidae, Iguanodontia, is a clade that dates back to the Late Jurassic (the earliest ages of *Camptosaurus* and *Dryosaurus*; probably near the boundary between the Kimmeridgian and Tithonian, approximately 151 mya) of western North America (Norman, 2004). Beyond that, several reasonably well-known taxa formerly thought to have been basal ornithopods (*Agilisaurus*, *Hexinlusaurus*, and others) have been shifted to more basal positions within Ornithischia (Butler et al., 2008). With these removed, sibling relationships are unresolved more basally than Rhabdodontidae + Iguanodontia, with *Thescelosaurus*, *Parksosaurus*, *Gasparinisaura*, and the latter clade forming a polytomy. Relationship with *Hypsilophodon* follows thereafter. *Parksosaurus* and *Thescelosaurus* have a North American distribution, while *Gasparinisaura* is South American and *Hypsilophodon* is European. Taken together, these dinosaurs indicate that the most parsimonious of source areas of the entire clade is European (Euramerican, taking into account the age of the basal *Hypsilophodon*), with dispersal of *Gasparinisaura*, *Thescelosaurus*, *Parksosaurus*, and Iguanodontia to the New World. *Zalmoxes* and *Rhabdodon* are part of the original European distribution (Fig. 7).

4.2.5. *Telmatosaurus transsylvanicus*

Nopcsa originally described what he considered hadrosaurid material from the Haţeg Basin in 1900 at the age of 22. Properly named *T. transsylvanicus* in 1903, Nopcsa considered this species to be positioned at the base of Hadrosauridae. In addition to Haţeg, specimens referred to *Telmatosaurus* have also been claimed in France and Spain (Lapparent, 1947; Le Loeuff et al., 1993), but they have not stood up to further investigation (Laurent et al., 1997). Currently *Telmatosaurus* is known only from Transylvania (Dalla Vecchia, 2006).

The first cladistic analysis to include *Telmatosaurus*, (Weishampel et al., 1993) confirmed Nopcsa's (1900) suggestion that it was the basal member of Hadrosauridae; that is, the sister-group of the clade consisting of lambeosaurines and hadrosaurines. This position has been confirmed over the ensuing years through the discovery of many new hadrosaurids and the application of cladistic methods with larger character-taxon matrixes to understand the general shape of the cladogram of the group (Weishampel et al., 1993; Godefroit et al., 1998; Norman, 2002, 2004; You et al. 2003a,b; Horner et al., 2004; Fig. 8). More recently, Forster (1997) argued that Hadrosauridae should consist solely of Lambeosaurinae and Hadrosaurinae, which places *Telmatosaurus* outside this clade. This alternative position of *Telmatosaurus*, just outside Hadrosauridae sensu stricto, was re-iterated recently by Sues and Averianov (2009). In both cases, the relationship of *Telmatosaurus*, lambeosaurines, and hadrosaurines is maintained and the issue becomes semantic (see Horner et al., 2004). Moreover, when analyzing the cladogram that depicts the preferred phylogenetic hypothesis of Sues and Averianov (2009), only details such as time of origin and dispersal of the *Telmatosaurus* lineage to Europe differ, compared to those derived from our preferred phylogenetic hypothesis.

Based on this phylogenetic position, with the closest relatives of *Telmatosaurus* being the more commonly known clade of Hadrosaurinae + Lambeosaurinae — called Euhadrosauria by Weishampel et al. (1993) — and successively more distant Asian and North American outgroups, the *Telmatosaurus* lineage must be as old as or older than the late Albian (the age of "*Trachodon*" *cantabrigiensis*, an indeterminate euhadrosaurian from England; Lydekker, 1888).

These relationships imply a ghost lineage for *Telmatosaurus* of 30 M.y.; the alternative hypothesis of Sues and Averianov (2009) suggests a somewhat shorter ghost lineage, of about 18 M.y.

Beyond the timing of these cladal origins, the palaeobiogeography of Hadrosauridae requires geographic locations of taxa farther down the cladogram. Unfortunately, the sister group of Euhadrosauria + *Telmatosaurus* (Hadrosauridae *sensu* Weishampel et al., 1993) as well as successive outgroups are not altogether certain. A few studies have indicated that forms like *Eolambia caroljonesa* and *Protohadros byrdi* (Kirkland, 1998; Head, 1998; You et al., 2003a), both from the earliest

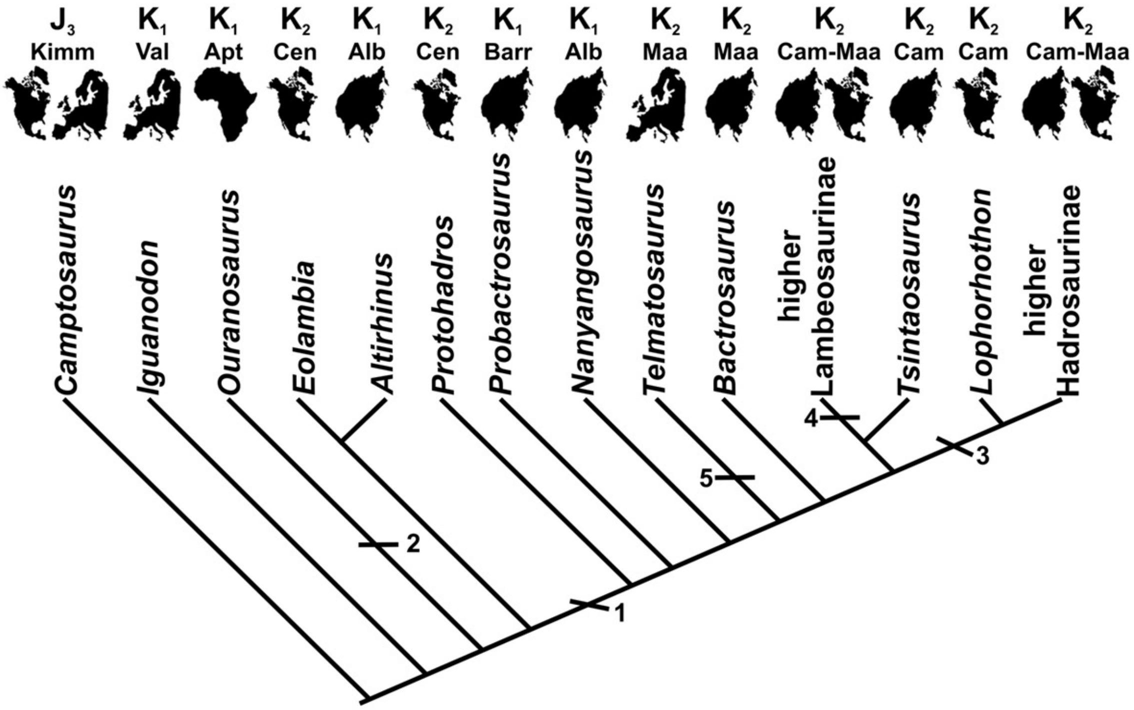

Fig. 8. Phylogenetic relationships of ankylopollexian ornithopods, with the position of *Telmatosaurus* (based on Weishampel et al., 1993; Horner et al., 2004; Butler et al., 2006). Events: 1 — isolation of the hadrosauroids in Asiamerica (after the Barremian), 2 — dispersal of *Ouranosaurus* from Europe to Africa (pre-Aptian; but see Canudo et al., 2009); 3 — dispersal of basal hadrosaurines from Asia to North America (prior to the Campanian); 4 — dispersal of derived lambeosaurines from Asia to North America (in several episodes after the Santonian, with occasional reversal of the dispersal direction; see also Godefroit et al., 2003); 5 — dispersal of *Telmatosaurus* from Asiamerica to Europe (probably before the Albian; see text).

Late Cretaceous (approximately 95 mya) of North America, are the next successive close relatives of Hadrosauridae. More distant relationships beyond this point are with a variety of Asian and North American taxa. Other, more recent work places one or several Asian taxa (among them, *Bactrosaurus*, *Probactrosaurus,* and *Nanyangosaurus*; Godefroit et al., 1998; Xu et al., 2000; Norman, 2002) as sister taxa of Hadrosauridae.

When locations of these taxa are optimized on the cladogram summarizing current understanding of higher ankylopollexian relationships (Fig. 8), the most parsimonious source area of the entire clade is Euramerica. The evolution of the clade of *Probactrosaurus* and higher taxa involves dispersal to Asia, with a second dispersal of the *Telmatosaurus* lineage to Europe. Finally, the Euhadrosauria/Hadrosauridae clade has an Asiamerican source. The notion of a North American origin for Hadrosauridae has a long history (e.g., Lull and Wright, 1942; Ostrom, 1961), but when Asian taxa are intermixed with those from North America as successive sister taxa to Hadrosauridae (as indicated above), then the source area becomes Asiamerica.

The European location of *Telmatosaurus*, combined with its relationship among ankylopollexian taxa, stands out against the otherwise Asian/Asiamerican distribution of closely related taxa. In lieu of the discovery of new taxa, *Telmatosaurus* is best interpreted as the terminus of a single European migration.

4.2.6. Other dinosaurs

Less is known about the relationships of the nodosaurid *Struthiosaurus transylvanicus*, a member of a clade of three described species distributed from Transylvania to Austria and the Ibero-Armorican landmass (see Garcia and Pereda-Suberbiola, 2003, Pereda-Suberbiola and Galton, 2009). The phylogenetic position of *Struthiosaurus* is somewhat uncertain; although usually considered a nodosaurid (e.g., Pereda-Suberbiola and Galton, 2001), this was considered not well supported by Vickaryous et al. (2004). It was recently included in two phylogenetic analyses (Ősi, 2005; Ősi and Makádi, 2009) that resolved its position at the base of Nodosauridae, followed by *Hungarosaurus* from the Santonian of Hungary, and, further up the tree, by a clade of late Early to Late Cretaceous North American taxa (*Silvisaurus*, *Sauropelta*, *Pawpawsaurus*, *Edmontonia*, and *Panoplosaurus*); unfortunately, its relationships to *Cedarpelta*, considered the oldest (Berriasian–Hauterivian of North America) and basalmost nodosaurid by Vickaryous et al. (2004) is unknown at present. Phylogenetic relationships of *S. transylvanicus* within the genus have not yet been investigated.

Based on available phylogenetic data (Fig. 9), the origin of the *Struthiosaurus* lineage extends into pre-early Aptian times (ghost lineage duration about 44 M.y.), but could go back as far as the earliest Cretaceous, depending on its relationships with *Cedarpelta* (estimated ghost lineage duration up to 75 M.y.). However, with its sister species ranging only as far as the Early Campanian (Garcia and Pereda-Suberbiola, 2003; Pereda-Suberbiola and Galton, 2001), the origin of *S. transylvanicus* itself extends back only to the Santonian–Campanian boundary; this suggests the presence of land connections between the different southern European landmasses during the second half of the Late Cretaceous. As for the origin of the *Struthiosaurus* lineage, *a posteriori* optimization using the tree topology found by Ősi and Makádi (2009) suggests that it (together with that of *Hungarosaurus*) can be traced to Euramerica, with their successively more derived relatives living in the Early Cretaceous of North America (Vickaryous et al., 2004). Thus, it seems reasonable that the common ancestor of *Struthiosaurus* and its closest relatives was Euramerican and dates to at least the late Aptian. The identification of a clade of derived late Early to Late Cretaceous North American nodosaurids suggests that isolation following the severing of land connections between the eastern and western parts of Euramerica (i.e., Europe and North America, respectively) might have been the driving factor for the endemic development of the *Struthiosaurus* lineage in Europe. Subsequently, eustasy-driven fragmentation of the different southern European landmasses might have produced the split of this lineage into the three known species inhabiting different islands. However, poor skeletal representation of the Transylvanian *Struthiosaurus*,

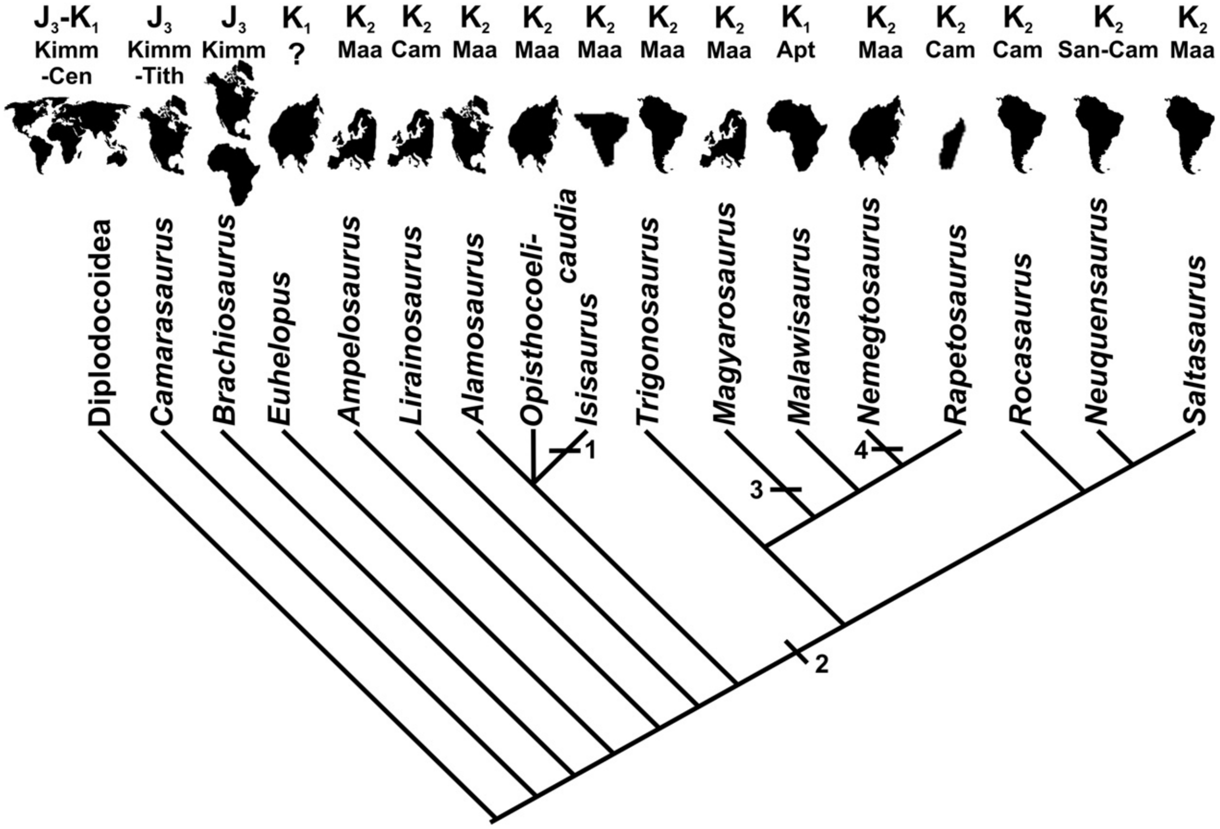

Fig. 9. Phylogenetic relationships of Macronaria, with the position of *Magyarosaurus* (based on Curry Rogers, 2005; Upchurch et al., 2004). Events: 1 — dispersal of the ancestors of *Isisaurus* from Laurasia to India (prior to the Maastrichtian); 2 — dispersal of the ancestors of '*Rapetosaurus* clade' + Saltasauridae from Laurasia to Gondwana (Africa) before the Aptian, 3 — dispersal and isolation of the ancestors of *Magyarosaurus* before the Aptian, 4 — reintroduction of the ancestors of *Nemegtosaurus* into Asia before the Maastrichtian.

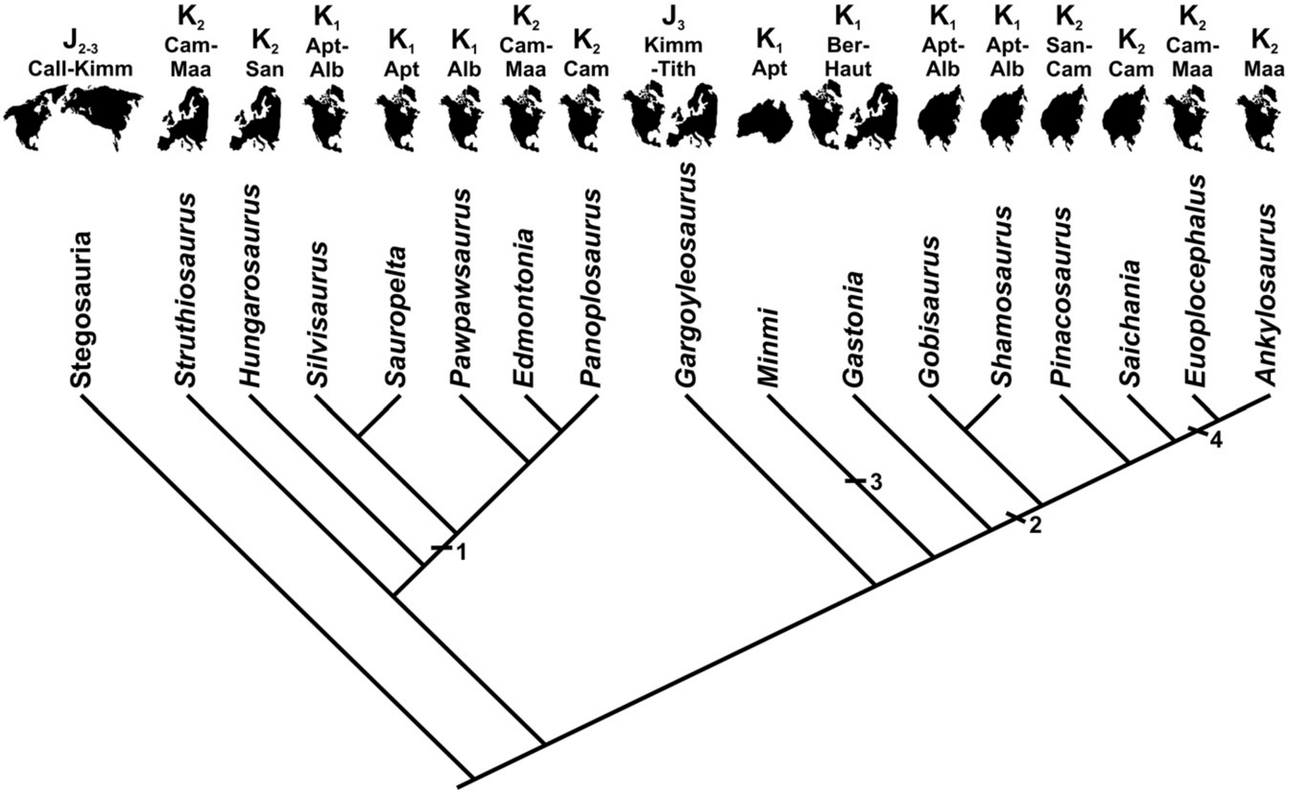

Fig. 10. Phylogenetic relationships of Ankylosauria, with the position of *Struthiosaurus* (based on Vickaryous et al., 2004; Ősi, 2005; Ősi and Makádi, 2009). Events: 1 — dispersal and/or isolation of the derived nodosaurids in North America after the Barremian, following the severing of the Euramerican land connections, 2 — dispersal of the ancestors of higher Ankylosauridae from Euramerica to Asia (before the Aptian), 3 — dispersal of the ancestors of *Minmi* from Euramerica to Australia (before the Aptian), and 4 — reintroduction of the most derived Ankylosaurinae from Asia to North America (before the Campanian).

together with the uncertainties regarding the exact phylogenetic position of the genus (compare Ősi and Makádi, 2009 with Vickaryous et al., 2004 and Carpenter, 2001), suggests that this palaeobiogeographic scenario must be treated with caution.

Unfortunately, far less is known about the relationships of the Transylvanian titanosaurs (*Magyarosaurus* and yet to be named forms) — where they might have originated and when they diverged — but efforts to obtain this information is now underway (e.g., Csiki et al., 2007, in press). Only one phylogenetic analysis including *Magyarosaurus* has been published so far (Curry Rogers, 2005). According to this study, *Magyarosaurus* clusters as a member of an informal '*Rapetosaurus* clade' (Fig. 10) alongside *Rapetosaurus* from the ?Campanian or ?Maastrichtian of Madagascar, *Trigonosaurus* from the Maastrichtian of Brazil, *Malawisaurus* from the Aptian of Malawi and *Nemegtosaurus* from the Maastrichtian of Mongolia (Upchurch et al., 2004). The sister group of the '*Rapetosaurus* clade' is the exclusively South American Late Cretaceous (Santonian–Maastrichtian) saltasaurine clade (*Saltasaurus*, *Neuquensaurus*, and *Rocasaurus*). Based on this topology, *Magyarosaurus* represents a late-surviving offshoot of an evolutionary lineage dating back to at least the Aptian, yielding a ghost lineage duration of about 50 M.y. Moreover, optimization of the biogeographic area of origin suggests a southern, Gondwanan (western Gondwanan) origin for the '*Rapetosaurus* clade', with introduction of the evolutionary lineage leading to *Magyarosaurus* from western Gondwana (probably Africa) into Europe some time during the Aptian or later. Interestingly, the earliest probable timing of this faunal exchange coincides closely with the opening of a dispersal route between Africa and Europe in the Barremian-Aptian, as hypothesized recently by Canudo et al. (2009).

Although the available data provide the basis for *a posteriori* optimization to determine the time and place of origin for *Magyarosaurus*, several lines of evidence suggest extreme caution must be taken in this respect. First, *Magyarosaurus* was coded in Curry Rogers (2009) on the assumption that all titanosaur remains from the Haţeg belong to one taxon (e.g., Le Loeuff, 1993). However, a recent revision of the available material suggests the presence of several taxa (e.g., Csiki et al., 2007, in press), which casts doubt on the codings supporting the phylogenetic position of *Magyarosaurus*. Moreover, the position of *Magyarosaurus* within its clade is unstable and poorly supported (see Curry Rogers, 2005, for details); consequently any palaeobiogeographic hypothesis based on this analysis rests on rather weak grounds. These phylogenetic uncertainties surrounding *Magyarosaurus*, and other taxa not yet included in cladistic analyses, suggest caution until a full revision of the Haţeg titanosaurs is published.

5. Discussion

From the foregoing, the biogeographic affinities of the Haţeg fauna point to a panoply of sources. First, in terms of faunistics, Haţeg is strongly endemic with respect to other European faunas. Second, phylogenetic analyses indicate a mixture of dispersal and vicariant explanations. Dispersal from Asiamerica accounts for the European (i.e., Transylvanian) distribution of *Telmatosaurus*. On the other hand, a broad European/Euramerican distribution argues for an early isolation, before the end of the Early Cretaceous, of core Late Cretaceous European taxa (e.g., multituberculate mammals, basal cryptodirans, hylaeochampsid-grade eusuchian crocodylians, basal ornithopods), with subsequent vicariant events involving Transylvanian taxa.

The above discussions suggest a complex palaeobiogeographic history of the Haţeg assemblage. The wider implications of these diversified palaeobiogeographic affinities, as outlined, will be discussed in the following.

5.1. The Haţeg Island — a refugium?

Insularity is often thought to represent an evolutionary dead-end, islands acting as refugia for the terminal members of a clade. The last surviving mammoths (*Mammuthus primigenius*) were reported to have inhabited small islands in the Arctic Ocean (Vartanyan et al., 1993, 1995, 2008; Guthrie, 2004). New Zealand and its neighbouring smaller islands represent sanctuaries within which endemic representatives of several primitive clades (e.g., Leiopelmatidae, Sphenodontia) survive (Mitchell et al., 2006; Worthy et al., 2006; Jones et al., 2009). Finally, a peculiar vertebrate assemblage described from the Albian Tlayua Formation, Mexico, including several basal forms (squamates, scincoids), was interpreted as an insular fauna (Reynoso, 2000).

Relatively early, Nopcsa (1915, 1923a) interpreted the Haţeg fauna in similar terms, as an assemblage composed of primitive taxa surviving within an island sanctuary, shielded from competition from more derived contemporaries by occupying an isolated region.

In the cases of most of the taxa discussed above, such an evolutionary history is certainly conceivable, especially in the case of those taxa for which a long ghost lineage can be reconstructed, and whose unexpectedly late stratigraphic occurrences contrast with their strikingly primitive morphology. *Kallokibotion* or *Telmatosaurus* certainly fit the case of survivors within an isolated island refuge. But even these two taxa imply different interpretations: while for *Kallokibotion* the Haţeg area acted as a *palaeorefugium*, an area circumscribing a fragment of a once-existing wider distribution (Nekola, 1999), for *Telmatosaurus* it represents a *neorefugium*, a sanctuary area formed after the geographic range expansion of the basal hadrosaurids into Europe (Nekola, 1999).

It should be emphasized, however, that the palaeobiogeographic significances of other members of the Haţeg fauna do not comply with such a simplistic refugium model. Although rhabdodontids and *Allodaposuchus*, together with *Struthiosaurus* and several other lower vertebrate taxa (i.e., *Bicuspidon*) represent isolated and late-surviving descendants of very old phylogenetic lineages, these taxa are by no means restricted to the Transylvanian area. All show a wider, southern European distribution, encountered on other landmasses as well (Weishampel et al., 2004; Makádi, 2006; Martin, in press). Here, they are represented eventually by different species, or closely related sister taxa, suggesting local evolution and speciation on the different landmasses. In some cases, the Haţeg taxa and their relatives from other parts of southern Europe are more or less contemporary, removing the Transylvanian taxa as the latest survivors of their clades. Accordingly, these taxa do not fit the model of insular relicts, but represent instead members of an endemic European faunal radiation implying clades isolated here after the Early Cretaceous. Moreover, presence of closely related, even sister-species taxa, across different parts of southern Europe calls for the presence of dispersal routes between these isolated landmasses. The time of opening of these dispersal routes, as well as their exact palaeogeographic position, nature, and selectivity, are poorly constrained and should represent an important direction for future studies of Late Cretaceous European palaeobiogeography.

Several other, less well-known clades from Haţeg are represented by taxa with a widespread distribution during the Late Cretaceous (see review in Pereda-Suberbiola, 2009); these include lepisosteids, discoglossids, albanerpetontids, basal alligatoroids, dromaeosaurids and other theropods with uncertain affinities (*Richardoestesia* and *Paronychodon*). Whether these represent descendants of older European taxa or immigrants from other (mainly Asiamerican) landmasses, remains undetermined until more diagnostic material is discovered that will allow a thorough comparison with their relatives from other palaeobiogeographic provinces. Even theropods whose affinities seem to point to Asiamerican connections during the Late Cretaceous (i.e., alvarezsaurids and caenagnathids; Osmólska et al., 2004; Padian, 2004; Longrich and Currie, 2009) have been interpreted previously as possible descendants of Early Cretaceous members of these clades present in Europe/Euramerica (Csiki and Grigorescu, 2005; Kessler et al., 2005).

Finally, the "Haţeg Island" can be interpreted as an evolutionary cradle (see Bellemain and Ricklefs, 2008 for modern examples) for at least kogaionid multituberculates. According to their known stratigraphic and geographic distribution, kogaionids were restricted to the Transylvanian area during the Late Cretaceous, but spread across southern Europe during the Palaeocene (Csiki and Grigorescu, 2002; Kielan-Jaworowska et al., 2004; Csiki et al., 2005 and references cited therein). Based on this distribution pattern, as well on the apparently basal position of most Transylvanian kogaionids compared to the Palaeocene representatives of this clade, it is tempting to hypothesize that the Transylvanian landmass, isolated for most of the Late Cretaceous from other emerged areas, represented the place of diversification, if not the origin, of Kogaionidae (Csiki and Grigorescu, 2002).

5.2. Haţeg Island and the Late Cretaceous European palaeobioprovince

As already noted in the faunal comparisons (4.1.), the overall composition of the Haţeg fauna is reminiscent of those from other emergent parts of southern Europe. However, although Late Cretaceous Europe is usually considered a coherent bioprovince in most models (Le Loeuff, 1997; Holtz et al., 2004), its unity is far from well supported (e.g., Upchurch et al., 2002). The faunal differences across the Late Cretaceous of Europe (e.g., Buffetaut and Le Loeuff, 1991; Le Loeuff and Buffetaut, 1995; Rage, 2002) can be ascribed both to the extreme geographical fragmentation of the region (Dercourt et al., 2000), and possibly to the differential palaeobiogeographic evolution of the segments of this bioprovince.

Geographically, it seems difficult to treat the different Late Cretaceous continental faunal assemblages of Europe as parts of a unique and homogenous bioprovince; this is contradicted by the palaeogeographic-palaeotectonic setting of Late Cretaceous Europe. The advanced geographical fragmentation of southern Europe arose both from the presence of epicontinental seaways transgressed over the stable European craton, and to the different deep-sea basins connected to the Neo-Tethys and Alpine Tethys oceans (e.g., Dercourt et al., 2000; Stampfli and Borel, 2002; Golonka, 2004; Schmid et al., 2008). An analogue probably can be found in the modern Malay Archipelago extending between mainland Asia and Australia.

A short survey of the most outstanding faunal differences reveals interesting distribution patterns across Europe. Despite the relatively high diversity of the Haţeg fauna, it is noteworthy that it lacks members of several clades represented in western European vertebrate faunas. For example, hadrosaurids appear to have been quite common in latest Cretaceous assemblages from Ibero-Armorica, with diverse basal lambeosaurines as a newly recognized hallmark feature (Pereda-Suberbiola et al., 2009; Prieto-Marquez and Wagner, 2009); these taxa are missing from hadrosaurid-bearing assemblages from southeastern Europe (Romania, Italy). Abelisauroid theropods were described from areas belonging to the partly submerged southern margin of the European mainland (France, the Netherlands; see Carrano and Sampson, 2008 and references therein), but not from more eastern areas, evolving as insular continental blocks within the northern part of the Tethys (Austria, Hungary, Italy, Slovenia, Romania). Rare records of European Late Cretaceous ceratopsians are known from north-western European sites (Godefroit and Lambert, 2007; Lindgren et al., 2007), but these are absent from more southern and eastern (including Haţeg) assemblages. The eutherian zhelestids are well represented in the Ibero-Armorica realm (see review by Kielan-Jaworowska et al., 2004), while rare marsupials were described from northwestern Europe (the Netherlands; Martin et al., 2005); both of these groups are absent from the eastern European faunas, including Haţeg. Besides these differences in faunal composition, each landmass harboured an array of endemic taxa, differentiated at least at specific, if not generic level (see Pereda-Suberbiola, 2009). Taken together, these faunal differences require a two-step hypothesis to explain: *minor differences* (clades represented by different species or genera on different European areas) most probably arose from differentiation from a common core assemblage, or by accidental dispersal of individual taxa from other palaeobioprovinces, while *major differences* (entire clades present in certain areas and absent from others) represent more substantial and more recent palaeobiogeographic ties with neighbouring palaeobioprovinces.

According to these alternative explanations, the following predictions can be advanced:

1. Minor differences will occur randomly between the different areas, because they result from local extinctions or speciations experienced by the different clades, or from random dispersal across existing barriers.
2. Major differences will occur non-randomly, as members of different clades appear associated recurrently in certain areas, while are missing, again recurrently, in others.
3. Clades occurring recurrently together share a common palaeobiogeographic affinity, usually pointing outside, towards a neighbouring palaeobioprovince. The identification of a dispersal route between the two areas, supported by independent (geological–geophysical) evidence, is to be expected.

Surveying the composition of the different Late Cretaceous local faunas of Europe, all three predictions are upheld. Especially significant is the occurrence, in close proximity, of a reconstructed northern, circum-Arctic dispersal route (Martin et al., 2005 and references therein), of such clearly Asiamerican faunal elements as neoceratopsians and herpetotheriid marsupials. The presence of basal lambeosaurines, suggesting faunal connections with Asian assemblages during earlier Late Cretaceous times (?Santonian–Campanian; Pereda-Suberbiola et al., 2009; Prieto-Marquez and Wagner, 2009), within the Ibero-Armorican Realm, at the opposite end of Europe from Haţeg, is intriguing and calls for the presence of a high-latitude dispersal route from Asia towards continental Europe. It is conceivable that this filter dispersal route was also responsible for the dispersal of neoceratopsians into the more northern parts of Europe (as also suggested by Prieto-Marquez and Wagner, 2009). On the other hand, the presence of abelisauroids (possibly even relatively derived abelisaurids; Carrano and Sampson, 2008), bothremydines (*Rosasia*; Gaffney et al., 2006) and relatively common madtsoiids, both clades with Gondwanan ties, on the Ibero-Armorican landmass, as well as their occurrence near a suggested Iberian dispersal route connecting with Africa (Gheerbrant and Rage, 2006) conforms again to predictions 2–3. The near-absence of all these groups in southeastern Europe (corresponding to Tethyan Europe, as opposed to cratonic Europe) suggests that the deep-sea trenches and basins transecting this area represented barriers effective enough to restrict dispersal of many western European taxa.

Again, the Malay Archipelago can offer a parallel to this phenomenon. The important biogeographic boundary dividing the archipelago (Wallace, 1860), called subsequently the Wallace Line, is presumably a by-product of the Lombok Strait, a deep-water trough separating the islands of Bali and Lombok. Although the nature, position, and effectiveness of this dividing line is still under discussion (cf., Mayr, 1944; Simpson, 1977; Brown and Guttman, 2002), biogeographic boundaries produced by deep-water barriers and affecting at least some continental vertebrate groups within an oceanic archipelago seem to be well established (Sweet and Pianka, 2003, 2007).

Similar to the present-day Malay Archipelago, biogeographic boundary lines dividing the European Archipelago (and especially its Tethyan segment) should be seen as the rule and not the exception. The peculiar composition of the Haţeg fauna, compared to those from the western part of Europe, supports the presence of such clear-cut boundaries within the “European palaeobioprovince”. This being the case, it raises questions about the reality of a unique European bioprovince, as hypothesized by several authors (e.g., Le Loeuff, 1997; Holtz et al., 2004; Pereda-Suberbiola, 2009). However, Late Cretaceous Europe cannot be described as a Euro-African Province (Le

Loeuff, 1991) either. Instead, the “European” bioprovince should be seen more as a mosaic within which the individuality of each particular faunal assemblage was shaped by different palaeobiogeographic events and influences.

6. Conclusions

Faunal analyses of the European Cretaceous identify the Haţeg fauna as part of a larger European bioprovince. However, it remains somewhat atypical because of extreme species-level endemism compared to contemporary terrestrial faunas from elsewhere in Europe. Phylogenetic analyses of five Haţeg species, calibrated by biostratigraphic occurrences, indicate long ghost lineages (30–80 M.y; mean = 57), in keeping with the dearth of preservation possibilities of insular faunas in the fossil record. Kogaionids, *Kallokibotion*, *Allodaposuchus*, and *Zalmoxes* (together with their European sister taxa) are thought to have arisen from vicariant events between western Europe and North America. In contrast, the geographic distribution of *Telmatosaurus* is an example of European endemism following an Asiamerican ancestry and immigration.

While Haţeg likely acted as a refugium for *Kallokibotion* and *Telmatosaurus*, other faunal members (together with their immediate sister taxa) are not restricted to Transylvania, but known otherwise from localities across southern Europe. In addition, Transylvania may have acted as an evolutionary cradle for kogaionids.

Transylvania and the other southern faunas of Europe seem to represent a distinct division of the Late Cretaceous European palaeobioprovince. A boundary between this Tethyan part of Europe and the more northern and western parts of the European palaeobioprovince would have functioned much like the Wallace Line in the Malay Archipelago, in which a seemingly homogeneous geographic region is divided into two (or more) biogeographic provinces that reflect different histories.

Acknowledgments

We are grateful to the many friends and colleagues (Attila Ősi, Márton Rabi — Budapest, Hungary; Xabier Pereda-Suberbiola — Bilbao, Spain; Jean Le Loeuff — Espéraza, France; Jeremy E. Martin — Corti, France; Francois Therrien — Drumheller, Alberta, Canada; Mike Habib — Baltimore, Maryland, USA; Cora Jianu — Deva, Romania) who were either willing or inadvertent commentators on this study. Thanks are given to the CNCSIS (National University Research Council) grants to DG (1163A/2004) and ZCs (95At/2003, 1930/2009), as well as the Synthesys grant GB-TAF 3417-2007 to ZCs, supporting field and museum research. Thanks to the Royal Society for funding the visit of ZCs to Bristol in 2006, through a RS International Incoming Short Visit grant, offering the opportunity to outline several topics discussed in this contribution. DBW thanks the National Science Foundation, the National Geographic Society, the Dinosaur Society, the Jurassic Foundation, and the Paleontological Society International Research Program (the latter two awarded to Coralia-Maria Jianu, who is also thanked for her contributions to this paper) for funds supporting field and museum research since 1987.

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