Latest Cretaceous Vertebrates from the Haţeg Basin, Romania

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SUMMARY

The Late Cretaceous was a crucial time for the evolution of life on land, and despite its importance, this period is incompletely understood in many places around the world. The uppermost Cretaceous continental deposits of the Haţeg Basin in western Romania have yielded one of the richest and most diverse vertebrate assemblages of Europe, thus being of paramount importance for understanding European Late Cretaceous ecosystems. Although the Haţeg Basin looks back on a research history of more than 120 years, many open questions about the latest Cretaceous vertebrate assemblages remain. This includes, in particular, their diversity, their phylogenetic and biogeographical relationships, as well as palaeoecological aspects. In order to assess these questions, four key specimens were examined for this thesis, a partial turtle skeleton, two ornithopod braincases and one partial skull of a rhabdodontid dinosaur. The first specimen can be confidently referred to the Dortokidae, a European endemic clade of basal Pleurodires. It is morphologically similar to the genus *Dortoka* but differs significantly from all previously described species of that genus and thus is assigned to a new species, *Dortoka vremiri*. Phylogenetic analyses recovered the new taxon in a sister-group relationship with a Paleocene dortokid from western Romania, indicating local survival of the lineage across the K/Pg extinction, as opposed to subsequent immigration, as well as the presence of two distinct dortokid lineages, an eastern and a western European one. Additionally, it was possible to demonstrate that the new species occupied a different ecological niche than the only other sympatric turtle taxon from the Haţeg Basin described before, *Kallokibotion bajazidi*. The two ornithopod braincase specimens have previously been referred to the rhabdodontid *Zalmoxes*, although they differ markedly from other braincase specimens of that genus described before. A detailed comparison with basal and more derived ornithopods demonstrated that the peculiar morphology of these two specimens is exclusively found in hadrosauroids. Therefore, the two specimens are re-assigned to the basal hadrosauroid *Telmatosaurus*. The final specimen examined is a partial skull that resembles rhabdodontid dinosaurs. Despite these similarities, the specimen differs considerably from all other rhabdodontid skulls reported thus far and shows a unique and highly autapomorphic anatomy, and therefore, it is assigned to a new genus and species, *Transylvanosaurus platycephalus*. Two sets of phylogenetic analyses placed the new taxon within Rhabdodontidae but were unable to resolve the in-group relationships. Based on the high degree of similarity between *Transylvanosaurus* and *Rhabdodon* from southern France, a particularly close relationship between those taxa is suggested, which indicates a more complex biogeographical history than previously recognised. In addition, *Transylvanosaurus* differs widely from the sympatric rhabdodontid *Zalmoxes* in its skull proportions, indicating a certain degree of niche partitioning between the two genera. The results of this dissertation show that the alpha-level taxonomic diversity of certain groups was higher than previously thought. Moreover, the phylogenetic relationships of the new taxa indicate more complex biogeographical histories than reconstructed before and differential distribution patterns for different vertebrate groups. Finally, it was possible to detect some degree of niche partitioning between the members of the vertebrate groups.

ZUSAMMENFASSUNG

Die Oberkreide (100.5–66 Ma) war eine entscheidende Periode in der Entwicklungsgeschichte des Lebens an Land und trotz dieser Bedeutung, ist dieser Zeitabschnitt in vielen Teilen der Erde nur unvollständig verstanden. Die kontinentale Oberkreide des Haţeg Beckens hat eine der reichhaltigsten und diversesten Ansammlungen von Wirbeltieren aus dieser Zeit geliefert, und ist daher von zentraler Bedeutung für unser Verständnis für die oberkretazischen Ökosysteme Europas. Obwohl das Haţeg Becken auf eine mehr als 120-jährige Forschungsgeschichte zurückblickt, bleiben viele Fragen über die oberkretazischen Wirbeltiere noch immer offen. Dies beinhaltet im Besonderen ihre Diversität, ihre phylogenetischen und biogeographischen Beziehungen, sowie paläoökologische Aspekte. Um diese Fragen zu beantworten, wurden vier Wirbeltierfossilien für diese Doktorarbeit untersucht, ein Teilskelett einer Schildkröte, zwei Hirnschädel ornithopoder Dinosaurier und ein Teilschädel eines rhabdodontiden Dinosauriers. Das erste Fossil kann eindeutig den Dortokiden zugeordnet werden, einer endemischen Gruppe basaler Pleurodiren. Es ähnelt morphologisch der Gattung *Dortoka*, unterscheidet sich aber erheblich von allen anderen bisher bekannten Arten dieser Gattung und wird daher einer neuen Art zugeordnet, *Dortoka vremiri*. Phylogenetische Analysen ergaben eine Schwestergruppen-Beziehung der neuen Art mit Dortokiden aus dem Paläozän West-Rumäniens, was auf das lokale Überleben dieser Gruppe während des K/T Aussterbeereignisses hindeutet und nicht auf spätere Immigration, sowie auf die Existenz zweier getrennter Dortokiden-Gruppen in Ost- bzw. Westeuropa. Des Weiteren konnte nachgewiesen werden, dass die neue Art eine andere ökologische Nische besetzte als die einzig andere bekannte Schildkröte aus dem Haţeg Becken, *Kallokibotion bajazidi*. Die zwei Ornithopoden Hirnschädel wurden zuvor dem Rhabdodontiden *Zalmoxes* zugeordnet, obwohl sie sich stark von anderen fossilen Hirnschädeln dieser Gattung unterscheiden. Ein detaillierter Vergleich mit basalen und abgeleiteten Ornithopoden zeigte, dass die eigenartige Morphologie dieser beiden Stück ansonsten ausschließlich bei Hadrosauroiden vorkommt. Daher werden beide Stücke stattdessen dem basalen Hadrosauroiden *Telmatosaurus* zugeordnet. Das letzte untersuchte Fossil ist ein Teilschädel der Ähnlichkeiten zu rhabdodontiden Dinosauriern aufweist. Trotz dieser Ähnlichkeiten, unterscheidet sich der Schädel deutlich von dem aller anderen Rhabdodontiden und zeigt eine einzigartige und stark autapomorphe Anatomie, und wird folglich einer neuen Gattung und Art zugeordnet, *Transylvanosaurus platycephalus*. Zwei voneinander unabhängige phylogenetische Analysen ergaben, dass das neue Taxon den Rhabdodontiden angehört, waren indes aber nicht in der Lage die Verwandtschaftsverhältnisse innerhalb der Gruppe aufzulösen. Aufgrund der starken Ähnlichkeit zwischen *Transylvanosaurus* und *Rhabdodon* aus Südfrankreich, wird eine besonders nahe Verwandschaft zwischen diesen Taxa angenommen, was wiederum auf eine kompliziertere biogeographische Vergangenheit hinweist als bisher vermutet. Zudem deutet die stark unterschiedliche Schädelanatomie zwischen *Transylvanosaurus* und dem sympatrischen *Zalmoxes* auf die Besetzung unterschiedlicher ökologischer Nischen hin. Die Ergebnisse diser Dissertation zeigen, dass die Diversität bestimmter Gruppen höher war als bisher gedacht. Des Weiteren deuten die phylogentischen Beziehungen der neuen Taxa darauf hin, dass die Biogeographie komplizierter war als zuvor rekonstruiert und dass die verschiedenen Wirbeltiergruppen unterschiedliche Verbreitungsmuster aufweisen. Schließlich war es möglich die Bestzung unterschiedlicher ökologischer Nischen bei angehörigen derselben Gruppe aufzuzeigen.

LIST OF PUBLICATIONS

Publications included in this thesis

All of the following publications have been fully published by the respective journals. The finally formatted and published version of the papers can be found attached as an appendix. The publications below are sorted according to their online publication date.

1.) **Augustin, F. J.**, Csiki-Sava, Z., Matzke, A. T., Botfalvai, G., & Rabi, M. 2021. A new latest Cretaceous pleurodiran turtle (Testudinata: *Dortokidae*) from the Haţeg Basin (Romania) documents end-Cretaceous faunal provinciality and selective survival during the K-Pg extinction. *Journal of Systematic Palaeontology*, *19*, 1059–1081.

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2.) **Augustin, F. J.**, Dumbravă, M. D., Bastiaans, D., & Csiki-Sava, Z. 2023. Reappraisal of the braincase anatomy of the ornithopod dinosaurs *Telmatosaurus* and *Zalmoxes* from the Upper Cretaceous of the Haţeg Basin (Romania) and the taxonomic reassessment of some previously referred specimens. *PalZ*, *97*, 129–145.

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(Online publication date: 04.06.2022)

3.) **Augustin, F. J.**, Bastiaans, D., Dumbravă, M. D., & Csiki-Sava, Z. 2022. A new ornithopod dinosaur, *Transylvanosaurus platycephalus* gen. et sp. nov. (Dinosauria: Ornithischia), from the Upper Cretaceous of the Haţeg Basin, Romania. *Journal of Vertebrate Paleontology*, *42*, e2133610 (1–23).

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Declaration according to § 5 Abs. 2 No. 8 of the PhD regulations of the Faculty of Science
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For Cumulative Theses Only!

Last Name, First Name: Augustin, Felix Justus

List of Publications

1. Augustin, F. J., Csiki-Sava, Z., Matzke, A. T., Botfalvai, G., & Rabi, M. 2021. A new latest Cretaceous pleurodiran turtle (Testudinata: Dortokidae) from the Haţeg Basin (Romania) documents end-Cretaceous faunal provinciality and selective survival during the K-Pg extinction. Journal of Systematic Palaeontology 19:1059–1081.
2. Augustin, F. J., Dumbravă, M. D., Bastiaans, D., & Csiki-Sava, Z. 2023. Reappraisal of the braincase anatomy of the ornithopod dinosaurs *Telmatosaurus* and *Zalmoxes* from the Upper Cretaceous of the Haţeg Basin (Romania) and the taxonomic reassessment of some previously referred specimens. PalZ 97:129–145.
3. Augustin, F. J., Bastiaans, D., Dumbravă, M. D., & Csiki-Sava, Z. 2022. A new ornithopod dinosaur, *Transylvanosaurus platycephalus* gen. et sp. nov. (Dinosauria: Ornithischia), from the Upper Cretaceous of the Haţeg Basin, Romania. Journal of Vertebrate Paleontology 42:e2133610.

Nr.	**Accepted publication yes/no**	**List of authors**	Position of candidate in list of authors	Scientific ideas by the candidate (%)	Data generation by the candidate (%)	Analysis and Interpretation by the candidate (%)	Paper writing done by the candidate (%)
1	yes	5	1	70	70	80	70
2	yes	4	1	80	70	90	90
3	yes	4	1	80	70	90	80

I confirm that the above-stated is correct.

Date, Signature of the candidate

I/We certify that the above-stated is correct.

Date, Signature of the doctoral committee or at least of one of the supervisors

Publications not included in this thesis that were written during the PhD

Most of the following publications either have been fully published by the respective journals or were accepted for publication. Moreover, four articles are currently under review. The publications below are sorted according to their online publication date.

a) Published articles

4.) **Augustin, F. J.**, Matzke, A. T., Maisch, M. W., & Pfretzschner, H.-U. 2020. First evidence of an ankylosaur (Dinosauria, Ornithischia) from the Jurassic Qigu Formation (Junggar Basin, NW China) and the early fossil record of Ankylosauria. *Geobios*, *61*, 1–10.

https://doi.org/10.1016/j.geobios.2020.06.005.

(Online publication date: 06.07.2020)

5.) Hinz, J. K., Matzke, A. T., **Augustin, F. J.**, & Pfretzschner, H.-U. 2020. A *Nothosaurus* (Sauropterygia) skull from Kupferzell (Triassic, late Ladinian; SW Germany). *Neues Jahrbuch für Geologie und Paläontologie — Abhandlungen*, *297*, 101–111.

https://doi.org/10.1127/njgpa/2020/0915.

(Online publication date: 09.07.2020)

6.) **Augustin, F. J.**, Matzke, A. T., Maisch, M. W., Hinz, J. K., & Pfretzschner, H.-U. 2020. The smallest eating the largest: the oldest mammalian feeding traces on dinosaur bone from the Late Jurassic of the Junggar Basin (northwestern China). *The Science of Nature*, *107*, 1–5.

https://doi.org/10.1007/s00114-020-01688-9.

(Online publication date: 19.07.2020)

7.) **Augustin, F. J.**, Matzke, A. T., Maisch, M. W., & Pfretzschner, H.-U. 2020. A theropod dinosaur feeding site from the Upper Jurassic of the Junggar Basin, NW China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *560*, 109999 (1–12).

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(Online publication date: 06.09.2020)

8.) **Augustin, F. J.**, Matzke, A. T., Maisch, M. W., & Pfretzschner, H.-U. 2021. New information on *Lonchognathosaurus* (Pterosauria: Dsungaripteridae) from the Lower Cretaceous of the southern Junggar Basin (NW China). *Cretaceous Research*, *124*, 104808 (1–12).

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9.) **Augustin, F. J.**, Matzke, A. T., Maisch, M. W., & Pfretzschner, H.-U. 2021. Dinosaur taphonomy of the Jurassic Shishugou Formation (Northern Junggar Basin, NW China) – insights from bioerosional trace fossils on bone. *Ichnos*, *28*, 87–96.

https://doi.org/10.1080/10420940.2021.1890590.

(Online publication date: 15.03.2021)

10.) **Augustin, F. J.**, Matzke, A. T., Maisch, M. W., & Csiki-Sava, Z. 2021. Pterosaur remains from the Lower Cretaceous Lianmuxin Formation (upper Tugulu Group) of the southern Junggar Basin (NW China). *Historical Biology*, *34*, 312–321.

https://doi.org/10.1080/08912963.2021.1910819.

(Online publication date: 05.04.2021)

11.) Kampouridis, P., Svorligkou, G., Kargopoulos, N., & **Augustin, F. J.** 2021. Reassessment of '*Chilotherium wegneri*' (Mammalia, Rhinocerotidae) from the late Miocene of Samos (Greece) and the European record of Chilotherium. *Historical Biology*, *34*, 412–420.

https://doi.org/10.1080/08912963.2021.1920939.

(Online publication date: 13.05.2021)

12.) Hartung, J., **Augustin, F. J.**, Kampouridis, P., & Chure, D. J. 2021. A unique notostracan trace fossil assemblage from the Upper Triassic Chinle Formation (northeastern Utah, USA) and its paleoecological and paleoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *583*, 110667 (1–11).

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13.) **Augustin, F. J.**, Matzke, A. T., Maisch, M. W., Kampouridis, P., & Csiki-Sava, Z. 2022. The first record of pterosaurs from the Lower Cretaceous Hutubei Formation (lower Tugulu Group) of the southern Junggar Basin (NW China) – A glimpse into an unusual ecosystem. *Cretaceous Research*, *130*, 105066 (1–8).

https://doi.org/10.1016/j.cretres.2021.105066.

(Online publication date: 21.10.2021)

14.) Massonne, T., **Augustin**, **F. J.**, Matzke, A. T., Weber, E., & Böhme, M. 2022. A new species of *Maomingosuchus* from the Eocene of the Na Duong Basin (northern Vietnam) sheds new light on the phylogenetic relationship of tomistomine crocodylians and their dispersal from Europe to Asia. *Journal of Systematic Palaeontology*, *19*, 1551–1585.

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(Online publication date: 18.05.2022)

15.) **Augustin, F. J.**, Kampouridis, P., Hartung, J., Albersdörfer, R., & Matzke, A. T. 2022. The geologically oldest specimen of *Pterodactylus*: a new exquisitely preserved skeleton from the Upper Jurassic (Kimmeridgian) Plattenkalk deposits of Painten (Bavaria, Germany). *Fossil Record*, *25*, 331–343.

https://doi.org/10.3897/fr.25.90692.

(Online publication date: 28.11.2022)

b) Accepted Articles

16.) **Augustin, F. J.**, Hartung, J., & Kampouridis, P. (in press). Dinosaur faunas of Egypt – the terrestrial Late Cretaceous vertebrate record. In: Z. Hamimi, H. Khozyem, T. Adatte, F. H. Nader, F. Oboh-Ikuenobe, M. K. Zobaa, H. El Atfy (Eds.), *The Phanerozoic geology and natural resources of Egypt*. Springer.

17.) Kampouridis, P., Hartung, J., & **Augustin, F. J.** (in press). The Eocene – Oligocene vertebrate assemblages of the Fayum Depression, Egypt. In: Z. Hamimi, H. Khozyem, T. Adatte, F. H. Nader, F. Oboh-Ikuenobe, M. K. Zobaa, H. El Atfy (Eds.), *The Phanerozoic geology and natural resources of Egypt*. Springer.

c) Submitted Articles

18.) Kampouridis, P., Hartung, J., **Augustin, F. J.**, & Ferreira, G. S. (submitted). The enigmatic ptolemaiid *Qarunavus meyeri* from the early Oligocene of the Fayum Depression (Egypt) – new insights from micro-computed tomography. Submitted to: *Zoological Journal of the Linnaean Society of London*. (Currently under review).

19.) Massonne, T., **Augustin, F. J.**, Ferreira, G. S., Matzke, A. T., & Böhme, M. (submitted). A new cryptodire from the Eocene of the Na Duong Basin (northern Vietnam) sheds new light on Pan-Trionychidae from South East Asia. Submitted to: *Journal of Systematic Palaeontology*. (Currently under review).

20.) **Augustin, F. J.**, Rabi, M., Spindler, F., Kampouridis, P., Hartung, J., & Matzke, A. T. (submitted). A new specimen of *Solnhofia parsonsi* from the Upper Jurassic (Kimmeridgian) Plattenkalk deposits of Painten (Bavaria, Germany) and comments on the relationship between limb taphonomy and habitat ecology in fossil turtles. Submitted to: *PLoS One*. (Currently under review).

1. INTRODUCTION

The Late Cretaceous (100.5–66 Ma) was a crucial period in the evolution of land living organisms, being a time of major upheavals, both on a regional and global scale. The period began with the major re-organization of terrestrial ecosystems (Lloyd et al., 2008; Benton et al., 2022), while at the end of the period, Earth underwent one of its most severe biotic crises (for an overview, see Archibald, 1996). However, our knowledge on Late and especially latest Cretaceous terrestrial ecosystems is largely limited to the extremely well studied North American deposits. Despite a considerable increase of our knowledge on the continental European Upper Cretaceous in the past decades (e.g., Csiki-Sava et al., 2015), many key aspects are still poorly understood. This applies in particular to the diversity, palaeobiogeographical relationships, and palaeoecology of the terrestrial vertebrates that inhabited nowadays Europe during the Late Cretaceous, which, during that time, constituted an extensive archipelago situated within a shallow subtropical sea. The dinosaur-bearing, continental uppermost Cretaceous deposits of the Haţeg Basin in western Romania (Fig. 1) represent an ideal place to address such issues as it yielded one of the richest and most diverse continental vertebrate faunas from the whole Upper Cretaceous of Europe (e.g., Grigorescu, 1983; Weishampel et al., 1991; Weishampel and Jianu, 2011; Csiki-Sava et al., 2015, 2016). Moreover, the fauna of the Haţeg Basin is the single most well-known and best-established island fauna from the whole pre-Cenozoic (Nopcsa, 1923a; Csiki and Grigorescu, 2007; Benton et al., 2010; Csiki and Benton, 2010), making it a prerequisite to study the evolutionary mechanisms on island ecosystems.

Although looking back on a research history of more than 120 years, and despite the large number of previous studies concerning the Haţeg vertebrate fauna (for an overview, see Grigorescu, 2010a), there remain considerable uncertainties regarding the alpha-level taxonomic diversity of several vertebrate clades. If the diversity is indeed found to be higher, the examination of the phylogenetic relationships of the new taxa has the potential to shed important new light on the palaeobiogeography of the terrestrial vertebrates from the Late Cretaceous of Europe. Furthermore, a higher palaeodiversity indicates the potential presence of niche partitioning among the vertebrates. In other words, there are three important open questions regarding the vertebrate assemblages from the Haţeg Basin: first, was the diversity of certain groups higher than previously thought, second, what are the implications of the phylogenetic relationships of the new taxa, and third, was there some kind of niche partitioning present between the members of those groups? In order to answer these questions, a re-evaluation of previously described specimens and the examination of new and so-far undescribed material is necessary. Four specimens in particular have the potential to shed important new light on these issues, one well-preserved turtle shell that has been provisionally referred to a dortokid turtle and three braincase specimens that supposedly belong to rhabdodontid ornithopod dinosaurs. Two of these specimens have already been described before, whereas the other two have never been studied in detail before. Based on these specimens and the open questions mentioned above, the following three hypotheses were formulated that serve as the rationale for this dissertation: first, the alpha-level taxonomic diversity of turtles and rhabdodontid dinosaurs was higher than previously thought, second, the phylogenetic relationships of the new taxa will allow new insights into the palaeobiogeography, and third, there was some degree of niche partitioning between the members of the two groups. Before evaluating these three hypotheses more in depth, an introduction to the latest Cretaceous vertebrate assemblages of the Haţeg Basin and the two respective groups that are the focus of this thesis is provided.

1.1. Research history of the latest Cretaceous vertebrates from the Haţeg Basin

In accordance with the importance of the Upper Cretaceous fossiliferous deposits of the Haţeg Basin, they repeatedly became the subject of systematic scientific study since their first scientific mention more than 120 years ago by Halaváts (1897). Whereas this first account dealt mainly with the lithology of the deposits, their fossil content soon aroused the interest of Franz Nopcsa (1877–1933), who subsequently published extensively on the sedimentology and palaeontology of his “Szentpéterfalva Sandstones”, amounting to thirteen papers (Lambrecht, 1933; Weishampel and Reif, 1984). From 1929 until 1976, only five contributions to the geology and paleontology of the Haţeg Basin were added, before the dinosaur-bearing beds received renewed attention (Grigorescu, 2010a). From 1977 onward, new surveys and systematic excavations at the old outcrops as well as in as-yet largely unexplored regions of the Haţeg Basin revealed many exciting discoveries and, combined with new approaches and sedimentological studies, have greatly expanded our knowledge of the geology and the palaeontology of the Haţeg Basin, resulting in a plethora of new studies. Despite these considerable advances in our understanding of the latest ‘Haţeg Island’ ecosystems, the tempo of discoveries and new studies being published has not diminished and the last years have seen an ever-increasing amount of research being conducted on the ‘island of the dwarf dinosaurs’.

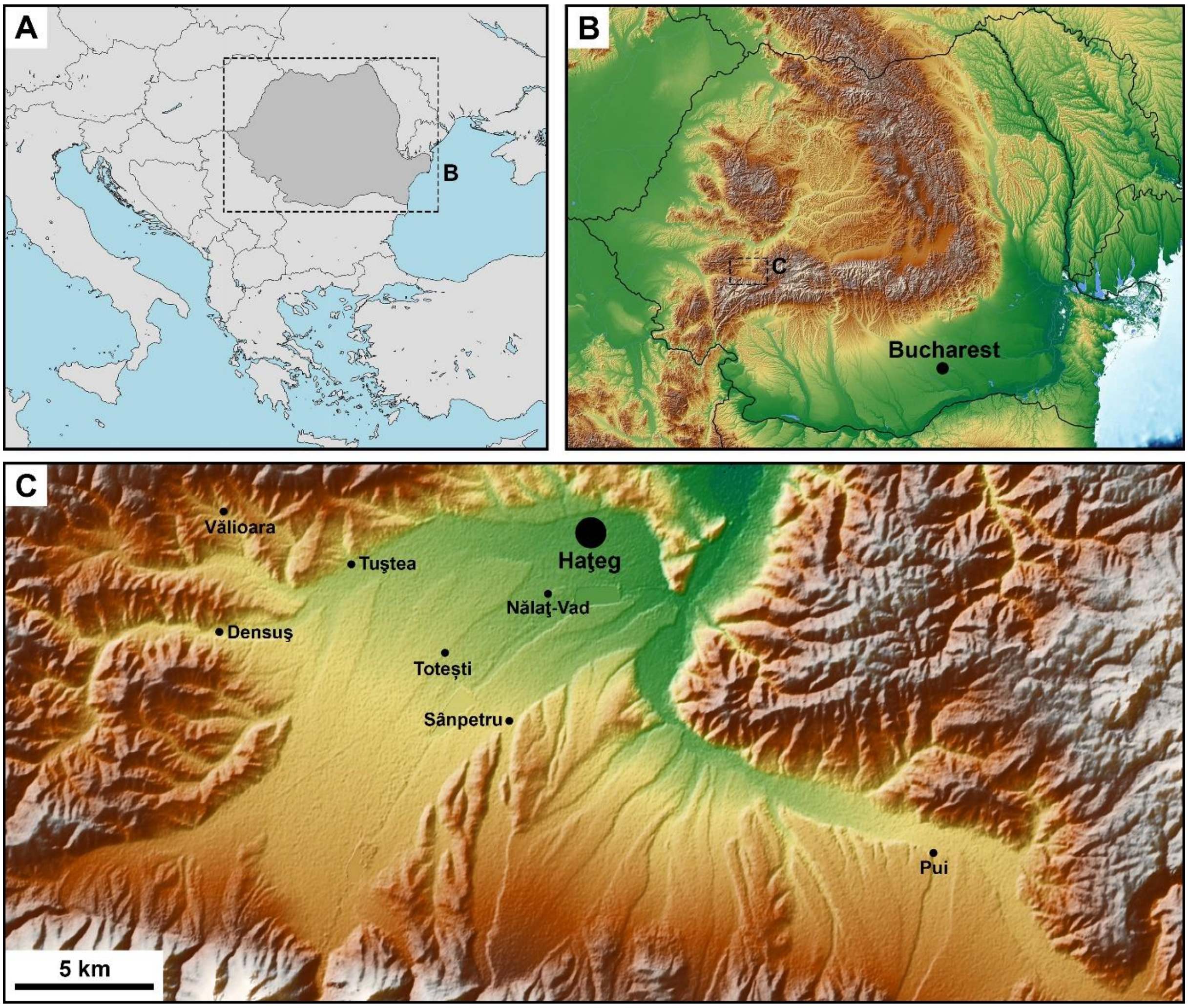

Figure 1. Geographic position of the Haţeg Basin. **A**, Map of Eastern Europe with the position of Romania. **B**, Topographical map of Romania with the position of the Haţeg Basin. **C**, Topographical map of the Haţeg Basin with selected cities and villages discussed in the text. The map was created with GMT6 (Wessel et al., 2013).

1.2.1. The early years – 1895 until 1933

The first observations of vertebrate fossils in the Haţeg area were certainly made by locals centuries ago, in a time when the term “dinosaur” was not even coined and the very concept of palaeontology was not existing (Grigorescu, 2010a). Nonetheless, the first modern scientific account of the geology of the continental deposits from the Haţeg Basin was given late in the nineteenth century by Halaváts (1897), a geologist from the Royal Hungarian Geological Institute in Budapest engaged in geological mapping in Transylvania. The report mainly describes the lithology and the extent of the deposits, which Halaváts (1897) suspected to be Miocene terrestrial sediments. In 1895, two years before the report was published, the young Ilona Nopcsa found some suspicious fossil bones on the family estate, which she gave to her elder brother, the Hungarian nobleman Franz Baron Nopcsa (Fig. 2). These immediately caught the attention of the young man and, in the same year, he showed them to the distinguished Eduard Suess, Professor for Geology at the University of Vienna (Weishampel and Reif, 1984). Suess, in turn, encouraged Nopcsa to study the fossiliferous rocks near his family estate and search for further specimens, which he did with great success in the years to follow.

Nopcsa not only shifted the age of these continental beds from Miocene to Danian (then being the last stage of the Cretaceous) in his first publication (Nopcsa, 1897), but also described the first dinosaur from the continental beds (Nopcsa, 1900), on the basis of a well preserved skull (Fig. 3A–B). He named this medium-sized herbivore *Limnosaurus transsylvanicus*, and recognised it as belonging to the family Hadrosauridae (Nopcsa, 1900). After learning that the genus name was preoccupied by a crocodilian (Marsh, 1872), he coined the new genus *Telmatosaurus* (Nopcsa, 1903a), which he hereafter synonymized with *Orthomerus* (Nopcsa, 1915), a hadrosaur from the latest Cretaceous of Belgium. The initial description of ‘*Limnosaurus*’ also included the mention of indeterminate chelonian and crocodilian remains, as well as of specimens that he interpreted as pertaining to three different basal ornithopod species (Nopcsa, 1900). Two years later these basal ornithopod remains were assigned to a single species, *Mochlodon suessi* (Fig. 3C–F) (Nopcsa, 1902a), otherwise known from the Gosau beds of Austria (Bunzel, 1871), but later referred to *Rhabdodon priscus* (Nopcsa, 1915, 1925). The sedimentologic record of alternating mud-, silt- and sandstones with occasional conglomerates and carbonate concretions, together with the occurrence of freshwater molluscs led Nopcsa to conclude that the bones were deposited in a freshwater environment (Nopcsa, 1900). In addition to isolated bones, he noted the peculiar occurrence of vertebrate fossils in locally restricted accumulations (German ‘Nester’), spread heterogeneously throughout the lithologic section, and containing the remains of multiple taxa (Nopcsa, 1900).

Moreover, Nopcsa elucidated the taphonomy of the vertebrate assemblages and provided the first fauna list (Nopcsa, 1902b), adding to the taxa mentioned above a pterosaur, a sauropod and a stegosaurid. The latter has afterwards been described as a primitive ankylosaur, *Struthiosaurus transsylvanicus* (Nopcsa, 1915). The sauropod specimens were later referred to the wastebasket taxon *Titanosaurus*, as the new species *T. dacus* (Nopcsa, 1915), but thereafter assigned to the new genus *Magyarosaurus* by Friedrich von Huene (1932), who also coined two more species, *M. transsylvanicus* and *M. hungaricus*. Moreover, Nopcsa reported the presence of further indeterminate vertebrate taxa, including squamates (Nopcsa, 1914a: p. 568), a crocodilian (cf. '*Crocodilus affulevensis*') (Nopcsa, 1915), turtles (cf. '*Pleurosternum*') (Nopcsa, 1915), a large-sized theropod ('*Megalosaurus* sp.') (Nopcsa, 1915), and pterosaurs (cf. *Ornithodesmus*) (Nopcsa, 1915, 1923a). The taphonomic observations and the discovery of the peculiar vertebrate accumulations prompted him to specify the depositional environment as a huge (i.e., approximately 150 km^2) freshwater lake (Nopcsa, 1902b). The accumulations, according to Nopcsa (1902b), represented the feeding places of the crocodilians, which, in the process, tore the carcasses apart and distributed them along the shoreline. Further geological mapping in Transylvania also clarified some important differences between the rocks of the northern and the more central parts of the basin, revealing the extent of the Late Cretaceous sediments and the influence of volcanism in the north (Nopcsa, 1905). During his fieldwork in the northwestern part of the Haţeg Basin near Vălioara and Densuş, Nopcsa also discovered a few vertebrate remains (Nopcsa, 1905).

Aside from his accounts on the geology, taphonomy and palaeontology of the continental deposits, Nopcsa also speculated on the habitat and paleoenvironment, concluding that the area was located on an island during the latest Cretaceous (Nopcsa, 1914b, 1923a). This notion was mainly derived from the observation that most dinosaur species were distinctively smaller than contemporaneous taxa from other continental vertebrate assemblages. In addition, the relatively high degree of 'primitiveness' of most dinosaurs, as well as the supposedly low diversity of the vertebrate assemblage, were also assumed to be consequences of the isolated island habitat (Nopcsa, 1915). Moreover, Nopcsa (1914a) specified that the sediments near Szentpéterfalva were deposited in a very shallow freshwater swamp, whereas those of Vălioara were deposited in deeper but flowing water, closer to the shore. Nopcsa also expressed some paleobiological hypotheses concerning the preferred habitats and the diet for the vertebrates from Szentpéterfalva (Nopcsa, 1914a), as well as sexual dimorphism in *Mochlodon*, pathologies and the extinction of the Transylvanian dinosaurs (Nopcsa, 1915). Due to financial difficulties, Nopcsa sold the largest part of his collection to the Natural History Museum of London (NHMUK), where it is still housed today. The material was purchased by the NHMUK at several occasions between 1906 and 1926 (Dalla Vecchia, 2009).

Figure 2. Hungarian nobleman Franz Baron von Nopcsa (1877–1933), the first researcher studying the vertebrate fossils from the Haţeg Basin. **A**, Photo of Franz Nopcsa as a young man in Shqiptar warrior costume, by C Pietzner, around 1913. **B**, Portrait of Franz Nopcsa by F. Márton, 1926. Modified after Grigorescu (2010). **C**, Photo of the Nopcsa family estate near Săcel, northwest of Sânpetru, by I. Leszay 1926.

Although Franz Nopcsa was the most famous of the early researchers working on the Szentpéterfalva sandstones, he was not the only one. Some bone fragments, collected by Nopcsa from the locality near Szentpéterfalva, were afterwards interpreted to belong to a large bird by the British palaeontologist Charles William Andrews, who named them *Elopteryx nopcsai*, in honour of their discoverer (Andrews, 1913). Later, two tibiotarsi from the same collection were also assigned to this species (Lambrecht, 1929). Schafarzik (1909) described the freshwater gastropods from the northwestern region of the Haţeg Basin near Densuş, which Nopcsa (1900) briefly mentioned a few years earlier from the central part, and thus provided the first detailed account on invertebrates. Complementing this work in the northern part, were the excavations of vertebrate remains by Hungarian geologist Ottokár Kadić from the Royal Hungarian Geological Institute in Budapest, who, like Schafarzik, was tasked with geological mapping in the northwestern part of the Haţeg Basin (Kadić, 1916). Kadić found numerous vertebrate specimens at several different sites near Vălioara and conducted systematic excavations over the course of four field seasons from 1912 until 1915 (for a historical overview of the excavations by Kadić, see Botfalvai et al., 2021). Finally, the work of Laufer (1925) is notable for it contained the first description of leaf impressions from Upper Cretaceous tuffs near Densuş and added further information on the petrographic characteristics and the areal extent of the continental beds, specifically in the northwestern region of the basin.

Among the late contributions by Franz Nopcsa to the palaeontology of the Haţeg Basin, one article is particularly noteworthy, in that it provides an overview of the fauna – along with the first description of the primitive turtle *Kallokibotion bajazidi* – as well as a discussion of the palaeogeographic and palaeoecological significance of this fauna (Nopcsa, 1923a). In the same year he also presented a more detailed treatise on *Kallokibotion*, which represents one of the most abundant vertebrate taxa, coining the new species *K. magnificum* (Nopcsa, 1923b). Since Nopcsa never mentioned the indeterminate turtle taxa (cf. ‘*Pleurosternum*’, see above) in these later papers, he likely considered it to be synonymous with *Kallokibotion*. Additional remains of ‘*Orthomerus*’ and ‘*Rhabdodon*’ lead to a comprehensive description of their axial anatomy (Nopcsa, 1925). Furthermore, in a monograph on extinct reptiles, Nopcsa assigned the crocodilian remains from Haţeg (cf. ‘*Crocodilus affulevensis*’, see above) to a new genus, *Allodaposuchus* (Nopcsa, 1928). The last contribution to the Upper Cretaceous beds of the Haţeg Basin by Nopcsa, was an extensive monograph on the armoured dinosaur

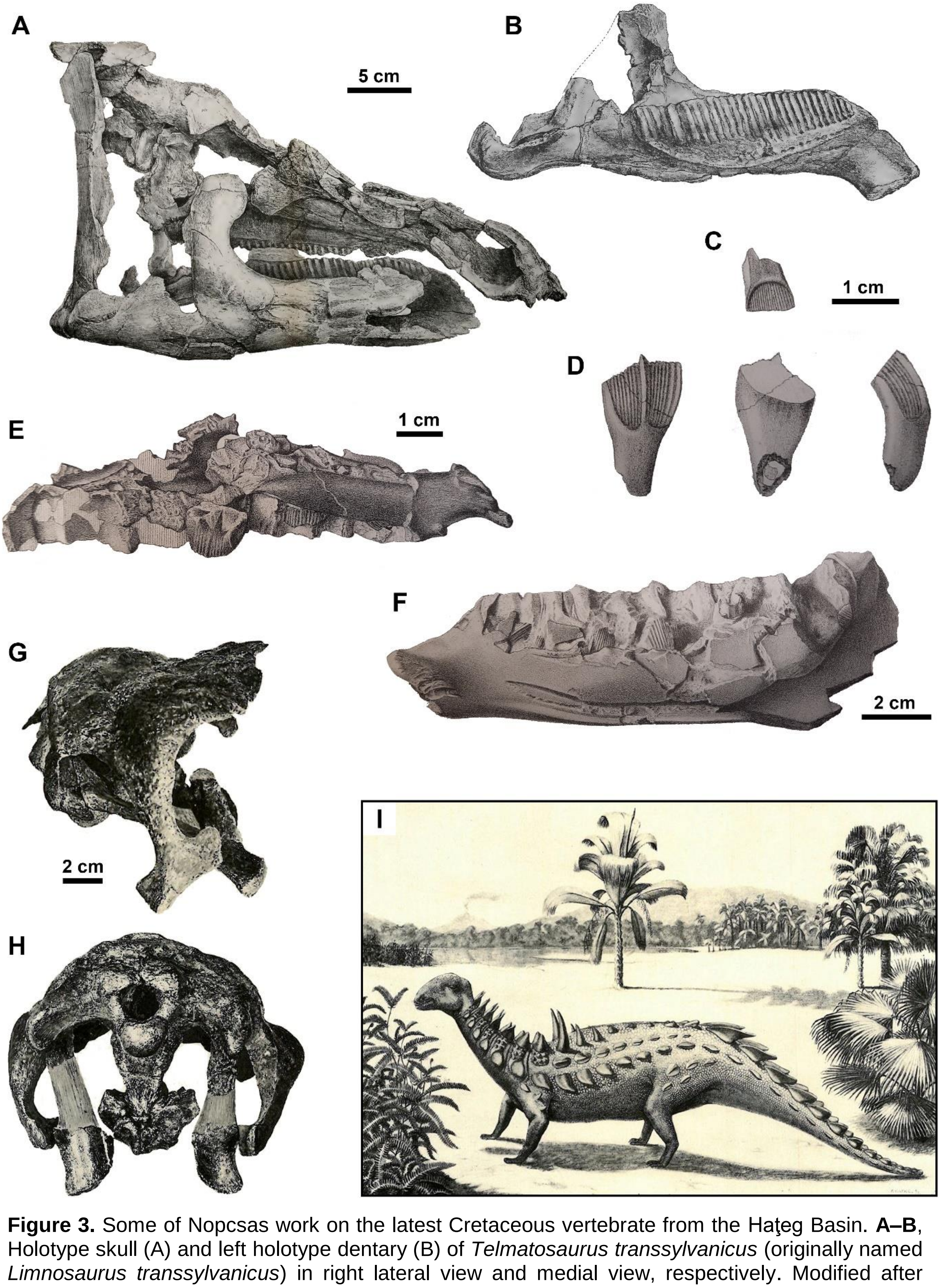

Figure 3. Some of Nopcsas work on the latest Cretaceous vertebrate from the Haţeg Basin. **A–B**, Holotype skull (A) and left holotype dentary (B) of *Telmatosaurus transsylvanicus* (originally named *Limnosaurus transsylvanicus*) in right lateral view and medial view, respectively. Modified after Nopcsa (1900). **C–F**, Maxillary tooth in buccal view (C), dentary tooth in (from left to right) lingual, buccal and mesial view (D), maxillary (E) and holotype dentary (F) of the rhabdodontid dinosaur '*Mochlodon robustum*' (now *Zalmoxes robustus*). Modified after Nopcsa (1902a). **G–H**, Skull of the nodosaurid ankylosaur *Struthiosaurus transsylvanicus* in right lateral view (G) and posterior view (H). Modified after Nopcsa (1929a). **I**, Life reconstruction of *Struthiosaurus transsylvanicus* as envisioned by Nopcsa. Modified after Nopcsa (1929a).

Struthiosaurus transsylvanicus (Fig. 3G–I), elucidating details of its anatomy and relationships (Nopcsa, 1929a). In 1933, at the age of 55, Franz Baron Nopcsa committed suicide in his apartment in Vienna (Lambrecht, 1933). A final treatise on the role of geological and climatological factors on the distribution of terrestrial reptiles, published in the year after his death, contained a brief notion on the insularity and primitiveness of the vertebrate fauna from Transylvania (Nopcsa, 1934).

1.2.2. Sliding into oblivion – 1934 until 1976

Following the death of Franz Nopcsa in 1933, the interest in the Upper Cretaceous deposits from the Haţeg Basin diminished suddenly and nearly ceased entirely. Subsequently, the first contributions were that of Mamulea nearly 20 years later, dealing with the geology of the region near Sânpetru, formerly Szentpéterfalva, and Pui in the central respectively eastern part of the basin (Mamulea, 1953a), as well as in the northwestern part around Răchitova (Mamulea, 1953b). In addition to his geological fieldwork, Mamulea collected several bones, which he assigned to the titanosaur *Magyarosaurus dacus* (Grigorescu, 2010a). Furthermore, leaf impressions of ferns and angiosperms have been described by Mărgărit and Mărgărit (1967), thus expanding our knowledge on the paleoflora of the Late Cretaceous from Transylvania. Like the leaf impressions mentioned earlier by Laufer (1925), they were found in tuffaceous sediments near Densuş, in the northwestern part of the Haţeg Basin. In accordance with the decision of the International Stratigraphic Committee, which shifted the Danian to the Tertiary, Dincă et al. (1972) assigned the Upper Cretaceous deposits of the Haţeg Basin to the Maastrichtian, since then the last stage of the Cretaceous. A new examination of the bird remains described by Andrews (1913) and Lambrecht (1929) as *Elopteryx nopcsai*, lead Harrison and Walker (1975) to conclude that the specimens, in fact, belong to three different genera, establishing a new family of Cretaceous owls (Bradycnemidae) based on the two new taxa *Bradycneme draculae* and *Heptasteornis andrewsi*.

1.2.3 Renewed interest – 1977 until today

From 1929 until 1980, only five contributions to the geology and palaeontology of the Haţeg Basin were published, before the dinosaur-bearing beds received renewed attention. From 1977 onwards, systematic excavations were again conducted in the Haţeg Basin led by Dan Grigorescu from the University of Bucharest (Grigorescu, 2005, 2010a). First, these excavations concentrated on the Sibişel Valley Section, where Nopcsa had uncovered the large majority of his specimens, and several important new localities were discovered here (see below). Later, systematic excavations were also conducted in other parts of the basin, such as the northwestern part near Densuş and Tuştea as well as the southeastern part the basin near Pui, which were known to yield vertebrate fossils since Nopcsas time but were not the focus of detailed study. These new efforts soon resulted in the publication of new papers on the vertebrate palaeontology of the Haţeg Basin, the first being a study describing new material of the enigmatic *Elopteryx nopcsai* (Grigorescu and Kessler, 1981). One of the most important contributions was published shortly thereafter – an overview of the latest Cretaceous vertebrates and their taphonomy as well as a new examination of the sedimentology and stratigraphy of the uppermost Cretaceous deposits (Grigorescu, 1983). Importantly, this study rejected Nopcsas idea of the Maastrichtian strata from the Haţeg Basin representing lacustrine deposits, and instead suggested that they were deposited on a poorly channelized alluvial plain drained by braided river systems, which comprised dry areas, wetlands and well-drained floodplains (Grigorescu, 1983). One year later, Grigorescu (1984) described the first remains of coelurosaurian theropods and multituberculate mammals from the Sibişel Valley. Briefly thereafter, Grigorescu et al. (1985) described remains of fishes, amphibians, squamates crocodilians, dinosaurs and multituberculates from Pui, located in the eastern part of the Haţeg Basin. Based on the new multituberculate material, Rădulescu and Samson (1986) erected the new taxon *Barbatodon transylvanicum* (later amended to *B*. *transylvanicus*). Additional teeth of multituberculates were reported later by Grigorescu and Hahn (1987) and referred to a new species within the genus *Paracimexomys*, *P*. *dacicus*, which, however, represents a junior synonym of *B*. *transylvanicus*.

Since the 1990s, the tempo of new discoveries being made and new studies being published accelerated greatly, which is the result of the huge efforts undertaken by Romanian scientists (mostly from the University of Bucharest and later from the Babes-Bolyai University of Cluj-Napoca) and fruitful collaborations with scientists from other countries (Fig. 4). Due to the ever-increasing speed at which the research progressed, the discoveries and publications are too numerous to list them all in detail here, and thus only an overview of the more recent developments is provided. One of the most remarkable among these is the discovery and description of the first dinosaur eggs and nests from the Haţeg Basin, which were discovered near Tuştea in 1988 and ascribed to the titanosaur *Magyarosaurus dacus* (Grigorescu et al., 1990). Later, the megaloolithid eggs from the 'Tuştea nesting site' were re-assigned to the hadrosaur *Telmatosaurus*, after hatchlings were recovered from the nests (Grigorescu et al., 1994, 2010; Grigorescu, 2010b, 2017). Since their initial discovery at Tuştea, dinosaur eggs and eggshells have been found also at other sites of the Haţeg Basin (Codrea et al., 2002; Grigorescu and Csiki, 2008; Grigorescu et al., 2010). Aside from megaloolithid eggshells, a variety of other eggshell morphotypes have been found in the uppermost Cretaceous deposits of the Haţeg Basin (Grigorescu et al., 1999, 2010).

Moreover, numerous studies on the taxonomy of the dinosaurs from the Haţeg Basin have been published since the 1990s. The first vertebrate taxon described by Nopcsa, *Telmatosaurus transsylvanicus*, was re-described in the early 1990s and recognised as one of the most basal hadrosaurids (Weishampel et al., 1993), although since then it has been mostly classified as a more basal hadrosauroid, lying outside of the Hadrosauridae (e.g., Sues and Averianov, 2009; Prieto-Márquez, 2010; McDonald, 2012). So far, all the hadrosauroid material from the Haţeg Basin has been referred to *T. transsylvanicus*, although the diversity was suggested to might have been higher (Dalla Vecchia, 2009). A revision of the other ornithopod from the Haţeg Basin, previously referred to as *Mochlodon* and *Rhabdodon* by Nopcsa, was provided by Weishampel et al. (2003), who erected the new genus *Zalmoxes* (containing the two species *Z*. *robustus* and *Z*. *shqiperorum*) and included it in the new family Rhabdodontidae (see below). In the past, all of the rhabdodontid material from the Haţeg Basin was assigned to a single genus, including the old Nopcsa specimens and countless new ones (Jianu, 1994; Weishampel et al., 2003; Godefroit et al., 2009; Brusatte et al., 2017). Recently, however, the indiscriminate assignment of all the rhabdodontid material to *Zalmoxes* has been questioned (Brusatte et al., 2017), and at least some specimens referred to *Zalmoxes* in the past differ considerably (see below). Although the nodosaurid *Struthiosaurus* is a rather rare faunal component, new specimens from the Haţeg Basin were described by Ősi et al. (2014) and referred to the only species known from the Haţeg Basin, *S*. *transsylvanicus*. Titanosaurian sauropods on the other hand, are abundant in the uppermost Cretaceous strata of the Haţeg Basin. Although the validity of *Magyarosaurus transsylvanicus* and *M*. *hungaricus* has been questioned, the co-occurrence of several titanosaurian taxa in the Maastrichtian strata of Romania has been proposed repeatedly (Csiki et al., 2010a; Stein et al., 2010; Mannion et al., 2019). The new genus and species *Paludititan* *nalatzensis*, was named by Csiki et al. (2010a) for material from Nălaţ-Vad, a relatively newly discovered vertebrate locality in the central part of the Haţeg Basin (Codrea et al., 2002). Recently, Mocho et al. (2022) argued that at least four distinct titanosaurians are present in the sample from the Haţeg Basin based on the morphology of the caudal vertebrae, *M*. *dacus* and *Paludititan* as well as two indeterminate taxa.

The first detailed evaluation of the taxonomy and diversity of the theropod dinosaurs from the Haţeg Basin was provided by Csiki and Grigorescu (1998) based on old and more recently collected material, comprising mostly isolated teeth and hind limb elements. The vertebrae referred by Nopcsa to a large-sized theropod (‘*Megalosaurus* sp.’, see above) were re-interpreted by these authors as belonging to a titanosaur (Csiki and Grigorescu, 1998). Moreover, the femoral fragments referred to *Elopteryx* were regarded as those of a derived non-avian maniraptoran, while *Bradycneme* and *Heptasteornis* (which are based on tibiotarsi) were considered to be synonymous and referable to a basal tetanuran; all three genera were further considered to represent nomina dubia (Csiki and Grigorescu, 1998). During the following years, however, the affinities of these taxa have proven to be rather controversial and they were later also regarded as dromaeosaurids, troodontids or alvarezsaurids (for a discussion, see Naish and Dyke, 2004; Kessler et al., 2005). The fragmentary femur described by Grigorescu and Kessler (1981) was re-identified as potentially belonging to a small abelisaurid (Csiki and Grigorescu, 1998). Based on small isolated teeth, Csiki and Grigorescu (1998) concluded that at least three different theropods are represented – a velociraptorine dromaeosaurid, an indeterminate troodontid and cf. *Euronychodon* (and possibly a fourth indeterminate theropod). Subsequently, small theropod teeth from various strata of the Haţeg Basin were referred to velociraptorine dromaeosaurids and troodontids as well as to the tooth genera *Richardoestesia*, *Euronychodon* and *Paronychodon* (Grigorescu et al., 1999; Codrea et al., 2002; Smith et al., 2002; Vasile, 2008; Csiki-Sava et al., 2016), the latter potentially also representing derived paravian theropods (Csiki-Sava et al., 2015). Besides teeth, a number of other theropod remains were reported from the Haţeg Basin, including a partial skull roof of a dromaeosaurid (Weishampel and Jianu, 1996), a dorsal vertebra of an indeterminate medium-sized theropod (Smith et al., 2002), and a sacrum of a small paravian (Ősi and Főzy, 2007). Aside from these fragmentary remains, Csiki et al. (2010b) described a new genus and species of dromaeosaurid, *Balaur bondoc*, based on a partial skeleton from the Transylvanian Basin, but the taxon seems to have been present in the Haţeg Basin

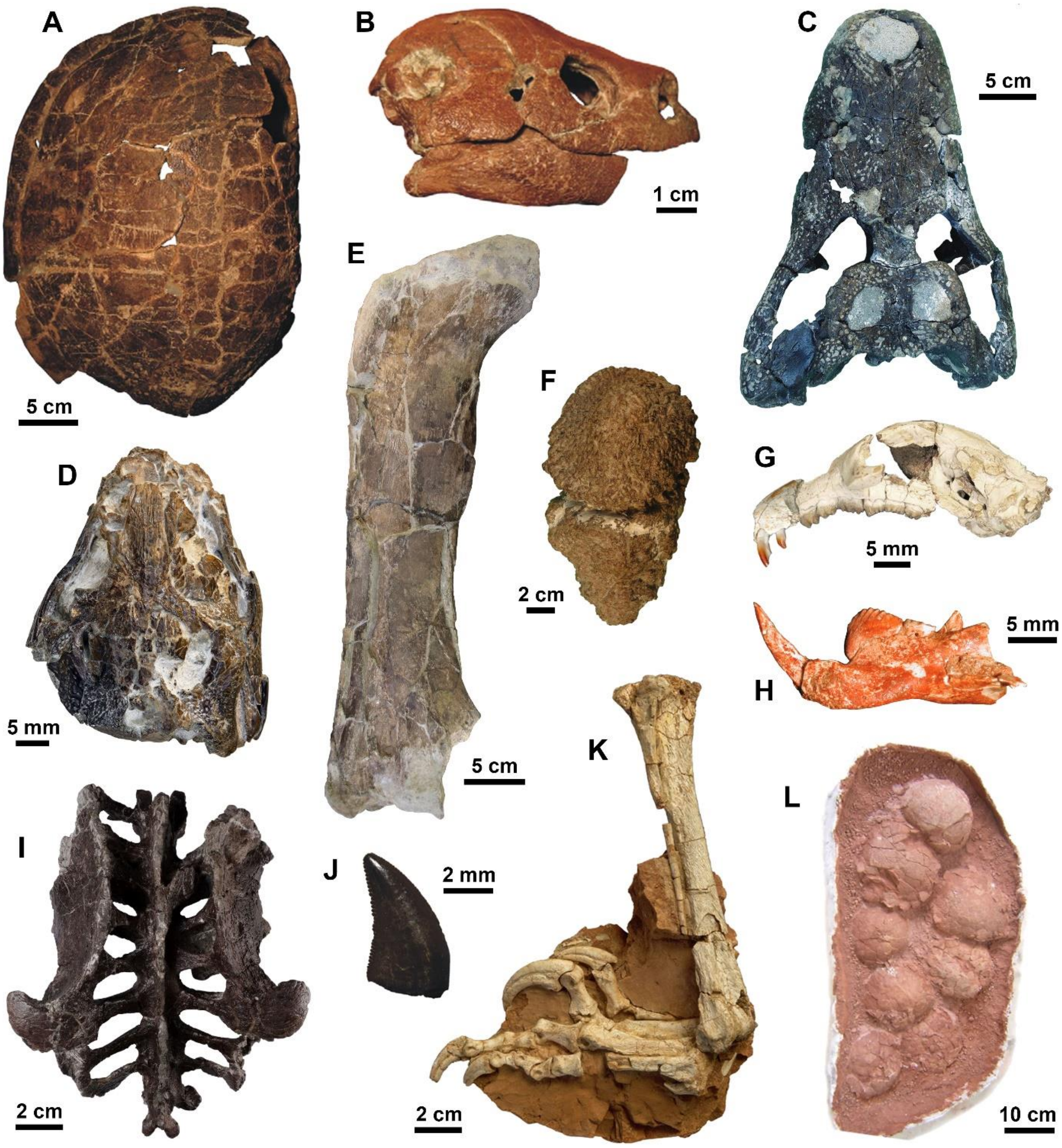

Figure 4. Representatives of the latest Cretaceous vertebrate assemblages from Transylvania. **A–B**, Shell (UBB NVK-31) in dorsal view (A) and skull (UBB ToK-2) in right lateral view (B) of *Kallokibotion bajazidi* from Totești and Nălaţ-Vad, respectively. Modified after Pérez-García and Codrea (2018). **C**, Skull of *Allodaposuchus precedens* (PSMUBB V 438) from Oarda de Jos (south-western Transylvanian Basin) in dorsal view. Modified after Csiki-Sava et al. (2015). **D**, Holotype skull of *Aprosuchus ghirai* (UBB V.662/1) from Pui in dorsal view. Modified after Venczel and Codrea (2019). **E**, Right femur of an indeterminate titanosaur (GPIT/RE/12880) from Sânpetru in anterior view. **F**, Titanosaur osteoderm (LPB (FGGUB) R.1902) from Sânpetru. Modified after Csiki-Sava et al. (2015). **G**, Holotype skull of *Litovoi tholocephalos* (LPB (FGGUB) M.1700) from Pui in left lateral view. Modified after Csiki-Sava et al. (2018). **H**, Right dentary of *Barbatodon transsylvanicus* (LPB (FGGUB) M.1635) from Pui in medial view. Modified after Csiki-Sava et al. (2015). **I**, Pelvis of a gargantuaviid bird (UBB V649) from Nălaţ-Vad in dorsal view. Modified after Mayr et al. (2020). **J**, Dromaeosaurid theropod tooth (LPB (FGGUB) R.2289) from Livezi in labial view. Modified after Csiki-Sava et al. (2016). **K**, Left distal hind limb of *Balaur bondoc* (EME PV.313) from Sebeș-Glod (southwestern Transylvanian Basin) in left lateral view. Modified after Csiki-Sava et al. (2015). **L**, Megaloolithid nest (LPB (FGGUB) R.2146) from Tuştea, ascribed to the hadrosaurian *Telmatosaurus transsylvanicus*. Modified after Botfalvai et al. (2017).

too, based on appendicular elements previously referred by Csiki and Grigorescu (2005) to an oviraptorosaurian (Csiki et al., 2010b; Brusatte et al., 2013a); for a potential avian status of *Balaur*, see Cau et al. (2015). The real alpha-level taxonomic diversity of non-avian theropods is difficult to assess due to the mostly isolated and non-overlapping material. The first definitive bird remains were reported by Wang et al. (2011a) and assigned to the Ornithurae and Enantiornithes, while Mayr et al. (2020) described a pelvis assignable to the large flightless avialan *Gargantuavis*, or a closely related taxon (Buffetaut and Angst, 2020).

Although turtles are among the most common vertebrates and their fossils are very abundant, the taxonomic diversity seems to have been rather low, and until the 1990s only one taxon has been identified, *Kallokibotion* (see above). A revision of *Kallokibotion* was published by Gaffney and Meylan (1992), who regarded *K. magnificum* as a junior synonym of the type species *K. bajazidi*. Subsequently, an additional turtle group was reported from the Haţeg Basin, the Dortokidae (Vremir 2004, Vremir and Codrea 2009, Vremir and Rabi 2011, Rabi et al. 2013), with some well-preserved specimens being referable to this family (see below). Additionally, Rabi et al. (2013) provided an extensive overview of the turtles from the uppermost Cretaceous of Transylvania and the whole Upper Cretaceous of central-eastern Europe. Recently, additional well preserved material of *Kallokibotion bajazidi* was described (Pérez-García and Codrea, 2018), as well as the detailed neuroanatomy of this taxon (Martín-Jiménez et al., 2021). As for the turtles, only one crocodilian has been reported from the Haţeg Basin until the 1990s, *Allodaposuchus precedens* (see above). However, since then, a much higher diversity of crocodyliforms has recognised, now including *Doratodon* sp. (Grigorescu et al., 1999; Martin et al., 2006; Vasile, 2008), *Acynodon* sp. (Martin et al., 2006; Vasile, 2008), and *Theriosuchus sympiestodon* (Martin et al., 2010, 2014). Recently, a new atoposaurid, the small-sized *Aprosuchus ghirai* was erected based on a near-complete skull from Pui (Venczel and Codrea, 2019). Finally, several important pterosaur specimens were discovered during the last decades, despite this group being exceedingly rare in the uppermost Cretaceous of the Haţeg Basin. Probably, the most important of these is the holotype of the giant azhdarchid *Hatzegopteryx thambema* (Buffetaut et al., 2002, 2003), which was recently suggested to be a terrestrially foraging animal and, in light of the absence of large theropods in the local fauna, to have occupied the niche of the terrestrial apex predator (Naish and Witton, 2017). Additional pterosaur material, exclusively referable to the Azhdarchidae, has since been reported from the Haţeg Basin, indicating the presence of at least two different taxa (Vremir et al., 2011, 2013, 2015b, 2018).

Concerning the smaller vertebrates from the uppermost Cretaceous of the Haţeg Basin, a high diversity – especially of amphibians, squamates, and mammals – was reported since the 1990s, mainly through intensified screen washing activity (Grigorescu et al., 1999), which also allowed the recognition of the high diversity of theropods and crocodyliforms mentioned above. Fish remains, in contrast, are relatively scarce but at least five different taxa have been reported thus far, indeterminate acipenseriforms, indeterminate characids, an indeterminate teleostean and two lepisosteids, *Lepisosteus* sp. and *Atracosteus* sp. (Grigorescu et al., 1985, 1999; Csiki et al., 2008). Several different amphibians have been recovered from the Haţeg Basin, and they currently comprise one albanerpetontid (*Albanerpeton* sp.) and at least five different anurans – *Eodiscoglossus* sp., *Paralatonia transylvanica* and *Hatzegobatrachus grigorescui*, cf. *Bakonybatrachus* sp., and an indeterminate potential pelobatid (Grigorescu et al., 1999; Venczel and Csiki, 2003; Folie and Codrea, 2005; Venczel et al., 2016); the previously reported cf. *Paradiscoglossus* (Folie and Codrea, 2005) has recently been assigned to *Paralatonia* (Venczel et al., 2016). Nevertheless, with at least five different anurans, western Romania has yielded the highest diversity of this group in the entire Upper Cretaceous record of Europe (Venczel et al., 2016). A variety of squamates were also reported during the last decades including an indeterminate anguimorph (Grigorescu et al., 1999), an amphisbaenian (?*Slavoia*) (Csiki et al., 2008), at least two different scincomorphs (the paramacellodids *Becklesius nopcsai* and *Becklesius* cf. *hoffstetteri*), two teiid lizards (*Bicuspidon hatzegiensis* and *Barbatteius vremiri*), and the madtsoiid snake *Nidophis insularis* (Grigorescu et al., 1999; Codrea et al., 2002; Folie and Codrea, 2005; Vasile et al., 2013a; Venczel and Codrea, 2016). The rather high diversity of mammals has only relatively recently been recognised, and so far, three genera containing five species have been reported, all belonging to the endemic Kogaionidae and some of them being known from comparatively well-preserved material – *Barbatodon transylvanicus*, *B*. *oardaensis*, *Kogaionon ungureanui*, *K*. *radulescui*, and *Litovoi tholocephalos* (Rădulescu and Samson, 1996; Csiki and Grigorescu, 2000; Csiki et al., 2005; Smith and Codrea, 2015; Solomon et al., 2016; Csiki-Sava et al., 2018, 2022; Smith et al., 2022); material previously assigned to a third kogaionid genus (*Hainina*) probably belongs to other kogaionids (Csiki-Sava et al., 2022).

Aside from the taxonomy and systematics, new research has also been conducted on the palaeoecology and taphonomy of the vertebrate assemblages of the Haţeg Basin, using various methods, such as the preservation and distribution pattern of the vertebrate remains (Csiki et al., 2008, 2010c; Botfalvai et al., 2017), bioerosional trace fossils on the bones (Csiki, 2006; Csiki et al., 2010c; Augustin et al., 2019), and stable isotope analysis of bones and teeth (Bojar et al., 2010a). Furthermore, a number of studies examined the potential effects of the insular habitat on the vertebrate fauna, including potential dwarfism, peculiar biogeographical relationships, and the 'primitiveness' of many taxa (Weishampel et al., 1991, 2010; Le Loeuff, 2005; Csiki and Grigorescu, 2007; Pereda-Suberbiola and Galton, 2009; Benton et al., 2010; Stein et al., 2010). The presence of insects was recently demonstrated through the identification of bioerosional trace fossils, which were ascribed to termites and dermestid beetles (Csiki, 2006; Vremir, 2009; Vasile et al., 2013b; Augustin et al., 2019), as well as possible insect eggs (Bodor et al., 2014; Heřmanová et al., 2017). The palaeoflora of the uppermost Cretaceous deposits of the Haţeg Basin was reconstructed using palynological data as well as meso- and macrofossils of plants, revealing an open vegetation composed of a diverse subtropical flora of ferns, bryophytes, gymnosperms and angiosperms (Van Itterbeeck et al., 2005; Csiki et al., 2008; May Lindfors et al., 2010; Popa et al., 2014, 2016). Finally, detailed sedimentological work allowed a refined reconstruction of the palaeoenvironment, the palaeoclimate, and the stratigraphic framework for the uppermost Cretaceous deposits of the Haţeg Basin (e.g., Van Itterbeeck et al., 2004; Bojar et al., 2005, 2010b; Therrien, 2005, 2006; Therrien et al., 2009; Panaiotu and Panaiotu, 2010; Csiki-Sava et al., 2016).

The overview of the research history of the latest Cretaceous vertebrates from the Haţeg Basin presented here is, naturally, missing many details and is not aimed at providing an exhaustive compilation. Nevertheless, this overview includes the most important findings and demonstrates how much research has already been conducted on the ‘island of the dwarf dinosaurs’. Several other publications have summarised the state of knowledge on the uppermost Cretaceous deposits of the Hateg Basin and their vertebrate assemblages before, often with different focuses, providing additional valuable overviews (Weishampel et al., 1991; Grigorescu, 2010a; Weishampel and Jianu, 2011; Csiki-Sava et al., 2015, 2016).

Tab. 1. Taxa list of the latest Cretaceous vertebrates from the Haţeg Basin. ‘Taxon 1’ corresponds to ‘class’, ‘order’ or similar rank, ‘Taxon 2’ corresponds to a rank between ‘class’ and ‘family’, and ‘Taxon 3’ corresponds to ‘family’ or similar rank.

Taxon 1	Taxon 2	Taxon 3	Genus	species	Reference
Pisces	Acipenseriformes	incertae sedis	Genus indet.	species indet.	(Grigorescu et al., 1985)
	Teleostei	Characidae	Genus indet.	species indet.	(Grigorescu et al., 1985)
		incertae sedis	Genus indet.	species indet.	(Csiki et al., 2008)
	Holostei	Lepisosteidae	*Lepisosteus*	species indet.	(Csiki et al., 2008)
			Atractosteus	species indet.	(Csiki et al., 2008)
Lissamphibia	Allocaudata	Albanerpetontidae	*Albanerpeton*	species indet.[2]	(Grigorescu et al., 1999)
	Anura	Alytidae[1]	*Eodiscoglossus*	species indet.	(Grigorescu et al., 1999)
			Paralatonia	*transylvanica*	(Venczel and Csiki, 2003)
			cf. *Bakonybatrachus*	species indet.	(Venczel et al., 2016)
		Bombinatoridae[1]	*Hatzegobatrachus*	*grigorescui*	(Venczel and Csiki, 2003)
		Pelobatidae?	Genus indet.	species indet.	(Venczel et al., 2016)
Squamata	Amphisbaenia	incertae sedis	?*Slavoia*	species indet.	(Csiki et al., 2008)
	Anguimorpha	incertae sedis	Genus indet.	species indet.	(Grigorescu et al., 1999)
	Lacertoidea	Teiidae	*Bicuspidon*	*hatzegiensis*[4]	(Folie and Codrea, 2005)
			Barbatteius	*vremiri*	(Venczel and Codrea, 2016)
	Scincomorpha	Paramacellodidae	*Becklesius*	*nopcsai*	(Folie and Codrea, 2005)
			Becklesius	cf. *B. hoffstetteri*	(Folie and Codrea, 2005)
	Serpentes	Madtsoiidae	*Nidophis*	*insularis*	(Vasile et al., 2013a)
Testudinata	‘Stem-Testudines’	Kallokibotionidae	*Kallokibotion*	*bajazidi*	(Nopcsa, 1923a)
	Pleurodira	Dortokidae	*Dortoka*	*vremiri*	(Augustin et al., 2021)
Metasuchia	Ziphosuchia[5]	incertae sedis	*Doratodon*	species indet.	(Grigorescu et al., 1999)
	Eusuchia[7]	Globidonta	*Acynodon*	species indet.	(Martin et al., 2006)
		Atoposauridae	*Theriosuchus*	*sympiestodon*	(Martin et al., 2010)
			Aprosuchus	*ghirai*	(Venczel and Codrea, 2019)
		Allodaposuchidae	*Allodaposuchus*	*precedens*	(Nopcsa, 1928)
Pterosauria	Pterodactyloidea	Azhdarchidae	*Hatzegopteryx*	*thambema*	(Buffetaut et al., 2002)
			Genus indet.	species indet.	(Vremir et al., 2015b)
Dinosauria	Ankylosauria	Nodosauridae	*Struthiosaurus*	*transsylvanicus*	(Nopcsa, 1929a)
	Ornithopoda	Rhabdodontidae	*Zalmoxes*	*robustus*	(Nopcsa, 1902a)
			Zalmoxes	*shqiperorum*	(Weishampel et al., 2003)
			Transylvanosaurus	*platycephalus*	(Augustin et al., 2022)
		Hadrosauroidea	*Telmatosaurus*	*transsylvanicus*	(Nopcsa, 1900)
	Sauropoda	Titanosauria	*Magyarosaurus*	*dacus*	(Huene, 1932)
			Paludititan	*nalatzensis*	(Csiki et al., 2010a)
			Genus indet.	species indet.	(Mocho et al., 2022)
			Genus indet.	species indet.	(Mocho et al., 2022)
	Theropoda	Velociraptorinae	Genus indet.	species indet.	(Csiki and Grigorescu, 1998)
		Troodontidae	Genus indet.	species indet.	(Csiki and Grigorescu, 1998)
		incertae sedis	*Euronychodon*	species indet.	(Csiki and Grigorescu, 1998)
		incertae sedis	*Paronychodon*	species indet.	(Codrea et al., 2002)
		incertae sedis	*Richardoestesia*	species indet.	(Codrea et al., 2002)
		incertae sedis	*Balaur*	*bondoc*	(Csiki et al., 2010b)
Aves	incertae sedis	Gargantuaviidae	*Gargantuavis*	species indet.	(Mayr et al., 2020)
	Ornithothoraces	Ornithurae	Genus indet.	species indet.	(Wang et al., 2011a)
		Enantiornithes	Genus indet.	species indet.	(Wang et al., 2011b)
Mammalia	Multituberculata	Kogaionidae	*Barbatodon*	*transylvanicus*	(Rădulescu and Samson, 1986)
			Barbatodon	*oardaensis*	(Csiki-Sava et al., 2022)
			Kogaionon	*ungureanui*	(Rădulescu and Samson, 1996)
			Kogaionon	*radulescui*	(Smith et al., 2022)
			Litovoi	*tholocephalos*	(Csiki-Sava et al., 2018)

1.2. The vertebrate assemblages of the Haţeg Basin and their significance

Over the past 120 years, an extremely diverse array of vertebrates has been recovered from the uppermost Cretaceous deposits of the Haţeg Basin including fishes, anurans, albanerpetontids, lizards, madtsoiid snakes, dortokid and kallokibotionine turtles, crocodyliforms, titanosaurian sauropods, non-avian maniraptoran theropods, birds, rhabdodontids, hadrosauroids, nodosaurid ankylosaurs, azhdarchid pterosaurs and kogaionid multituberculate mammals (see above). Overall, more than 50 vertebrate taxa have so far been described from the Maastrichtian strata of the Haţeg Basin (for a complete taxa list, see Tab. 1). Apart from the diversity, the vertebrate assemblages from the Haţeg Basin are remarkable for being highly unusual in several respects. Perhaps most striking is the small size of most dinosaurian taxa (Fig. 5), particularly when compared to their equivalents from other Late Cretaceous continental faunas (Nopcsa, 1914b, 1923a; Jianu and Weishampel, 1999; Csiki and Grigorescu, 2007; Benton et al., 2010; Csiki and Benton, 2010; Stein et al., 2010; Csiki-Sava et al., 2016). Moreover, several of the vertebrate taxa from the uppermost Cretaceous beds of the Haţeg Basin are basal representatives within their respective clades and are endemic, indicating some degree of isolation (Nopcsa, 1923a; Weishampel et al., 1991, 2010; Csiki and Grigorescu, 2007; Benton et al., 2010). The unusual faunal composition, as exemplified by the lack of large predatory dinosaurs (e.g., Csiki and Grigorescu, 1998), represents another peculiarity of these fossil assemblages, and recently giant azhdarchid pterosaurs have been suggested as potential apex predators in these ecosystems (Naish and Witton, 2017). Most of these peculiarities have been ascribed to the notion that the Haţeg area was situated on an island in the Late Cretaceous – a suggestion brought forward as early as 1914 by Franz Nopcsa (Nopcsa, 1914b, 1923a), and later revived by several authors (Weishampel et al., 1991, 2010; Csiki and Grigorescu, 2007; Benton et al., 2010; Csiki and Benton, 2010; Csiki-Sava et al., 2015, 2016).

In fact, during the Late Cretaceous, the entire present-day European continent consisted of an extensive Archipelago of small and large islands situated in a warm and subtropical sea (Fig. 6), the Late Cretaceous European Archipelago (Csiki-Sava et al., 2015). In this context, the latest Cretaceous vertebrates of the Haţeg Basin lived on a relatively small island with an area of approximately 80,000 km^2 (Benton et al., 2010) in the eastern part of this archipelago (Csiki-Sava et al., 2015), usually referred to as the ‘Haţeg Island’ or the ‘Transylvanian Island’. Despite the importance of the vertebrate assemblages of the Haţeg Basin, they are not the only ones from the Late Cretaceous Haţeg Island. Aside from the Haţeg Basin, uppermost Cretaceous continental strata crop out in several additional areas in Transylvania, including the southwestern, western and northwestern parts of the Transylvanian Basin, the Rusca Montană Basin and the southern Apuseni Mountains (Codrea et al., 2010; Csiki-Sava et al., 2016). Notably, all of these deposits are roughly coeval and they have in common a comparable geotectonic setting, and a similar lithology (Csiki-Sava et al., 2016). The most important of these deposits (in terms of richness in vertebrate fossils) are those from the southwestern part of the Transylvanian Basin, where uppermost Cretaceous rocks crop out near the cities of Sebeș and Alba-Iulia along the Mureş River (Codrea et al., 2010; Vremir et al., 2015a; Csiki-Sava et al., 2016). Although these outcrops have been assigned to several different lithostratigraphic units in the past, they were recently all included in the upper Campanian–late Maastrichtian Sebeș Formation (Vremir et al., 2015a; Csiki-Sava et al., 2016). The vertebrate assemblage recovered from the Sebeș Formation is relatively similar to that recovered from the Haţeg Basin, and most taxa (at least on the family level) that are present in the latter also occur in the southwestern Transylvanian Basin (Codrea et al., 2010; Vremir et al., 2015a; Csiki-Sava et al., 2016). Intriguingly, it has been suggested that the Sebeș Formation of the southwestern Transylvanian Basin documents more lowland paleoenvironments, whereas the deposits of the Haţeg Basin represent more upland palaeoenvironments (e.g., Csiki-Sava et al., 2016).

Looking outside the Transylvanian area, terrestrial vertebrates from the later part of the Late Cretaceous (Santonian–Maastrichtian) have been uncovered in various places in Europe, which mostly correspond to different emergent landmasses of the Late Cretaceous European Archipelago. The most important Late Cretaceous continental vertebrate assemblages of Europe – besides the ones from Transylvania – are those from Spain, southern France, eastern Austria, and western Hungary (Csiki-Sava et al., 2015). In Spain, latest Cretaceous vertebrates are known chiefly from the southern Pyrenees of northeastern Spain, but also from northern Spain (e.g., Laño), central Spain (e.g., Lo Hueco, Armuña), and eastern Spain, where they occur in various different formations ranging in age from late Campanian to late Maastrichtian (Csiki-Sava et al., 2015; Ortega et al., 2015; Pereda-Suberbiola et al., 2015; Pérez-García et al., 2016). In southern France, latest Cretaceous vertebrates have been

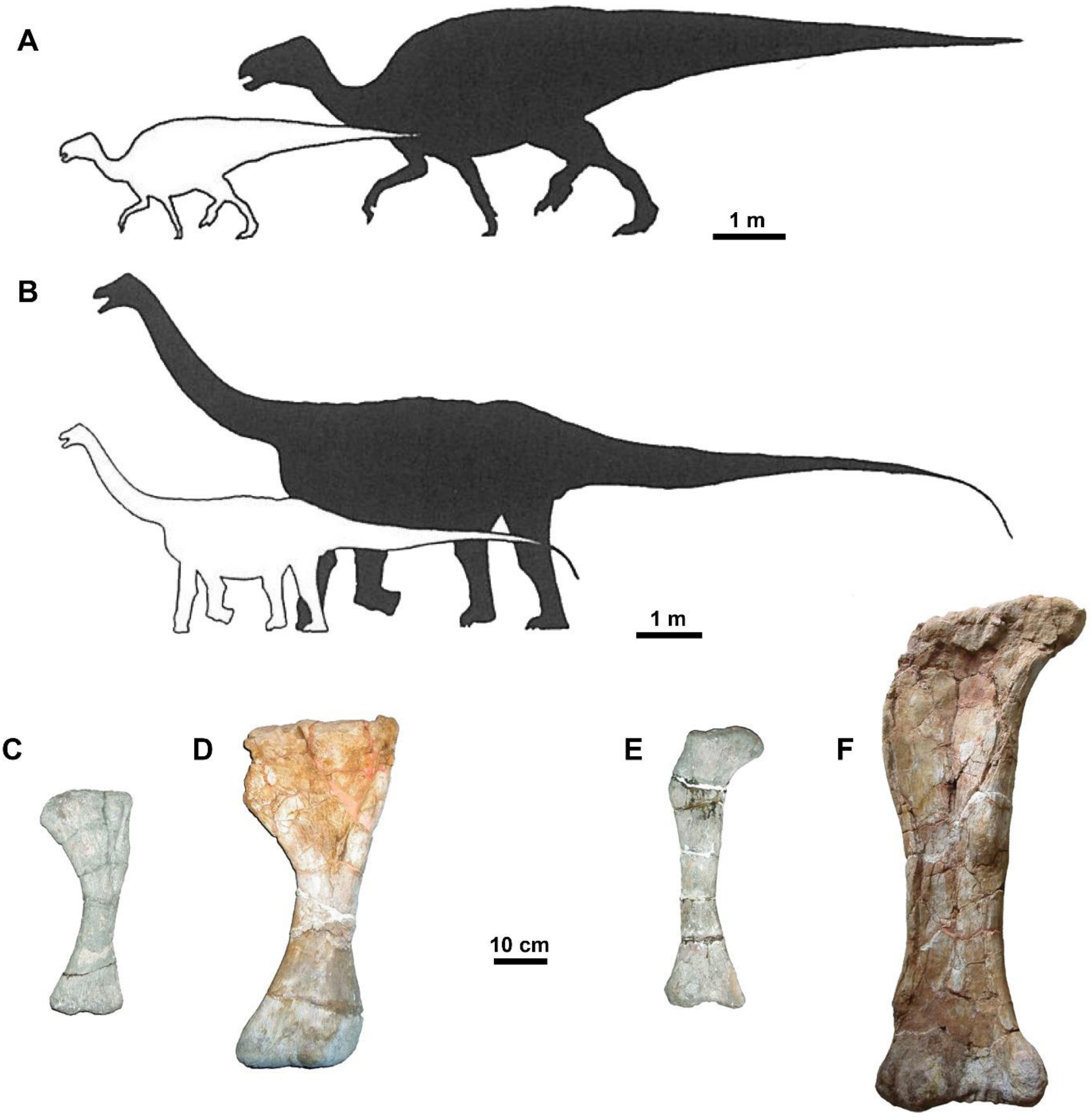

Figure 5. Dwarfing of the dinosaurs from the Haţeg Island. **A**, Size comparsion between *Magyarosaurus* (white silhouette) and a titanosaurian of ancestral body size. Modified after Weishampel and Jianu (2011). **B**, Size comparsion between *Telmatosaurus* (white silhouette) and an iguanodontian of ancestral body size. Modified after Weishampel and Jianu (2011). **C–D**, Size comparison between a left humerus of *Magyarosaurus* (LPB (FGGUB) R.1047) from the Haţeg Island (C) and the same element of *Ampelosaurus* (MDE C3-86) from the Ibero-Armorican landmass (D). Modified after Csiki-Sava et al. (2015). **E–F**, Size comparison between the left femur of Magyarosaurus (LPB (FGGUB) R.1046) from the Haţeg Island (E) and the right femur of Ampelosaurus (MDE C3-86) from the Ibero-Armorican landmass (F). Modified after Csiki-Sava et al. (2015). Note the much larger size of *Ampelosaurus* as compared to *Magyarosaurus*.

found at numerous localities distributed over a large area and come from several different lithostratigraphic units, whose age ranges from the early Campanian to the late Maastrichtian (Buffetaut and Le Loeuff, 1991a; Buffetaut et al., 1997; Csiki-Sava et al., 2015). The vertebrate assemblage from eastern Austria was found in the 'coal-bearing series' of Muthmannsdorf, which was mined until the end of the 19th century and which is assignable to the lower Campanian Grünbach Formation of the Gosau Group (Bunzel, 1871; Seeley, 1881; Summesberger et al., 2007; Csiki-Sava et al., 2015). In western Hungary, terrestrial Late Cretaceous vertebrates come from two sites, an abandoned bauxite mine near Iharkút, yielding the large majority finds, and waste dumps of the subterranean Ajka coalmines near Ajka, both of which are Santonian in age and belong to the Csehbánya Formation, respectively the Ajka Coal Formation (Ősi et al., 2012b; Csiki-Sava et al., 2015).

During the Late Cretaceous, both the Iberian Peninsula and southern France were located on the Ibero-Armorican Island, which was one of the largest islands of the Late Cretaceous European Archipelago and was located in its western part (Csiki-Sava et al., 2015). The Grünbach Formation of Muthmannsdorf and the Csehbánya Formation of Iharkút on the other hand, were probably deposited on the Austroalpine landmass (Csiki-Sava et al., 2015). Although the vast majority of vertebrate finds from the Upper Cretaceous of Europe come from continental deposits, a number of important specimens have been found in near-shore marine settings, which were probably situated close to the islands. This includes material from the Santonian of central Belgium, the lower Santonian to lower Campanian of western Bulgaria, the lower Campanian of northeastern Italy and southern Sweden, the Campanian to lower Maastrichtian of southwestern Russia, the upper Campanian to Maastrichtian of central-western Portugal, the upper Maastrichtian of the southeastern Netherlands and northeastern Belgium, the upper Maastrichtian of southern Germany, the upper Maastrichtian of southwestern Slovenia, the upper Maastrichtian of southeastern Poland (footprints only), the upper Maastrichtian of northwestern Bulgaria, and the upper Maastrichtian of Crimean Peninsula, Ukraine (for an overview of the occurences of Late Cretaceous terrestrial vertebrates throughout Europe, see Csiki-Sava et al., 2015).

In general, the terrestrial Late Cretaceous vertebrate faunas of Europe are characterised by a unique taxonomic composition and complex biogeographical relationships. Several suprageneric taxa seem to have ben endemic to the Late Cretaceous of Europe such as palaeobatrachid frogs among amphibians, kallokibotionines, solemydids and dortokids among turtles, allodaposuchids among crocodyliforms, struthiosaurines and rhabdodontids among dinosaurs, as well as kogaionids and lainodontines among mammals (Csiki-Sava et al., 2015; Joyce et al., 2016;

Blanco, 2021). Furthermore, within the Late Cretaceous European Archipelago, not all taxa share the same distribution. Some taxa (at least on the ‘familial’ level) have a particularly wide, trans-European distribution – occurring throughout all of the best-sampled faunas (i.e. northeastern Spain, southern France, eastern Hungary, western Austria, western Romania) – including dortokids (see below), azhdarchids (e.g., Buffetaut, 1999, 2008; Buffetaut et al., 2011; Ősi et al., 2011; Vremir et al., 2015b), struthiosaurine ankylosaurs (Ősi and Prondvai, 2013; Ősi et al., 2014), and rhabdodontids (see below); to this list could be added atoposaurid crocodyliforms (Martin et al., 2014) and allodaposuchid eusuchians (Blanco, 2021; Rabi pers. com.) if Muthmannsdorf (the least well-sampled of these faunas) is excluded. Other clades only occur in certain parts of the Late Cretaceous European Archipelago, often being limited to either the western or the eastern realm. For example, helochelydrids (Joyce et al., 2016), lainodontine zhelestids (Gheerbrant and Astibia, 2012) and lambeosaurine hadrosaurids (Prieto-Márquez et al., 2013) are only known from the western Ibero-Armorican landmass, whereas kallokibotionine turtles (Rabi et al., 2013) and kogaionid multituberculate mammals (Smith et al., 2022; Csiki-Sava et al., 2022) are only known from the eastern part of the archipelago, the latter being restricted to the Haţeg Island. However, even within widely distributed clades, there are distinct lineages with a disjunct distribution pattern, such as dortokids (see below), allodaposuchids (Narváez et al., 2016; Blanco, 2021), and rhabdodontids (see below).

Taken together, the vertebrate assemblages from the Transylvanian area appear to be more similar to those from eastern Austria and western Hungary than to those from Spain and southern France, likely due to geographical proximity (Rabi et al., 2013; Csiki-Sava et al., 2015; see below). This dichotomous distribution pattern (i.e., eastern vs. western European) indicates some degree of faunal separation between the Ibero-Armorican landmasses on the one hand, as well as the Austroalpine and Transylvanian landmasses on the other. However, there are also some taxa that occurred on the Ibero-Armorican Island and the Haţeg Island but not on the Austroalpine landmass, like, for example, hadrosaurs (Csiki-Sava et al., 2015), derived titanosaurs (Csiki-Sava et al., 2015; Ősi et al., 2017), and peculiar large flightless birds, the Gargantuaviidae (Buffetaut and Angst, 2020; Mayr et al., 2020). Finally, the Haţeg Island also differs from all other landmasses of the Late Cretaceous European Archipelago (regarding faunal composition) in, for example, the absence of bothremydid turtles that are present on the Austroalpine (Iharkút) and Ibero-Armorican landmasses, and in the absence of large, non-coelurosaurian theropods (Csiki-Sava et al., 2015). Interestingly, the Transylvanian landmass is further characterised by relative faunal stability when compared to the Ibero-Armorican Island (Csiki-Sava et al., 2015, 2016). In the Ibero-Armorican realm, the titanosaur-rhabdodontid-nodosaurid fauna of the early Maastrichtian is replaced by a hadrosauroid-titanosaur dominated fauna in the Maastrichtian, with rhabdodontids and nodosaurids apparently dying out in the early late Maastrichtian (Le Loeuff et al., 1994; Buffetaut et al., 1997; Vila et al., 2016). Such a faunal succession did not occur in the Transylvanian realm and all major taxa survived for the entire recorded time span, i.e., from the late Campanian to late Maastrichtian (Csiki-Sava et al., 2016). This further indicates that the Haţeg Island was somewhat decoupled from the western European realm and evolved in its own, unique way. It should be noted, however, that especially on lower taxonomic levels, the faunas of the different landmasses of the Late Cretaceous European Archipelago generally show a relatively high degree of endemism, probably due to geographic isolation and potentially their temporal separation (Csiki-Sava et al., 2015).

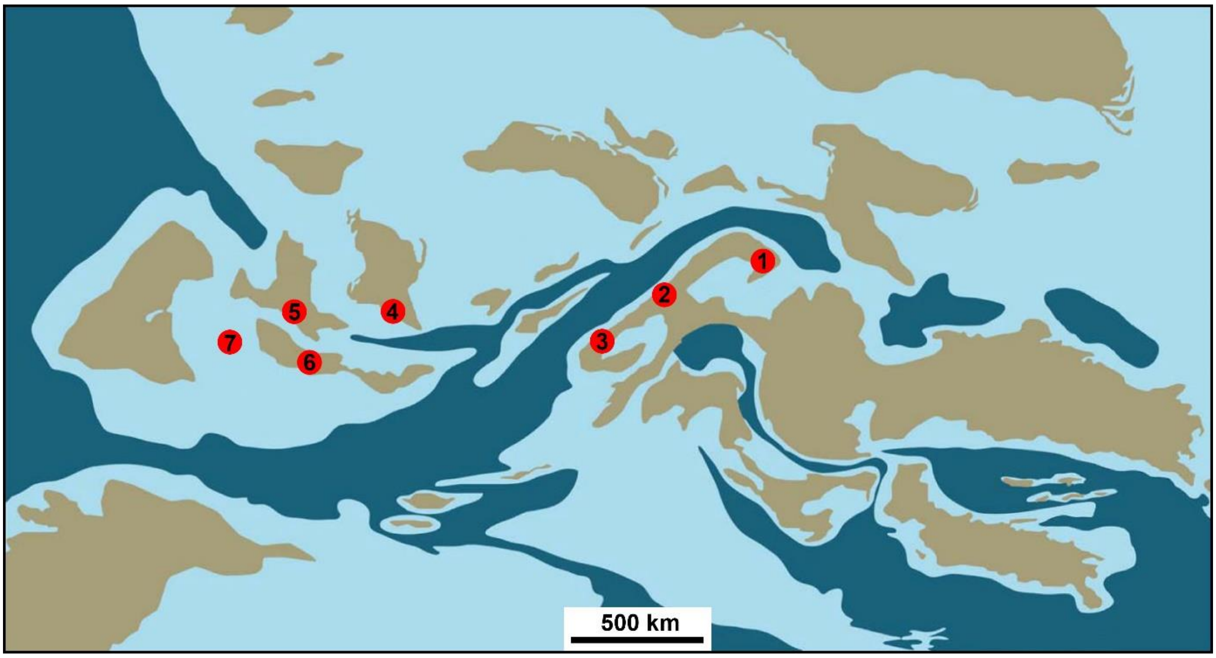

Figure 6. Palaeogeographic map of Europe during the latest Cretaceous (late Campanian), with the location of the most important vertebrate assemblages. **1**, Transylvania (including the Haţeg, Transylvanian and Rusca Montană basins), western Romania. **2**, Iharkút, western Hungary. **3**, Muthmannsdorf, eastern Austria. **4**, Eastern southern France. **5**, Western southern France. **6**, Northern Spain. **7**, Central Spain. Note that the position and the extent of the different islands was slightly different before and after the late Campanian. In particular, during the Maastrichtian, the emergent landmasses were more extensive, meaning that the uppermost Cretaceous strata from central Spain (7) were deposited in a predominantly continental environment. The 'Haţeg Island' (1) was located at approximately 22.6–28.5° northern latitude during the Maastrichtian. Numerous additional latest Cretaceous vertebrate fossils have been uncovered in near-shore marine settings (see text). Modified after Blanco (2021).

1.3. Geological setting

The Haţeg Basin is an intramontane basin situated in the southwestern Carpathians, western Romania. The basin formed by extensional deformation during and after the latest Cretaceous phase of the Carpathian orogeny, and thereafter was supplied with detritus from the adjacent Poiana Ruscă and Retezat mountains, located to the west and the south, respectively (Bojar et al., 1998; Willingshofer et al., 2001). Tectonically, the Haţeg Basin belongs to the Tisia-Dacia block or microplate, which during the latest Cretaceous formed a subtropical island (also called 'Haţeg Island' or 'Transylvanian Island'), located at 22.6–28.5° northern latitude in the eastern part of the Late Cretaceous European Archipelago (Panaiotu and Panaiotu, 2010; Csiki-Sava et al., 2015). The climate on this island has been reconstructed as strongly seasonal and warm, with a mean annual temperature of 10–14°C (Bojar et al., 2005, 2010a; Therrien, 2005; Therrien et al., 2009). Upper Cretaceous sedimentary rocks crop out in four main regions in the Haţeg Basin and each of these deposits probably corresponds to a distinct lithostratigraphic unit (Fig. 8). Of these four units, two have been formally defined and assigned to formations, i.e., the Sînpetru Formation of the south-central Haţeg Basin and the Densuş-Ciula Formation in the northwestern part of the basin.

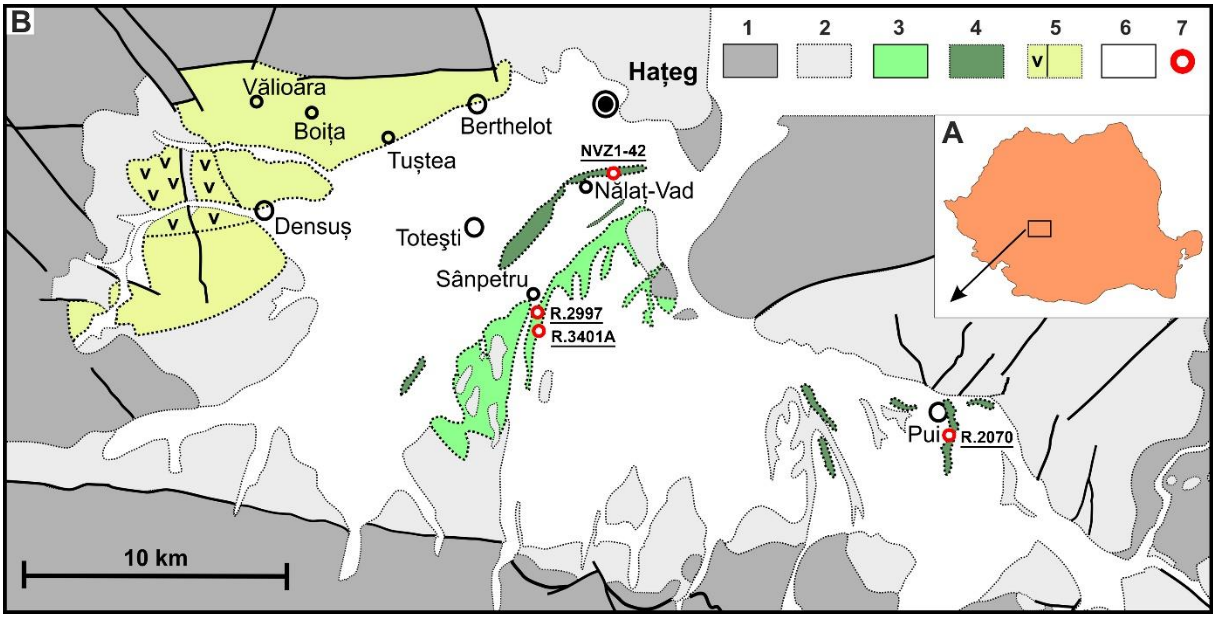

Figure 7. Locality information and the geology of the Haţeg Basin. **A**, Position of the Haţeg Basin in Romania. **B**, Geological map of the Haţeg Basin. **Legend: 1**, Crystalline basement; **2**, Pre-Quaternary sedimentary rocks, with 3–5 denoting the Upper Cretaceous continental deposits. **3**, Sînpetru Formation; **4**, Deposits formerly correlated with the Sînpetru Formation (Râul Mare and Bărbat river sections in the central and southeastern part of the basin, respectively, see text for explanations); **5**, Densuş-Ciula Formation (v, volcanoclastic subunit); **6**, Quaternary deposits; **7**, Localities yielding the specimens studied for this thesis (underlined numbers are the inventory numbers lacking the institutional abbreviation). Modified after Augustin et al. (2021).

Conversely, the Upper Cretaceous deposits cropping out in the central part of the basin near Nălaţ-Vad and in the southeastern part of the basin near Pui have only relatively recently been suggested to represent distinct lithostratigraphic units, and they are now usually informally referred to as the Râul Mare River section' and the 'Pui Beds', respectively (Csiki-Sava et al. 2016). The age of these deposits ranges from early to late Maastrichtian (for details on the chronostratigraphic age, see Csiki et al. 2016). Generally, all of these units are composed of reddish to greyish siliciclastic sedimentary rocks that were deposited by meandering and braided river systems, although significant sedimentological differences are present between them. The specimens that are the focus of this dissertation have been found at three of these four lithostratigraphic units – the Sînpetru Formation of the Sibişel Valley section, the Râul Mare River section, and the 'Pui Beds' – and accordingly, these three units are introduced in more detail below (for an overview, see also Tab. 2).

1.3.1. The Sînpetru Formation of the 'Sibişel Valley section'

Virtually all of the original Nopcsa specimens and numerous more recent finds have been collected from the Sînpetru Formation in the south-central part of the Haţeg Basin. The rocks of the Sînpetru Formation mainly crop out along the Sibişel River Valley (Therrien et al., 2009). These strata, also called the 'Sibişel Valley section' (Fig. 8), represent the stratotype section of the Sînpetru Formation and has been have been estimated to be early to early late Maastrichtian in age (Therrien, 2004; Panaiotu and Panaiotu, 2010). The sedimentary rocks of the Sibişel Valley section comprise coarse-grained and fine-grained layers arranged in multiple fining-upward sequences, which were laid down on a poorly channelized alluvial plain drained by braided river systems (Grigorescu, 1983; Therrien, 2006; Therrien et al., 2009). Abundant and well-developed palaeosols have further been used to infer a heterogeneous environment composed of wetlands, seasonal wetlands and well drained floodplains (Therrien et al., 2009). The palaeoclimate during the time of deposition was likely semi-arid to sub-humid, seasonal and warm (Bojar et al., 2005; Therrien, 2005; Therrien et al., 2009). The vertebrate assemblage of the type section of the Sînpetru Formation includes amphibians, multituberculate mammals, squamates, turtles, crocodyliforms, pterosaurs, as well as ankylosaurs, ornithopods, theropods and sauropods among dinosaurs (Nopcsa, 1900, 1902a, 1904; Andrews, 1913; Nopcsa, 1929a; Grigorescu, 1984; Rădulescu and Samson, 1996; Csiki and Grigorescu, 1998; Martin et al., 2014). In general, the vertebrate remains often show complex taphonomic histories and occur either as isolated bones and teeth, or as associated and partly articulated remains, the latter sometimes occurring also in restricted multitaxic bonebeds or 'fossil-pockets' (Nopcsa, 1902b; Grigorescu, 1983; Csiki et al., 2010c; Augustin et al., 2019).

The large majority of the original Nopcsa specimens – including the ornithopod braincase specimen NHMUK R.3401A studied during this dissertation (see below) – were discovered in such a fossil pocket, representing the single most prolific locality excavated by Nopcsa, his Quarry 1 (German 'Nest 1'). Quarry 1 was mentioned in several Nopcsa publications (Nopcsa, 1900, 1902b, 1902a, 1904), one of which was devoted specifically to the description of this fossil site (Nopcsa 1902b). Nopcsa discovered the locality in 1895 on the 'left side' of the Sibişel Valley near the Temesel forest (Nopcsa, 1902b), which, according to the local villagers, is located on the eastern side of the river and placed near the entrance of the Sibişel Valley (Fig. 1B). Nopcsa recognised the importance of this site soon after its discovery and excavated 'Nest 1' for several years, until it was almost fully exploited (Nopcsa, 1904). At the locality, the vertebrate fossils exclusively occur in a blueish to greenish grey mudstone horizon that overlies a reddish grey mudstone layer and which is overlain by a fine-grained yellow sandstone layer, each with a thickness of about 50 cm (Nopcsa, 1902b). However, the fossils are not distributed evenly in this blueish to greenish mudstone horizon but are rather restricted to an elongated to ellipsoidal body (the actual 'Nest') measuring 15 m in length (German '20 Schritte') and 3 m in depth. In addition, the fossils seem to have been concentrated near the middle of this sediment body, where they lie extremely close to each other. The preservation of the bones is diverse and ranges from nearly perfectly preserved to fragmentary and abraded. Despite being largely disarticulated, many of the bones probably belong to the same individuals, as already noted by Nopcsa. In general, the bones are not sorted, neither according to their size nor to their preservation. Overall, 185 identifiable bones and numerous fragments were found in 'Nest 1' belonging to at least five taxa, including the turtle *Kallokibotion*, indeterminate pterosaurs, the titanosaur *Magyarosaurus*, the hadrosauroid *Telmatosaurus* and the rhabdodontid *Zalmoxes* (Nopcsa, 1900, 1902a, 1902b, 1904).

The turtle specimen LBP (FGGUB) R.2297, which was studied in the course of this dissertation (see below), has been found in 1995 at the 'La Cărare' fossil locality, which represents one of the richest sites in the Sibişel Valley section. The locality is situated on the eastern side of the Sibişel Valley, close to the entrance of the valley near the village of Sânpetru (Csiki et al., 2010c: fig. 1), and was quarried between 1993 and 1997 until it was nearly fully exploited (Csiki, 2006). Thereafter, only few additional specimen have been recovered from this locality (e.g., Ősi et al., 2014). The deposits at the locality consist of interbedded greenish conglomeratic sandstones and brownish mudstones (Csiki, 1999). The large majority of fossils at 'La Cărare' were found in a grey-greenish conglomeratic sandstone horizon, which grades into a sandy siltstone towards the top (Csiki, 2006; Ősi et al., 2014). Like many other sandstone bodies in vicinity, the fossiliferous basal conglomeratic sandstone seems to be laterally restricted and lens-shaped. As is usually the case with vertebrate remains from the Sînpetru Formation, the fossils at 'La Cărare' occur mostly isolated, but very few specimens also show skeletal association and even articulation with specimen LBP (FGGUB) R.2297 representing such an exception. In some instances, matching sizes and a similar preservation indicate skeletal association of isolated elements (pers. com. Z. Csiki-Sava); in this regard, the 'La Cărare' site thus resembles 'Quarry 1' (see above). Based on the taphonomical characteristics of the fossils and the sedimentology of the site, the fossils were likely accumulated by river channels (Csiki, 2006). Besides LPB (FGGUB) R.2297, the 'La Cărare' bonebed yielded many more vertebrate remains, including the turtle *Kallokibotion*, the crocodyliform *Allodaposuchus*, pterosaurs, titanosaurian sauropods, coelurosaurian theropods, nodosaurid ankylosaurs, hadrosauroid ornithopods, and rhabdodontid ornithopods (Jianu, 1994; Csiki and Grigorescu, 1998; Csiki, 1999, 2006; Martin et al., 2014; Ősi et al., 2014).

1.3.2. The 'Râul Mare River section'

The braincase specimen UBB NVZ1-42, which was studied in the course of this dissertation (see below), was discovered in the Râul Mare River section near Nălaţ-Vad in the central part of the Haţeg Basin. Here, strongly tilted uppermost Cretaceous rocks are exposed by the river Râul Mare, being accessible within and along its river course (Fig. 8). More specifically, the deposits crop out in three distinct areas, from oldest to youngest, near the village of Nălaţ-Vad, near Totești and near Unciuc (Csiki-Sava et al., 2016). Lithologically, the strata consist predominantly of fine-grained, dark-grey floodplain deposits and lenticular channel sandstones (Smith et al., 2002; Van Itterbeeck et al., 2004; Csiki-Sava et al., 2016). The depositional environment has been interpreted as a meandering river floodplain with dispersed freshwater ponds and a relatively high groundwater table, especially compared to other sites of the Haţeg Basin (Van Itterbeeck et al., 2004; Ciobanete et al., 2011; Săsăran et al., 2011).

Stratigraphically, the Râul Mare River section was considered to belong to the Sînpetru Formation (Codrea et al., 2002; Therrien, 2006; Therrien et al., 2009), the Densuş-Ciula Formation (Panaiotu et al., 2011), or to represent its own lithostratigraphic unit (Csiki-Sava et al., 2016). Regardless of the precise lithostratigraphic relationships, the age of the succession has been reconstructed as 'middle' Maastrichtian (Van Itterbeeck et al., 2005) or late Maastrichtian (Ciobanete et al., 2011; Panaiotu et al., 2011) based on palynostratigraphy and magnetostratigraphy, respectively, thus representing one of the youngest deposits from the entire Haţeg Basin (Csiki-Sava et al., 2016).

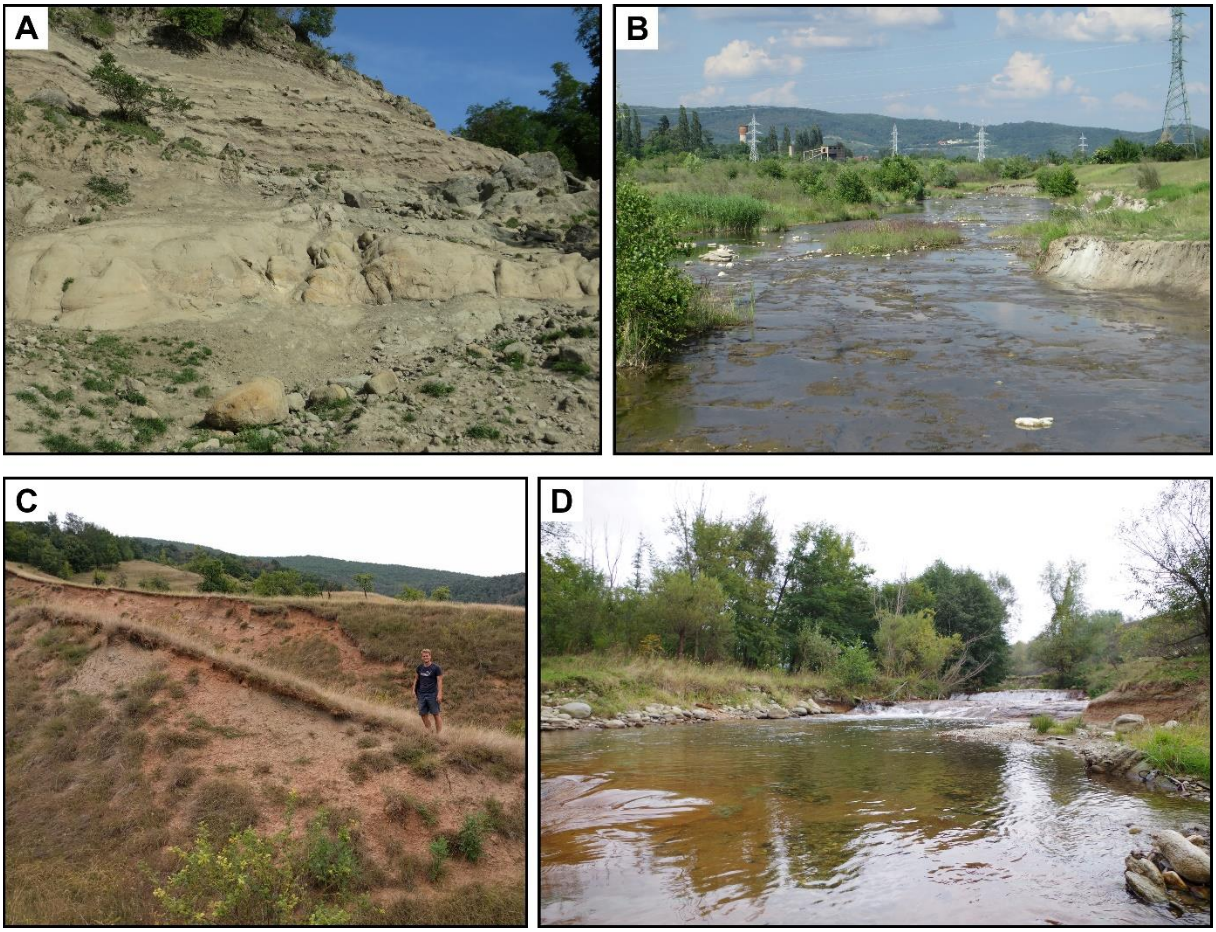

Figure 8. Outcrops of the different Upper Cretaceous units of the Haţeg Basin. **A**, The western side of the Sibişel Valley section (Sînpetru Formation), close to the entrance of the valley near Sânpetru in the south-central part of the basin. Photo by L. Eger. **B**, The Râul Mare River section (for stratigraphic relationships, see text), near Nălaţ-Vad in the central part of the basin. Photo by L. Eger. **C**, Outcrops near the village of Livezi (Densuş-Ciula Formation) in the northwestern part of the basin, northwest of Tuştea. Photo by A. Daranyi. **D**, Bărbat River Valley section (for stratigraphic relationships, see text), near Pui in the southeastern part of the basin. Photo by C. Dietzel.

Originally discovered at the beginning of the 20th century (Nopcsa, 1905), systematic excavations near Nălaţ-Vad and Totești have only relatively recently been conducted (Codrea et al., 2002; Smith et al., 2002). However, since then, the Râul

Mare River section has yielded one of the most diverse vertebrate assemblages from the Haţeg Basin, including amphibians, squamates, turtles, crocodyliforms, pterosaurs, non-avian dinosaurs, birds and multituberculate mammals as well as dinosaur eggs (Codrea et al., 2002; Smith et al., 2002; Godefroit et al., 2009; Csiki et al., 2010a; Wang et al., 2011a; Csiki-Sava et al., 2016; Brusatte et al., 2017; Mayr et al., 2020). As is often the case in the Haţeg Basin, the vertebrate remains from the Râul Mare River section mostly occur as isolated finds but sometimes also in local accumulations or fossil pockets (see above). In the latter case, the bones are occasionally associated or articulated, an example for this being the holotype specimen of the titanosaur *Paludititan* (Csiki et al., 2010a). Moreover, the braincase specimen studied for this dissertation, UBB NVZ1-42, was found in such a fossil pocket together with numerous disarticulated bones referred to a single individual of the rhabdodontid *Zalmoxes shqiperorum* (Godefroit et al., 2009). Although the specimens from this fossil pocket have been suggested to almost exclusively belong to this one individual of *Z. shqiperorum*, at least one undisputed hadrosauroid element (a left quadrate assigned to *Telmatosaurus*) has been recovered as well, demonstrates the presence of one more taxon in this fossil pocket (Godefroit et al., 2009).

1.3.3. The ‘Pui Beds’

The braincase specimen LPB (FGGUB) R.2070, which was studied in the course of this dissertation (see below), was found in uppermost Cretaceous strata near Pui, in the eastern part of the Haţeg Basin. In this part of the basin, continental Upper Cretaceous sedimentary rocks are exposed in and along the Bărbat River Valley (Fig. 8). Here, the uppermost Cretaceous sedimentary rocks comprise red mudstones and grey-greenish sandstones with interspersed dark-grey mudstone layers (Van Itterbeeck et al., 2004; Therrien, 2005; Csiki-Sava et al., 2016). The depositional environment has been reconstructed as a meandering river floodplain, while the climate during the time of deposition was likely seasonal and semi-arid (Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005; Csiki-Sava et al., 2016). As is the case for the Râul Mare River section, the lithostratigraphic relationships of the deposits from the Bărbat River Valley are contentious. Previously, these strata have been assigned to the Sînpetru Formation (Nopcsa, 1905; Mamulea, 1953a; Grigorescu, 1992) or to a separate unit that has been informally named the 'Bărbat Formation' (Therrien, 2005) or the Pui Beds' (Csiki-Sava et al., 2016, 2018). Irrespective of the precise lithostratigraphic relationships of the Bărbat River Valley section, the age of these strata has been confined to the early–late Maastrichtian boundary based on palynostratigraphy (Van Itterbeeck et al., 2005). The vertebrate assemblage from Pui includes fishes, amphibians, squamates, turtles, crocodyliforms, azhdarchid pterosaurs, rhabdodontid and hadrosauroid ornithopods, titanosaurs, coelurosaurian theropods and kogaionid multituberculates (Rădulescu and Samson, 1986; Grigorescu et al., 1999; Csiki et al., 2005; Folie and Codrea, 2005; Codrea and Solomon, 2012; Smith and Codrea, 2015; Vremir et al., 2015b; Solomon et al., 2016; Venczel and Codrea, 2016, 2019; Csiki-Sava et al., 2018; Vasile et al., 2019). Although isolated vertebrate remains dominate the sample, associated and even articulated remains are comparatively common in these deposits (Csiki et al., 2010c; Csiki-Sava et al., 2018), which includes, among others, the partial skull described here, LPB (FGGUB) R.2070 (see below).

Tab. 2. Overview of the uppermost Cretaceous continental deposits of the Haţeg Basin.

Occurrence/ distribution	Outcrops	Formation	Age	Lithology	Depositional environment
South-central Haţeg Basin	Sibişel River Valley	Sînpetru Formation	early–‘middle’ Maastrichtian	coarse-grained and fine-grained layers arranged in multiple fining-upward sequences	poorly channelized alluvial plain drained by braided river systems
South-east Haţeg Basin	Bărbat River	Sînpetru Formation? Distinct unit? (‘Pui Beds’, ‘Bărbat Fm.’)	‘middle’ Maastrichtian	red mudstones and grey-greenish sandstones with interspersed dark-grey mudstone layers	meandering river floodplain
Central Haţeg Basin	Râul Mare River	Sînpetru Fm.? Densuş-Ciula Fm? Distinct unit? (unnamed)	‘middle’–late Maastrichtian	mainly fine-grained, dark-grey floodplain deposits and lenticular channel sandstones	meandering river floodplain with freshwater ponds
North-west Haţeg Basin	various	Densuş-Ciula Formation	early–late Maastrichtian	reddish to greyish sandstones and conglomerates, variegated mudstones, volcanoclastics	alluvial fans and plains with channel and floodplain deposits

1.4. Dortokid turtles

The Dortokidae is an endemic family of turtles, known exclusively from the Lower Cretaceous to lower Eocene of Europe (Lapparent de Broin et al., 2004; Cadena and Joyce, 2015; Pérez-García et al., 2017). The phylogenetic relationships of the family are poorly understood but they probably represent basally-branching members of the Pan-Pleurodira (Lapparent de Broin et al., 2004; Gaffney et al., 2006; Rabi et al., 2013; Cadena and Joyce, 2015). Currently, the Dortokidae includes at least two different genera and four species, all of which are known from postcranial remains only (see below). In general, dortokids are relatively small pleurodires, with a carapace length of approximately 20 cm in the largest members. Moreover, dortokids are highly autapomorphic and one of the key features characterising the family being primarily characterised by their peculiar micro-reticulate shell ornamentation. Based on the overall morphology of their shells and their taphonomy, they have been hypothesized to represent semiaquatic to aquatic freshwater turtles, although direct evidence for their ecology is sparse (see below). The large majority of dortokid fossils have been recovered from Upper Cretaceous strata of northern and central Spain, southern France, eastern Austria, and western Romania (Lapparent de Broin and Murelaga, 1999; Rabi et al., 2013; Cadena and Joyce, 2015). However, the group is also known from Lower Cretaceous deposits of northeastern Spain (Pérez-García et al., 2014, 2017). Interestingly dortokid remains have also been discovered in Palaeocene and Eocene deposits of Romania (Lapparent de Broin in Gheerbrant et al., 1999; Vremir, 2013), demonstrating that the clade Dortokidae survived the end-Cretaceous mass extinction, which, in turn, allows potential insights into the selection and survival mechanisms across the K-Pg boundary. In the section to follow, a brief overview of the taxonomy and phylogenetic relationships, as well as the palaeoecology of the Dortokidae is presented.

1.4.1. The taxonomic history of the Dortokidae

The eponymous *Dortoka vasconica* (Fig. 9) was the first dortokid taxon described (Lapparent de Broin and Murelaga, 1996). The holotype of this taxon consists of a partial shell comprising the anterior part of the carapace and plastron, and has been found at the uppermost Cretaceous (late Campanian) deposits at Laño, northern Spain (Lapparent de Broin and Murelaga, 1996). In same publication, Lapparent de Broin and Murelaga (1996) also erected the family Dortokidae. Numerous additional shell elements (>460 specimens in total) of *D. vasconica* are known from the type locality, together covering a large part of the shell (Lapparent de Broin and Murelaga, 1996, 1999). Aside from shell elements, the type locality also yielded several pelvic elements as well as isolated cervical and caudal vertebrae, which could not be assigned to any of the other local turtle taxa and thus were referred to *D. vasconica* (Lapparent de Broin and Murelaga, 1996, 1999). Further material that has been referred to *Dortoka* sp. comes from the Upper Cretaceous (Campanian–Maastrichtian) of southern France (Lapparent de Broin and Murelaga, 1996, 1999). Interestingly, dortokid remains are much rarer in southern France than at the type locality (Lapparent de Broin et al., 2004: p. 206). Abundant new material of *D. vasconica* from the type locality was described by Pérez-García et al. (2012), which demonstrates a high degree intraspecific variability and the presence of two morphotypes of the plastron, the latter perhaps indicating sexual dimorphism in this species (Pérez-García et al., 2012), a hypothesis later reinforced by incorporating a more extensive comparative framework (Guerrero and Pérez-García, 2021). Recently, *Dortoka vasconica* has also been reported from the Upper Cretaceous (late Campanian) of Armuña, central Spain, based on several isolated carapacial and plastral elements (Pérez-García et al., 2016), as well as from the Upper Cretaceous (Campanian) of Cruzy, southern France, based on an isolated first costal (Tong et al., 2022), representing the only two definitive occurrences of this species besides Laño.

A second dortokid, named *Ronella botanica* (Fig. 9), was described a few years after *Dortoka* and was based on a partial plastron and pubis from the upper Paleocene of northwestern Romania (Lapparent de Broin in Gheerbrant et al., 1999). The type specimen was discovered in the botanical garden of the city Jibou (hence the species name), where it was found in the lacustrine Rona Limestone that belongs to the upper Paleocene (Thanetian) Jibou Formation (Lapparent de Broin in Gheerbrant et al., 1999; Lapparent de Broin et al., 2004). Additional material of *Ronella botanica* from the type locality was described later including a nearly complete carapace and plastron, as well as the posterior half of a carapace and plastron, among other more fragmentary shell and pelvic elements (Lapparent de Broin et al., 2004). More recently, Vremir (2013) described a costal bone fragment from the Eocene (Ypresian) of the Şimleu Basin, northwestern Romania, that he referred to cf. *Ronella botanica* because of its microreticulate shell ornamentation (typical for dortokids, see above), which is relatively weakly developed and most closely resembles *R. botanica* in this respect. However, as also noted by Vremir (2013), the assignment of the costal is not conclusive and thus, for the time being, unambiguous remains of *Ronella botanica* have only been reported from the type locality. In their review of the fossil record of dortokids, Cadena and Joyce (2015) referred *R. botanica* to the genus *Dortoka* and accordingly regarded *Ronella* as a junior synonym of the latter, because the two taxa differ only in minor features of the shell morphology – a view followed for the description of specimen LPB (FGGUB) R.2297 (see below, and Augustin et al., 2021). However, this view has not been accepted by some subsequent studies (Pérez-García et al., 2017; Tong et al., 2022).

Eodortoka morellana (Fig. 9) represents the third named member of the Dortokidae. This taxon is exclusively known from Lower Cretaceous (late Barremian) Arcillas de Morella Formation of northeastern Spain, and solely from the Mas de la Parreta Quarry (Pérez-García et al., 2014, 2017). The holotype of this taxon consists of a left hyoplastron, but additional shell material has been assigned to it, including several carapacial and plastral elements (Pérez-García et al., 2014). Due to the fragmentary material assigned to *Eodortoka morellana*, Cadena and Joyce (2015) have considered the taxon as a nomen dubium, pending the discovery and description of more complete and diagnostic specimens. Although *Eodortoka* is the first dortokid taxon from deposits younger than Late Cretaceous, the presence of dortokids in the Lower Cretaceous has been established before. During the late 1990s, shortly after the recognition of the family by Lapparent de Broin and Murelaga (1996), several fragmentary shell elements from the Lower Cretaceous (Barremian) of Vallipón have been referred to an indeterminate dortokid (Murelaga Bereikua, 1998). Following the description of *Eodortoka*, an indeterminate dortokid has been reported from the Lower Cretaceous (Hauterivian–Barremian) El Castellar Formation, representing the oldest record of the family Dortokidae so far (Pérez-García et al., 2017).

Aside from these taxa, additional indeterminate dortokids have been reported from the Upper Cretaceous of Central and Eastern Europe. Three isolated costals from the Upper Cretaceous (lower Campanian) Grünbach Formation (Gosau Group) of Muthmannsdorf, eastern Austria, were described by Rabi et al. (2013) and referred to Dortokidae indet. In addition, several isolated carapacial and plastral elements from Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút, western Hungary, are also referable to indeterminate dortokids (Ősi et al., 2012b; Rabi et al., 2013). The referral of these elements to the Dortokidae was mostly based on the characteristic microreticulate shell ornamentation of the clade, but a more precise taxonomic assignment of the material has to await the discovery of more complete specimens. Generally, the post-Barremian/pre-Santonian record of dortokids (i.e., younger than *Eodortoka* but older than the material from Iharkút) is extremely sparse and so far, the only purported evidence for the group during this time interval are two isolated pelvic bones from the early Late Cretaceous (early Cenomanian) paralic deposits of Charentes, western France that have been referred to cf. Dortokidae (Vullo et al., 2010).

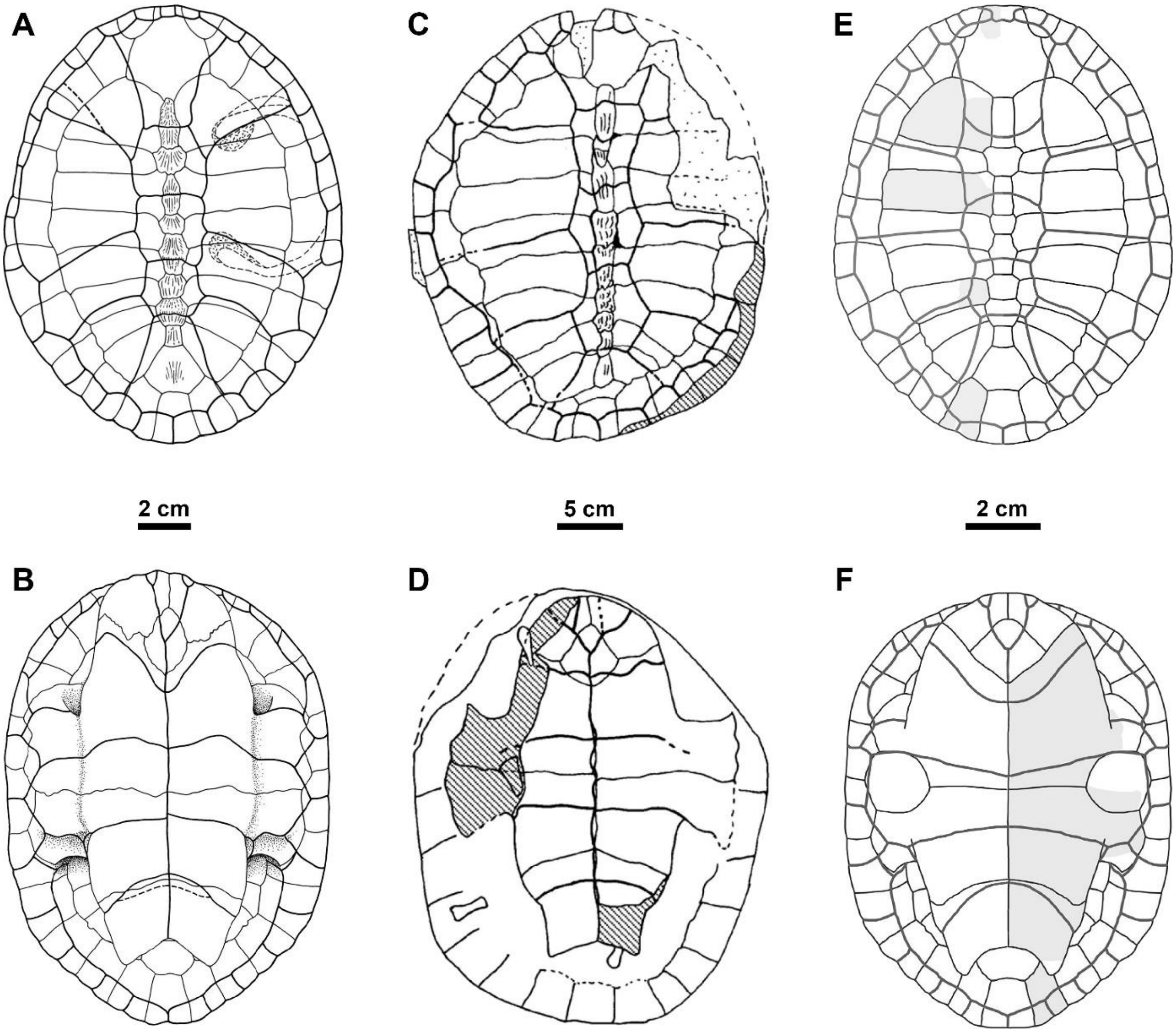

Figure 9. Anatomy of the Dortokidae. **A–B**, Drawing of the carapace (A) and plastron (B) of *Dortoka vasconica* in dorsal and ventral view, respectively. Modified after Lapparent de Broin and Murelaga (1999). **C–D**, Drawing of the carapace (C) and plastron (D) of *Dortoka* (=*Ronella*) *botanica* in dorsal and ventral view, respectively. Modified after Lapparent de Broin et al. (2004). **E–F**, Drawing of the carapace (E) and plastron (F) of *Eodortoka morellana* in dorsal and ventral view, respectively (preserved parts in grey). Modified after Pérez-García et al. (2014).

The presence of dortokid turtles in the Upper Cretaceous deposits of the Transylvanian region was first recognised by Vremir (2004), who reported on fragmentary remains from the uppermost Cretaceous (Maastrichtian) of the Transylvanian Basin. Subsequently, a new dortokid genus and species, '*Muehlbachia nopcsai*', was erected for material collected from several localities of the Transylvanian Basin, all belonging to the Sebeș Formation (upper Campanian to Maastrichtian), as well as from Pui of the southeastern Haţeg Basin (Vremir and Codrea, 2009). The designated holotype of '*Muehlbachia nopcsai*' consists of a partial plastron and associated carapacial elements from the lower part of the Sebeș Formation (lower Maastrichtian) near Vurpăr in the Transylvanian Basin (Vremir and Codrea, 2009). The first description of ‘*Muehlbachia nopcsai*’, based on the holotype and referred specimens, was provided by Vremir (2010). However, this taxon was later shown to be a nomen nudum, as it was named in an abstract volume (Vremir and Rabi, 2011). A new and well-preserved partial shell of a dortokid turtle, LPB (FGGUB) R.2297, from the Sînpetru Formation of the south-central Haţeg Basin was reported by Vremir and Rabi (2011) but not described. Rabi et al. (2013) described additional dortokid material from different uppermost Cretaceous (Maastrichtian) formations of the Haţeg and Transylvanian basins and assigned them to a new, unnamed dortokid genus and species (‘Dortokidae gen. et sp. nov.’). The best-preserved dortokid specimen from the Upper Cretaceous of Romania, LPB (FGGUB) R.2297, was studied for this dissertation (see below), and referred to a new species (Augustin et al., 2021).

1.4.2. The phylogenetic relationships of the Dortokidae

Ever since the first description of a dortokid (*Dortoka vasconica*) and the recognition of the family Dortokidae in the same paper, they were assigned to the Pleurodira (Lapparent de Broin and Murelaga, 1996). More specifically, Lapparent de Broin and Murelaga (1996) considered *Dortoka* to be the sister-group to either Eupleurodira or Pelomedusoides, i.e., within the clade Eupleurodira (sensu Gaffney et al., 2006). Shortly thereafter, the relationships of *Dortoka* were explored within the framework of a phylogenetic analysis for the first time (Lapparent de Broin and Murelaga, 1999). In the preferred cladogram of Lapparent de Broin and Murelaga (1999), *Dortoka* is placed within Eupleurodira (sensu Gaffney et al., 2006) and recovered in a sister-group relationship with Pelomedusoides, confirming their earlier assessment. The phylogenetic position of the Dortokidae (at this time only including *Dortoka* and *Ronella*) was again assessed by Lapparent de Broin et al. (2004) based mainly on the morphology of the cervical vertebrae, concluding that dortokids are best regarded as pleurodires outside of Eupleurodira. In their classic monograph on the evolution of pleurodires, Gaffney et al. (2006) explored the phylogenetic relationships of Pleurodira using an extensive dataset that included also dortokids (i.e., *Dortoka vasconica* but not *Ronella botanica*, the only other dortokid known at the time). In this analysis, *Dortoka* was found to be a basal pleurodire and the sister-group to Eupleurodira (i.e., Pelomedusoides + Chelidae), and as such, was placed in the newly erected clade Megapleurodira (Gaffney et al., 2006). At the same time, however, Gaffney et al. (2006) cautioned that, due to the lack of any skull material, the phylogenetic relationships of dortokids are not entirely clear. Nevertheless, since then, the Dortokidae has been universally recovered as a group of stem-pleurodires (i.e., a member of Pan-Pleurodira sensu Joyce et al., 2004, 2021) by subsequent phylogenetic analyses (Fig. 10) (e.g., Ferreira et al., 2018; Hermanson et al., 2020).

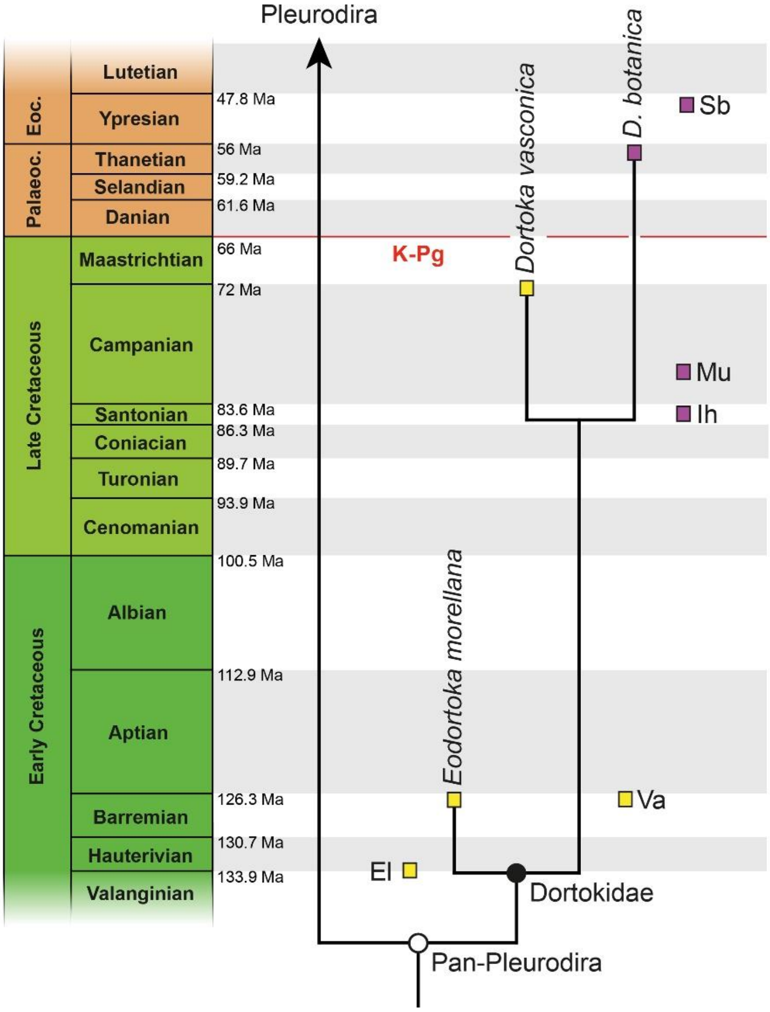

Figure 10. Phylogenetic relationships and temporal distribution of the Dortokidae. The relationships within Dortokidae follow Pérez-García et al. (2017). The relationships of the indeterminate dortokids have not yet been explored by a phylogenetic analysis, and thus they are not included in the cladogram; however, their position next to certain clades indicates proposed close relationships based on morphological grounds (for details, see text). The colour of the boxes denotes their distribution (yellow for Western Europe, purple for Eastern Europe). **Abbreviations: El**, Indeterminate dortokid from the Lower Cretaceous of El Castellar, Spain; **Ih**, Indeterminate dortokid from the Upper Cretaceous of Iharkút, Hungary; **Mu**, Indeterminate dortokid from the Upper Cretaceous of Muthmannsdorf, Austria; **Sb**, Indeterminate dortokid from the lower Eocene of the Şimleu Basin, Romania; **Va**, Indeterminate dortokid from the Lower Cretaceous of Vallipón, Spain.

The in-group relationships of the Dortokidae were first assessed by Lapparent de Broin et al. (2004). According to these authors, the Early Cretaceous Vallipón dortokid shares certain derived features with *Dortoka vasconica* and thus they might together form a lineage distinct from the Paleocene *Dortoka* (= *Ronella*) *botanica* (Lapparent de Broin et al., 2004). Subsequently, the in-group relationships of the Dortokidae were examined in some detail by Rabi et al. (2013), who suggested that the dortokid(s) from the Maastrichtian strata of the Haţeg and Transylvanian basins (‘Dortokidae gen. et sp. nov.’), as well as the dortokids from the lower Campanian Grünbach Formation of Muthmannsdorf (Austria) and the Santonian Csehbánya Formation of Iharkút (Hungary), are closer related to each other than to the western European dortokids. Accordingly, there were two distinct lineages of dortokids, one with an eastern European distribution and the other with a western European distribution, indicating biogeographical separation between both regions during the Cretaceous (Rabi et al., 2013). The relationships of *Dortoka* (= *Ronella*) *botanica* from the upper Paleocene (Thanetian) Jibou Formation of northwestern Romania were not explored by these authors (Rabi et al., 2013). In their description of the Early Cretaceous *Eodortoka,* Pérez-García et al. (2014) considered this taxon to be the most primitive member of the family Dortokidae and the sister-taxon to all other dortokids. The first, and so far only (but see below), phylogenetic analysis of the in-group relationships of dortokids was conducted several years later and included *Dortoka vasconica*, *Dortoka* (= *Ronella*) *botanica*, and *Eodortoka morellana* (Pérez-García et al., 2017). This analysis recovered *Eodortoka* in a basal position within Dortokidae, i.e., in a sister-taxon relationship with the clade comprising *D*. *vasconica* and *D.* (= *Ronella*) *botanica* (Pérez-García et al., 2017). The indeterminate dortokids from the Lower Cretaceous of Spain as well as from the Upper Cretaceous of Austria and Hungary were not included in the phylogenetic analysis. However, Pérez-García et al. (2017) noted that the indeterminate dortokid from Vallipón and those from Iharkút and Muthmannsdorf are likely more derived than *Eodortoka* (Fig. 10).

1.4.3. The palaeoecology of the Dortokidae

Several hypotheses regarding the palaeoecology of dortokids have been put forward since the 1990s. The first to speculate about the preferred habitat of dortokids were Lapparent de Broin and Murelaga (1996), who considered *Dortoka vasconica* as a freshwater turtle. Some years later, the same authors noted that *D. vasconica* is morphologically similar to the extant pleurodires *Pelomedusa* and *Pelusios*, both of which are semiaquatic freshwater turtles capable of estivation during the dry season (Lapparent de Broin and Murelaga, 1999). Based on the taphonomy of the turtle remains at Laño, it was suggested that *D. vasconica* might have lived relatively close to the shore and was not a particularly good swimmer compared to, for example, the bothremydid pleurodire *Polysternon* that was also found at Laño (Lapparent de Broin and Murelaga, 1999). In addition, Lapparent de Broin and Murelaga (1999) noted that *D. vasconica* was a continental turtle and not capable of crossing sea barriers. Subsequently, the palaeoecology of *D. vasconica* was re-evaluated in light of new material from Laño (Pérez-García et al., 2012). The presence of a large pair of fontanelles in the carapace of *D. vasconica*, which are also found in adult individuals, is a feature typically present in more aquatic turtles (Pérez-García et al., 2012). The analysis of the shell bone microstructure of *D. vasconica* corroborated this hypothesis, revealing similar compactness values to aquatic tetrapods (Pérez-García et al., 2012). Both the presence of fontanelles and the shell bone microstructure led Pérez-García et al. (2012) to conclude that *D. vasconica* was more aquatic than previously recognised. The high abundance of *D. vasconica* at Laño, as well as the unusually high degree of intraspecific variability of its shell morphology, could indicate especially favourable environmental and ecological conditions for this taxon at Laño (for considerations on the palaeoecological implications of intraspecific shell variability in turtles, see Matzke and Maisch, 2004).

Rabi et al. (2013) investigated the palaeoecology of dortokids and other turtles from the Upper Cretaceous of Central and Eastern Europe, based mainly on the relative abundances of taxa in different sedimentary facies. According to this survey, dortokids appear to be most common in sedimentary rocks deposited by relatively low hydrodynamic conditions, typically present in, for example, ponds, slow-flowing creeks, swamps, and oxbow lakes on floodplains (Rabi et al., 2013). Based on this distribution pattern and the comparatively small size of dortokids, Rabi et al. (2013) suggested that dortokids probably inhabited quieter water bodies. In contrast, *Kallokibotion*, the only other turtle taxon currently known from the Upper Cretaceous of Romania, is more common in overbank deposits and in palaeosoils indicating a more terrestrial lifestyle (Rabi et al., 2013). A semi-terrestrial lifestyle in *Kallokibotion* is also indicated by several anatomical features such as the high and domed shell or the dorsoventrally expanded skull (Rabi et al., 2013), as well as by its neuroanatomy (Martín-Jiménez et al., 2021). Interestingly, it was noted by these authors that the supposedly semi-terrestrial *Kallokibotion* and dortokids seem to never co-occur in the same horizon, even when occurring at the same outcrop. Generally, dortokids occur in a broad range of depositional settings and aside from strictly continental deposits, their remains have also been found in sedimentary rocks laid down on coastal plains and in near-marine settings (e.g., Muthmannsdorf, see Rabi et al., 2013; Armuña, see Pérez-García et al., 2016). Additionally, a purported indeterminate dortokid (from the Cenomanian of Charentes, see above) has been found in paralic deposits (Vullo et al., 2010). So far, most palaeoecological considerations have focused on the preferred habitat of dortokids, while other aspects are difficult to address due to the incomplete understanding of their anatomy. A good example of this is the diet of dortokids, which is completely unknown and currently impossible to assess owing to the lack of any cranial remains referable to this family.

1.5. Rhabdodontid dinosaurs

Among the various dinosaur groups that inhabited the Late Cretaceous European Archipelago, the Rhabdodontidae is one of the most important, because these animals seem to have been exceptionally common – in fact, no group of medium-sized vertebrates is more abundant in the Upper Cretaceous deposits of Europe. Interestingly, unquestionable remains of rhabdodontids are currently only known from Upper Cretaceous (i.e., Santonian and younger) strata of Europe and accordingly, the clade appears to have been endemic to the Late Cretaceous European Archipelago (Bunzel, 1871; Nopcsa, 1902a; Weishampel et al., 2003; Ősi et al., 2012a; Godefroit et al., 2017; Párraga and Prieto-Márquez, 2019). A potential Lower Cretaceous rhabdodontid from northern Spain, the unnamed 'Vegagete ornithopod', has been described recently and referred to the clade (Dieudonné et al., 2016, 2020; Yang et al., 2020), but according to a subsequent assessment, it might instead be a close relative of the Rhabdodontidae (Dieudonné et al., 2021). Within Ornithopoda, the Rhabdodontidae has consistently been found to be a basal clade of iguanodontians (see below), which, combined with their fossil record being limited to the Late Cretaceous, results in a particularly long ghost lineage. In general, rhabdodontids are small- to medium-sized, probably bipedal animals characterised by a rather stocky build, with strong hind limbs, short forelimbs, a long tail and a comparatively large, triangular skull that tapers anteriorly and ends in a pointy snout (Fig. 11). Currently, nine species within six genera of rhabdodontids have been described (see below), which have been found in southern France, northern Spain, eastern Austria, western Hungary and western Romania. The uppermost Cretaceous deposits of the Haţeg Basin – as well as other, roughly coeval strata from Transylvania – have yielded one of the best records for rhabdodontids, and, until very recently, all of this material has been referred to the genus *Zalmoxes*. However, research conducted in the course of this dissertation has shown that at least one more rhabdodontid inhabited the 'Haţeg Island' during the latest Cretaceous (Augustin et al., 2022). In the following section, a brief overview of the taxonomy, the phylogenetic relationships, and the palaeoecology of the Rhabdodontidae is presented.

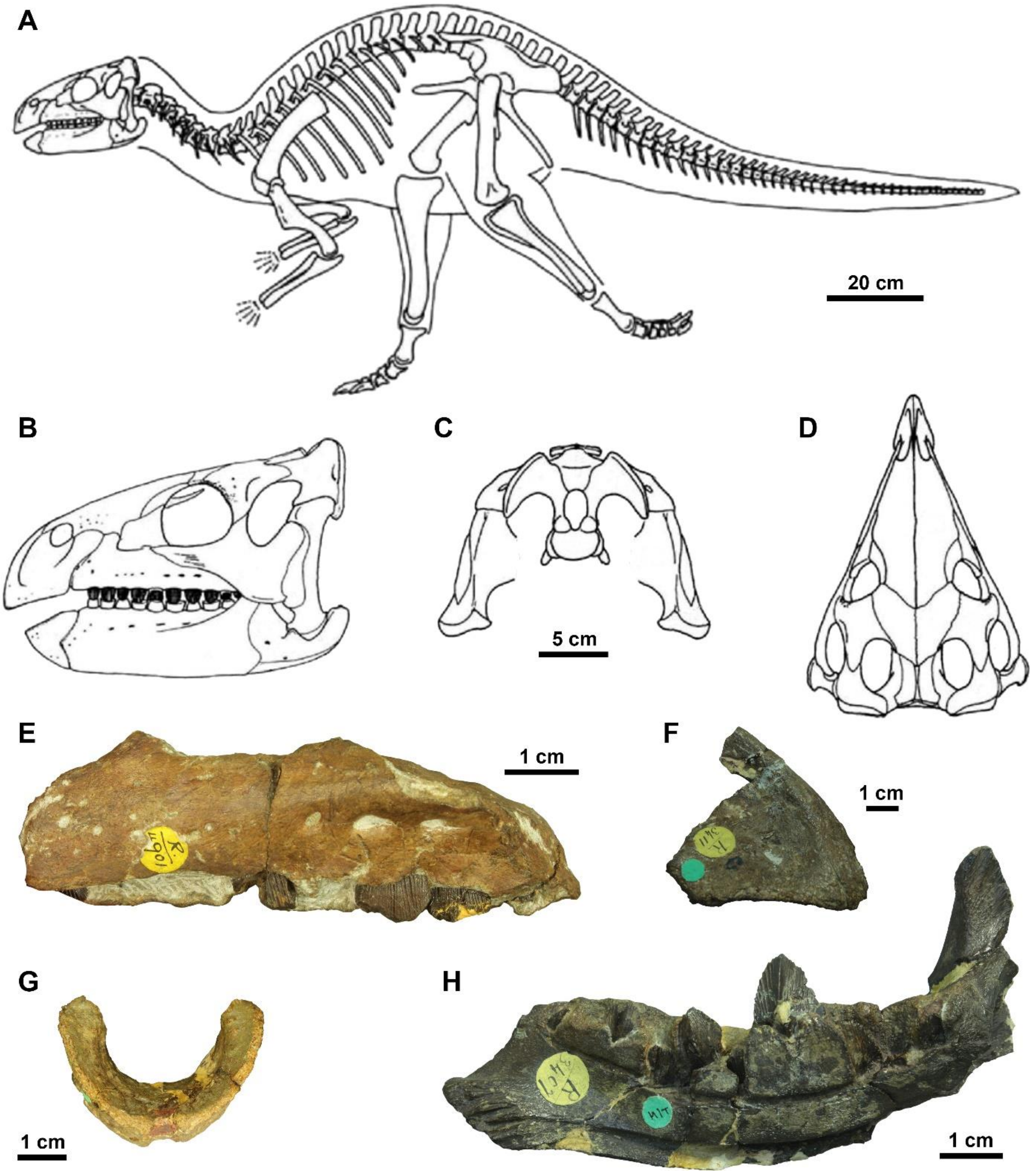

Figure 11. Anatomy of the Rhabdodontidae. **A**, Skeletal reconstruction of *Zalmoxes robustus*. Modified after Weishampel et al. (2003). **B–D**, Skull reconstruction of *Z. robustus* in left lateral view (B), posterior view (C), and dorsal view (D). Modified after Weishampel et al. (2003). **E**, Maxillary of *Z. robustus* (NHMUK R.4901) in medial view. **F**, Premaxillary of *Z. robustus* (NHMUK R.3411) in right lateral view. **G**, Predentary of *Z. robustus* (NHMUK R.3410) in dorsal view. **H**, Right dentary of *Z. robustus* (NHMUK R.3407) in medial view. All specimens figured (i.e., E-F) are historical Nopcsa specimens from his Quarry 1 (for details, see text). Photos kindly provided by J. Magyar.

1.5.1 The taxonomic history of the Rhabdodontidae

The first rhabdodontid that was scientifically described and which later served as the basis for the name of the family is *Rhabdodon priscum* (later amended to *R. priscus* by Brinkmann, 1986) from the uppermost Cretaceous (Campanian–middle Maastrichtian) of France (Matheron, 1869). Initially based on a fragmentary dentary and some postcranial elements, *Rhabdodon* is now known from numerous specimens from southern France (Lapparent, 1947; Garcia et al., 1999; Pincemaille-Quillevere, 2002; Pincemaille-Quillevere et al., 2006; Chanthasit, 2010). Additionally, *Rhabdodon* has also been reported from the Upper Cretaceous of northeastern Spain (e.g., Pereda-Suberbiola and Sanz, 1999; Ortega et al., 2006, 2015; Pereda-Suberbiola et al., 2015). However, the referral of this material to just one species or even genus is currently debated and usually at least a second species, *R. septimanicus* from southern France, is recognised (Buffetaut and Le Loeuff, 1991b; Allain and Suberbiola, 2003; Ősi et al., 2012a). Soon after the description of *Rhabdodon*, a closely related taxon from the Upper Cretaceous (lower Campanian) of Austria was reported by Bunzel (1871), *Iguanodon suessi*, for which Seeley (1881) coined the new genus name *Mochlodon*. The material assigned to *Mochlodon suessi* comprises a right dentary, a partial parietal and fragmentary postcranial elements (Bunzel, 1871; Seeley, 1881), of which the dentary (PIUW 2349/2) was selected as the lectotype of the taxon by Sachs and Hornung (2006). Although *Mochlodon* was later synonymised with *Rhabdodon* by Nopcsa (1915), a view held up for decades (e.g. Abel, 1919; Romer, 1933, 1956; Huene, 1956; Müller, 1968; Steel, 1969; Brinkmann, 1988; Norman and Weishampel, 1990), subsequent work showed that *Mochlodon* indeed likely represents a valid genus that is distinct from *Rhabdodon* (Ősi et al., 2012a). More recently, a second species of *Mochlodon*, *M. vorosi*, was described by Ősi et al. (2012a) based on a left dentary (holotype), as well as a referred left postorbital, two right quadrates, additional dentaries, isolated teeth and postcranial elements from the Upper Cretaceous (Santonian) of Hungary. It is noteworthy that the name *Rhabdodon* was abandoned in favour of *Mochlodon* for several years during the 1980s (Bartholomai and Molnar, 1981; Weishampel and Weishampel, 1983; Milner and Norman, 1984; Norman, 1984, 1985; Weishampel, 1984; Sereno, 1986), when it was recognised that the genus name *Rhabdodon* was pre-occupied by a colubrid snake (Fleischmann, 1831). However, following the submission of a case to the ICZN (No. 2536) by Brinkmann (1986) to conserve the name for the dinosaur, *Rhabdodon* has become the valid genus name of the taxon described and named by Matheron (1869).

The first reports of basal ornithopods from the Haţeg Basin, were made by Nopcsa (1897, 1899a, 1899b) in three short notes on the geology of the region around Sânpetru ('Szentpéterfalva'), referring the material to the genera *Mochlodon* (then only known from the Upper Cretaceous of Austria) and *Camptosaurus* (known from the Upper Jurassic of the United States). Subsequently, Nopcsa (1900), in his monograph on the hadrosauroid dinosaur *Telmatosaurus* (originally named '*Limnosaurus*'), commented on three lower jaws that were found together with the type material of *Telmatosaurus* at his most prolific site, Quarry 1 (German 'Nest 1'), and which he referred to basal ornithopods. Two of these jaws were assigned to new species, *Camptosaurus inkeyi* and *Mochlodon robustum*, whereas the third was referred to *Mochlodon suessi* (see above). Despite erecting two new species and reporting the presence of a third one, Nopcsa (1900) did not figure the dentaries in this monograph and only very briefly described the element he assigned to *Camptosaurus inkeyi* in a footnote. The first thorough study of rhabdodontid material from the Haţeg Basin was published by Nopcsa (1902a). In this monograph, he described the cranial elements and synonymised *Mochlodon robustum* with *Mochlodon suessi*. Two years later, Nopcsa published a second monograph on the cranial anatomy of *Mochlodon* reporting new elements from Sânpetru (Nopcsa, 1904). In this publication, Nopcsa also re-identified the type dentary of *Camptosaurus inkeyi* as a maxilla and considered it to be a junior synonym of *Mochlodon* (Nopcsa, 1904: p. 245-246). Subsequently, Nopcsa (1905) regarded *Mochlodon robustum* as a valid species again and listed both *M. robustum* and *M. suessi* as occurring at Sânpetru (Nopcsa, 1905: p. 170). After first-hand examination of the *Rhabdodon* material from southern France described by Matheron (1869), Nopcsa (1915) synonymised *M. robustum* and *M. suessi* with *Rhabdodon priscum* and regarded the two former *Mochlodon* species as sexual variants of a single species (Nopcsa, 1915: p. 4-7). Several years later, Nopcsa published his third monograph on the rhabdodontids from the Haţeg Basin, this time describing the vertebral column and mentioning the new inventory numbers in the London collection (NHMUK), to which Nopcsa sold his collection shortly before (Nopcsa, 1925). In this third monograph, Nopcsa again noted two morphotypes within his '*Rhabdodon*' sample that he interpreted as most likely representing male and female of one species (Nopcsa, 1925), a view which he later reiterated in an article on sexual dimorphism in ornithopod dinosaurs (Nopcsa, 1929b), his last work dealing with ornithopod dinosaurs from the Haţeg Basin.

Following the work of Nopcsa, the rhabdodontids and, in fact, the whole uppermost Cretaceous vertebrate fauna from the Haţeg Basin slid into oblivion for several decades (see above). Renewed interest began to form again in the 1970s and 1980s, with systematic excavations taking place at several of Nopcsas classical sites as well as at new localities (for an overview, see Grigorescu, 2010a). As a consequence, an extensive review of the geology, taphonomy and palaeontology of the Haţeg Basin was given by Grigorescu (1983), incorporating both old and new data. Additionally, Weishampel (1991) provided an updated overview of the dinosaur fauna from the Haţeg Basin with a detailed treatment of *Rhabdodon priscus*, mainly based on the original Nopcsa specimens but also by reporting newly discovered material. A few years later, Jianu (1994) described a new dentary from Sânpetru and assigned it to *Rhabdodon priscus*. Eventually, an extensive revision of the rhabdodontid material from the Haţeg Basin, both old and new, was published by Weishampel et al. (2003), in which the authors noted several important differences between *Rhabdodon* from France and the material from Romania. Consequently, the new genus *Zalmoxes* was erected for the rhabdodontid material from Romania, containing two species, *Z. robustus* and *Z. shqiperorum*. The former represents a resurrection of Nopcsas *Mochlodon robustum* (amended to *robustus*), whereas the latter is a new species based on a partial skeleton excavated by Nopcsa. In the same publication, Weishampel et al. (2003) also formally established the family Rhabdodontidae, at that time including *Rhabdodon*, *Mochlodon* and *Zalmoxes*. During the following years, additional material referred to *Zalmoxes* was described from various parts of the Haţeg and Transylvanian basins (Brusatte et al., 2013b, 2017; Dumbravă et al., 2013; Vremir et al., 2014, 2017; Botfalvai et al., 2015). Among these newly discovered specimens, a partial skull and skeleton of *Z. shqiperorum* from Nălaţ-Vad is particularly noteworthy, as it represents one of the most complete individuals known so far (Godefroit et al., 2009).

The braincase specimen LPB (FGGUB) R.2070, which was the focus of this dissertation, has been discovered at the ‘middle’ Maastrichtian ‘Pui Beds’ of the southeastern Haţeg Basin and comprises a well-preserved and nearly complete basicranium and the associated paired frontals. Previously, this specimen was preliminarily identified as *Zalmoxes* sp. (Csiki et al., 2010c). However, detailed study of it, conducted in the course of this dissertation, has shown that it cannot be reconciled with *Zalmoxes* and instead belongs to a new and hitherto unnamed genus and species of rhabdodontid dinosaur (see below), which has been named *Transylvanosaurus platycephalus* (Augustin et al., 2022). In addition to *Rhabdodon*, *Mochlodon*, *Zalmoxes*, and *Transylvanosaurus*, the family Rhabdodontidae contains two more monospecific genera. The first of these is *Matheronodon provincialis*, which was based on a single, well preserved right maxilla from the Upper Cretaceous (late Campanian) of the Aix-en-Provence Basin in southern France (Godefroit et al., 2017). The second, *Pareisactus evrostos*, is known from a nearly complete left scapula that was discovered in the Upper Cretaceous (lower Maastrichtian) Tremp Formation (Conques Member) of northeastern Spain (Párraga and Prieto-Márquez, 2019). To date, no further material has been assigned to either *Matheronodon* nor to *Pareisactus* and thus both taxa are only known from their respective holotypes. For the taxonomic history of the Rhabdodontidae presented here, only unquestionable members of the family were considered; for other putative rhabdodontids that were, however, mostly placed outside of the Rhabdodontidae (within the more inclusive clade Rhabdodontomorpha), see below.

1.5.2. The phylogenetic relationships of the Rhabdodontidae

From the very beginning on, the close relationship between rhabdodontids and iguanodontian ornithopods was recognised. In fact, already Matheron (1869) in his initial description of *Rhabdodon* noted the similarity of this form to *Iguanodon*, as did Bunzel (1871) by assigning the rhabdodontid from Muthmannsdorf to *Iguanodon*, as the new species *I. suessi* (later placed in its own genus *Mochlodon*, see above). Nopcsa (1901) was the first to assign the rhabdodontids known at the time to a higher clade, placing *Rhabdodon* and *Mochlodon* (the latter also including the rhabdodontid material from the Haţeg Basin later to be named *Zalmoxes*) within the Hypsilophodontidae. This clade was, in turn, considered to be part of the family Kalodontidae, a newly erected, paraphyletic grouping of non-hadrosaurid ornithopods (Nopcsa, 1901). Later, Nopcsa (1902b) confirmed this assignment in his first monograph on the rhabdodontid dinosaurs from the Haţeg Basin, noting the close resemblance of this material to *Hypsilophon* from the Lower Cretaceous of England. After the examination of further cranial material, Nopcsa (1904), in his second monograph on the rhabdodontids from the Haţeg Basin, still regarded *Mochlodon* as a close relative of *Hypsilophodon*, although he noted that it also appears to be similar to *Camptosaurus* (see also Nopcsa, 1903b). His view, however, changed again several years later, when he regarded *Rhabdodon* (now including *Mochlodon* and *Zalmoxes*) as a member of the more derived Camptosauridae (Nopcsa, 1915), an opinion also expressed in his later works (Nopcsa, 1923a, 1934). During the next decades, most authors followed this classification and *Rhabdodon* was assigned to the Camptosauridae or, alternatively, to the Iguanodontidae, which, during that time, was often used as a somewhat more inclusive clade containing taxa traditionally placed within Camptosauridae such as *Camptosaurus* (Abel, 1919; Romer, 1933, 1945, 1956; Huene, 1956; Müller, 1968; Steel, 1969).

In the early 1980s, however, this view was challenged by some workers, who classified *Mochlodon* (at this time including *Rhabdodon* and the Romanian rhabdodontid material, see above) as a non-iguanodontid ornithopod (Bartholomai and Molnar, 1981), as a potential hypsilophodontid (Norman, 1985), or at least questioned its iguanodontid affinities (Weishampel and Weishampel, 1983). All of these views have in common that *Rhabdodon* was considered a more basal ornithopod than previously thought. The advent of cladistics in ornithischian systematics during the mid-1980s (Norman, 1984; Sereno, 1984, 1986; Cooper, 1985; Maryanska and Osmólska, 1985), also had a profound impact on the classification of *Mochlodon* and *Rhabdodon* within the dinosaur family tree. In the framework of these first cladistic analyses, *Mochlodon* (including *Rhabdodon*) was regarded as a dryosaurid (Milner and Norman, 1984), or as a basal member of the clade Iguanodontia (Sereno, 1986). Based on the suggested more basal position and the hypsilophodontid-like tooth morphology, Brinkmann (1988) classified *Rhabdodon* as a member of the Hypsilophodontidae. Norman (1990) rejected dryosaurid affinities of *Rhabdodon* and instead considered it to be a hypsilophodontian. In contrast, Norman and Weishampel (1990) followed Sereno (1986) and classified *Rhabdodon* as Iguanodontia incertae sedis. Similarly, Weishampel et al. (1998) and Pincemaille-Quillevere (2002) regarded *Rhabdodon* as a basal iguanodontian.

In his extensive revision of the rhabdodontid material from the Haţeg Basin, Weishampel (2003) finally erected the family Rhabdodontidae (at this time containing *Rhabdodon*, *Zalmoxes* and, provisionally, *Mochlodon*), and in their phylogenetic analysis recovered them as the sister-clade to Iguanodontia. Since then, the Rhabdodontidae has been consistently placed at the base of the iguanodontian radiation (Butler et al., 2008; McDonald, 2012; Ősi et al., 2012a; Boyd, 2015; Dieudonné et al., 2016, 2021; Bell et al., 2018, 2019; Madzia et al., 2018; Verdú et al., 2018, 2020; Yang et al., 2020; Poole, 2022). This basal phylogenetic position within Iguanodontia, combined with their fossil record being limited to the Upper Cretaceous, indicates an exceptionally long ghost lineage for rhabdodontids. Potential close relatives of the Rhabdodontidae, which might belong to the more inclusive clade Rhabdodontomorpha, are the 'Vegagete ornithopod' from the Lower Cretaceous (Barremian–Aptian) of northern Spain (Dieudonné et al., 2016), *Muttaburrasaurus* from the Lower Cretaceous (Albian) of northeastern Australia (Bartholomai and Molnar, 1981), and *Fostoria* from the Upper Cretaceous (lower Cenomanian) of eastern Australia (Bell et al., 2019). It should be noted however, that alternative positions for all of these three taxa within Iguanodontia have been suggested. The 'Vegagete ornithopod' has been proposed to be the basal-most and earliest member of the Rhabdodontidae (Dieudonné et al., 2016), a derived member of the family and the sister-taxon to *Mochlodon vorosi* (Yang et al., 2020), or, more recently, the closest outgroup of Rhabdodontidae within Rhabdodontomorpha (Dieudonné et al., 2020, 2021). *Muttaburrasaurus* is usually regarded as a basal rhabdodontomorph (Dieudonné et al., 2016, 2021; Bell et al., 2018; Madzia et al., 2018; Barta and Norell, 2021), but it has also been proposed to be a member of the Rhabdodontidae (McDonald et al., 2010; McDonald, 2012), or has been recovered as a more basal (Bell et al., 2019) or derived iguanodontian (Boyd, 2015; Herne et al., 2019). *Fostoria* on the other hand has been found to be either a basal rhabdodontomorph (Dieudonné et al., 2021) or a more basal iguanodontian (Bell et al., 2019).

In addition to the phylogenetic position of the Rhabdodontidae within Ornithopoda, the interrelationships of the different rhabdodontids have been examined as well (Fig. 12). In most previous phylogenetic analyses, *Rhabdodon* spp. from southern France and northeastern Spain has been recovered as the sister-taxon to a clade comprising *Mochlodon* spp. from Austria and Hungary and *Zalmoxes* spp. from Romania (Ősi et al., 2012a; Madzia et al., 2018; Verdú et al., 2018, 2020; Barta and Norell, 2021; Dieudonné et al., 2021). Notably, only a single phylogenetic analysis has found a closer relationship between *Rhabdodon* and *Zalmoxes* instead (Dieudonné et al., 2016). Based on the results of the phylogenetic analyses and the respective distribution pattern of the then-known rhabdodontids, the presence of two rhabdodontid lineages has been suggested, one from Western Europe and the other from Eastern Europe (Ősi et al., 2012a). The phylogenetic relationships of *Pareisactus evrostos* from northeastern Spain were explored only by a single phylogenetic analysis that found it to be the sister-taxon to *Rhabdodon priscus*, in which case it belongs to the first rhabdodontid lineage with a western European distribution (Párraga and Prieto-Márquez, 2019). *Matheronodon* from southern France has never been included in a phylogenetic analysis and thus its relationships with the other rhabdodontids remain currently unknown. A comparable 'eastern vs. western' dichotomous distribution pattern has been previously suggested for some other continental vertebrate groups as well, such as turtles (Rabi et al., 2013; Csiki-Sava et al., 2015), mammals (Csiki-

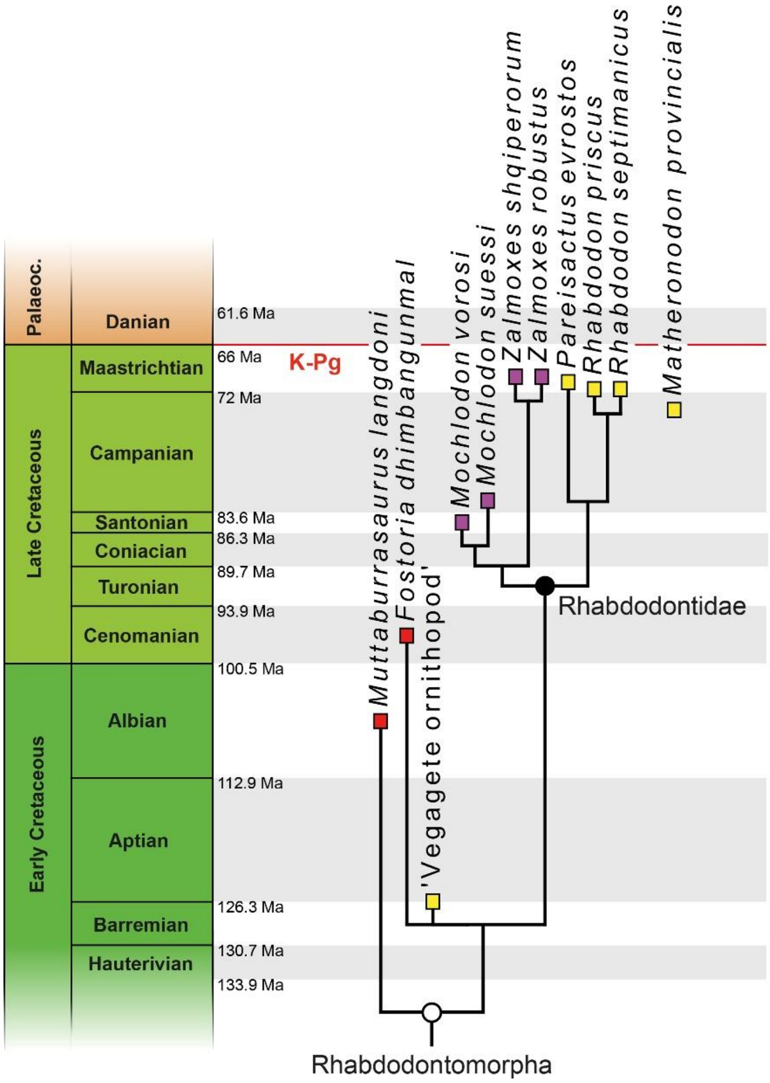

Figure 12. Phylogenetic relationships and temporal distribution of the Rhabdodontidae. The relationships within Rhabdodontidae primarily follow Dieudonné et al. (2021), as well as Párraga and Prieto-Márquez (2019) for the relationships of *Pareisactus*. The relationships of *Matheronodon* have not yet been explored by a phylogenetic analysis, and thus it is not included in the cladogram. The colour of the boxes denotes their distribution (yellow for Western Europe, purple for Eastern Europe, red for Australia).

Sava et al., 2015; Gheerbrant and Teodori, 2021) and allodaposuchid crocodyliforms (Narváez et al., 2016; Blanco and Brochu, 2017; Blanco, 2021). Such a high degree of regional faunal differences and endemism is usually linked to geographical isolation of the different islands of the Late Cretaceous European Archipelago (for an overview, see Csiki-Sava et al., 2015). However, the relationships of the new rhabdodontid dinosaur from the Haţeg Basin studied for this dissertation, *Transylvanosaurus platycephalus*, challenge this hypothesis and instead indicate a different biogeographical history of the Rhabdodontidae (see below).

1.5.3. The palaeoecology of the Rhabdodontidae

Notions about the palaeoecology of rhabdodontids have been made early on, and one of the first to hypothesise rather extensively on this topic was, again, Franz Nopcsa, who is considered one of the pioneers of dinosaur palaeobiology (Weishampel and Reif, 1984). In his detailed description of the skull anatomy of '*Mochlodon*' (i.e., *Zalmoxes*), Nopcsa (1902a) concluded that, based on tooth morphology, the movement of the jaws was only vertically and that the abrasion of the teeth indicates a scissor-like shearing action of the teeth. He was, however, not the first to propose this kind of mastication and two decades before, Seeley (1881) suggested a scissor-like chewing action based on tooth wear of *Mochlodon suessi*. In addition, Nopcsa (1914a), assumed that the sharp beak and the teeth adapted for chewing indicate that the dinosaur ate food items that were hard on the outside but soft on the inside. He further reasoned that the rhabdodontids from 'Szentpéterfalva' (= Sânpetru) were living in the same area where their remains have been found, because they are so abundant at this locality and because juveniles have been found there (Nopcsa, 1914a). Since he interpreted the deposits at Szentpéterfalva as those of a shallow freshwater swamp, he regarded the rhabdodontids as swamp dwellers (Nopcsa, 1914a), a notion that he reiterated thereafter (Nopcsa, 1915, 1923a). Contrary to Nopcsas interpretation, more recent sedimentological investigations demonstrated that the sedimentary rocks of Szentpéterfalva (i.e., the stratotype section of the Sînpetru Formation) were in fact deposited on a poorly channelised alluvial plain drained by braided river systems, which comprised dry areas, wetlands and well-drained floodplains (for details, see above).

This alternative sedimentological and palaeoenvironmental interpretation was first proposed by Grigorescu (1983), who also noted that, based on taphonomical considerations, rhabdodontids (along with hadrosaurs and turtles) were likely residents of swampy areas within this diverse palaeoenvironmental setting. Subsequently, however, an extensive survey of the taphonomy of latest Cretaceous vertebrates from the Haţeg Basin demonstrated that rhabdodontid remains are present in all different palaeoenvironmental settings recorded in the Haţeg Basin and, despite earlier claims to the contrary, are commonly found in well-drained palaeoenvironments (Csiki et al., 2010c). Therefore, these animals were almost certainly not limited to swamps or lacustrine environments as suggested before, but instead were inhabiting all palaeobiotopes represented in the deposits of the Haţeg Basin (Csiki et al., 2010c). Interestingly, rhabdodontid remains with similar taphonomic features – and thus common taphonomic histories – pertaining to several different individuals of different sizes have been found together in some bonebeds in the Haţeg Basin, suggesting that these animals might have been gregarious (Csiki et al., 2010c). A similar conclusion is suggested by the occurrence of at least six individuals of different sizes at the monotaxic Vegagete fossil locality that all belong to the 'Vegagete ornithopod', an indeterminate iguanodontian probably belonging to Rhabdodontomorpha (Dieudonné et al., 2020, 2021, 2023).

During the past decades, especially the feeding behaviour and potential diet of rhabdodontids received a great deal of attention. In his monograph on ornithopod jaw mechanisms, Weishampel (1984) described the intracranial joints in more than 50 ornithopod taxa, including '*Mochlodon*' (most specimens examined pertain to *Zalmoxes*, but a few also belong to *Rhabdodon* and *Mochlodon*). Based on the morphology and the distribution of these joints, it was concluded that the more derived ornithopods (including '*Mochlodon*') utilised a transverse power stroke to chew their food that was accomplished by the mobilization of the upper jaws (Weishampel, 1984). This kind of cranial kinesis and the associated chewing mechanism was later confirmed for *Zalmoxes* by Weishampel et al. (2003), although the authors noted a deviation from the general bauplan of derived ornithopods that probably limited the degree of intracranial mobility and might represent an adaptation to process hard food items. Apart from that, large jaw adductor muscle chambers in *Zalmoxes* coupled with the robust jaws and the well-developed coronoid process of the lower jaw are indicators of a high bite strength (Weishampel et al., 2003). Taken together with the mesiodistally enlarged teeth and the high-angled wear-surface of the teeth, these features indicate that the masticatory apparatus of rhabdodontids was adapted for powerful slicing action (Godefroit et al., 2017), an interpretation very similar to that of Seeley (1881) and Nopcsa (1902a) discussed above. Moreover, it was suggested that the relatively narrow jaw tips, which in life were most likely covered by a keratinous beak, could indicate that *Zalmoxes* was a selective feeder (Weishampel et al., 2003). Godefroit et al. (2017) further argued that the enlarged teeth of rhabdodontids (taken to the extreme in *Matheronodon* from southern France) represent an adaptation for the crushing of tough and woody or fibrous food items. Taking the palaeobotanical data of various rhabdodontid-bearing localities into consideration, Godefroit et al. (2017) hypothesised that rhabdodontids fed primarily on tough plant parts with a high sclerenchyma fibre content like the palms *Sabalites* and *Pandanites*, the former genus being known also from the Haţeg Basin (Popa et al., 2014).

Apart from cranial anatomy, two independent lines of evidence have been used to infer the feeding ecology of rhabdodontids – stable isotope analysis and multiproxy dentition analysis. Stable isotope analysis of rhabdodontid teeth from the Haţeg Basin suggested that these animals mainly ingested C3 plants (Bojar et al., 2010a). Remarkably, the similarity of the *δ*13C values between the rhabdodontid and the hadrosaur teeth from the Haţeg Basin was interpreted by Bojar et al. (2010a) to reflect the absence of large-scale habitat partitioning between the two ornithopods. Furthermore, dental microwear analysis has been applied to teeth of *Mochlodon vorosi* from Iharkút (Hungary) revealing straight and parallel micro striations that likely reflect orthal jaw movement, while the high tooth formation rates in this taxon imply an abrasive diet (Virág and Ősi, 2017). Recently, dental microwear analysis of *Mochlodon vorosi* further indicated that this animal was a low-browsing herbivore (browsing height up to 1m above ground level) that fed on particularly tough vegetation (Ősi et al., 2022). Differences in the microwear pattern of the rhabdodontid *Mochlodon vorosi* and hadrosaurs likely reflect differences in feeding ecology (Ősi et al., 2022). Despite a similar and partially overlapping browsing height in *Mochlodon* and hadrosaurs, the rhabdodontid probably fed on higher-growing plants, which were either tougher or were processed more vigorously (Ősi et al., 2022). Similarly, a different microwear pattern in the sympatric ankylosaur *Hungarosaurus* (as compared to *M. vorosi*) demonstrates different feeding strategies and niche partitioning between the two sympatric herbivorous dinosaurs, with *Hungarosaurus* probably feeding on softer plants and/or processing its fodder less intensively (Ősi et al., 2022).

In addition to the habitat preferences and feeding ecology of rhabdodontids, several remarks about their posture and locomotion have been made. In their monograph on *Zalmoxes*, Weishampel et al. (2003) noted about *Zalmoxes* that it was a medium-sized ornithopod with a comparatively stocky build. Several peculiarities of the postcranium indicated to these authors that the locomotion *Zalmoxes* differed from that of other ornithopods and that it had a particularly wide gait when walking and running. Subsequently, Dumbravă et al. (2013) reconstructed the musculature of the hind limb based mainly on the partial *Zalmoxes shqiperorum* skeleton from Nălaţ-Vad (see also Godefroit et al., 2009) and other material from this site, concluding, among other things, that the rather ventral position of the fourth trochanter on the femur indicates that *Z. shqiperorum* was not a particularly fast runner. Although rhabdodontids are mostly envisioned as bipedal animals (for *Zalmoxes*, see Weishampel et al., 1991: fig. 11, and Weishampel et al. 2003: fig. 36; for *Rhabdodon*, see Garcia et al., 1999: fig. 2; for *Mochlodon*, see Ősi et al., 2012a: fig. 15), at least *Rhabdodon* was also portrayed as quadrupedal (Pincemaille-Quillevere, 2002: fig. 1; Chanthasit, 2010: p. 121). Part of this uncertainty concerning the posture of rhabdodontids is due to the fact that complete and articulated skeletons are presently lacking (but see Vremir et al., 2017). Recently, Dieudonné et al. (2023) used several proxies for the posture of ornithopods (based on hind limb morphology) to evaluate the posture of rhabdodontomorphs. They concluded that the 'Vegagete ornithopod' and *Mochlodon vorosi* switched from quadrupedality to bipedality during ontogeny, whereas *Muttaburrasaurus* and some derived rhabdodontids of the Late Cretaceous (i.e., *Zalmoxes* and *Rhabdodon*) retained a quadrupedal posture until late in ontogeny or even into adulthood (Dieudonné et al., 2023). Moreover, based on the histology of long bones, these authors suggested that the 'Vegagete ornithopod' grew very rapidly and likely had a high basal metabolic rate (Dieudonné et al., 2023). Conversely, the bone histology of *Zalmoxes* likely indicates relatively slow growth (Benton et al., 2010).

1.6. Objectives

The Haţeg Basin has yielded one of the richest and best-known vertebrate assemblages from the entire Upper Cretaceous record of Europe (see above). Despite the large numbers of studies dealing with the latest Cretaceous vertebrates from the Haţeg Basin, there remain some open questions, especially regarding the alpha-level taxonomic diversity of certain vertebrate clades. During the last few decades, several new and as-yet largely unstudied vertebrate specimens have been discovered, which differ considerably from previously described taxa and thus can potentially yield significant new insights into the composition of the vertebrate fauna of the uppermost Cretaceous of the Haţeg Basin. Moreover, a critical re-assessment of already described material has shown that some specimens cannot be reconciled with the taxa they were originally referred to. The main goals of this thesis are threefold: first, to re-evaluate the diversity of the latest Cretaceous vertebrates from the Haţeg Basin based on four key specimens that potentially belong to new taxa, second, to reconstruct the phylogenetic and palaeobiogeographic relationships of these new taxa, and third, to reconstruct the palaeoecology of these new taxa and to detect possible niche partitioning. The four key specimens (Tab. 3) comprise two well-preserved specimens that have never been described before and almost certainly represent new taxa, as they differ considerably from previously described reported ones, and two already described specimens that are, however, very different in morphology and thus cannot be referred to the taxa they have been assigned to.

The first of these key specimens is a well-preserved partial turtle skeleton, LPB (FGGUB) R.2297, which differs completely from the only other turtle taxon previously recognised from the Haţeg Basin on the species-level – *Kallokibotion bajazidi*. The specimen instead shares numerous features with the Dortokidae, a European endemic family of pleurodirans that has been previously reported from the Upper Cretaceous of the Haţeg Basin (see above); however, all of these remains were considered indeterminate thus far. The second and third key specimens are two already described ornithopod braincases, NHMUK R.3401A and UBB NVZ1-42, which in the past years have been assigned to the rhabdodontids *Zalmoxes robustus* and *Z. shqiperorum*, respectively. However, both specimens differ significantly from all other rhabdodontid braincases reported so far and assigned to *Z. robustus* and *Rhabdodon*. Consequently, if indeed belonging to a rhabdodontid, they would probably represent a new taxon, as the morphology cannot be reconciled with that previously reported for the genus *Zalmoxes*. The fourth, and final, of these key specimens, LPB (FGGUB) R.2070, is a partial skull of an ornithopod dinosaur that shows certain similarities with *Z. robustus* and *Rhabdodon*, and thus likely belongs to a rhabdodontid. Nonetheless, it differs considerably from all rhabdodontid skulls described thus far, indicating the presence of a new rhabdodontid in the uppermost Cretaceous deposits of the Haţeg Basin. In order to evaluate the taxonomic status of these four specimens, a detailed osteological description and a thorough comparison with all other dortokids, respectively, rhabdodontids is necessary. Moreover, for the reconstruction of the phylogenetic relationships, the specimens have to be included into phylogenetic analyses. The results of these analyses, combined with the results of the comparisons, can then be used to infer the phylogenetic and, by extension, the palaeobiogeographical relationships. As a final step, the anatomy of the specimens and taphonomic considerations can offer insights into the palaeoecology and potential niche partitioning if the diversity is indeed found to be higher than previously thought.

Tab. 3. Overview of the four key specimens examined for this dissertation.

Specimen	Description	Locality	Stratigraphy	Age	Previous Assignment
LPB (FGGUB) R.2997	partial skeleton	La Cărare quarry, near Sânpetru Sibişel Valley section	Sînpetru Formation	early–'middle' Maastrichtian	Gen. et sp.es nov. Dortokidae
NHMUK R.3401A	partial braincase	Nopcsas quarry 1, near Sânpetru, Sibişel Valley section	Sînpetru Formation	early–'middle' Maastrichtian	*Zalmoxes robustus*, Rhabdodontidae
UBB NVZ1-42	basicranium	Fossil Pocket 3, near Nălaţ-Vad, Râul Mare River section	Sînpetru Fm.? Densuş-Ciula Fm.? Distinct unit?	'middle'–late Maastrichtian	*Zalmoxes shqiperorum*, Rhabdodontidae
LPB (FGGUB) R.2070	partial skull	'middle part of succession', Bărbat River Valley, near Pui	Sînpetru Fm.? Distinct unit?	'middle' Maastrichtian	*Zalmoxes* sp., Rhabdodontidae

2. RESULTS

The main results of the three papers that are included in this dissertation are summarised below. The complete papers are attached as an appendix at the end of this dissertation thesis, in their finally formatted and published version.

2.1. A new pleurodiran turtle from the Sînpetru Formation of the Haţeg Basin

The first specimen studied for this dissertation is LPB (FGGUB) R.2297 (Fig. 13), a well-preserved partial turtle skeleton comprising the majority of the carapace, the almost complete plastron and some appendicular elements preserved in situ (the right scapula and right pubis). The material was found in 1995 at the locality 'La Cărare', one of the most important fossil sites of the Sibişel Valley section (for an overview of the geological setting and the vertebrate assemblage of this locality, see above). The specimen was briefly mentioned and figured by Vremir and Rabi (2011) in a conference abstract but it has never been described in detail. A full osteological description of the specimen and a detailed comparison with all previously described dortokids can be found in Augustin et al. (2021), which is attached in the appendix. Notably, the interpretation of the osteology differs markedly from that provided by Vremir and Rabi (2011). LPB (FGGUB) R.2297 clearly belongs to the Dortokidae based on the presence of the peculiar microreticulate shell ornamentation that constitutes a widely accepted synapomorphy of the clade (Lapparent de Broin and Murelaga, 1996, 1999; Lapparent de Broin et al., 2004; Rabi et al., 2013; Pérez-García et al., 2014; Cadena and Joyce, 2015). Although dortokid turtles have been reported from the Haţeg Basin before (see above), they are not assigned to a specific taxon, and thus *Kallokibotion bajazidi* represents the only previously defined turtle species from the uppermost Cretaceous of the Haţeg Basin.

Specimen LPB (FGGUB) R.2297 closely resembles the derived dortokids *Dortoka vasconica* (Lapparent de Broin and Murelaga, 1996) and *Dortoka* (= *Ronella*) *botanica* (Lapparent de Broin in Gheerbrant et al., 1999). Additionally, it shares all of the synapomorphies of the genus *Dortoka*, i.e., the characteristic shell ornamentation of the neurals that consists of anteroposteriorly elongate grooves, the absence of a sutural contact between the first peripheral and the first costal, irregularly shaped neurals, the second pleural overlapping the first costal, and the absence of mesoplastra (Cadena and Joyce, 2015). Therefore, the specimen can be confidently assigned to the genus *Dortoka*. Nonetheless, LPB (FGGUB) R.2297 differs from both

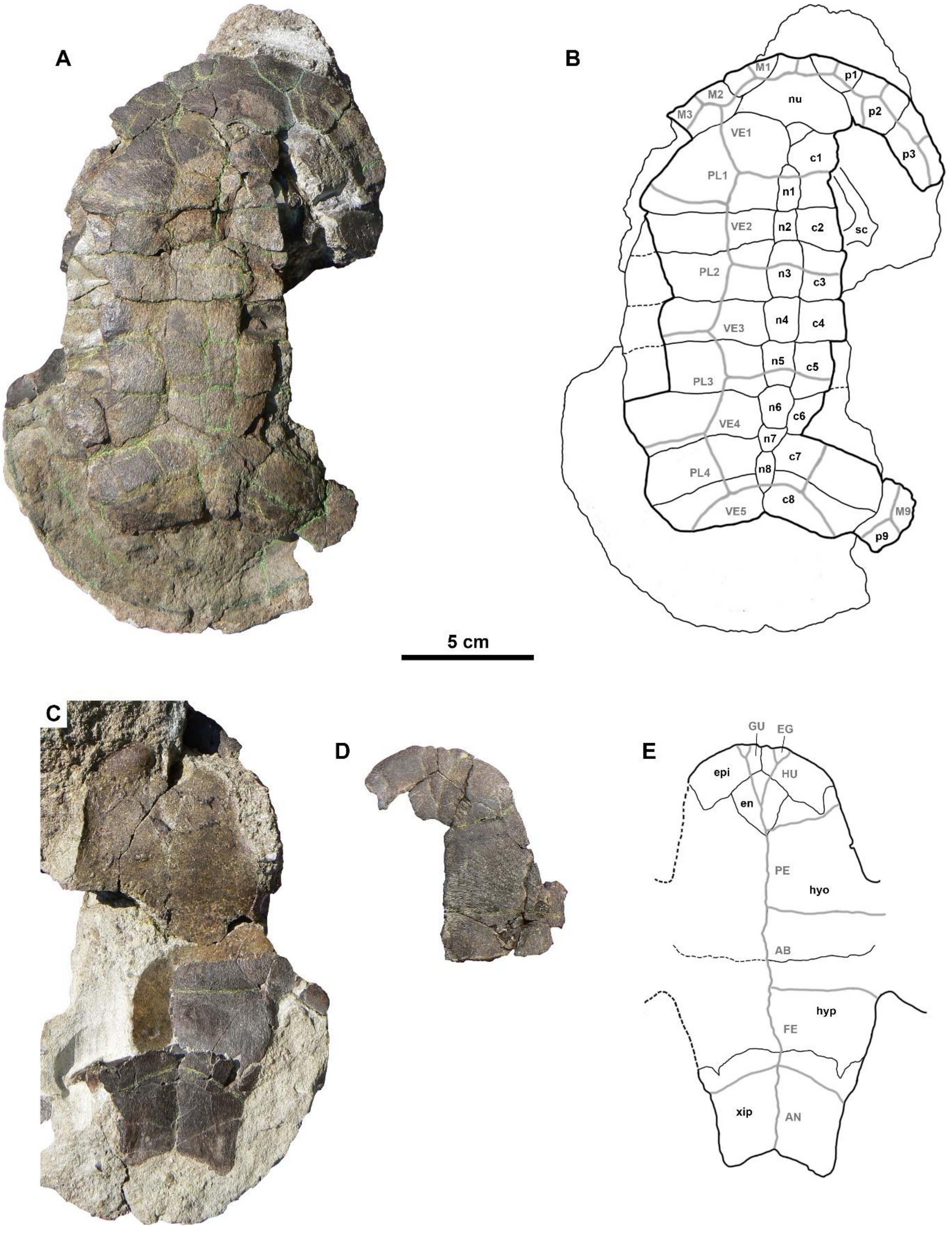

Figure 13. Holotype of *Dortoka vremiri*, LPB (FGGUB) R.2997, from the Sînpetru Formation of the Haţeg Basin. **A–B**, Photograph (A) and drawing (B) of the carapace in dorsal view. **C–E**, Photographs of the posterior part (C) and the anterior part of the plastron (D), as well as drawing of the plastron (E) in ventral view. **Abbreviations**: **AB**, abdominal scale; **AN**, anal scale; **c**, costal; **EG**, extragular scale; **en**, entoplastron; **epi**, epiplastron; **FE**, femoral scale; **GU**, gular scale; **HU**, humeral scale; **hyo**, hyoplastron; **hyp**, hypoplastron; **M**, marginal scale; **n**, neural; **nu**, nuchal; **p**, peripheral; **PE**, pectoral scale; **PL**, pleural scale; **VE**, vertebral scale; **xip**, xiphiplastron. Modified after Augustin et al. (2021).

D. vasconica and *D. botanica* in several important features and, due to these differences, is assigned to a new species, *Dortoka vremiri* (Augustin et al., 2021). *Dortoka vremiri* can be diagnosed by the following unique combination of characters (after Augustin et al., 2021): (1) a first pair of costals that meet anterior to neural 1 along a midline suture; (2) a last pair of costals that meet posterior to neural 8 along a midline suture; (3) the lack of a cervical scale, a first pair of pleural scales that is entirely restricted to the first costals; (4) a second pair of pleural scales that does not contact the fifth pair of costals; (5) the position of the sulcus between vertebrals 4 and 5 being located on the last neural; (6) a fifth vertebral that does not contact the seventh pair of costals; (7) an entoplastron being widest in the anterior third of the bone; (8) pectoral scales that contact the entoplastron; (9) small extragulars that are at least three times shorter than the gular. Several of these features are variously shared with *D*. *vasconica*, *D*. *botanica*, *Eodortoka morellana* and the indeterminate dortokids from the Csehbánya Formation of Iharkút and the Grünbach Formation of Muthmannsdorf. Moreover, three of the features listed above are only found in *Dortoka vremiri* and thus constitute potential autapomorphies of the taxon, i.e., the first pair of costals that meet anterior to neural 1, the posterior position of the sulcus between vertebrals 4 and 5 (located on the last neural), and the fifth vertebral that does not contact the seventh pair of costals.

In order to explore the phylogenetic relationships of the new taxon within Dortokidae, two sets of phylogenetic analyses were performed – a global one within Pan-Pleurodira based on the dataset of Hermanson et al. (2020), and an in-group analysis within the Dortokidae based on the dataset of Pérez-García et al. (2017). For the two analyses, several modifications to both character-taxon matrices were made including the revision of some incorrectly coded characters in the first matrix, as well as the addition of new outgroup taxa, the ordering and deletion of certain characters, and the addition of two new characters in the second matrix (for the complete set of changes to both matrices and the complete matrices, see online supplementary files of Augustin et al., 2021). Additionally, the two analyses were run with slightly different settings (for the detailed settings, see Augustin et al., 2021). The first, global analysis recovered *D*. *vremiri* within the Dortokidae at the base of Pan-Pleurodira but, unsurprisingly, was unable to resolve the relationships between the dortokids included in the analysis (i.e., *D*. *vasconica*, *D*. *botanica* and *D*. *vremiri*), which formed a polytomy. For this reason, a second analysis was performed, using the dataset of Pérez-García et al. (2017), which represents the most recent dortokid matrix specifically designed to test the relationships of the Dortokidae. The second analysis recovered *Dortoka vremiri* in a sister-taxon relationship with the Paleocene *D. botanica*, together forming the sister-clade to the Campanian–Maastrichtian *D. vasconica*, whereas the Early Cretaceous *Eodortoka morellana* was found to be the basal-most member of the family (Fig. 14). The different indeterminate dortokids (see above) were not included in the analysis. The clade comprising *D. vremiri* and *D. botanica* is supported by two synapomorphies, i.e., the first pair of pleural scales being restricted to the first pair of costals and the

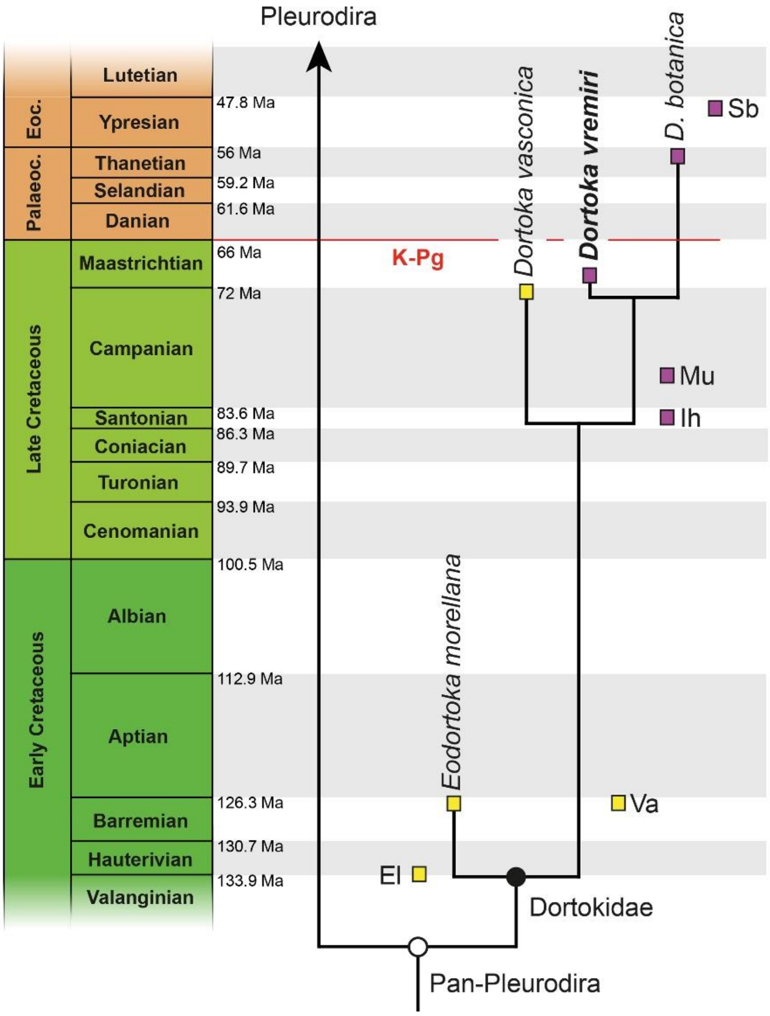

Figure 14. Phylogenetic relationships of *Dortoka vremiri* and temporal distribution of the Dortokidae. The relationships depicted are based on the results of the second phylogenetic analysis of Augustin et al. (2021). The relationships of the indeterminate dortokids have not yet been explored by a phylogenetic analysis, and thus they are not included in the cladogram; however, their position next to certain clades indicates proposed close relationships based on morphological grounds (for details, see text). The colour of the boxes denotes their distribution (yellow for Western Europe, purple for Eastern Europe). **Abbreviations: El**, Indeterminate dortokid from the Lower Cretaceous of El Castellar, Spain; **Ih**, Indeterminate dortokid from the Upper Cretaceous of Iharkút, Hungary; **Mu**, Indeterminate dortokid from the Upper Cretaceous of Muthmannsdorf, Austria; **Sb**, Indeterminate dortokid from the lower Eocene of the Şimleu Basin, Romania; **Va**, Indeterminate dortokid from the Lower Cretaceous of Vallipón, Spain. Modified after Augustin et al. (2021).

pectorals partially covering the entoplastron. The first of these is also found in the indeterminate dortokids from the Santonian of Iharkút and the Campanian of Muthmannsdorf.

The results of the second phylogenetic analysis demonstrate the presence of two distinct dortokid lineages, a western one consisting of *D. vasconica* from the Ibero-Armorican landmass (Spain and southern France), and a second lineage including *D. vremiri* and *D. botanica* from the Transylvanian landmass (western Romania). At least the latter clade also survived into the Paleogene (and potentially into the Eocene, see above). The two indeterminate dortokids from the Austroalpine landmass (i.e., from Iharkút in western Hungary and Muthmannsdorf in eastern Austria) likely belong to the second lineage as well, as indicated by the shared presence of one of the synapomorphies of the clade comprising *D. vremiri* and *D. botanica*. This dichotomous distribution pattern fits the previously recognised faunal separation between the western Ibero-Armorican landmass on the one hand, and the eastern Austroalpine and Transylvanian landmasses on the other (for other examples, see above). The sister-taxon relationship between *D. vremiri* and *D. botanica* further indicates local survival of the Transylvanian dortokids across the K-Pg boundary, as opposed to immigration from elsewhere in the Paleocene. In the Paleocene of Western Europe, dortokids are completely absent thus far, which suggests some selectivity across the K-Pg extinction event for the family. Due to the low morphological disparity of dortokids, ecological variability was probably low as well, which in turn indicates geographical selectivity. Such a geographical selectivity across the K-Pg extinction event may also have played a role in the survival of kogaionid mammals, which are found in the uppermost Cretaceous and Paleocene of Transylvania, whereas the other endemic mammal clade from the Ibero-Armorican Island (the zhelestid eutherians) apparently died out at the end of the Cretaceous. In this context, the palaeogeographic position of the more remote Haţeg Island could have been crucial in the survival of certain vertebrate groups across the K-Pg boundary.

Ecologically, dortokids have been reconstructed as semi-aquatic or aquatic freshwater turtles, based on shell morphology, bone microstructure and taphonomy (for details, see above). Based on the taphonomy, Rabi et al. (2013) noted that dortokids are most common in deposits accumulated under lower hydrodynamic conditions and seemingly never co-occur with the presumably more terrestrial turtle

Kallokibotion, thus likely inhabited quieter water bodies. In contrast to this conclusion, the holotype specimen of *Dortoka vremiri* comes from a hydrodynamically active depositional environment (see above), while other dortokid remains from the uppermost Cretaceous of Transylvania were found in well-drained floodplain deposits, sometimes even alongside *Kallokibotion* fossils. Therefore, dortokid remains are not restricted to sediments accumulated by very slowly moving waters but instead occur in a variety of depositional environments, ranging from hydrodynamically active river channels, to slow-flowing waters and ponds and well-drained floodplains. However, novel taphonomical data still indicate a semi-aquatic to aquatic lifestyle for dortokids. More specifically, a striking difference in preservation between the two turtle taxa from the Haţeg Basin likely reflect distinct ecologies for *Kallokibotion* on the one hand, and dortokids on the other. In the uppermost Cretaceous deposits of the Haţeg Basin, remains of dortokids are notably rare and, except for LPB (FGGUB) R.2297, usually occur as isolated and fragmentary elements, whereas *Kallokibotion* is known from numerous partial to near-complete shells and skeletons. Experimental work previously demonstrated that turtle carcasses decompose and disintegrate much faster when submerged in water than in terrestrial environments. In this context, the abundance of articulated *Kallokibotion* specimens suggests a preference for well-drained habitats, while the rarity of (mostly fragmentary) dortokid remains indicates a more aquatic lifestyle. Additionally, the occurrence of dortokid fossils in well-drained environments (e.g., at the Tuştea site) is best explained by post-mortem transport during flood events. In contrast to dortokids, the more terrestrial *Kallokibotion* went extinct during the K-Pg extinction event. The novel taphonomical data, combined with the local survival of dortokids in Transylvania based on the newly recognised phylogenetic relationships (see above), indicates preferential survival of freshwater versus terrestrial turtles, which agrees well with the observed patterns from other continental vertebrate assemblages (particularly those of North America).

2.2. A re-evaluation of the braincase anatomy of the ornithopods from the Haţeg Basin

For the second paper of this dissertation, two ornithopod braincase specimens were examined, NHMUK R.3401A and UBB NVZ1-42. The first of these, NHMUK R.3401A, is a historical Nopcsa specimen and was discovered by him in 'Nest 1' (Nopcsa, 1904), his most prolific locality (see above). It comprises the basioccipital, both exoccipital-opisthotic complexes, the supraoccipital, and the anterior portion of the basisphenoid-parasphenoid complex. Although Nopcsa never described nor figured the specimen, he referred it to the hadrosaur *Telmatosaurus* (see Nopcsa, 1904: tab. 1), an interpret-tation followed by Weishampel et al. (1993). Subsequently, however, Weishampel et al. (2003) re-assigned the specimen to the rhabdodontid *Zalmoxes robustus*. The latter authors also briefly described and figured specimen NHMUK R.3401A (Weishampel et al., 2003: p. 78, fig. 11). The second specimen UBB NVZ1-42 was discovered in 2002 by a joint Belgian-Romanian team near Nălaţ-Vad (Godefroit et al., 2009). The specimen preserves the basioccipital, both exoccipitals, and the basisphenoid-parasphenoid complex. Because it was preserved in a local accumulation of vertebrate fossils that mostly belong to *Zalmoxes shqiperorum*, it was referred to this taxon as well (Godefroit et al., 2009); it is noteworthy, however, that at least some hadrosaurian bones were among the recovered specimens, demonstrating that it actually represents a multitaxic assemblage (Godefroit et al., 2009). The specimen was briefly described and figured by Godefroit et al. (2009: p. 533, fig. 8). A detailed description of the two specimens, NHMUK R.3401A and UBB NVZ1-42, can be found in Augustin et al. (2023) which is attached as an appendix.

Both specimens exhibit a remarkably similar morphology that is completely different from that of other braincases referred to *Zalmoxes robustus*. More specifically, both specimens have an anteroposteriorly short basioccipital that is directly connected to two well-developed bulbous sphenoccipital tubercles (= the basal tubera) with a deep depression separating the tubercles (Fig. 15), whereas the braincase specimens referred to *Z*. *robustus* have an elongated basioccipital neck and conjoined, crest-like basal tubera that extend mediolaterally. This distinct and peculiar morphology, which is very different from that of *Z*. *robustus*, was already noted by Godefroit et al (2009: p. 534, 546, 548), and explained as an autapomorphic feature of *Zalmoxes shqiperorum*, setting it apart from *Z*. *robustus*. However, the braincase specimens referred to

Zalmoxes robustus (NHMUK R.3408, NHMUK R.3409, FGGUB (LPB) R.1629, and FGGUB (LPB) R.1723) are overall much more similar to those of *Rhabdodon*, the only other rhabdodontid for which braincases are known (Pincemaille-Quillevere et al., 2006; Chanthasit, 2010), than to both NHMUK R.3401A and UBB NVZ1-42. Accordingly, if indeed belonging to a rhabdodontid, the specimens would, more likely, be referable to a new genus (distinct from both *Zalmoxes* and *Rhabdodon*) due to its highly aberrant braincase morphology.

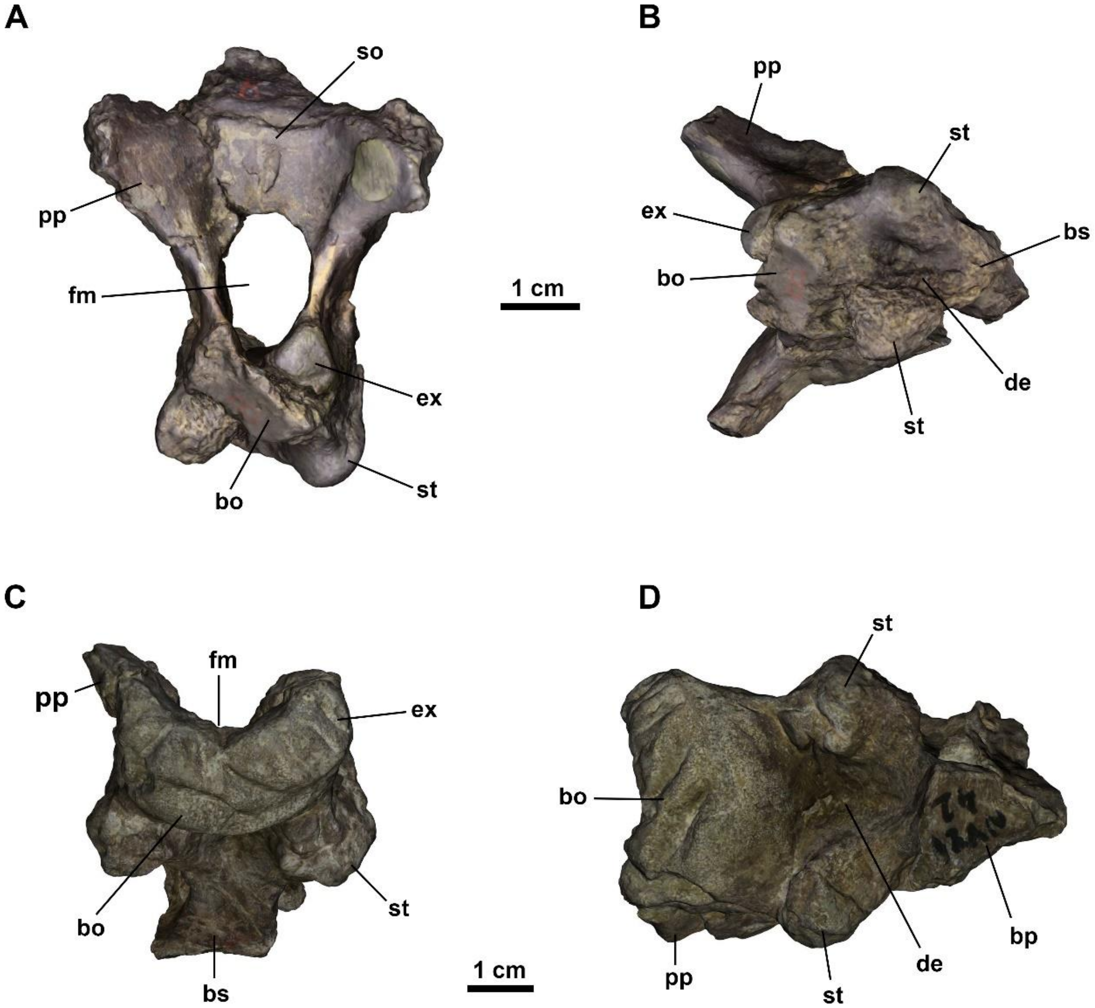

Figure 15. The ornithopod braincase specimens re-examined for this thesis. Both specimens were previously referred to the rhabdodontid ornithopod *Zalmoxes* but a detailed comparison showed that they actually belong to a hadrosauroid ornithopod, most likely *Telmatosaurus transsylvanicus*. The anatomical features shared with hadrosauroids are an anteroposteriorly short basioccipital, two well-developed bulbous sphenoccipital tubercles (= the basal tubera) that lie directly anterior to the basioccipital, and a deep depression separating the sphenoccipital tubercles (for details, see text). **A–B**, Specimen NHMUK R.3401A from the Sînpetru Formation of the Haţeg Basin in posterior (A) and ventral view (B). **C–D**, Specimen UBB NVZ1-42 from the Râul Mare River section of the Haţeg Basin in posterior (C) and ventral view (D). **Abbreviations: bo**, basioccipital; **bp**, basisphenoid platform on the ventral aspect of the basisphenoid; **bs**, basisphenoid-parasphenoid complex; **de**, depression on the ventral aspect of the basicranium between the sphenoccipital tubercles; **ex**, exoccipital; **fm**, foramen magnum; **pp**, paroccipital process formed by the exoccipital-opisthotic complex; **so**, supraoccipital; **st**, sphenoccipital tubercle. Modified after Augustin et al. (2023).

A detailed comparison with basal ornithischians, basal neornithischians, basal ornithopods, basal iguanodontians, basal hadrosauroids and hadrosaurids showed that this braincase morphology (i.e., a short basioccipital connected to two sphenoccipital tubercles that are separated by a deep depression) occurs exclusively among hadrosauroids. The complete comparisons (in total with 49 taxa, including 15 basal iguanodontians, 12 basal hadrosauroids and 16 hadrosaurids), can be found in Augustin et al. (2023). Moreover, all members of the Hadrosauroidea examined, which includes a large portion of the taxa for which this area is well preserved, exhibit this characteristic basicranial morphology. Therefore, specimens NHMUK R.3401A and UBB NVZ1-42 definitively belong to hadrosauroid dinosaurs and not, as previously suggested, to rhabdodontids. Remarkably, both specimens very closely resemble the only hadrosauroid taxon presently known from the Upper Cretaceous of the Haţeg Basin, *Telmatosaurus*. Indeed the holotype specimen of *Telmatosaurus transsylvani-*

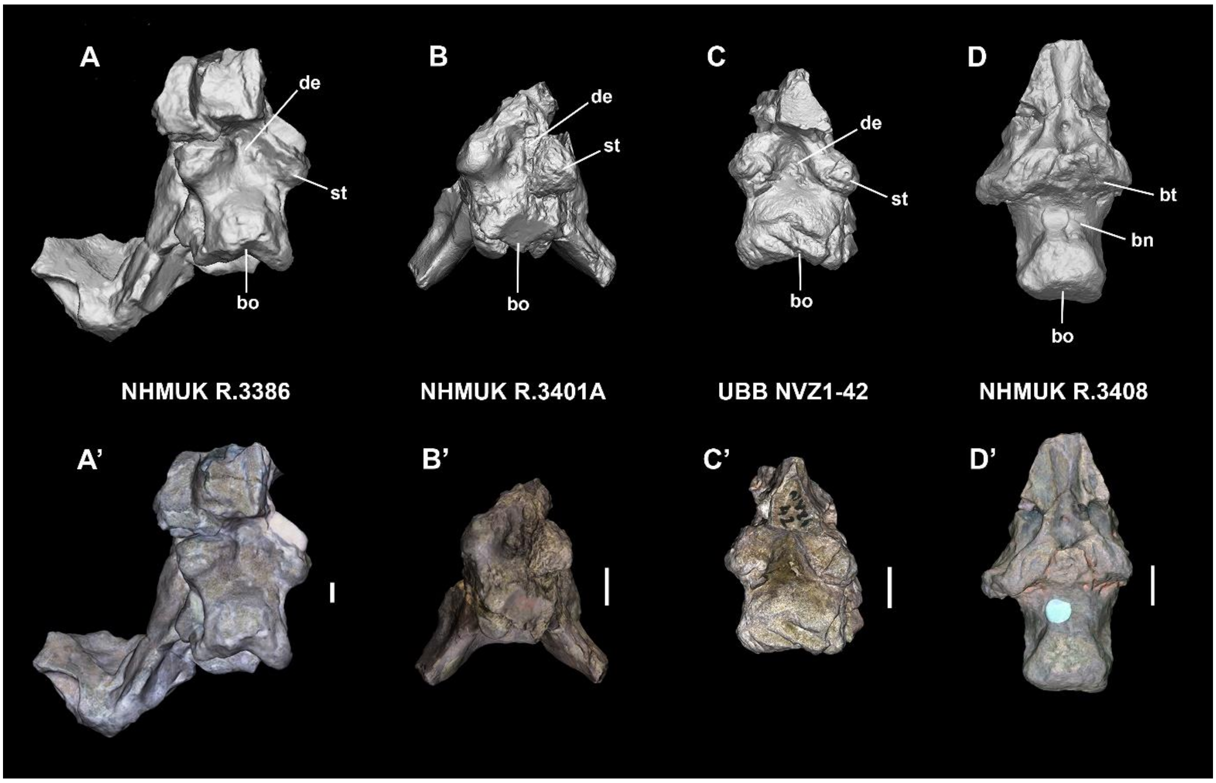

Figure 16. Comparison of NHMUK R.3401A and UBB NVZ1-42 with the basicranium of *Telmatosaurus* and *Zalmoxes*. **A–A'**, Surface model of the holotype skull of *Telmatosaurus*, NHMUK R.3386 witihout texture (A) and with texture (A') in ventral view. **B–B'**, Surface model of NHMUK R.3401A without texture (B) and with texture (B') in ventral view. **C–C'**, Surface model of UBB NVZ1-42 without texture (C) and with texture (C') in ventral view. **D–D'**, Surface model of the *Zalmoxes* basicranium NHMUK R.3408 without texture (D) and with texture (D') in ventral view. Note the high degree of morphological similarity between NHMUK R.3401A, UBB NVZ1-42 and the holotype specimen of *Telmatosaurus*, NHMUK R.3386, which all differ considerably from NHMUK R.3408. **Abbreviations: bo**, basioccipital; **de**, depression on the ventral aspect of the basicranium between the sphenoccipital tubercles; **st**, sphenoccipital tubercle. Modified after Augustin et al. (2023).

cus, NHMUK R.3386, and the referred basicranium NHMUK R.3387, both described and figured by Nopcsa (1900), are very similar in morphology to NHMUK R.3401A and UBB NVZ1-42, suggesting that they too belong to *Telmatosaurus*. The extensive comparisons further demonstrate that hadrosauroids differ from rhabdodontids and all other ornithopods in their derived braincase morphology, which allows the confident identification of even isolated and fragmentary skulls. Finally, the re-assignment of UBB NVZ1-42 to a hadrosauroid prompts a revised diagnosis for *Zalmoxes shqiperorum* as the supposedly autapomorphic basicranial morphology of that taxon (Godefroit et al., 2009: p. 528) is based on this specimen.

2.3 A new rhabdodontid dinosaur from the 'Pui Beds' of the Haţeg Basin

The final specimen studied in the course of this dissertation is LPB (FGGUB) R.2070, a partial skull of an ornithopod dinosaur from the 'Pui Beds' cropping out along the Bărbat River Valley near Pui, in the eastern part of the Haţeg Basin (for an overview of the geological setting and the vertebrate assemblage of this locality, see above). The specimen comprises the articulated basicranium composed of the basioccipital, the exoccipital-opisthotic complexes, the basisphenoid-parasphenoid complex, the prootic, and the laterosphenoid, which were found associated with the articulated left and right frontals (Fig. 17). Interestingly, the frontals were found slightly above and anterior to the basicranium in their roughly correct anatomical position, indicating that, originally, some soft tissues were probably still connecting the basicranium with the frontals. Previously, LPB (FGGUB) R.2070 has been figured by Csiki et al. (2010c) as it was found in the field, and has been preliminarily referred to as *Zalmoxes* sp. by these authors, although it has never been described. Generally, the specimen is well preserved and undistorted, with small foramina and processes being still discernible. A full osteological description of the specimen can be found in Augustin et al. (2022), which is attached in the appendix. The specimen can be confidently assigned to the Rhabdodontidae as it exhibits the characteristic basicranial morphology of the group (for details, see Augustin et al., 2023). Thorough comparisons with all rhabdodontid braincase specimens reported so far have been conducted and can be found in Augustin et al. (2022), which is attached in the appendix. These comparisons clearly support the interpretation of it being referable to a rhabdodontid. However, at the same time, LPB (FGGUB) R.2070 differs considerably from all other rhabdodontid crania reported so far, both from Romania and from southern France.

Based on these differences, a new genus and species of rhabdodontid dinosaur is erected for specimen LPB (FGGUB) R.2070, *Transylvanosaurus platycephalus* (Augustin et al., 2022). The new taxon shows a number of unique features that overall demonstrate a peculiar and highly autapomorphic skull anatomy of this animal. More specifically, *Transylvanosaurus platycephalus* is diagnosed as a small- to medium-sized rhabdodontid ornithopod dinosaur characterised by the following seven autapomorphies (after Augustin et al., 2022): (1) proportionately wide frontals with a length to width ratio of 1.38; (2) presence of a well-developed, mediolaterally extending frontal crest that borders the sutural contact with the nasal and the prefrontal; (3)

elongated and straight paroccipital processes being only modestly curved laterally; (4) presence of massive prootic processes extending mainly anterolaterally and ventrally; (5) mediolaterally wide, crest-like basal tubera that meet the long axis of the braincase at a very flat angle of approximately 140°; (6) widely splayed basipterygoid processes (diverging approximately 25° from the sagittal plane) that extend mostly ventrolaterally and, to a lesser degree, anteriorly; (7) presence of a well-developed, anteroventrally inclined notch on the lateral side of the basicranium, directly anterior to the basal tubera, which is continuous and straight. Moreover, *Transylvanosaurus* differs from all other rhabdodontids by the following unique combination of characters (after Augustin et al., 2022): the basioccipital being convex and trapezoidal in ventral view; a heart-shaped foramen magnum being wider high; a straight endocranial floor that posteriorly becomes wider; a weakly developed crista tuberalis; an elongated basisphenoid; a high basisphenoid-parasphenoid complex; the posterior surface of the basal tubera having a wrinkled posterior surface and a midline process that does not extend for the entire height of the basal tubera.

In order to assess the relationships of *Transylvanosaurus* two different phylogenetic analyses were performed, the first being based on the dataset of Dieudonné et al. (2021) and the second on the dataset of Madzia et al. (2018). Aside from the addition of *Transylvanosaurus* to the datasets, no additional changes to the character-taxon matrices were made and, for the analyses, no taxon was excluded nor pruned. Two different approaches were used for the two analyses (for the detailed settings, see Augustin et al., 2022). The first analysis recovered *Transylvanosaurus* in a polytomy with the undisputed rhabdodontids *Rhabdodon*, *Mochlodon*, and *Zalmoxes*, as well as with *Fostoria* and the ‘Vegagete ornithopod’, together constituting the sister-group to *Muttaburrasaurus*. The second analysis placed *Transylvanosaurus* in a polytomy with *Zalmoxes* and *Mochlodon*, together forming the sister-clade to *Rhabdodon*, while *Muttaburrasaurus* was recovered in a more basal position (*Fostoria* and the ‘Vegagete ornithopod’ were not included in the second analysis). It should be noted however, that the grouping of *Transylvanosaurus*, *Zalmoxes* and *Mochlodon* as the sister-clade to *Rhabdodon* in the second analysis is not supported by any synapomorphy, but is due to the latter showing several autapomorphic features, which are not preserved in *Transylvanosaurus*. Recently, the Rhabdodontidae was formally defined as the smallest clade containing *Rhabdodon priscus* and *Zalmoxes robustus* (Madzia et al., 2021), and thus *Transylvanosaurus* is, by definition, a member of the Rhabdodontidae

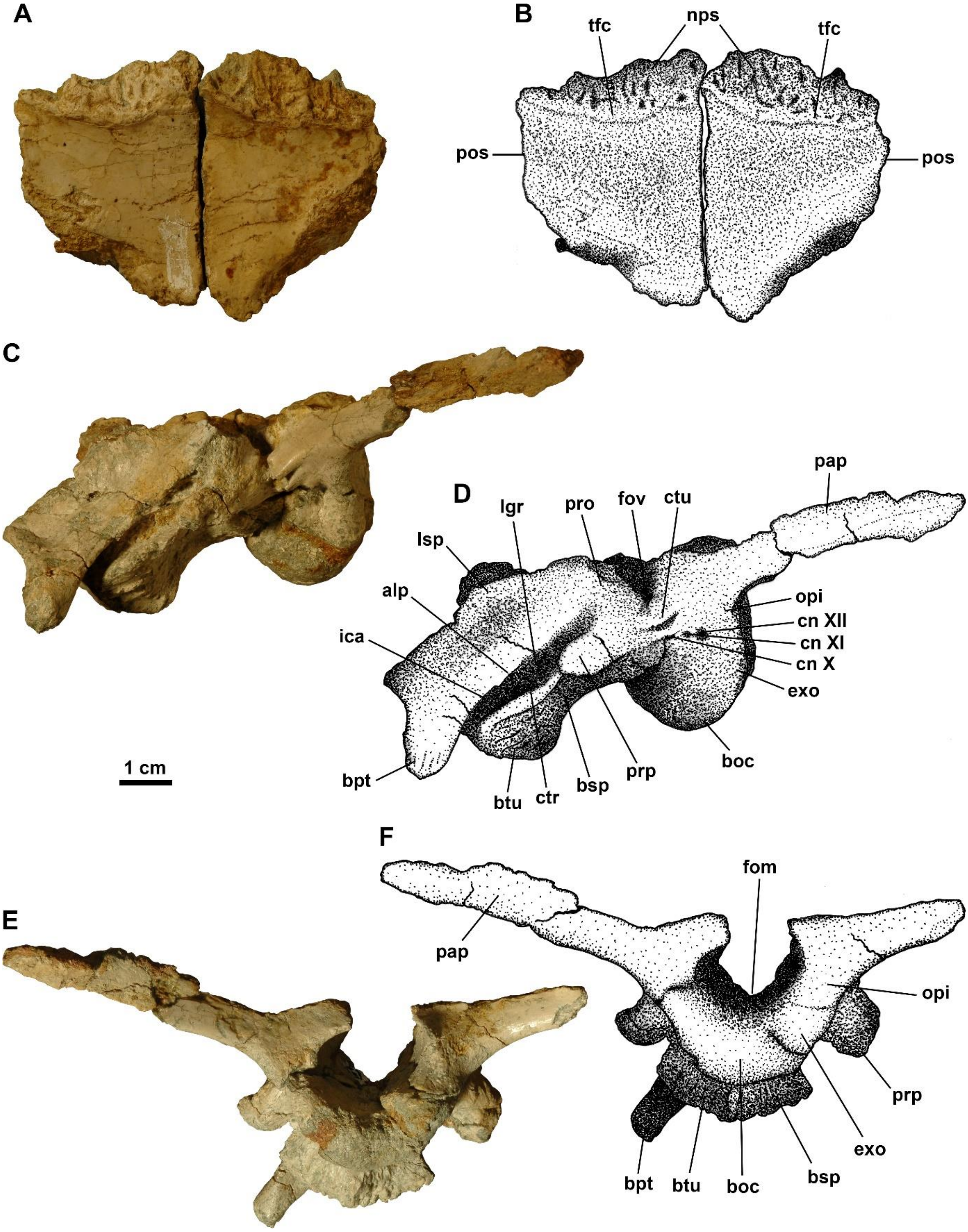

Figure 17. The holotype specimen of *Transylvanosaurus platycephalus*, LPB (FGGUB) R.2070, from the 'Pui Beds' of the Haţeg Basin. **A–B**, Photograph (A) and drawing (B) of the frontals in dorsal view. **C–D**, Photograph (C) and drawing (D) of the basicranium in left lateral view. **E–F**, Photograph (E) and drawing (F) of the basicranium in posterior view. **Abbreviations**: **alp**, alar process; **boc**, basioccipital; **bpt**, basipterygoid process; **bsp**, basisphenoid; **btu**, basal tubera; **cn**, cranial nerve; **ctr**, crista transversalis; **ctu**, crista tuberalis; **exo**, exoccipital; **fov**, foramen ovalis; **ica**, opening for the internal carotid artery; **lgr**, lateral groove; **lsp**, laterosphenoid; **nps**, confluent nasal-prefrontal suture; **opi**, opisthotic; **pap**, paroccipital process; **pas**, parietal suture; **pos**, postorbital suture; **pro**, prootic; **prp**, prootic process; **tfc**, transverse frontal crest. Modified after Augustin et al. (2022).

according to the results of both phylogenetic analyses. This provides additional strong evidence for the rhabdodontid affinities of *Transylvanosaurus*, especially given that the analyses are based on two different and largely independent data sets.

Due to the poor resolution of the phylogenetic analyses (i.e., *Transylvanosaurus* being recovered in a polytomy with the other rhabdodontids) and the scarcity of braincase characters in both datasets, the relationships of *Transylvanosaurus* within the Rhabdodontidae were assessed based on detailed morphological comparisons with the rhabdodontid braincases reported so far. Interestingly, the holotype of *Transylvanosaurus* is overall more similar to the braincase specimens from southern France previously assigned to *Rhabdodon* than to those described from Romania and assigned to *Zalmoxes*. More specifically, *Transylvanosaurus* shares with *Rhabdodon* dorsoventrally deep basal tubera that project anteroventrally, an anterior portion of the basisphenoid-parasphenoid complex that is inclined anterodorsally, as well as paroccipital processes that are only modestly curved, and thus relatively straight for most of their length. Therefore, a particularly close relationship between *Transylvanosaurus* and *Rhabdodon* from southern France is suggested (Fig. 18), which in turn, has important implications for the biogeographical history of the Rhabdodontidae. As outlined above, two distinct rhabdodontid lineages have been previously identified, one comprising *Rhabdodon* spp. from southern France and northeastern Spain (and potentially *Pareisactus* from northeastern Spain), whereas the other comprises *Zalmoxes robustus* and *Z*. *shqiperorum* from Romania as well as *Mochlodon suessi* and *M*. *vorosi* from Austria and Hungary, respectively. The close relationship between *Rhabdodon* and *Transylvanosaurus* postulated here challenges this concept of two geographically separated rhabdodontid lineages inhabiting the western and the eastern part of the Late Cretaceous European Archipelago, which were thought to have evolved in isolation since the Coniacian (as indicated by the Santonian age of *Mochlodon*). Therefore, allopatric speciation alone cannot account for the distribution pattern, and at least one dispersal event of the ‘western’ European rhabdodontid lineage must have taken place – either from west towards the eastern European realm (i.e., the Transylvanian area) or from east towards the western European realm (i.e., the Ibero-Armorican area), depending on the place of origin for the Rhabdodontidae.

Moreover, the recognition of *Transylvanosaurus* has some palaeoecological implications. The new taxon represents only the second rhabdodontid genus from the uppermost Cretaceous deposits of western Romania, aside from *Zalmoxes*. Generally, the family is characterised by a relatively high taxonomic diversity and, in many cases, by the co-occurrence of at least two rhabdodontid taxa. In the upper Campanian–lower Maastrichtian of northeastern Spain, *Rhabdodon* spp. occurs alongside *Pareisactus evrostos*, while coeval deposits of southern France yielded *Rhabdodon priscus* and *R. septimanicus* as well as *Matheronodon provincialis*. Likewise, with the description of

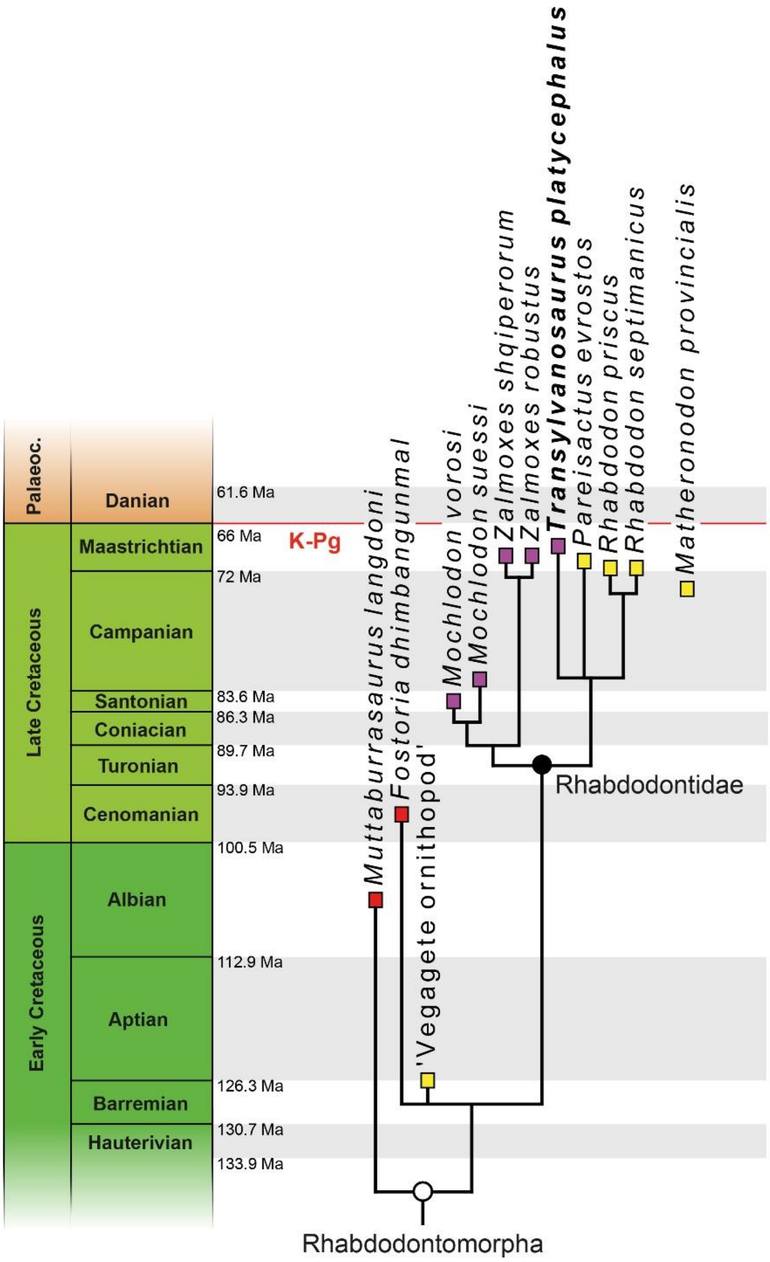

Figure 18. Phylogenetic relationships of *Transylvanosaurus platycephalus* and temporal distribution of the Rhabdodontidae. The relationships depicted are based on the results of the two phylogenetic analysis and the extensive comparisons of Augustin et al. (2022). The relationships of *Mochlodon* and *Pareisactus* primarily follow Dieudonné et al. (2021), as well as Párraga and Prieto-Márquez (2019). The relationships of *Matheronodon* have not yet been explored by a phylogenetic analysis, and thus it is not included in the cladogram. The colour of the boxes denotes their distribution (yellow for Western Europe, purple for Eastern Europe, red for Australia).

Transylvanosaurus, three rhabdodontids are now known from the Maastrichtian of western Romania (the others being *Zalmoxes robustus* and *Z*. *shqiperorum*), and thus their diversity seems to have been similar to that of the latest Cretaceous of the Ibero-Armorican landmass. Conversely, only one rhabdodontid has so far been described from the slightly older European deposits, including *Mochlodon vorosi* from the Santonian of western Hungary, *Mochlodon suessi* from the lower Campanian of eastern Austria (see above), and cf. *Rhabdodon priscus* from the lower Campanian of southern France (Buffetaut et al., 1996). Interestingly, the different sympatric rhabdodontids largely overlapped in body size, as is the case for *Rhabdodon* and *Pareisactus* from northern Spain (Párraga and Prieto-Márquez, 2019), *Rhabdodon* and *Matheronodon* from southern France (Chanthasit, 2010; Godefroit et al., 2017), as well as *Zalmoxes robustus* and *Z*. *shqiperorum* from western Romania (Weishampel et al., 2003; Ősi et al., 2012a). The holotype specimen of *Transylvanosaurus* likely belongs to a subadult individual based on the degree of fusion between the skull bones, and regarding its size, compares well with cranial elements referred to *Zalmoxes*. Accordingly, three rhabdodontids of a roughly similar body were present on the Haţeg Island during the Maastrichtian. However, *Transylvanosaurus* differs considerably from the sympatric *Zalmoxes* in its cranial morphology and had a much wider and lower skull. The widely different skull proportions in *Transylvanosaurus* certainly correlate with a different size of certain muscles such as a larger attachment site for m. rectus capitis ventralis and m. protractor pterygoideus in *Transylvanosaurus* (for details, see Augustin et al., 2022). Ultimately, such differences might reflect differences in feeding adaptations and niche partitioning between the sympatric rhabdodontids from the Haţeg Basin.

3. CONCLUSION

The uppermost Cretaceous deposits of the Haţeg Basin have yielded one of the richest vertebrate assemblages from the Upper Cretaceous of Europe. Consequently, they are of paramount importance for understanding the evolution of life on land during the Late Cretaceous. Despite the long research history of the latest Cretaceous vertebrates from the Haţeg Basin, major aspects remain poorly known, such as their alpha-level taxonomic diversity, their phylogenetic and palaeobiogeographical relationships, as well as their palaeoecology. In order to evaluate these issues, four key specimens were examined for this thesis that have the potential to shed new light on these poorly known aspects. The first of these specimens, LPB (FGGUB) R.2997, is a partial, articulated turtle skeleton from the Sînpetru Formation that preserves most of the carapace, the complete plastron, and some appendicular elements. The specimen can be assigned to the dortokid stem-pleurodiran *Dortoka* based on the presence of the full set of shared derived characters of the genus. At the same time, the new specimen differs considerably from all other species of the genus and thus is referred to a new species, *D*. *vremiri*. Two sets of phylogenetic analyses recovered the new taxon as being firmly placed within the Dortokidae and, more specifically, as the sister-taxon to *D*. *botanica* from the Palaeocene of western Romania. The third species of the genus, *D*. *vasconica* is known from the Upper Cretaceous of northern Spain, central Spain and southern France. This distribution pattern indicates the presence of two distinct and geographically separated dortokid lineages. Two indeterminate dortokids from the Upper Cretaceous of eastern Austria and western Hungary resemble the Romanian taxa and, in particular, share one synapomorphy of the eastern European dortokid clade (*D*. *vremiri* + *D*. *botanica*), thus likely belonging to this clade as well. The phylogenetic relationships indicate the local survival of dortokids across the K/Pg extinction event, as opposed to subsequent immigration. Meanwhile dortokids are absent from the Palaeogene of Western Europe and thus appear to have died out during the K/Pg extinction event. Moreover, new taphonomical data demonstrates that the only other local turtle taxon, the stem-testudine *Kallokibotion bajazidi*, was more terrestrial than the supposedly semi-aquatic *D*. *vremiri*. Interestingly, the former apparently died out during the K/Pg extinction event. This suggests both geographical and ecological extinction selectivity across the K/Pg extinction in Europe.

Tab. 4. Summary of the most important results of this dissertation thesis.

Specimen	Initial taxonomic hypothesis	Final taxonomic assessment	Phylogenetic relationships	Biogeographic implications	Ecology and niche partitioning
LPB (FGGUB) R.2997	Dortokidae, gen. et sp. nov.	Dortokidae, *Dortoka vremiri* sp. nov.	Sister-taxon to *Dortoka botanica*, close relatives from Hungary and Austria	Closest relatives from E-Europe, presence of an eastern European lineage (i.e., dichotomous distribution)	Probably freshwater aquatic, different niche than the (supposedly semi-terrestrial) sympatric turtle *Kallokibotion bajazidi*
NHMUK R.3401A	Rhabdodontidae, gen. et sp. nov.?	Hadrosauroidea, *Telmatosaurus transsylvanicus*	—	—	—
UBB NVZ1-42	Rhabdodontidae, gen. et sp. nov.?	Hadrosauroidea, *Telmatosaurus transsylvanicus*	—	—	—
LPB (FGGUB) R.2070	Rhabdodontidae, gen. et sp. nov.	Rhabdodontidae, *Transylvanosaurus platycephalus* gen. et sp. nov.	Sister-taxon to *Rhabdodon* spp.	Closest relative(s) from W-Europe, at least one rhabdodontid lineage with a trans-European distribution	Markedly different skull shape than the sympatric rhabdodontid *Zalmoxes* spp. that likely reflects different feeding ecology

The second and third key specimens examined for this thesis are two ornithopod braincases, NHMUK R.3401A and UBB NVZ1-42, from the Sînpetru Formation and the Râul Mare River Section, respectively. Both of these specimens have been described before and were previously assigned to the rhabdodontid ornithopod dinosaur *Zalmoxes*. Notably, NHMUK R.3401A closely resembles UBB NVZ1-42 morphologically, despite being much smaller. However, they differ considerably from other braincases assigned to the Rhabdodontidae, including *Zalmoxes* from western Romania and *Rhabdodon* spp. from southern France, and thus, a taxonomic re-evaluation is necessary. A detailed comparison with basal ornithischians as well as basal and derived ornithopods showed that the basicranial morphology seen in the two braincase specimens (a short basioccipital that is connected to two well-developed bulbous sphenoccipital tubercles separated by a deep depression) is otherwise only and found in more derived hadrosauroid ornithopods, which consistently exhibit this morphology. In addition, NHMUK R.3401A and UBB NVZ1-42 closely resemble the only local hadrosauroid taxon *Telmatosaurus* and accordingly are re-assigned to this taxon. The last specimen examined for this thesis is a partial skull of an ornithopod dinosaur, LPB (FGGUB) R.2070, from the Pui Beds of the southeastern Haţeg Basin. Generally, this specimen resembles rhabdodontid dinosaurs, although it differs considerably from all other rhabdodontid skulls reported thus far and shows a unique and highly autapomorphic anatomy. Therefore, the skull is assigned to a new genus and species, *Transylvanosaurus platycephalus*. Two sets of phylogenetic analyses placed the new taxon within Rhabdodontidae but were unable to resolve the in-group relationships. Based on the high degree of similarity between *Transylvanosaurus* and *Rhabdodon* from southern France, a particularly close relationship between those taxa is suggested, which indicates a more complex biogeographical history than previously recognised. In addition, *Transylvanosaurus* differs widely from the sympatric rhabdodontid *Zalmoxes* in its skull proportions, indicating a certain degree of niche partitioning between the two genera.

Figure 19. Life reconstruction of the two new taxa described for this dissertation thesis, the rhabdodontid dinosaur *Transylvanosaurus platycephalus* (foreground, right) and the dortokid turtle *Dortoka vremiri* (foreground, left). In the background are other vertebrate taxa from the Haţeg Island, (from left to right) the crocodilian *Allodaposuchus precedens*, the giant azhdarchid pterosaur *Hatzegopteryx thambema*, two dromaeosaurid theropods, and titanosaurian sauropods. The environment depicted is based on the ‘Pui Beds’, the type locality of *Transylvanosaurus* that also yielded remains of dortokid turtles. Artwork by Peter Nickolaus, who also holds the copyright. Used with permission.

The examination of the four specimens allowed important new insights into the composition, relationships, and palaeoecology of the uppermost Cretaceous vertebrate assemblages from the Haţeg Basin (Fig. 19). In particular, it was possible to confirm the three hypotheses formulated above. First, the in-group diversity of turtles and rhabdodontids was higher than previously thought, and accordingly, two new taxa were recognised (*D*. *vremiri* and *Transylvanosaurus platycephalus*). Both taxa differ markedly from all previously described members of their respective clades and especially *Transylvanosaurus* is highly autapomorphic in its skull anatomy. Second, the phylogenetic relationships of the two new taxa offer important insights into the evolution and palaeobiogeography of their respective clades, as dortokids seem to exhibit a dichotomous, east/west distribution pattern (as suggested before), whereas rhabdodontids are characterised by a more complex biogeographical history than previously recognised, including at least one more dispersal event. Consequently, the vertebrates of the Late Cretaceous European Archipelago exhibit differential distribution patterns, each group being characterised by its own unique biogeographical history. The new phylogeny of dortokids presented here further indicates geographical and ecological extinction selectivity. Third, a certain degree of niche partitioning was present between the two turtles (*D*. *vremiri* and *Kallokibotion*) and the rhabdodontids (*Zalmoxes* and *Transylvanosaurus*). Therefore, the higher taxonomic diversity within the respective clades can be explained, at least partially, by niche partitioning.

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APPENDIX

FIRST PAPER

A NEW LATEST CRETACEOUS PLEURODIRAN TURTLE (TESTUDINATA: *DORTOKIDAE*) FROM THE HAŢEG BASIN (ROMANIA) DOCUMENTS END-CRETACEOUS FAUNAL PROVINCIALITY AND SELECTIVE SURVIVAL DURING THE K-PG EXTINCTION

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A new latest Cretaceous pleurodiran turtle (Testudinata: *Dortokidae*) from the Haţeg Basin (Romania) documents end-Cretaceous faunal provinciality and selective survival during the K-Pg extinction

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Dortokidae is an endemic family of stem-pleurodiran turtles, known exclusively from the Cretaceous and early Paleogene of Europe. Here we describe a new dortokid taxon from the Upper Cretaceous (Maastrichtian) Sînpetru Formation of the southern Haţeg Basin, Romania. The type material of *Dortoka vremiri* sp. nov. comprises a well-preserved carapace and a nearly complete plastron as well as the *in situ* right scapula and right pubis. Phylogenetic analyses performed to assess the position and interrelationships of *Dortoka vremiri* sp. nov. within *Dortokidae* as well as within the wider *Pleurodira* recovered the new taxon firmly nested within *Dortokidae*, and together with other dortokids, placed along the stem lineage of pleurodires. Our analysis provides evidence for allopatric speciation in *Dortoka* through the presence of two distinct lineages – an eastern and a western European lineage, respectively. A similar east/west disjunct distribution pattern has also been established previously for several vertebrate groups such as other turtles, dinosaurs and mammals, probably resulting from isolation due to the particular palaeogeographical setting of the Late Cretaceous European Archipelago. The phylogeny demonstrates local survival of *Dortoka* across the K-Pg boundary as the sister-taxon of *D. vremiri* is *D. botanica* from the uppermost Paleocene deposits of Romania and points to geographical selectivity, as the western lineage of *Dortoka* went extinct before the Paleogene. Osteology and novel taphonomical data imply a semi-terrestrial lifestyle for *Kallokibotion bajazidi*, a turtle occurring in coeval faunas with the aquatic and smaller-sized *D. vremiri* and most likely going extinct at the K-Pg boundary. Altogether, this pattern is consistent with selective extinction of terrestrial taxa previously observed for other continental vertebrate assemblages across the end-Cretaceous mass extinction with only two other examples from turtles.

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Keywords: Pleurodira; Haţeg Basin; Upper Cretaceous; Sînpetru Formation; palaeobiogeography; Cretaceous-Paleogene extinction

Introduction

The uppermost Cretaceous continental strata of the Haţeg Basin have long been known for their richness in vertebrate fossils (e.g. Nopcsa 1923a), yielding one of the most diverse vertebrate faunas from the continental Late Cretaceous of Europe (Weishampel *et al.* 1991, 2010; Csiki-Sava *et al.* 2015). Moreover, the Haţeg Basin is notable for the supposed insular endemism and dwarfism of its vertebrate fauna (Csiki & Grigorescu 2007; Benton *et al.* 2010; Csiki & Benton 2010). Since the early palaeontological studies by Nopcsa more than 120 years ago (e.g. Nopcsa 1897, 1900), subsequent discoveries revealed an array of vertebrate groups, including fishes, amphibians, squamates, turtles, crocodyliforms, pterosaurs, non-avian dinosaurs, birds and mammals (Grigorescu 1983; Weishampel *et al.* 1991; Csiki-Sava *et al.* 2016). Turtles are among the most abundant vertebrates from the Late Cretaceous deposits of the Haţeg Basin as well as in the adjacent Transylvanian and Rusca Montană basins (e.g. Vremir & Codrea 2009; Codrea *et al.* 2010, 2012; Vremir 2010). So far, two distinct taxa have been recognized – the stem-turtle *Kallokibotion bajazidi* (Nopcsa 1923a, b; Gaffney & Meylan 1992; Pérez-García & Codrea 2018), and as yet unnamed member(s) of the *Dortokidae* (Vremir 2004; Vremir & Codrea 2009; Rabi *et al.* 2013; Vremir *et al.* 2014, 2015). A more complete dortokid

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*Corresponding authors. Email: felix.augustin@uni-tuebingen.de specimen represented by a partial plastron and associated carapacial fragments from the Late Cretaceous (early Maastrichtian) Vurpăr locality of the Transylvanian Basin has previously been referred to a new genus and species, '*Muehlbachia nopcsai*' (Vremir & Codrea 2009), but this taxon was subsequently shown to be a *nomen nudum* (Rabi *et al.* 2013; Cadena & Joyce 2015).

Dortokidae is a clade of semiaquatic to aquatic freshwater pan-pleurodiran turtles, endemic to Europe and ranging from the Early Cretaceous to the Eocene (Lapparent de Broin *et al.* 2004; Cadena & Joyce 2015; Pérez-García *et al.* 2017). No skull is known for any dortokid, which precludes a firm establishment of their relationships to other pleurodires, yet all previous phylogenies recovered them as stem-pleurodires (e.g. Gaffney *et al.* 2006; Hermanson *et al.* 2020). *Dortokidae* is primarily characterized by its unique micro-reticulate shell ornamentation and currently comprises at least two different genera and three species (Lapparent de Broin & Murelaga 1996; Gheerbrant *et al.* 1999; Pérez-García *et al.* 2014; Cadena & Joyce 2015). The eponymous *Dortoka vasconica* is represented by extensive material from the Late Cretaceous (Campanian–Maastrichtian) of Laño and Armuña, northern and central Spain respectively, as well as southern France (Lapparent de Broin & Murelaga 1996, 1999; Pérez-García *et al.* 2012, 2016). *Dortoka* (= *Ronella*) *botanica* was based on a partial plastron and pubis from upper Paleocene beds of the Jibou Formation in Romania (Lapparent de Broin in Gheerbrant *et al.* 1999), and additional material has been also described later (Lapparent de Broin *et al.* 2004). This taxon was originally named a new genus, *Ronella botanica*, by Lapparent de Broin (in Gheerbrant *et al.* 1999), but it was later referred to *Dortoka botanica* by Cadena & Joyce (2015). The supposedly more basal dortokid *Eodortoka morellana* is represented by fragmentary and disarticulated material from the Lower Cretaceous (Barremian–Aptian) Arcillas de Morella Formation of north-eastern Spain (Pérez-García *et al.* 2014). Although this taxon has recently been considered a *nomen dubium* by Cadena & Joyce (2015), we here tentatively treat it as valid (see below). An indeterminate dortokid has been reported from the Lower Cretaceous (Hauterivian–Barremian) El Castellar Formation, representing the oldest record of the family so far (Pérez-García *et al.* 2017). Additionally, indeterminate dortokids have been described from the Upper Cretaceous (lower Campanian) Gosau Group of Austria, as well as from the Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút, Hungary, besides the already mentioned disarticulated material from the uppermost Cretaceous (Maastrichtian) of Transylvania (Ősi *et al.* 2012b; Rabi *et al.* 2013). The geologically youngest record of the family *Dortokidae* has been reported from the lower Eocene of the Şimleu Basin, north-western Romania, and was referred to cf. *Dortoka* (= *Ronella*) *botanica* (Vremir 2013).

Here we describe a new species of the derived dortokid *Dortoka* from the Upper Cretaceous Sînpetru Formation of the Haţeg Basin. *Dortoka vremiri* sp. nov. is represented by a fairly well-preserved specimen (LPB [FGGUB] R.2297) comprising the complete plastron and the nearly complete carapace in association with the scapula and parts of the pelvis preserved *in situ*. The taxonomical status of the fragmentary dortokid specimens reported in Rabi *et al.* (2013) will be clarified elsewhere but they may represent the same taxon. In order to assess the phylogenetic relationships of the new taxon, we perform two sets of phylogenetic analyses – a global one within the *Pan-Pleurodira* and an in-group analysis within the *Dortokidae*. Based on the phylogenetic relationships of the new taxon within *Dortokidae*, the palaeobiogeography of dortokids and allopatric speciation in the genus *Dortoka* are discussed. In addition, the survival of the lineage comprising *D. vremiri* sp. nov. across the K-Pg boundary has important implications for the patterns of survival and extinction on the Late Cretaceous European Archipelago.

Institutional abbreviations

LPB (FGGUB), Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania.

Taxonomical nomenclature

We follow the phylogenetic nomenclature of Joyce *et al.* (2021) and highlight all therein defined clade names in italics according to the PhyloCode.

Geological setting

The intramontane Haţeg Basin is located in the south-western Carpathians, western Romania (Fig. 1A). It is a synorogenic sedimentary basin that formed during and subsequent to the latest Cretaceous phase of the Carpathian orogeny (Bojar *et al.* 1998, 2010; Willingshofer *et al.* 2001). The continental Upper Cretaceous (Maastrichtian) sedimentary rocks of the Haţeg Basin comprise at least two main lithostratigraphical units (Fig. 1B) – the Densuş-Ciula Formation in the north-western part of the basin as well as the Sînpetru Formation in the southern and central parts of the basin

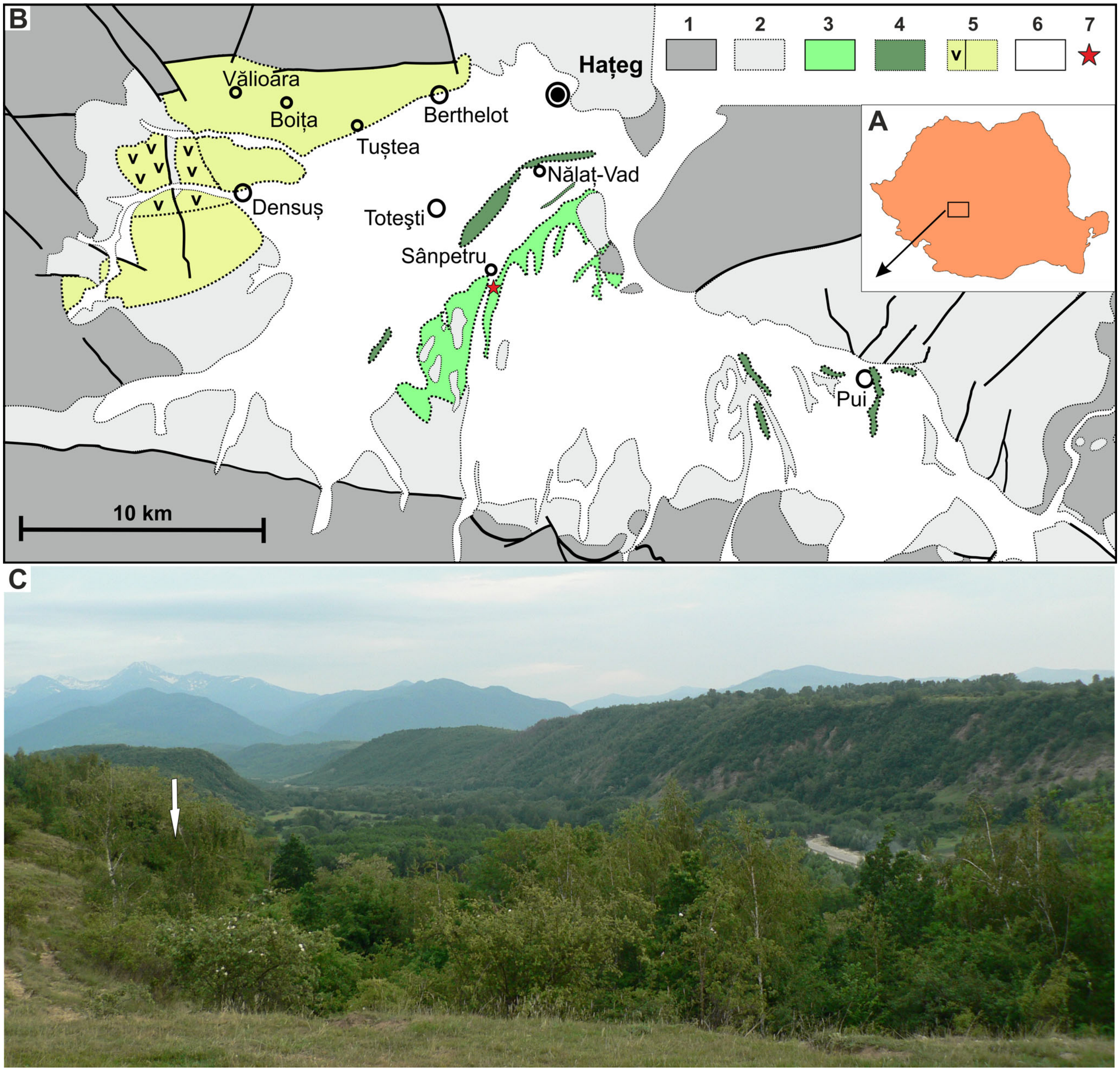

Figure 1. Geological setting of the type locality of *Dortoka vremiri* sp. nov. **A,** inset contour map of Romania showing the position of the Haţeg Basin. **B,** simplified geological map of the Haţeg Basin with the most important latest Cretaceous fossiliferous localities, highlighting the type locality (updated from Csiki-Sava *et al.* 2016). **C,** overview of the Sibişel Valley, with the stratotype deposits of the Sînpetru Formation cropping out along the hills flanking the valley. Arrow shows the approximate position of the type locality (not visible; see also Fig. 2A). In the background, the Retezat Mountains of the Southern Carpathians border the basin towards the south. **Legend: 1**, Pre-Alpine crystalline basement units surrounding the Haţeg Basin; **2**, outcropping areas of pre-Quaternary sedimentary rocks of the basin, with 3–5 highlighting the distribution of the uppermost Cretaceous continental beds: **3**, Sînpetru Formation; **4**, deposits tentatively correlated with the Sînpetru Formation (see Csiki-Sava *et al.* 2016); **5**, Densuş-Ciula Formation (**v**, volcanoclastic subunit); **6**, Quaternary deposits; **7**, type locality of *Dortoka vremiri* sp. nov.

(Grigorescu 1992; Therrien 2005; Csiki-Sava *et al.* 2016). The holotype specimen of the new dortokid taxon reported here, LPB (FGGUB) R.2297, was discovered in 1995 at the locality 'La Cărare', which is located near the village of Sânpetru in the south-central part of the Haţeg Basin, on the eastern side of the Sibişel Valley (Figs 1B, C, 2A). The outcrops that include the locality (Fig. 2B) belong to the lower part of the Maastrichtian Sînpetru Formation (Grigorescu 1983; Grigorescu & Csiki 2002; Panaiotu & Panaiotu 2010; Csiki-Sava *et al.* 2016).

The Sibişel Valley outcrop section that includes the 'La Cărare' locality (Figs 1C, 2A) exposes an 860 m thick succession of alluvial sediments representing the type section of the Sînpetru Formation (Grigorescu 1992). These sediments are mainly reddish to brownish, more rarely grey-greenish conglomerates, sand-, silt- and mudstones in alternating layers of coarse and fine-grained material that are arranged in multiple fining-upward sequences. They were probably laid down on a poorly channelized alluvial plain drained by braided river systems (Grigorescu 1983; Bojar *et al.* 2005; Therrien 2005, 2006; Therrien *et al.* 2009). Abundant palaeosols indicate the presence of drier areas interspersed within a mosaic of wetlands and well-drained floodplains (Therrien *et al.* 2009). The palaeoclimate during the time of deposition of the Sînpetru Formation has been reconstructed as warm, semi-arid and seasonal (Bojar *et al.* 2005; Therrien 2005; Therrien *et al.* 2009).

The Sînpetru Formation primarily yields disarticulated remains of vertebrates, including multituberculate mammals, turtles and crocodyliforms, as well as ankylosaur, ornithopod, theropod and sauropod dinosaurs (e.g. Nopcsa 1900, 1902a, b, 1904, 1929; Andrews 1913; Grigorescu 1983, 1984; Rădulescu & Samson 1996; Csiki & Grigorescu 1998; Csiki *et al.* 2010; Martin *et al.* 2014). Generally, the vertebrate occurrences can be grouped into distinct taphonomical categories, ranging from isolated bones and teeth to associated and partly articulated remains, or else to small, mainly lenticular multitaxic bonebeds, the so-called 'fossil-pockets' (Nopcsa 1902b; Grigorescu 1983; Csiki *et al.* 2010). Some of the bones from the Sînpetru Formation of the Sibişel River section show bioerosional trace fossils, documenting the feeding activity of insects (termites and coleopterans), multituberculate mammals, as well as theropod dinosaurs and/or ziphodont crocodyliforms (Csiki 2006; Augustin *et al.* 2019).

Sedimentology, palaeontology and taphonomy of the 'La Cărare' locality

The 'La Cărare' locality represents one of the richest fossil accumulations in the Sibişel Valley section. The sedimentology, palaeontology and taphonomy of this site, however, has never been described in detail yet. It was quarried over a span of several years during the 1990s (Csiki 1999; Csiki *et al.* 2010; Fig. 2C, E), and despite being abandoned after exhaustion (Fig. 2D), it continues to be occasionally resurveyed during more recent fieldtrips in order to identify and recover – often with success (e.g. Ősi *et al.* 2014, fig. 4; Fig. 2F) – fossil specimens that eventually still erode out from the otherwise largely excavated bonebed. Aside from the holotype material of *Dortoka vremiri* sp. nov., remains of several other vertebrates were recovered from this lenticular bonebed, including crocodyliforms (Martin *et al.* 2014), titanosaurs (Csiki 1999), theropods (Csiki & Grigorescu 1998), nodosaurid ankylosaurs (Ősi *et al.* 2014), and rhabdodontid ornithopods (Jianu 1994), besides other turtles (*Kallokibotion*; Fig. 2F), rare hadrosauroids, and possible pterosaurs (see Csiki *et al.* 2010). Although the accumulation is clearly multitaxic, it is nevertheless highly dominated by remains of the rhabdodontid ornithopod *Zalmoxes*, with turtle fossils second in abundance (see below).

The sedimentary rocks in the vicinity of the site are represented by decimetre-thick lens-shaped greenish conglomerates and sandstones intercalated with several decimetre-thick brownish red and variegated fine sandy and silty mudstones, representing channel fills and relatively well-drained floodplain deposits, respectively; the entire local succession is strongly tilted, dipping at an angle of about 45° towards the south-west (Csiki 1999; Fig. 2B). The fossiliferous body itself consists of a basal lens-shaped, grey-greenish coarse pebbly sandstone that grades upwards into a massive, rather soft brownish, fine sandy siltstone (Fig. 2C). The matrix-supported coarse-grained basal horizon, locally floored by a coarser channel lag conglomerate, shows some degree of sorting with a fining-upward tendency, and is locally cemented by hard siliceous cement that makes extracting fossils difficult. Although the strongly tilted nature of the beds, almost parallel with the slope of the hillside outcrop that hosts the 'La Cărare' site, makes it hard to ascertain this, the basal coarse conglomeratic sandstone seems laterally pinched out, lens-shaped, just as many other coarse sandstone bodies present in the local succession (Fig. 2B), passing into brownish sandy siltstones similar to those overlying the sandstone. The coarse, pebbly sandstone appears to rest on top of poorly consolidated yellowish medium-grained sandstones. On the upstream (southern) end of the quarried bonebed, there is tectonic contact along a small-scale sub-vertical fault between the fossil-bearing rocks and these presumably underlying poorly consolidated sandstones.

The largest number of fossils (>180 specimens) recovered from this site were concentrated within the basal coarse-grained member of the bonebed (Fig. 2E), and especially in its lower part, with fewer fossils discovered up-section (Fig. 2F). As the siltstones are capped immediately by the grass-bearing recent soil horizon, many of the yellowish-reddish light brown

Figure 2. Sedimentary and palaeontological context of the type locality of *Dortoka vremiri* sp. nov. **A,** detail of the right-side flank of the Sibişel Valley (river visible in bottom left), with outcropping deposits of the uppermost Cretaceous (Maastrichtian) Sînpetru Formation. Black arrow points to the location of the 'La Cărare' quarry, type locality of *Dortoka vremiri* sp. nov., white arrow, to the position of the succession shown in 2B. **B,** detail of the Maastrichtian continental beds cropping out in the surroundings of the 'La Cărare' quarry, showing the repetitive cycles of thin channel sandstones (ch ss), respectively floodplain fine siltstones-mudstones (fp ss-ms). **C,** excavations at the 'La Cărare' quarry in 1994, showing the local succession made up of basal, greenish coarse pebbly sandstones (cg ss) yielding the type specimen of *Dortoka vremiri* sp. nov., overlain by brownish silty mudstones (s ms). **D,** the abandoned 'La Cărare' quarry, in 2008. **E,** the main fossil-bearing greenish pebbly sandstone, with *in situ* fossils (in 1995), in the centre, a tibia of the rhabdodontid dinosaur *Zalmoxes*; hammer for scale. **F,** partial carapace of the stem-testudine *Kallokibotion bajazidi*, discovered in 2009 in the overlying brownish silty mudstones; hammer for scale.

coloured fossils recovered from the siltstones show signs of recent weathering, being affected through physical damage (to the degree of actual cracking) as well as through etching by root activity. On the other hand, fossils discovered in deeper levels of the bonebed, within the coarse sandstone – including the holotype of *Dortoka vremiri* sp. nov. – have a dark brown colour; these are often remarkably well preserved, with a pristine, shiny periosteal surface and with delicate processes or thin crests/ridges still present. Nevertheless, these specimens, especially those of more pristine preservation, are often brittle and prone to easy flaking/cracking, which makes their preparation rather difficult.

The samples recovered from the 'La Cărare' quarry are dominated by relatively small (<6 cm long) elements, a part of these being represented by fragments (including a large number of turtle plates), although relatively large (>30 cm long) specimens also occur occasionally. Most of the specimens were found isolated, and skeletal association, let alone articulation, within the site is extremely rare (the holotype of *Dortoka vremiri* sp. nov. represents one remarkable exception). Nonetheless, skeletal association can be reasonably inferred for several sets of otherwise isolated specimens based on their matching sizes and taphonomical characteristics (e.g. Csiki 1999; Z.C., pers. obs.), although these elements now occur dispersed within the fossiliferous lithon. These observations support the contribution of fluvial transport to the genesis of the bonebed, and corresponding dispersal and winnowing of the elements during transport, as well as attrition of specimens that underwent very different taphonomical histories (e.g. Csiki 1999; see below). Such a conclusion is consistent with the identification of these lenticular and fining-upward pebbly sandstones as channel deposits. If fluvial processes were indeed important during the formation of the basal part of the bonebed, it appears that at least some of the specimens, those represented by associated material, were probably moved as partial carcasses, as suggested by their potential skeletal association as well as their sometimes remarkably good preservation state.

Turtle remains at 'La Cărare' are dominated by those of the stem-testudine *Kallokibotion bajazidi*, but this taxon is usually represented by plate fragments, as well as by rare and isolated axial and appendicular elements, found both in the basal channel deposits and the overlying floodplain fines. In the latter sediments, such fragmentary elements are also associated with the best-preserved specimen referable to *Kallokibotion* from this site, a partial carapace found eroding out from the already abandoned quarry and preserving a good part of the peripheral region, while the central, more domed part of the carapace is missing (Fig. 2F).

Unlike *Kallokibotion*, which is generally common in the Transylvanian uppermost Cretaceous (e.g. Csiki *et al.* 2010; Rabi *et al.* 2013), the new dortokid is rare at 'La Cărare', but it is represented by a significantly better-preserved individual with the almost complete carapace and plastron in articulation, as well as with at least some elements of the right-side girdles also preserved *in situ* within the shell and exposed during preparation (Figs 3–6). The carapace exhibits two bilaterally symmetrical domed areas in the posterior half as well as a less bulging dome in the left side of the anterior half, both produced by moderate dorsoventral crushing (most probably due to lithostatic pressure). The specimen itself was found in a hydrodynamically stable position, lying quasi-horizontally on its plastron, within the basal, very coarse pebbly sandstone part of the 'La Cărare' succession. When discovered, only parts of the dorsal surface of the carapace were visible, and the presence of the rest of the skeleton was revealed only much later (2010–2011) during preparation. The plastron, exposed at that stage, is warped, dorsally bulging at mid-length, suggesting that lithostatic pressure deformed its central parts that were less well braced internally than the more anterior and more posterior parts of the shell, which were supported by the *in situ* girdles. As a final note, it is worth emphasizing that specimen LPB (FGGUB) R.2297 is currently the only fossil found at the 'La Cărare' locality – an attritional fossil assemblage recovered mainly from a channel deposit suggesting a relatively energetic fluvial setting – that shows a high degree of skeletal completeness, and even skeletal articulation with elements preserved in their lifetime position.

Systematic palaeontology

Testudinata Klein, 1760
Testudines Batsch, 1788
Pan-Pleurodira Joyce *et al.*, 2004
Dortokidae Lapparent de Broin & Murelaga, 1996

Remarks. *Dortokidae* contains three genera according to Lapparent de Broin *et al.* (2004) and Pérez-García *et al.* (2014) – *Dortoka vasconica*, *Ronella botanica* and *Eodortoka morellana*. *Ronella* was synonymized with *Dortoka* by Cadena & Joyce (2015), an opinion which we follow herein. The same authors considered *Eodortoka morellana* as a *nomen dubium* due to the fragmentary nature of the material and the utility of the species. However, we here treat it as a valid taxon because of the presence of diagnostic characters such as the unique possession of mesoplastra among dortokids (see Pérez-García *et al.* 2014) and because of its basal placement in the phylogeny (see below).

Dortoka Lapparent de Broin & Murelaga, 1996

Diagnosis. Members of the genus are characterized by the possession of the following synapomorphies: (1) distinct microsculpturing of the shell, consisting of a micro-reticulate pattern; (2) distinct macrosculpturing of the neurals, consisting of anteroposteriorly elongate pits and ridges; (3) absence of contact between the first peripheral and the first costal; (4) irregularly shaped neurals; (5) the second pleural overlaps the first costal; and (6) absence of mesoplastra (modified after Cadena & Joyce 2015).

Dortoka vremiri sp. nov.

(Figs 3–6)

Diagnosis. Medium-sized dortokid turtle characterized by the following unique combination of characters: (1) first pair of costals meet anterior to neural 1 and are sutured to one another near the midline; (2) last pair of costals meet posterior to neural 8 and have a well-developed median suture; neural 8 thus does not make contact with the suprapygal (also present in some specimens of *D. vasconica*); (3) cervical scale is absent (also seen in some specimens of *D. vasconica*); (4) first pair of pleural scales restricted to the first costals, not contacting the second costals (also present in *D. botanica*, an indeterminate dortokid from the Csehbánya Formation of Iharkút, and an indeterminate dortokid from the Gosau Group of Muthmannsdorf, see below); (5) second pair of pleurals not contacting costals five (also present in *D. botanica*); (6) the sulcus between vertebrals 4 and 5 is located far posteriorly on the last neural and the last, fifth vertebral does not contact costals 7; (7) greatest width of entoplastron in the anterior third of the bone; (8) pectoral scales contacting the entoplastron (also present in *D. botanica*); (9) small extragulars, at least three times shorter than the gular (also present in *D. vasconica* and *Eodortoka morellana*).

Derivation of name. The species is named in honour of our late colleague Mátyás Vremir, who passed away in June 2020, who skilfully prepared and studied the holotype specimen, and whose research greatly improved our understanding of fossil vertebrate faunas from Romania, including turtles.

Holotype. LPB (FGGUB) R.2297, a partial skeleton with most of the carapace and the complete plastron preserved in contact, together with the exposed *in situ* right scapula and right pubis; the left-side counterparts of these girdle elements are potentially also preserved inside the shell (see above).

Type locality. The holotype was found in 1995 at the locality 'La Cărare' in the Sibişel Valley (see also Csiki *et al.* 2010), near Sânpetru, central Haţeg Basin, Hunedoara County, Romania (Figs 1B, 2). The holotype was discovered in a bone-bed layer that also yielded several other vertebrate remains (see above).

Type stratum. Basal, coarse pebbly sandstone bed of the 'La Cărare' locality in the lower part of the Sînpetru Formation. The age of the Sînpetru Formation has been estimated as early–late Maastrichtian (Grigorescu 1983; Grigorescu & Csiki 2002; Panaiotu & Panaiotu 2010; Csiki-Sava *et al.* 2016), and based on the relative position of the type locality within the formation, it is most probably of early (at most earliest late) Maastrichtian in age.

Remarks. According to the most recent comprehensive review of the *Dortokidae*, there are two valid species of *Dortoka* that are very closely related and only differ in some minor aspects of their shell morphology, *D. vasconica* and *D.* (= *Ronella*) *botanica* (Cadena & Joyce 2015). Since the new taxon from the Late Cretaceous of the Haţeg Basin described here closely resembles both formerly recognized species of *Dortoka*, shares exclusive characters with both of these, and was found in our phylogenetic analysis to be the sister-taxon to *D. botanica* (see below), we here refer the new dortokid to the genus *Dortoka*.

Comments. The presence of dortokid turtles in the Late Cretaceous of the Transylvanian area was first reported by Vremir (2004). Subsequently, a new dortokid genus and species from the Transylvanian Basin, '*Muehlbachia nopcsai*', was erected by Vremir & Codrea (2009) based on a partial, disarticulated plastron and associated carapace fragments from the Late Cretaceous of Vurpăr. This taxon, however, was named in an abstract book and therefore does not fulfil the requirements defined by the ICZN (1999) (see also Cadena & Joyce 2015). The genus and species was thus subsequently considered to be invalid by several authors (Rabi *et al.* 2013; Cadena & Joyce 2015). The holotype specimen from the Haţeg Basin described here, LPB (FGGUB) R.2297, was briefly mentioned in Rabi *et al.* (2013) as belonging to a new but unnamed dortokid genus and species.

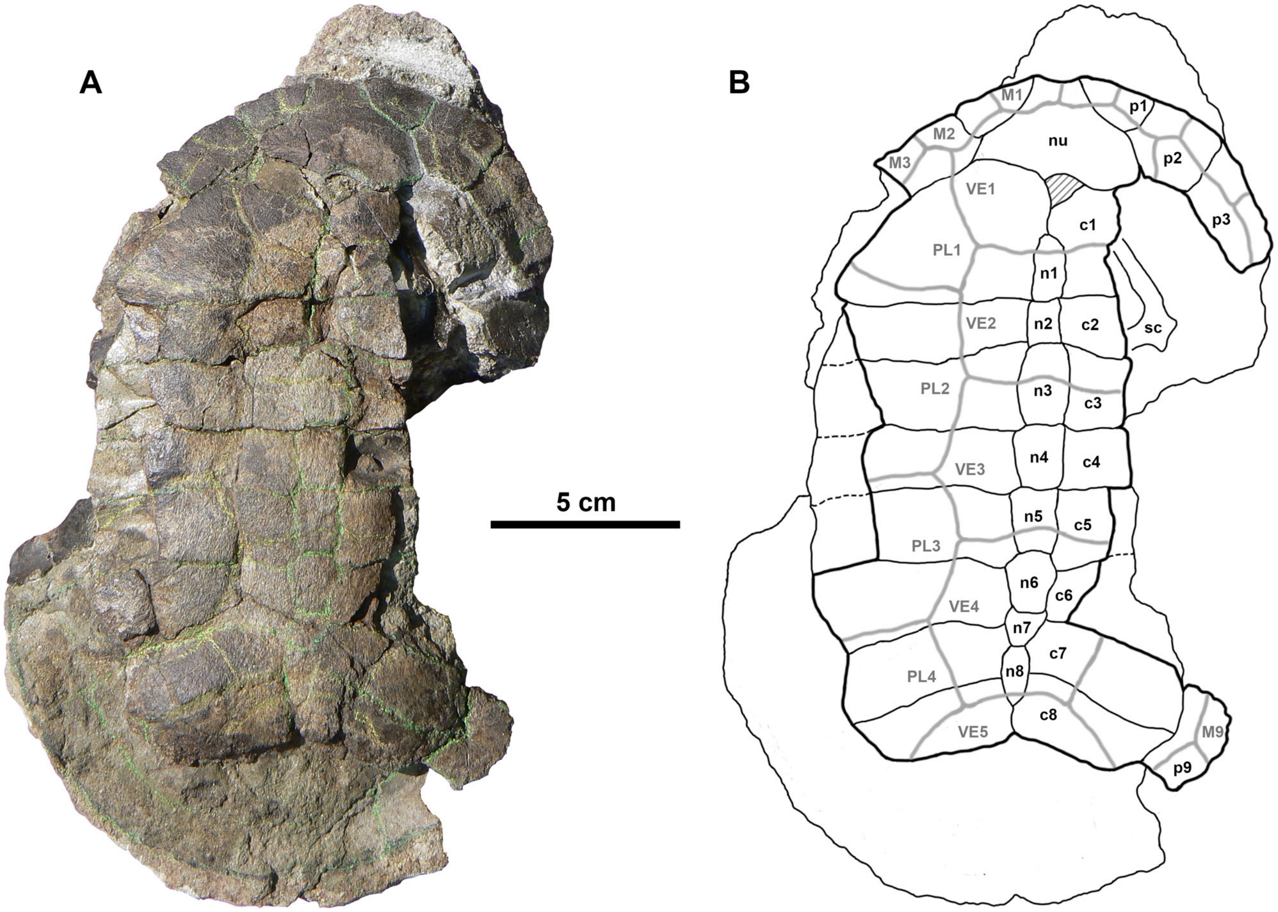

Figure 3. Holotype carapace of *Dortoka vremiri* sp. nov., LPB (FGGUB) R.2297, from the Upper Cretaceous Sînpetru Formation of the south-central Haţeg Basin, near Sânpetru. **A,** photograph and **B,** drawing of the carapace in dorsal view, both to the same scale. **Abbreviations**: **c**, costal; **M**, marginal scale; **n**, neural; **nu**, nuchal; **p**, peripheral; **PL**, pleural scale; **VE**, vertebral scale.

Description

The carapace of LPB (FGGUB) R.2297 is well-preserved and comprises the nuchal, all eight neurals, remnants of all eight costals on the left and right side, as well as left peripherals 1–2 and right peripherals 1–3 and 9 (Fig. 3). The specimen does not show any evidence for fontanelles, though it should be acknowledged that some of the respective segments (i.e. the lateral parts) of the carapace are incompletely known in the holotype. Most peripherals, the lateral parts of some costals, as well as the suprapygal and the pygal are missing. Nevertheless, the matrix of the block containing the carapace and the posterior part of the plastron (Fig. 3) preserves the impression of the missing posterior margin of the carapace, whereas the larger block that preserves the anterior-middle sections of the plastron also shows impressions of the missing, most distal right-side peripherals, allowing a reliable estimate both of the size and general contour of the shell, as well as of its morphology. When complete, the carapace would have been approximately 19 cm long and oval in shape. The carapace is still partly embedded in the original sandstone matrix but it was separated from the plastron during preparation.

The plastron is almost complete, comprising both epiplastra, the entoplastron, both hyoplastra, hypoplastra and xiphiplastra (Figs 4, 5). The mesoplastra are absent. The plastron is currently preserved in two different sandstone slabs, resulting from the preparation process, with the anterior part and the posterior part, respectively, separated. The anterior part is exposed in dorsal view and has subsequently been partly removed from the sandstone matrix in order to expose its ventral side as well. The posterior part is exposed in ventral view only. The plastron is generally long and narrow, and has a length of approximately 15.5 cm. Both the carapace and the plastron exhibit the micro-reticulate shell ornamentation that is typical for dortokids. The plates of the carapace and plastron are relatively thin, especially when compared to the contemporaneous and sympatric turtle *Kallokibotion*.

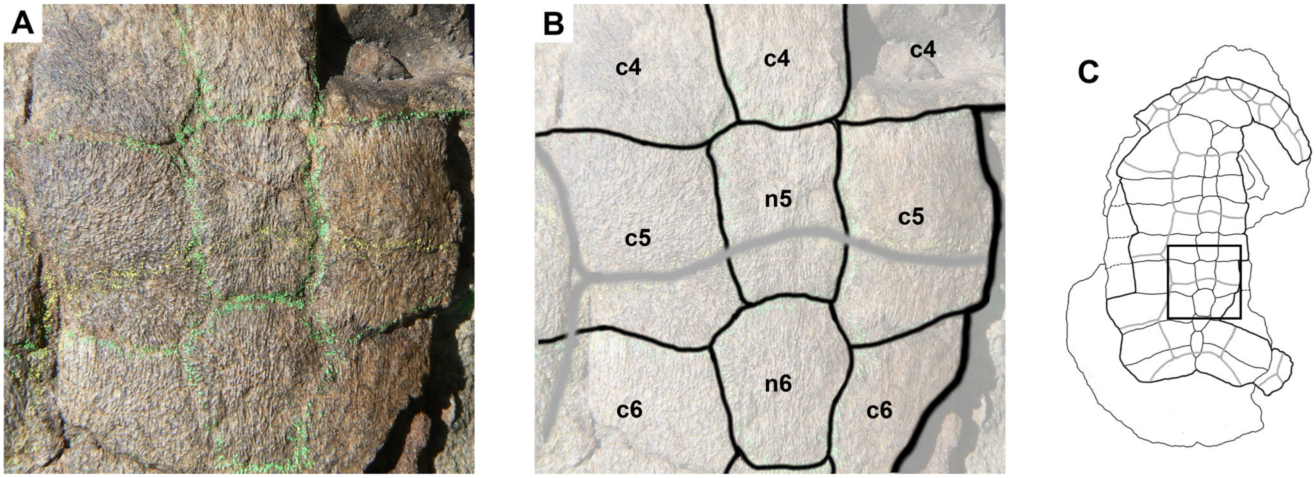

Figure 4. Detail of the holotype carapace of *Dortoka vremiri* sp. nov., LPB (FGGUB) R.2297, from the Upper Cretaceous Sînpetru Formation of the south-central Haţeg Basin, near Sânpetru showing the characteristic texture of the shell. The microsculpturing consists of a microreticulate pattern. The macrosculpturing, particularly of the neurals, comprises anteroposteriorly elongate pits and ridges. **A,** photograph and **B,** drawing of the middle part of the carapace in dorsal view, both to the same scale. **C,** overview drawing of the carapace highlighting the position of A and B. **Abbreviations**: **c**, costal; **n**, neural.

Carapacial bones. The nuchal is a trapezoidal element and wider mediolaterally than long anteroposteriorly with a width to length ratio of approximately 1:1.5. The element is slightly asymmetrical as the right side is generally larger and extends farther posteriorly. There is a small nuchal emargination. The nuchal is sutured to the first and second peripherals as well as to the first costals. The lateral suture to the first peripherals and the first costals is concave, whereas it is somewhat convex between the nuchal and the second peripherals. Posterior to the nuchal, a small and roughly triangular part of the carapace is missing and the sedimentary matrix below is exposed. Because the posterior margin of the nuchal shows internal bone structure at this part, the nuchal is probably broken posteriorly and thus its true posterior extension cannot be assessed.

The neural series is complete and consists of eight elongated elements. The neurals exhibit a distinct pattern of shell macrostructure consisting of shallow anteroposteriorly oriented grooves and ridges. The first neural is long and narrow and bordered by the first pair of costals anteriorly, thus not contacting the nuchal. The second neural is rectangular, relatively short and narrow. The third neural is large, almost rectangular in shape and much broader than the more anterior neurals. Neurals 4, 5 and 6 are also relatively large and broad, but have a more trapezoidal to hexagonal morphology, their broadest part being located anteriorly. Neural 7, trapezoidal to roughly triangular in shape, is the smallest element of the series. Neural 8 is very narrow and elongated, with a pointy end posteriorly.

Eight costals are present in the new dortokid from the Haţeg Basin but only costal 1 and 6 of the left side, as well as costals 7 and 8 of both sides are virtually complete. The remaining costals of the left side (i.e. 2, 3, 4 and 5) are almost complete, and impressions of these costals on the rock matrix extend some centimetres beyond the breakages. On the right side, only the medial part of costals 1–6 is preserved. The first costal is large and much wider anteroposteriorly than the other elements in the series. It has a trapezoidal to triangular outline with a slightly rounded anterior margin. The first costal makes contact with the nuchal, neural 1, and at least with peripherals 2 and 3. Additionally, the first costals meet each other at around midline, separating the first neural from the nuchal anteriorly. Costals 2–6 are comparatively straight and rectangular, extending mainly mediolaterally. Additionally, they are the longest costals in the series. The suture between these costals is straight and slightly undulating. The second costal makes contact only with the second neural, the third costal with neurals 2–4, the fourth costal with neurals 4 and 5, the fifth costal with neurals 5 and 6, the sixth costal with neurals 6 and 7, and the seventh costal with neurals 7 and 8. Costals 7 and 8 are shorter and directed posterolaterally. Like the previous costals, these are also rectangular to slightly trapezoidal in shape. The eighth costal is only sutured to neural 8; in addition, these last costals meet one another at midline posterior to neural 8. Therefore, neural 8 does not have contact with the suprapygal.

In LPB (FGGUB) R.2297, only the first two peripherals are preserved on the left side and the first three peripherals on the right side. Moreover, one of the posterior peripherals (peripheral 9) is present on the right side. Imprints of peripherals 7, 8 and 9 on the left side

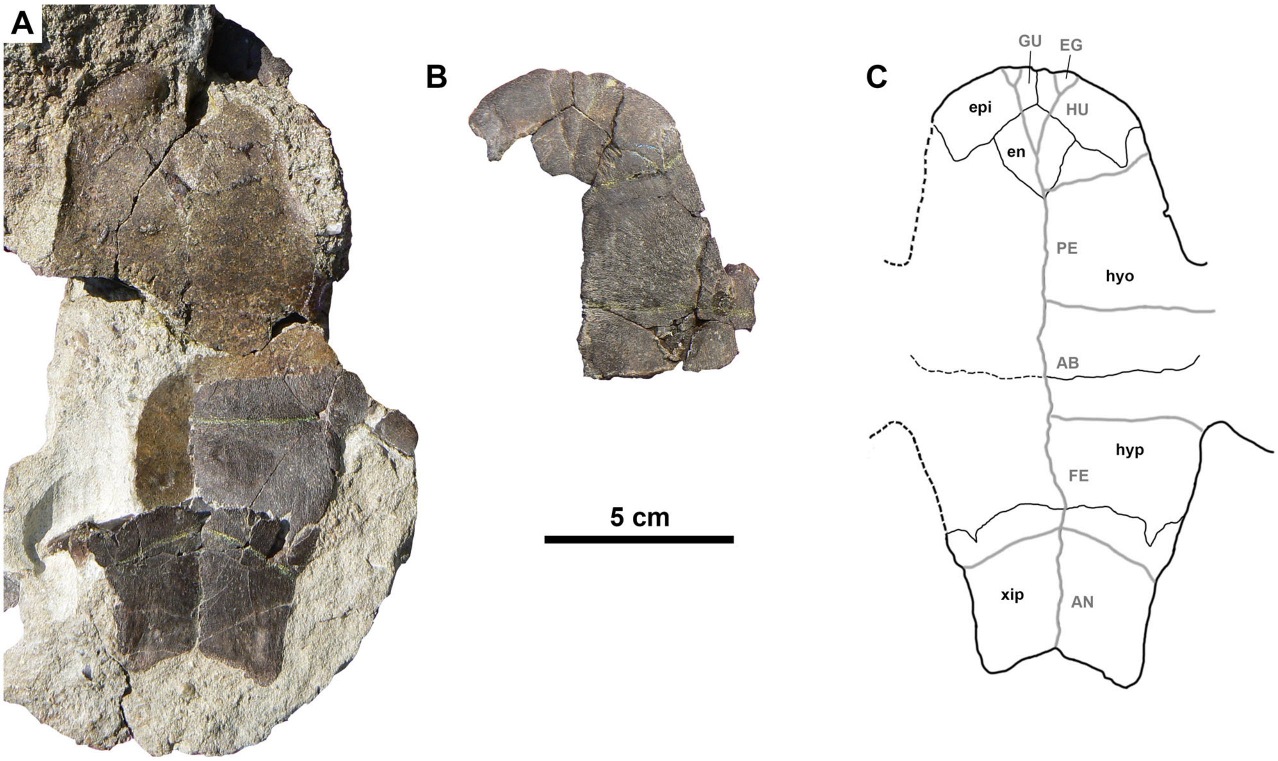

Figure 5. Holotype plastron of *Dortoka vremiri* sp. nov., LPB (FGGUB) R.2297, from the Upper Cretaceous Sînpetru Formation of the south-central Haţeg Basin, near Sânpetru. The plastron is preserved in two different sandstone slabs, the posterior part being exposed in ventral view (A) and the anterior part in dorsal view; later, the anterior part was partially removed from the rock matrix (B). **A,** photograph of the posterior lobe of the plastron in ventral view. **B**, photograph of the anterior part of the plastron in ventral view. **C**, drawing of the plastron in ventral view. All to the same scale. **Abbreviations**: **AB**, abdominal scale; **AN**, anal scale; **EG**, extragular scale; **en**, entoplastron; **epi**, epiplastron; **FE**, femoral scale; **GU**, gular scale; **HU**, humeral scale; **hyo**, hyoplastron; **hyp**, hypoplastron; **PE**, pectoral scale; **xip**, xiphiplastron.

as well as the anterior part of peripheral 10 on the right side are partially visible. Peripheral 1 is elongated, asymmetrical and narrow. Peripherals 2 and 3 are much wider mediolaterally and have a trapezoidal to rectangular shape. Peripherals 1 and 2 are sutured to the nuchal. The posterior-most peripheral preserved in the series is a rectangular element and represents probably peripheral 9, making contact with costals 7 and 8.

Carapacial scales. The carapace exhibits impressions of the five vertebral scales, four pleural scales and the first three marginal scales. A cervical scale is absent. The first vertebral is trapezoidal in outline and covers most of the nuchal, the anterior part of neural 1, the anteromedial part of costals 1, and to a much lesser degree the posteromedial parts of peripherals 1 and 2. The second vertebral scale has a quadrangular shape and covers the posterior part of neural 1, neural 2, the anterior part of neural 3, and the medial parts of costals 1–3. The third vertebral is hexagonal in shape, covering the posterior part of neural 3, neural 4, and the anterior part of neural 5, as well as the posteromedial part of costal 3, the medial part of costal 4, and the anteromedial part of costal 5. The fourth vertebral is also hexagonal in outline and covers the posterior part of neural 5, neurals 6 and 7 together with the anterior part of neural 8, as well as the anteromedial part of costal 5, the medial part of costals 6–7, and the anteromedial part of costal 8. The fifth and last vertebral is only partly preserved but seems to be more rounded at least anteriorly. It covers only the posterior-most part of neural 8 and the posterior part of costal 8; its posterior extent cannot be assessed due to the lack of the suprapygal and the pygal.

The first pleural scale is triangular in outline and covers only the lateral part of costal 1, the posteromedial part of peripheral 2, the medial part of peripheral 3, and probably also the anteromedial part of peripheral 4. Pleurals 2, 3 and 4 are only partly preserved as most of the lateral portion is missing. The second pleural scale covers the posterior-most part of costal 1, the lateral part of costals 2 and 3 as well as the anterior part of costal 4. The third pleural scale extends over the posterior-most part of costal 4, the lateral part of costal 5, and the anterior part of costal 6. The fourth pleural covers

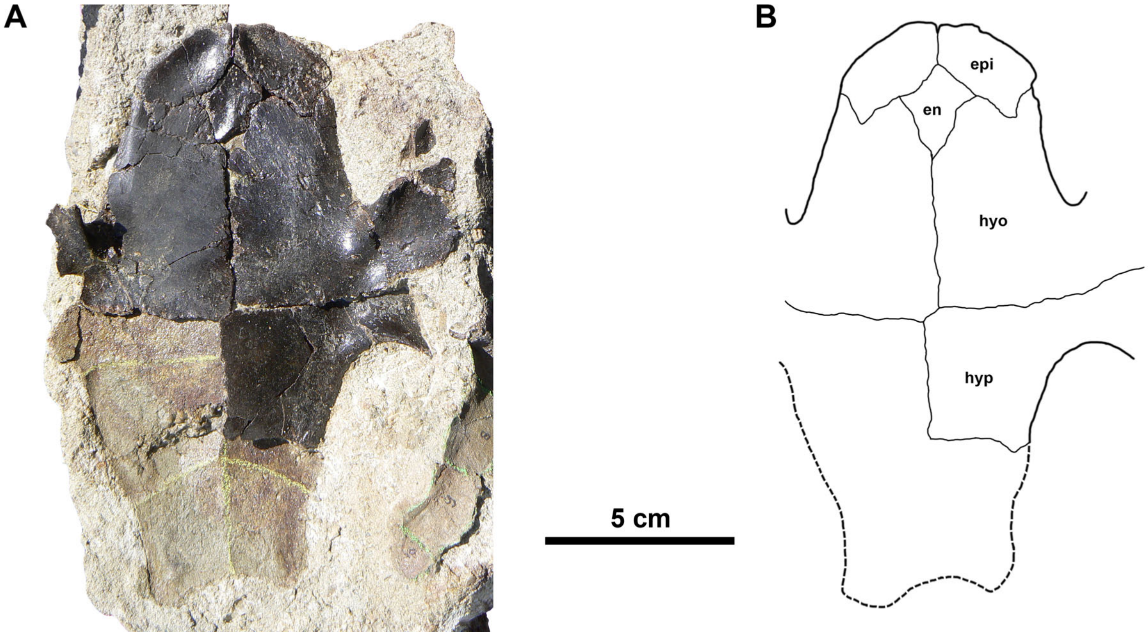

Figure 6. Holotype plastron of *Dortoka vremiri* sp. nov., LPB (FGGUB) R.2297, from the Upper Cretaceous Sînpetru Formation of the south-central Haţeg Basin, near Sânpetru. The plastron is preserved in two different sandstone slabs, the posterior part being exposed in ventral view (see also Fig. 4A) and the anterior part in dorsal view; later, the anterior part was partially removed from the rock matrix (Fig. 4B). **A,** photograph and **B,** drawing of the anterior part of the plastron in dorsal view, both to the same scale. **Abbreviations**: **en**, entoplastron; **epi**, epiplastron; **hyo**, hyoplastron; **hyp**, hypoplastron.

the posterior-most part of costal 6, the lateral part of costal 7, and the anterior part of costal 8, as well as the medial part of peripheral 9.

Marginal scale 1 extends over the anterolateral part of the nuchal and the anterior part of peripheral 1. The second marginal covers the posterolateral part of peripheral 1 and the anterolateral part of peripheral 2. The third marginal extends over the posterolateral part of peripheral 2 and the anterolateral part of peripheral 3. The sulci of the remaining marginals are not discernible.

Plastral bones. The epiplastra are elongated and trapezoidal in morphology, extending mainly posterolaterally. The anterior margin of the epiplastra is rounded and they have a straight median suture. The suture with the hyoplastron is triangular with a pointy tip reaching far posteriorly. The entoplastron is diamond-shaped, being slightly longer anteroposteriorly than wide mediolaterally. The broadest part of the entoplastron is at the level of the epiplastron–hyoplastron suture, approximately at the anterior third of the bone. The entoplastron is narrower and slightly more elongated in dorsal view than in ventral view. The hyoplastra are in contact with the epiplastron anteriorly, with the entoplastron anteromedially, and with the hypoplastron posteriorly. The suture between the hyoplastron and the hypoplastron is rather straight and located near the middle of the plastron. The hypoplastron is considerably smaller than the hyoplastron and is sutured to the xiphiplastron posteriorly. The suture between the hypoplastron and the xiphiplastron is relatively straight, although the hypoplastron forms a small triangular posterior protrusion close to the lateral margin. The suture between the hyo- and hypoplastron with the carapace is not preserved. The xiphiplastra form slightly more than half of the posterior lobe. A well-developed anal notch is present between the two xiphiplastra. The posterior part of the xiphiplastra is triangular in dorsal and ventral view. The midline suture between the xiphiplastra, the hypoplastra and the hyoplastra is straight in dorsal and ventral view.

Plastral scales. A single gular scale is present that is triangular and anteroposteriorly elongated, covering the medial part of the epiplastron and the anteromedial part of the entoplastron. The sulcus between the gular and the humeral splits anteriorly, thus enclosing a small and triangular extragular scale that is located at the anterior margin of the anterior lobe between the gular and the humeral. The humeral is trapezoidal to triangular in shape and covers the posterolateral part of the epiplastron and the posterolateral part of the entoplastron. The pectoral is almost as long anteroposteriorly as it is wide mediolaterally. It covers a small portion of the posterior entoplastron and the anterior part of the hyoplastron.

The sulcus between the pectoral and the humeral is straight and directed anterolaterally, the sulcus between the pectoral and the abdominal is straight and directed mediolaterally. The abdominal is rectangular with a straight sulcus anteriorly and posteriorly, both directed mediolaterally. It equally covers the posterior part of the hyoplastron and the anterior part of the hypoplastron. The femoral is rectangular to trapezoidal in morphology and covers the posterior part of the hypoplastron and to a lesser degree the anterior part of the xiphiplastron. The posterior sulcus of the femoral is straight and directed posterolaterally. The anal is quadrangular to trapezoidal in shape and covers the posterior part of the xiphiplastron. The median sulcus between the paired anal, femoral, abdominal, and pectoral scales is nearly straight and runs anteroposteriorly up to the centre of the entoplastron, where it splits and thus creates the unpaired gular.

Appendicular bones. The specimen exposes the right scapula *in situ*, still partially covered by the shell (Fig. 3). The length of the elements cannot be fully assessed but the angle between the dorsal process and the acromial process is close to 90°. The pubis is also preserved *in situ*, but the morphology is difficult to discern because it is still partly embedded in the sediment matrix and covered by the plastron. From what can be seen, however, it is evident that the pubis was sutured only to the xiphiplastron and is not contacting the hypoplastron.

Comparisons

Dortoka vremiri sp. nov. can be referred to *Dortoka* based on the presence of the following diagnostic features of the genus (see Cadena & Joyce 2015): (1) distinct microsculpturing of the shell, consisting of a microreticulate pattern; (2) distinct macrosculpturing of the neurals, consisting of anteroposteriorly elongate pits and ridges; (3) absence of contact between the first peripheral and the first costal; (4) irregularly shaped neurals; (5) the second pleural overlaps the first costal; and (6) absence of mesoplastra. This assignment is consistent with the results of the phylogenetic analysis performed here (see below) that recovered the new taxon as the sister-taxon of *Dortoka botanica*, together forming the sister-group to *D. vasconica*. In the following comparison, the holotype specimen described here is compared to all other known members of the *Dortokidae* – *Dortoka vasconica* from the Late Cretaceous of Spain and France (Lapparent de Broin & Murelaga 1996, 1999), *Dortoka* (= *Ronella*) *botanica* from the uppermost Paleocene of Romania (Gheerbrant *et al.* 1999; Lapparent de Broin *et al.* 2004), and *Eodortoka morellana* from the Early Cretaceous of Spain (Pérez-García *et al.* 2014). For an overview of the fossil record of the *Dortokidae*, as well as the diagnosis of *Dortoka vasconica* and *Dortoka* (= *Ronella*) *botanica*, see Cadena & Joyce (2015). We here tentatively regard the genus *Eodortoka* as valid (*contra* Cadena & Joyce 2015), although it is known from relatively fragmentary remains lacking the neurals, most peripherals and most costals, as well as the epiplastron and the entoplastron (Pérez-García *et al.* 2014), thus limiting the comparison with the new Romanian taxon.

Carapacial bones. The nuchal of *Dortoka vremiri* sp. nov. is relatively wide and short, which is similar to the condition seen in *D. botanica*, but different from the somewhat longer nuchal in *D. vasconica* and *Eodortoka*. The first neural is somewhat elongated in all dortokids. In all dortokids except *D. vremiri*, the first neural contacts the nuchal anteriorly. The second neural is small, rectangular and narrow in *D. vremiri* and *D. botanica*, whereas it is much wider and trapezoidal in morphology in *D. vasconica*. The third neural is large and rectangular in all dortokids. The fourth neural is proportionally larger in *D. vremiri* and *D. botanica* than in *D. vasconica*. Neurals 5 and 6 are hexagonal in all dortokids; however, the sixth neural is somewhat more elongated in *D. vremiri* than in other members of the family. Neural 7 is triangular and very small in *D. vremiri* but much larger and hexagonal in the other dortokids. The eighth neural is short and quadrangular in *D. vasconica* and thus differs from the more elongated neural 8 of *D. vremiri* and *D. botanica* that additionally has a pointy posterior tip. *D. botanica* differs from other dortokids in the possession of a ninth neural that is elongated and trapezoidal. Some specimens of *D. vasconica* have an incomplete neural series with some posterior elements missing. The neurals of *D. vasconica* and *D. botanica* exhibit very prominent and well-developed anteroposteriorly oriented grooves and ridges, while the holotype of *D. vremiri* only shows relatively shallow grooves and ridges on its neurals.

The morphology of the costals also closely resembles that of the other members of the family in that the first costal is generally a large, triangular to trapezoidal element, costals 2–6 are mediolaterally elongated with straight to undulating sutures, whereas costals 7 and 8 are the shortest elements in the series, being mainly posterolaterally oriented. However, the sutures between the costals and neurals differ within dortokids. *D. vremiri* differs from all other dortokids in that the first pair of costals meet each other near the midline, anterior to the first neural, along a well-developed suture. Additionally, the first costal contacts the nuchal and first neural in *D. vremiri*, whereas it is sutured to neurals 1 and 2 in other dortokids. The second costal is in contact only with the second neural in all dortokids. The third costal meets neurals 2, 3 and 4 in all dortokids except *D. botanica*, in which it sutures only to neurals 3 and 4. The sutures of costals 4–6 to the neurals do not vary within the family – costal 4 is sutured to neurals 4 and 5, costal 5 to neurals 5 and 6, and costal 6 to neurals 6 and 7. Costal 7 is in contact only with neural 7 in *D. vasconica*, which contrasts with the condition seen in *D. vremiri* and *D. botanica*, in which costal 7 meets both neurals 7 and 8. The last costal contacts neurals 7 and 8 in *D. vasconica* and *Eodortoka*, whereas it only contacts neural 8 in *D. vremiri*. Additionally, *D. vremiri* differs from most dortokid specimens in that the eighth costals meet each other posterior to neural 8 and have a well-developed midline suture; consequently, there is no contact between the suprapygal and neural 8 in *D. vremiri*. The same condition is seen in some specimens of *D. vasconica*, in which the posterior neurals are reduced. In *D. botanica*, costal 8 is sutured to neurals 8 and 9. The preserved peripherals of *D. vremiri* are generally very similar to that of the other dortokids in being quadrangular to rectangular.

Carapacial scales. The carapacial scales are overall similar in all dortokids. The cervical scale is absent in *D. vremiri* and some specimens of *D. vasconica*, while it is present in most other dortokids. In *D. botanica* and also most specimens of *D. vasconica* it is usually small and restricted to the anterior portion of the nuchal. In contrast, the cervical scale of *Eodortoka* is anteriorly splayed and also contacts the first peripherals. The first vertebral scale is more elongated in *D. vasconica* and *Eodortoka* than in *D. botanica* and *D. vremiri*. Vertebrals 2 and 3 are wider mediolaterally in *D. vremiri* than in the other dortokids. In addition, the anterior and posterior sulci of the second vertebral are concave in *Eodortoka* as opposed to the straight sulci in *D. vasconica*, *D. botanica* and *D. vremiri*. The fourth vertebral is the smallest in the series in *D. vasconica*, whereas it is equal in size to the other vertebrals in *D. vremiri* and *D. botanica*. Vertebral 5 is narrower mediolaterally in *D. vasconica* than in *D. vremiri* and *D. botanica*. *D. vremiri* differs from all other dortokids in that the sulcus between vertebral scales 4 and 5 runs across neural 8; in the other members of the family it runs across neural 7, or across the posterior costals in some specimens of *D. vasconica*. The second pleural of *D. vasconica* is proportionally much larger than in *D. vremiri* and *D. botanica*. Moreover, pleurals 1 and 3 are directed more anterolaterally and posterolaterally in *D. vasconica*, whereas they are directed more laterally in the other dortokids. Pleural 4 is similar in all dortokids. The marginalia are also very similar in all dortokids, with marginal 1 covering the nuchal and peripheral 1, marginal 2 covering peripherals 1 and 2, and marginal 3 covering peripherals 2 and 3.

Plastral bones. The anterior plastral lobe of *D. vremiri* resembles that of *D. vasconica* in being long and narrow anteroposteriorly when compared to *D. botanica* and *Eodortoka*. In contrast to all other members of the family, the epiplastron of *D. vremiri* is relatively narrow anteroposteriorly. In *D. vremiri* the epiplastron has a prominent posteriorly directed triangular protrusion that is also present in *D. vasconica* but absent in *D. botanica* and *Eodortoka*. The entoplastron is diamond-shaped in most dortokids except some specimens of *D. vasconica*, in which it is more oval. The entoplastron of *D. vremiri* differs from that of the other dortokids in being broadest anteriorly. The hyo- and hypoplastron are similar in all dortokids and have a more or less rectangular morphology. However, the hypoplastron has a prominent posteriorly directed triangular protrusion in *D. vremiri* that is absent in *D. vasconica*, *D. botanica* and *Eodortoka*. Similar to the condition reported in *D. vasconica* and *D. botanica*, *D. vremiri* lacks mesoplastra, and *Eodortoka* is the only dortokid known so far with mesoplastra. All dortokids have a well-developed anal notch and triangular posterior xiphiplastra.

Plastral scales. Small triangular extragulars, less than one-third the length of the gular scale, are present in both *D. vremiri* and *D. vasconica*. In *D. botanica*, they are significantly larger, amounting to more than half of the length of the gular scale, and extending over nearly half of the epiplastron. The gular scale is triangular and anteroposteriorly elongated in all dortokids, covering the anterior portion of the entoplastron and the anteromedial part of both epiplastra. In *D. vremiri* and *D. botanica,* the pectoral scale partly overlies the entoplastron, whereas the entoplastron is only covered by the humeral in *D. vasconica* and *Eodortoka*. Additionally, the pectoral curves strongly posteriorly in *D. vasconica* and *Eodortoka*, while it is straight in *D. vremiri* and *D. botanica*. The femoral covers both the hypoplastron and xiphiplastron in all dortokids, although it is largely restricted to the hypoplastron in *D. vasconica* and barely extends over the xiphiplastron. The abdominal scale is very similar in all dortokids and covers both the hyo- and the hypoplastron. The anal scale is restricted to the xiphiplastron in *D. vremiri*, *D. botanica* and *Eodortoka*, whereas in most specimens of *D. vasconica* the anals also cover the hypoplastron to a small extent.

Phylogenetic analysis

In order to assess the phylogenetic relationships of *Dortoka vremiri* sp. nov., we performed two sets of parsimony analyses, one using the global pan-pleurodiran matrix of Hermanson *et al*. (2020) and another using the dortokid matrix of Pérez-García *et al*. (2017).

Global pleurodiran phylogenetic analysis

In order to assess the global phylogenetic relationships of the new dortokid species *Dortoka vremiri* within *Pan-Pleurodira*, a global pleurodiran phylogenetic analysis was performed. For the analysis the character-taxon matrix of Hermanson *et al*. (2020) was used, which is the most recent pleurodiran matrix available, and includes 285 characters for 132 in-group taxa with *Proganochelys* as the outgroup. The data-matrix is an expansion of the global pleurodiran matrix of Ferreira *et al*. (2018), which in turn builds upon the classic pleurodiran matrix of Gaffney *et al*. (2006), but includes many additional postcranial characters. We revised six incorrectly coded characters for *Dortoka botanica* and *D. vasconica* (chs. 171, 175, 205, 224, 237 and 285; see Supplemental material S5). We included the herein described *Dortoka vremiri* sp. nov., for which we could score 48 characters (the complete data matrix can be found in the Supplemental material). We treated all characters as equally weighted and some multistate characters as ordered (following Hermanson *et al*. 2020). The dataset was run in TNT v. 1.5 (Goloboff & Catalano 2016) with Traditional Search and two rounds of tree bisection reconnection algorithm using 1000 replicates (second round applied to all trees in memory). The analysis recovered 480 equally parsimonious trees of 1511 steps. *Dortokidae* forms the sister group of *Pleurodira* in the strict consensus tree. The absence of seven character states support the placement of *Dortokidae* outside the crown-group of pleurodires in all trees (see Supplemental material S1 for list). The three species of *Dortokidae* included in this matrix, *Dortoka vasconica*, *D. botanica*, and *D. vremiri*, are unresolved, which is unsurprising because this dataset is not sampling dortokid-specific characters.

In-group phylogenetic analysis of *Dortokidae*

In order to assess the phylogenetic relationships of *Dortoka vremiri* sp. nov. within *Dortokidae*, a second in-group phylogenetic analysis was also performed. For this analysis the character–taxon matrix of Pérez-García *et al*. (2017) was used, which is the most recent dortokid matrix; it includes 30 characters for three in-group taxa and *Platychelys* as the outgroup. We kept the stem-pleurodire *Platychelys oberndorferi* in our version of the dataset but owing to its highly specialized morphology, which in many aspects is likely not plesiomorphic for *Pan-Pleurodira*, we no longer used it as outgroup. Instead, we added the paracryptodire *Pleurosternon bullocki*. In addition, we added three extant pleurodires: *Podocnemis lewyana*, *Pelomedusa subrufa*, and *Hydromedusa tectifera*. We ordered character 18 because it forms a clear morphocline and deleted characters 15 and 19 (see Supplemental material S1). Moreover, we included two new characters (see Supplemental material S1) and the new species *D. vremiri* described here. This resulted in a new data matrix with nine taxa and 32 characters. We could score a total of 22 characters for the new taxon (the complete data matrix can be found in the Supplemental material S2). The dataset was run in TNT v. 1.5 (Goloboff & Catalano 2016) with Traditional Search and a single round of tree bisection reconnection algorithm using 1000 replicates. We added a molecular backbone constraint as the dataset of Pérez-García *et al.* (2017) is not designed to reconstruct the phylogeny of extant taxa. The constraint ((*Hydromedusa tectifera* (*Podocnemis lewyana* + *Pelomedusa subrufa*)) follows Pereira *et al.* (2017) and all fossil taxa except the outgroup were allowed to float into the constrained topology. Forcing all these fossil taxa outside the constraint topology did not affect the relationships of *Dortokidae*. The parsimony analysis recovered a single most parsimonious tree (Fig. 8A; Fig. S4) with a length of 43 steps. *Dortoka vremiri* sp. nov. was placed as the sister taxon of *Dortoka botanica* from the uppermost Paleocene of Romania. *Dortoka vasconica* from the Late Cretaceous of Spain forms the sister-taxon to this eastern European clade, while *Eodortoka morellana* from the Early Cretaceous of Spain is found to be the most basal dortokid.

Discussion

Phylogenetic relationships

The global pleurodiran phylogenetic analysis performed in this study recovers *Dortoka vremiri* nov. sp. nested within *Dortokidae* (Fig. 7), the clade forming the stem lineage of *Pleurodira*. In the in-group phylogenetic analysis of *Dortokidae* performed here (Fig. 8A), the sister-taxon relationship of *D. vremiri* and *D. botanica* is supported by two synapomorphies: first pleural scales that are restricted to the first costals and pectorals that partially cover the entoplastron. The exclusion of pleural 1 from costal 2 is unique to this clade among turtles. However, *D. vremiri* also shares the particularly small extragulars with *D. vasconica* to the exclusion of *D. botanica.* As in Pérez-García *et al.* (2017), *Eodortoka*

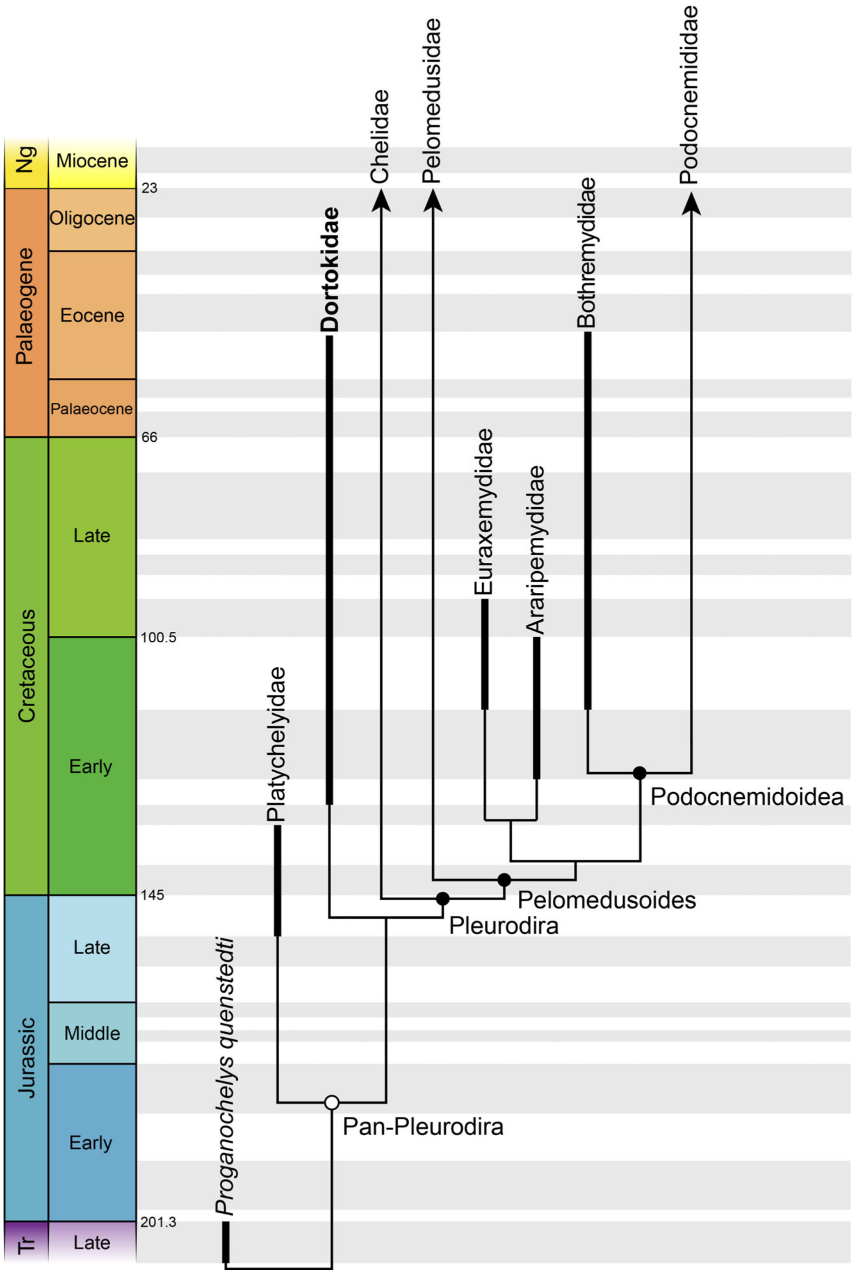

Figure 7. Phylogenetic and temporal relationships of the *Dortokidae* within the wider *Pleurodira*. The phylogenetic relationships are indicated by a simplified and time-calibrated strict consensus tree of the global pleurodiran phylogenetic analysis performed here using the data matrix of Hermanson *et al*. (2020). *Dortoka vremiri* sp. nov. is recovered as deeply nested within the *Dortokidae* in a polytomy with *Dortoka vasconica* and *Dortoka botanica*. For the in-group relationships of the *Dortokidae*, see Figure 8. For the complete strict consensus tree, see Supplemental material (Fig. S7). Modified after Hermanson *et al*. (2020). **Abbreviations**: **Ng**, Neogene; **Tr**, Triassic.

is the most basal dortokid due to the retention of mesoplastra and the pleural 1-2 sulcus not contacting costal 1. In addition, the present phylogenetic analysis recognizes two distinct lineages of *Dortoka*, comprising *D. vasconica* on the one hand and *D. vremiri* + *D. botanica* on the other.

Although not included in the phylogeny, the fragmentary indeterminate Hungarian dortokid from the Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút (Ősi *et al.* 2012b; Rabi *et al.* 2013) shares a synapomorphy with the lineage comprising *D. vremiri* and *D. botanica*, a first pleural that is restricted to the first costal and does not reach the second costal (Rabi *et al.* 2013). The similarly indeterminate Austrian dortokid, known from isolated costals only, from the Upper Cretaceous (early Campanian) Gosau Group of

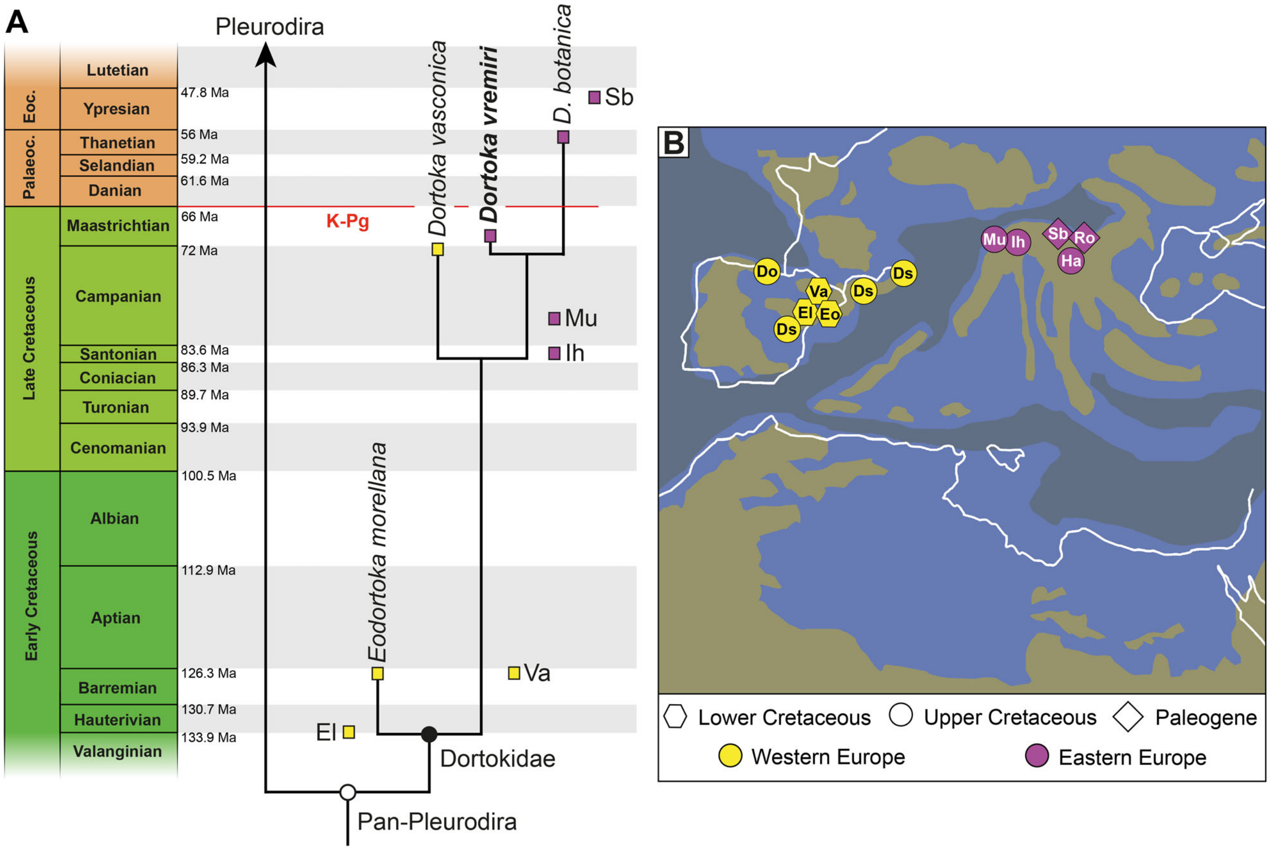

Figure 8. Phylogenetic relationships, as well as temporal and palaeogeographical position of *Dortoka vremiri* sp. nov. within the *Dortokidae*. **A,** strict consensus tree of the in-group phylogenetic analysis of the *Dortokidae* performed here using the modified data matrix of Pérez-García *et al.* (2017). For explanation of colours, see legend in B. There are two distinct lineages of derived dortokids, a western lineage comprising *Dortoka vasconica* from the Late Cretaceous of Spain and France as well as an eastern European lineage comprising *Dortoka vremiri* sp. nov. from the Late Cretaceous of Romania and *Dortoka botanica* from the uppermost Paleocene of Romania. **B,** palaeogeographical map of the Late Cretaceous European Archipelago depicting the distribution of the different dortokids. Modified after Rabi *et al.* (2013). **Abbreviations**: **Do**, *Dortoka vasconica* from the Late Cretaceous of Laño and Armuña, Spain; **Ds**, *Dortoka* sp. (*Dortoka vasconica*?) from the Late Cretaceous of southern and south-eastern France; **El**, indeterminate dortokid from the Early Cretaceous of El Castellar, Spain; **Eo**, *Eodortoka morellana* from the Early Cretaceous of Morella, Spain; **Ha**, *Dortoka vremiri* sp. nov. from the Late Cretaceous of the Haţeg Basin, Romania; **Ih**, indeterminate dortokid from the Late Cretaceous of Iharkút, Hungary; **Mu**, indeterminate dortokid from the Late Cretaceous of Muthmannsdorf, Austria; **Ro**, *Dortoka botanica* from the uppermost Paleocene of Rona, Romania; **Sb**, indeterminate dortokid from the lower Eocene of the Şimleu Basin, Romania; **Va**, indeterminate dortokid from the Early Cretaceous of Vallipón, Spain.

Muthmannsdorf also has a first pleural that is restricted to the first costal (Rabi *et al.* 2013), like *D. vremiri*, *D. botanica* and the Iharkút dortokid.

Allopatric speciation in *Dortoka* spp.

The phylogenetic analysis presented here suggests the presence of two distinct lineages of *Dortoka* during the Late Cretaceous, an eastern European lineage from the Tisia-Dacia block (including Transylvania from present day) and a western European lineage from the Ibero-Armorican area (Fig. 8B). The eastern lineage comprises *D. vremiri* from the Late Cretaceous (Maastrichtian) and *D. botanica* from the uppermost Paleocene (Thanetian), both from Romania. Based on a shared, unique synapomorphy (the restriction of pleural 1 to costal 1), the indeterminate Austroalpine (present day Hungary and Austria) dortokids most likely belong to this eastern European lineage as well (see also Rabi *et al.* 2013; Pérez-García *et al.* 2017). The western European lineage so far includes only *D. vasconica* from the Late Cretaceous (upper Campanian–lower Maastrichtian) of Spain and possibly southern France. The Hungarian and Austrian dortokids suggest that the split between the eastern and western European lineages occurred before the Santonian.

A faunal separation between the western Ibero-Armorican area and the more eastern Austroalpine and

Tisia-Dacia areas has previously been recognized for other vertebrate groups (Csiki-Sava *et al.* 2015), including turtles (Fig. 8B). The basal testudine turtle *Kallokibotion bajazidi* is only known from the eastern, Austroalpine and Transylvanian areas, whereas helochelydrid (= solemydid, see Joyce *et al.* 2016) turtles are restricted to the western, Ibero-Armorican landmasses (Rabi *et al.* 2013; Csiki-Sava *et al.* 2015). Similarly, kogaionid multituberculates have been discovered only in the Transylvanian area, in Eastern Europe, for the latest Cretaceous, whereas the Ibero-Armorican landmasses have yielded exclusively remains of eutherians, including lainodontine zhelestids (Gheerbrant & Astibia 2012; Csiki-Sava *et al.* 2015; Gheerbrant & Teodori 2021) from the same time period; remains of latest Cretaceous mammals are as yet completely unknown from the Austroalpine landmass. Remarkably, both of these regionally restricted mammalian groups are known to be endemic to Europe (Csiki & Grigorescu 2002; Gheerbrant & Astibia 2012; Smith & Codrea 2015), just as are two of the turtle clades cited above (dortokids and *Kallokibotion*).

Phylogenies and distribution of rhabdodontid ornithopod dinosaurs and allodaposuchid crocodilians suggest a similar regional east–west differentiation within their clades during the Late Cretaceous (e.g. Ősi *et al.* 2012a; Narváez *et al.* 2016; Dieudonné *et al.* 2021; although see Dieudonné *et al.* [2016] or Yang *et al.* [2020] for slightly different interpretations of the intra-clade relationships of rhabdodontids). Again, rhabdodontids are considered a clade of basal iguanodontians endemic to Europe (e.g. Weishampel *et al.* 2003, 2010; Ősi *et al.* 2012a; Csiki-Sava *et al.* 2015; Dieudonné *et al.* 2016), similarly to the dortokids, other testudinate clades as well as the different mammal groups, which show the clear eastern Europe–western Europe dichotomy in their distribution.

Palaeoecology of *Dortoka vremiri*

Dortokids have been interpreted either as semiaquatic (Lapparent de Broin & Murelaga 1999) or as aquatic freshwater turtles (Pérez-García *et al.* 2012). Lapparent de Broin and Murelaga (1999) based their interpretation mainly on the shell morphology of *D. vasconica* and its resemblance to that of the extant freshwater pleurodires such as *Pelomedusa* and *Pelusios*. Subsequently, Pérez-García *et al*. (2012) reassessed the palaeoecology of *D. vasconica* based on additional material as well as on the microstructure of the shell bones. They observed that the shell bones of *D. vasconica* exhibit compactness values similar to aquatic tetrapods and that this taxon accordingly was likely an aquatic turtle (Pérez-García *et al.* 2012). In addition, the new material of *D. vasconica* indicated the presence of fontanelles that remain open throughout ontogeny, also pointing to an aquatic lifestyle (Pérez-García *et al.* 2012). Rabi *et al*. (2013) furthermore noted that dortokid remains in Transylvania are most common in deposits accumulated under lower hydrodynamic conditions, such as within ponds, slow-flowing creeks, swamps, and oxbow lakes on the floodplain area. This distribution, together with their small size, led Rabi *et al*. (2013) to conclude that dortokids preferably inhabited quieter water bodies. Thus, based on all these different lines of evidence, *Dortoka* spp. are best regarded as semiaquatic to aquatic freshwater turtles.

Although Rabi *et al*. (2013) identified deposits formed in low-velocity to stagnant water bodies as preferential burial substrates for dortokid remains, it is worth emphasizing that actually some of the best-preserved and most complete dortokid specimens originate from different lithotypes. The holotype of *Dortoka vremiri* was discovered in a rather coarse channel sandstone (see above), suggesting a more hydrodynamically active depositional environment than that envisaged by Rabi *et al*. (2013). The associated remains of the Vurpăr specimen described as '*Muehlbachia nopcsai*' by Vremir & Codrea (2009) were discovered in red palaeosol-dominated deposits, and another associated dortokid specimen (partial plastron with attached pelvic elements) comes from dark red silty floodplain mudstones at Pui, in the Haţeg Basin. Also in Haţeg, at the Tuştea nesting site, isolated shell elements of dortokids were found alongside *Kallokibotion* fossils showing similar preservation style, in a brick red to dark red, micaceous and pedogenetically modified silty mudstone, of well-drained floodplain origin (Botfalvai *et al*. 2017). Finally, the only diagnostic turtle shell elements reported from the red, palaeosol-bearing lowermost portion of the continental Sebeș Formation exposed at Petrești-Arini, in the south-western Transylvanian Basin, were referred to dortokids by Vremir *et al*. (2014), whereas remains of *Kallokibotion* appear to be missing from these deposits. All these observations suggest that although *D. vremiri* was a semiaquatic to aquatic taxon, dortokid remains in the Maastrichtian of Transylvania are not restricted to sediments accumulated in ponding or very slowly moving waters.

Rabi *et al.* (2013) also noted that dortokids and *Kallokibotion* appear to never co-occur in the same sedimentary layer, even if they occur within the same outcrop. Recently, several localities in the Haţeg Basin yielded both *Kallokibotion* and dortokid remains from the same fossiliferous horizon, and among these, first of all is the type locality of *Dortoka vremiri*, the 'La Cărare' quarry. Here, remains referable to *Kallokibotion* (albeit, admittedly, almost exclusively in the form of isolated plates) were also recovered from the greyish-greenish coarse sandstones from which the type specimen LPB (FGGUB) R.2297 originate, whereas more complete *Kallokibotion* remains originate from the overlying brownish siltstones (Fig. 2F). Other important Transylvanian fossil localities where remains of the two taxa co-occur include the Tuştea nesting locality in the Haţeg Basin (e.g. Botfalvai *et al.* 2017) and the Vurpăr locality (south-western Transylvanian Basin) that yielded the associated dortokid shell remains formerly referred to as '*Muehlbachia nopcsai*' by Vremir (2010; for an overview of these localities, see Vremir *et al*. 2015).

Geographical selectivity across the Cretaceous–Paleogene extinction

A large number of the continental vertebrate groups that inhabited the latest Cretaceous European Archipelago have been reported to go extinct around the K-Pg boundary (Csiki-Sava *et al*. 2015). The reports of *Dortoka botanica* from the latest Paleocene of the former Tisia-Dacia block (including present day Transylvania in western Romania) have previously demonstrated that *Dortokidae* survived the K-Pg mass extinction (Gheerbrant *et al.* 1999; Lapparent de Broin *et al.* 2004; Rabi *et al.* 2013). However, in the absence of a phylogenetic framework for the Late Cretaceous dortokids from the Tisia-Dacia block, it has so far remained unclear whether *D. botanica* represents a Paleocene external immigrant or a local survivor. This is why the phylogenetic placement of the herein described latest Cretaceous *Dortoka vremiri* is particularly relevant, and its sister-taxon relationship with *D. botanica* suggests local survival of *Dortoka* on the Tisia-Dacia block. Whether the lineage survived elsewhere in eastern Europe remains uncertain in the absence of Maastrichtian and Paleocene vertebrate-bearing fossiliferous continental rocks. On the other hand, the western European Paleocene is better sampled for turtles, and here no dortokids have been identified from early Paleocene (Danian) or younger rocks (e.g. Groessens-Van Dyck 1985; Pérez-García 2020, and references therein), suggesting selectivity across the K-Pg extinction event for the group. This selectivity is best interpreted geographically as the low morphological disparity within the derived *Dortokidae* implies low ecological variability (based on the available evidence from shell morphology).

Another group where geographical selectivity may have played a role in survival are the kogaionid multituberculate mammals, an endemic clade and the only mammal group in the Transylvanian area during the Late Cretaceous (Csiki & Grigorescu 2002) and also recorded from the latest Paleocene vertebrate assemblage that yielded *Dortoka botanica* (Gheerbrant *et al.* 1999). The survival of the supposedly omnivorous kogaionids (e.g. Wilson *et al.* 2012; Augustin *et al.* 2019) and the extinction of the insectivorous zhelestid eutherians in western Europe contrasts with the pattern of the North American mammal turnover around the K-Pg boundary, where the mainly insectivorous eutherians show lower extinction rates than the dominantly omnivorous, more generalized multituberculates (Wilson 2013, 2014; Csiki-Sava *et al.* 2015). Ultimately, one cannot exclude that the preferential survival of some taxa in Transylvania (geographical selectivity) was due to special ecological properties of the local habitat. The more remote and thus potentially more protected palaeogeographical setting of the Transylvanian landmass (a neotethyan, intra-oceanic island, as opposed to the cratonic nature of the Ibero-Armorican landmass, surrounded at least in part by shallower epicontinental seas; Csiki-Sava *et al*. 2015) may have played a role in the differential survival of the eastern European dortokids and kogaionids.

Ecological extinction selectivity

As with geographical selection, testing for ecologically selective extinction also requires a phylogenetic framework of the taxa in question. With the newly identified sister-taxon relationship of the Late Cretaceous *Dortoka vremiri* and the Paleocene *D. botanica*, which suggests local survival of the eastern European derived dortokid lineage across the K-Pg boundary, a pattern of preferential survival of freshwater versus terrestrial turtles emerges for the mass extinction in Transylvania. *Kallokibotion bajazidi*, the only other turtle taxon currently known from the Late Cretaceous of Romania, had a more terrestrial lifestyle than *D. vremiri* based on its high domed carapace, dorsoventrally expanded skull, curved femur and humerus, and also supported independently by a recent investigation of its neuroanatomy (Rabi *et al.* 2013; Martín-Jiménez *et al.* 2021). In addition, a striking difference in taphonomical preservation between the two turtle taxa from the Haţeg Basin may reflect distinct ecologies. Except for the holotype of *D. vremiri*, all dortokid remains are markedly rare, isolated shell or other skeletal elements (e.g. LPB [FGGUB] R.1749, R.2015, R.2016, R.2398), whereas all the known partial shells and skeletons (e.g. LPB [FGGUB] R.1465, R.1466, R.1948, R.1960, R.1964, R.1996, R.2000–2003, R.2298, R.2710) belong to the far more common *Kallokibotion bajazidi.* Based on previous experimental work, turtle carcasses immersed in water degrade predominantly by bacterial decay and most of the skeleton disarticulates within 20 weeks, while in a terrestrial environment, insect larvae remove soft tissues and leave dry skin and bones; thereby, portions of the shell remain articulated even after three years (Brand *et al.* 2003). Following this empirical context, the relative abundance of articulated *K. bajazidi* materials from the Haţeg Basin suggests a preference for well-drained habitats. This pattern is consistent with the well-documented taphonomy of the Tuştea site, which is dominated by parautochthonous terrestrial fauna elements such as *Zalmoxes* and *Telmatosaurus*, while aquatic or semiaquatic taxa (anurans, *Albanerpeton*, the crocodyliform *Allodaposuchus*, and dortokids) are subordinately present (about 5%, see Botfalvai *et al.* 2017). The preservation mode (articulated and associated partial shells) and the frequency of *K. bajazidi* remains (about 21.4%) suggest that they were accumulated under similar taphonomical conditions as the parautochthonous fossils of terrestrial dinosaurs (Botfalvai *et al.* 2017) and were buried without significant transportation into a well-drained, more distal floodplain environment (Csiki *et al.* 2010). Meanwhile, dortokid remains, similarly to other aquatic or semiaquatic taxa, are rare at this site (about 0.8%) and are considered as allochthonous faunal elements, which were transported by periodic floods from the proximal, more water-logged settings to a more distal, floodplain environment (Botfalvai *et al.* 2017). *Kallokibotion bajazidi* is by far the most frequent turtle in the Haţeg Basin, where most of the bonebeds indicate a terrestrial depositional environment dominated by a terrestrial vertebrate assemblage (Csiki *et al.* 2010; Csiki-Sava *et al.* 2015; Botfalvai *et al.* 2021). This is in marked contrast with the predominantly aquatic fauna of Iharkút in Hungary (Ősi *et al.* 2012b, Botfalvai *et al.* 2015) where dortokid remains are far more common than those of *Kallokibotion* sp. (Rabi *et al.* 2013).

The extinction of *K. bajazidi* most likely occurred near or at the K-Pg boundary together with that of many other of the terrestrial Transylvanian vertebrates such as different groups of dinosaurs, as well as borioteiioid lizards or madtsoiid snakes (Csiki-Sava *et al.* 2015). The ecological selectivity of survival favouring aquatic taxa agrees well with the observed patterns from other continental vertebrate assemblages (particularly those of North America), where more terrestrial and larger vertebrates were found to be impacted the most by the extinction event (e.g. Archibald & Bryant 1990; Sheehan & Fastovsky 1992; Archibald 1996). The only other examples of terrestrial turtle extinctions across the K-Pg boundary include the clades Nanhsiungchelyidae and Helochelydridae (Hutchison & Archibald 1986; Lapparent de Broin & Murelaga 1999; Holroyd & Hutchison 2002; Joyce *et al.* 2011) but the list could prove to be more extensive with the clarification of the stratigraphical distribution, phylogeny, and ecology of several Late Cretaceous–Paleocene taxa.

Conclusions

A new species of dortokid pleurodiran turtle, *D. vremiri*, from the Upper Cretaceous Sînpetru Formation of the Haţeg Basin is described. The holotype specimen of the new taxon consists of a complete plastron and a nearly complete carapace with the right scapula and right pubis exposed *in situ*. *Dortoka vremiri* sp. nov. is clearly a member of the *Dortokidae* based on the presence of several synapomorphies of the family. Moreover, it differs from all other previously known dortokids in the possession of a unique combination of characters. Two phylogenetic analyses were performed to assess the position and interrelationships of *D. vremiri* within *Dortokidae* as well as within the wider *Pleurodira*. The global pleurodiran analysis recovered the new taxon to be firmly nested within *Dortokidae*, the latter placed as the sister-taxon of crown-pleurodires. In addition, the more exclusive phylogenetic analysis to assess the in-group relationships of dortokids recovered *Eodortoka* as the most basal dortokid, while the remaining members of the family form a clade of derived dortokids all belonging to the genus *Dortoka*. Within this more derived subclade, a sister-group relationship between *D. vremiri* and *D. botanica* was found.

The phylogenetic hypothesis presented here documents allopatric speciation through the presence of two distinct lineages of derived dortokids, an eastern European lineage distributed across the Austroalpine and Transylvanian areas (*D. vremiri* and *D. botanica*) as well as a western European lineage known from the Ibero-Armorican area (*D. vasconica*). The presence of two distinct dortokid lineages in eastern and western Europe supports previous hypotheses that identified biogeographical separation between the two areas during the Late Cretaceous. Such a faunal provinciality between the western and eastern European landmasses has previously been recognized for several groups, including *Kallokibotion* and helochelydrid (= solemydid, see Joyce *et al.* 2016) turtles as well as rhabdodontid dinosaurs, allodaposuchid crocodyliforms and mammals (Csiki-Sava *et al.* 2015). Moreover, the presence of *D. botanica* in uppermost Paleocene rocks of Romania together with the apparent extinction of dortokids in western Europe suggest some degree of geographical selectivity in the extinction patterns of terrestrial vertebrates on the Late Cretaceous European Archipelago. Since the only other turtle known from the Upper Cretaceous of the Transylvanian area, *Kallokibotion bajazidi*, was likely more terrestrial than the dortokids and probably went extinct at the K-Pg boundary, ecological selectivity of survivorship favouring aquatic over terrestrial taxa appears to have played an additional role during the K-Pg extinction event.

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SECOND PAPER

REAPPRAISAL OF THE BRAINCASE ANATOMY OF THE ORNITHOPOD DINOSAURS *TELMATOSAURUS* AND *ZALMOXES* FROM THE UPPER CRETACEOUS OF THE HAŢEG BASIN (ROMANIA) AND THE TAXONOMIC REASSESSMENT OF SOME PREVIOUSLY REFERRED SPECIMENS

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RESEARCH PAPER

Reappraisal of the braincase anatomy of the ornithopod dinosaurs *Telmatosaurus* and *Zalmoxes* from the Upper Cretaceous of the Haţeg Basin (Romania) and the taxonomic reassessment of some previously referred specimens

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Abstract

The hadrosauroid *Telmatosaurus* and the rhabdodontid *Zalmoxes* were the first and second dinosaur taxa that were described in detail from the famous Upper Cretaceous continental deposits of the Haţeg Basin by Franz Baron Nopcsa at the beginning of the twentieth century. Although they are among the most common and best-known dinosaurs discovered from these deposits, there are still many open questions as to their taxonomy and anatomy. Here, we re-describe two partial braincases from the uppermost Cretaceous of the Haţeg Basin that have been recently referred to the rhabdodontid *Zalmoxes* and re-assign them to hadrosauroids, possibly to *Telmatosaurus*. These specimens both exhibit basicranial features that are characteristic of derived hadrosauroids but are absent in more basal iguanodontians. These include an antero-posteriorly short basioccipital lacking a distinct neck, the presence of two well-developed sphenoccipital tubercles on the ventral aspect of the braincase and that are directly positioned anterior to the basioccipital, as well as a deep depression on the ventral aspect of the braincase between the sphenoccipital tubercles. The comparison provided herein demonstrates several important differences between the basicranium of hadrosauroids and that of rhabdodontids, which allows for the confident identification of even isolated and incomplete specimens. Moreover, the removal of the only basicranium that has been referred to *Zalmoxes shqiperorum* prompts a revised diagnosis of that species.

Keywords *Telmatosaurus* · Hadrosauroidea · *Zalmoxes* · Rhabdodontidae · Haţeg Basin · Braincase anatomy

Introduction

The hadrosauroid dinosaur *Telmatosaurus transsylvanicus* was the first vertebrate taxon named from the famous Upper Cretaceous vertebrate-yielding continental deposits of the Haţeg Basin in western Romania. It was described in detail by the renowned palaeontologist Franz Nopcsa based on a largely complete but crushed skull (Nopcsa 1900). In the following years, Nopcsa described a diverse vertebrate fauna from the Haţeg Basin including turtles, crocodyliforms, and dinosaurs (e.g., Nopcsa 1902a, b, 1904, 1923, 1929), which now is one of the best-known Late Cretaceous vertebrate assemblages of Europe (for an overview, see Weishampel et al. 1991; Grigorescu 2010; Csiki-Sava et al. 2015, 2016). A number of additional specimens referred to *Telmatosaurus* have been discovered and reported since the initial description by Nopcsa, both by himself as well as by other researchers more recently, making it one of the better-known taxa from the Haţeg Basin and the whole Upper Cretaceous of Europe (Weishampel et al. 1993; Dalla Vecchia 2006, 2009a); it is conceivable, however, that hadrosauroid fossils from the Transylvanian area that were customarily assigned to *Telmatosaurus transsylvanicus* may represent instead several, possibly closely related taxa (e.g., Dalla Vecchia

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2009a). Despite being hailed as the basal-most hadrosaurid dinosaur (e.g., Weishampel et al. 1993), *Telmatosaurus* is now generally regarded as a basal hadrosauroid, lying outside the radiation of derived hadrosaurids (Sues and Averianov 2009; Prieto-Márquez and Norell 2010; Godefroit et al. 2012a; McDonald et al. 2012). During the last decades, additional hadrosauroid taxa have been discovered in several different Upper Cretaceous units across Europe, revealing that the group was very successful and widespread on the Late Cretaceous European Archipelago (for an overview, see Dalla Vecchia 2006, 2009a, 2014; Prieto-Márquez et al. 2013). Most of these hadrosauroids, however, represent different hadrosaurid subclades more derived than the position reconstructed for *Telmatosaurus* (e.g., Pereda-Suberbiola et al. 2009; Cruzado-Caballero et al. 2010; Prieto-Márquez et al. 2013, 2019), with the notable exception of *Tethyshadros* from northeastern Italy (Dalla Vecchia 2009b) and *Fylax* from northeastern Spain (Prieto-Márquez and Carrera Farias 2021).

Despite being a relatively well-known taxon, there has been considerable debate over the referral of isolated and disarticulated remains to *Telmatosaurus*, primarily involving the other ornithopod dinosaur known from the Haţeg Basin, the rhabdodontid *Zalmoxes* (Weishampel et al. 1993, 2003; Brusatte et al. 2017). In fact, *Zalmoxes* was the second taxon that was described in detail by Nopcsa, although he originally referred the rhabdodontid material from the Haţeg Basin to *Mochlodon* and subsequently to *Rhabdodon* (Nopcsa 1902a, 1904, 1915, 1928). Only later, Weishampel et al. (2003) erected the new genus *Zalmoxes* for the rhabdodontid material from the Transylvanian area with the type species *Z. robustus* and its newly recognized sister-species *Z. shqiperorum*. The Rhabdodontidae is an endemic clade of Cretaceous European basal iguanodontians that are among the most common and abundant terrestrial vertebrates known to have inhabited the Late Cretaceous European Archipelago (e.g., Buffetaut and Le Loeuff 1991; Pereda-Suberbiola 1999; Weishampel et al. 2003; Ősi et al. 2012; Csiki-Sava et al. 2015; Dieudonné et al. 2016; Godefroit et al. 2017; Párraga and Prieto-Márquez 2019).

A recent re-investigation of the rhabdodontid cranial material from the Haţeg Basin also led to the re-examination of two partial ornithopod braincases that have been referred to *Zalmoxes* in the past. The first of these, UBB NVZ1-42 has been discovered from the Râul Mare River section near Nălaţ-Vad and was referred to *Zalmoxes shqiperorum* (Godefroit et al. 2009). The second, NHMUK R.3401A, is a historical Nopcsa specimen that was collected at the beginning of the twentieth century from the Sibişel Valley section of the Sînpetru Formation near Sânpetru. The latter specimen was, together with most of the original Nopcsa collection, later purchased by the Natural History Museum of London, where it is still deposited today. We here re-describe these specimens and, based on a through comparison with hadrosauroids as well as basal iguanodontians, we reject their rhabdodontid affinities and re-assign them tentatively to the hadrosauroid dinosaur *Telmatosaurus*.

Geological setting

The intramontane Haţeg Basin is located in the southwestern Carpathians, western Romania (Fig. 1a). Upper Cretaceous sedimentary rocks crop out mainly in the southcentral, central, southeastern and northwestern parts of the basin (Fig. 1b). The strata cropping out along the Sibişel Valley in the south-central parts of the Haţeg Basin represent the stratotype section of the Sînpetru Formation and yielded the quasi-totality of the original finds of Franz Nopcsa. The deposits in the northwestern parts of the basin have been referred to the Densuş-Ciula Formation, which differs from the Sînpetru Formation mainly in its higher content of volcanoclastic sediments mixed with the siliciclastics. Although other uppermost Cretaceous continental deposits in the central and southeastern parts of the basin are of a roughly similar age and yielded an overall similar vertebrate fauna with these two formally defined units, their precise correlation with either of the abovementioned formations has been rather contentious and they are often simply referred to as the ‘Râul Mare River section’ and the ‘Pui Beds’, respectively (see Csiki-Sava et al. 2016).

The first specimen re-described and re-assigned here (UBB NVZ1-42) was discovered in the Râul Mare River section near Nălaţ-Vad in the central part of the Haţeg Basin (Fig. 1b). The rocks of the Râul Mare River section crop out in, and along, the river Râul Mare and are strongly tilted, dipping almost vertically. The succession comprises siliciclastic sedimentary rocks that were likely deposited in a meandering river system (Therrien 2004; Săsăran et al. 2011). In the past, these deposits have been correlated with the upper part of the type Sînpetru Formation (Codrea et al. 2002; Therrien 2006; Therrien et al. 2009), or else were assigned tentatively to the Densuş-Ciula Formation (Panaiotu et al. 2011), or to a separate lithostratigraphic unit (Csiki-Sava et al. 2016). The age of the succession has been estimated as ‘middle’ (i.e., close to the early/late Maastrichtian boundary; Van Itterbeeck et al. 2005) or late Maastrichtian (Panaiotu et al. 2011; Ciobanete et al. 2011). Only relatively recently have systematic excavations along the Râul Mare revealed rich and diverse vertebrate assemblages comprising amphibians, turtles, squamates, pterosaurs, different dinosaurs including birds and multituberculate mammals as well as dinosaur eggs (Smith et al. 2002; Codrea et al. 2002; Godefroit et al. 2009; Csiki et al. 2010a; Wang et al. 2011; Csiki-Sava et al. 2016; Brusatte et al. 2017; Mayr et al. 2020). Some of the most important finds occurred in so-called fossil pockets,

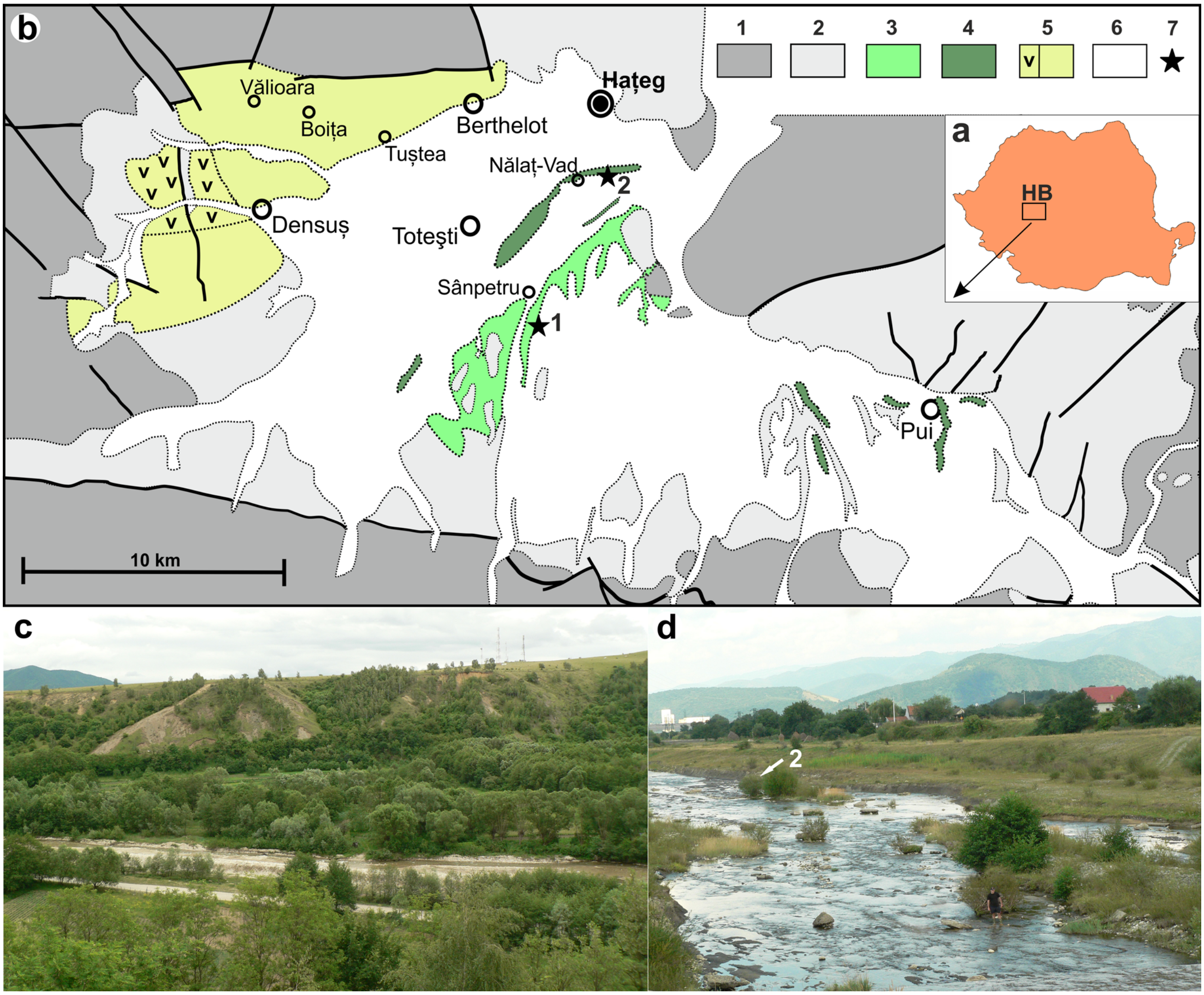

Fig. 1 Geological setting of the specimens UBB NVZ1-42 and NHMUK R.3401A. **a** Position of the study area within Romania. **b** Simplified geological map of the Haţeg Basin, highlighting the distribution of the uppermost Cretaceous continental deposits. Stars mark the origin of the braincases re-identified here as of hadrosauroid affinities: 1—approximate location of Nopcsa's Quarry 1, yielding specimen NHMUK R.3401A, 2—location of the fossiliferous pocket yielding specimen UBB NVZ1-42 (site 5 in Smith et al. 2002). 1—Pre-Alpine crystalline basement units surrounding the Haţeg Basin; 2—outcropping areas of pre-Quaternary sedimentary rocks of the basin, with 3–5 highlighting the distribution of the uppermost Cretaceous continental beds: 3—Sînpetru Formation; 4—deposits tentatively correlated with the Sînpetru Formation (see Csiki-Sava et al. 2016); 5—Densuş-Ciula Formation (v—volcanoclastic subunit); 6—Quaternary deposits; 7—stars mark the origin of the braincases re-identified here as of hadrosauroid affinities (see above). **c** View of the right-side flank of the Sibişel Valley south of Sânpetru, with exposures of the stratotype Sînpetru Formation. Approximate location of Nopcsa's Quarry 1 can be constrained to somewhere in the middle part of the section represented in the photo. **d** Overview of the Nălaţ-Vad locality, looking towards north. The approximate position of site (fossiliferous lens) NV5 (see Smith et al. 2002) pointed by arrow

local accumulations of vertebrate fossils that are sometimes associated or even partially articulated such as the holotype of the titanosaur *Paludititan* (Csiki et al. 2010a). The braincase described here, UBB NVZ1-42, was recovered from a fossil pocket that almost exclusively yielded disarticulated rhabdodontid remains assigned to *Zalmoxes shqiperorum* and assumed to represent a single individual (Godefroit et al. 2009). Notably, however, a left quadrate was found in the same fossil pocket that apparently does not belong to a rhabdodontid and instead is probably assignable to the hadrosauroid *Telmatosaurus* (Godefroit et al. 2009), thus indicating the presence of at least one more taxon in this fossil pocket. The presence of more than one taxon within the commonly occurring fossiliferous pockets from the uppermost Cretaceous of the Haţeg Basin is a widespread phenomenon (e.g., Nopcsa 1902b; Csiki et al. 2010b), and the case for such a multitaxic composition would be strengthened now for the NVZ1 fossil pocket as well by our re-assignment of the basicranium UBB NVZ1-42 to *Telmatosaurus* as argued below.

The second specimen that is re-examined here (NHMUK R.3401A) was collected by Franz Nopcsa from the Sibişel Valley section near Sânpetru in the south-central part of the Haţeg Basin (Fig. 1b). This sedimentary succession is exposed along a 2.5 km long natural valley carved by the Sibişel River and exposing an 860 m thick sequence of terrestrial Upper Cretaceous sediments. The sedimentary rocks comprise coarse-grained and fine-grained layers arranged in multiple fining-upward sequences, which were laid down on a poorly channelized alluvial plain drained by braided river systems (Grigorescu 1983; Therrien 2006; Therrien et al. 2009). Stratigraphically, the Sibişel Valley section represents the stratotype section of the Sînpetru Formation and has been estimated to be early to early late Maastrichtian in age (Therrien 2004; Panaiotu and Panaiotu 2010). The Sibişel Valley section includes many classical Nopcsa localities and has ever since yielded rich and diverse vertebrate assemblages comprising fishes, amphibians, turtles, squamates, crocodyliforms, pterosaurs, dinosaurs and multituberculate mammals (Nopcsa 1900, 1902a, b, 1904, 1923, 1929; Andrews 1913; Grigorescu 1983; Csiki and Grigorescu 1998; Csiki et al. 2010b; Martin et al. 2014; Csiki-Sava et al. 2016; Augustin et al. 2021). The fossil vertebrate remains often show complex taphonomic histories and can occur isolated, associated and partly articulated or in local multitaxic concentrations, so-called fossil pockets (Nopcsa 1902b; Grigorescu 1983; Csiki et al. 2010b; Augustin et al. 2019). The second specimen re-described here, NHMUK R.3401A, was discovered in such a multitaxic fossil concentration, identified as Quarry 1 by Nopcsa, together with different skull and postcranial bones of both rhabdodontids and hadrosauroids among others (Nopcsa 1904, and comments below).

Materials and methods

Two specimens are re-described herein. The first, UBB NVZ1-42, is a partial basicranium that was recovered together with other vertebrate remains (see below) in 2002 from the Râul Mare River section, near Nălaţ-Vad (Godefroit et al. 2009); the specimen is currently housed at the Palaeontological Collection of the Babeş-Bolyai University. The second specimen, NHMUK R.3401A, consists of a partial braincase and was collected by Franz Nopcsa from his 'Quarry 1' (see below), which he discovered in 1895 on the eastern side of the Sibişel Valley section near Sânpetru (Nopcsa 1902a, b; Grigorescu 2010); the specimen is currently stored at the Natural History Museum London. Both specimens were digitalized using the photogrammetry technique detailed by Mallison and Wings (2014) as well as the software Agisoft Photoscan Professional, in order to create surface models. In addition, 3D prints were produced based on the surface models, which are deposited in the Palaeontological Collection of the University of Tübingen.

Institutional abbreviations. LPB (FGGUB)—Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; NHMUK—Natural History Museum, London, UK; UBB—Babeş-Bolyai University, Cluj-Napoca, Romania.

Systematic Palaeontology

Dinosauria Owen (1842)
Ornithischia Seeley (1888)
Ornithopoda Marsh (1881)
Iguanodontia Baur (1891)
Hadrosauroidea Cope (1869)

Telmatosaurus transsylvanicus Nopcsa (1900)

Holotype. NHMUK R.3386, an almost complete but crushed skull.

Referred material. UBB NVZ1-42, a partial basicranium composed of the basioccipital, the partial exoccipital–opisthotic complexes, and the basisphenoid–parasphenoid complex from the Râul Mare River section, near Nălaţ-Vad, central Haţeg Basin, as well as NHMUK R.3401A, the posterior part of a skull composed of the basioccipital, both exoccipital–opisthotic complexes, the posterior part of the basisphenoid, and the supraoccipital from the Sibişel Valley section near Sânpetru, southern Haţeg Basin.

Remarks on UBB NVZ1-42. Specimen UBB NVZ1-42 has been previously referred to the rhabdodontid ornithopod dinosaur *Zalmoxes shqiperorum* (Godefroit et al. 2009). This referral was primarily based on the association of UBB NVZ 1-42 with other disarticulated bones in the 'third fossil pocket' at the Nălaţ-Vad locality, remains that almost exclusively belong to *Zalmoxes shqiperorum* and apparently represent a single individual (Godefroit et al. 2009). Recent investigations of the rhabdodontid fossils from the Haţeg Basin also led to a re-examination of UBB NVZ 1-42 and, based on comparison with several hadrosauroid and rhabdodontid basicrania from the Haţeg Basin as outlined below, we here confidently identify UBB NVZ1-42 as a hadrosauroid basicranium and refer it to the only known local hadrosauroid taxon, *Telmatosaurus*. Interestingly, Godefroit et al. (2009) also reported the presence of a second type of quadrate from the same fossil pocket, which they did not refer to *Zalmoxes shqiperorum* but instead noted that it closely resembles in morphology that of *Telmatosaurus*. In the original description, Godefroit et al. (2009) referred to the braincase as UBB NVZ1-40, although this number actually identifies a rhabdodontid left quadrate from this fossil site. The assignment of UBB NVZ 1-42 to *Zalmoxes shqiperorum* has previously been questioned by Brusatte et al. (2017), who also noted that it might instead belong to *Telmatosaurus*.

Remarks on NHMUK R.3401A. The braincase specimen NHMUK R.3401A is part of the original Nopcsa Collection that was later purchased by the Natural History Museum in London (e.g., Dalla Vecchia 2009a). As already pointed out by Dalla Vecchia (2009a), and as with most registry entries of the Nopcsa collection, the inventory number NHMUK R.3401 identifies a large number of different specimens, belonging to several individuals that actually represent more than one taxon. Furthermore, skeletal remains included under this specimen number are assumedly originating from individuals whose other (usually postcranial) remains are now registered under different entry numbers (for a more detailed discussion of this issue, see Dalla Vecchia 2009a: pp. 6–7).

Intriguingly, the same fossil pocket, from which braincase NHMUK R.3401A has been recovered, also yielded disarticulated, but fairly complete and definitively diagnostic skull bones, including dentaries, of both *Telmatosaurus transsylvanicus* and *Zalmoxes robustus*. These specimens had been lumped together under the same original specimen number NHMUK 3401, from which at one point certain specimens, some showing definitive hadrosauroid characters and also including the partial braincase discussed here, have been separated as NHMUK 3401A. It is worth noting that the fossil pocket that yielded this mixed material (mentioned as Quarry 1 in the NHMUK registry book) contains a similar mix of rhabdodontid and hadrosauroid remains just as the one reported for the (smaller) *Zalmoxes*-lens from Nălaţ-Vad from where the partial braincase UBB NVZ1-42 originates. This mixture of disarticulated skeletal remains belonging to different individuals and representing different taxa is a hallmark feature of the so-called ‘fossiliferous pockets’ that represent one of the main types of fossil occurrences in the Haţeg Basin (Nopcsa 1914; Csiki et al. 2010b), one for which Quarry 1 of Nopcsa is among the first and best examples.

These complications, together with the absence of original field notes or quarry maps to document the discovery conditions of the different specimens excavated by Nopcsa at Sânpetru, seriously hindered the understanding of the taxonomic identity and potential skeletal association of the specimens that make up this mixed fossil assemblage, including that of the partial braincase NHMUK R.3401A discussed here. Indeed, this specimen has been referred to *Telmatosaurus transsylvanicus* by Weishampel et al. (1993), who also used it to reconstruct the braincase anatomy of that taxon (Weishampel et al. 1993: Fig. 2). This taxonomic choice appears to be in accordance with Nopcsa’s original taxonomic identification of this specimen (see Nopcsa 1904, Table 1) who reported it as belonging to a second individual (Individual B) of *Telmatosaurus* (see also Dalla Vecchia 2009a). Subsequently, however, the specimen was re-assigned to *Zalmoxes robustus* by Weishampel et al. (2003), albeit without providing any arguments in favor of this view. Similar to UBB NVZ1-42, recent investigations of the rhabdodontid material from the Haţeg Basin also led to a re-examination of NHMUK R.3401A, and this resulted in the re-interpretation of this specimen as belonging to *Telmatosaurus transsylvanicus*, as originally proposed by Nopcsa (1904), respectively by Weishampel et al. (1993).

Description of UBB NVZ1-42

The specimen UBB NVZ1-42 includes the complete basioccipital, the partial exoccipital–opisthotic complexes, and most of the basisphenoid–parasphenoid complex (Fig. 2). Aside from the missing parts, the basicranium is well-preserved with delicate processes and small foramina still present. The occipital condyle is u-shaped to kidney-shaped in posterior view and composed of the basioccipital ventrally and the exoccipital–opisthotic complexes dorso-laterally (Fig. 2a). The suture between the basioccipital and the exoccipital–opisthotic complexes is not discernible. In ventral view, the occipital condyle is somewhat rectangular in outline with a convex surface (Fig. 2b). In lateral view, the occipital condyle is ellipsoidal and exhibits three large foramina, two openings next to each other for cranial nerve XII (hypoglossal nerve) and cranial nerves X (vagus nerve) and XI (accessory nerve), respectively, as well as one foramen located antero-ventrally to the latter, possibly for the exit of the jugular vein (Fig. 2c). Immediately above the opening for cranial nerve XII, the braincase is broken and the paroccipital process (mainly composed of the opisthotic) is largely missing, although the bone gets markedly thinner just above the opening for cranial nerve XII, likely indicating the ventral part of the paroccipital process.

On the ventral aspect of the braincase, directly adjacent to the basioccipital condyle, there are two round processes lying anteriorly and slightly laterally to the condyle (Fig. 2b). These processes, the sphenoccipital tubercles or basal tubera, are directed ventro-laterally and have a deep depression between them that is roughly triangular in outline. The suture between the basioccipital and the basisphenoid is hardly visible on the ventral aspect of the braincase but is probably present as a shallow indentation running across the sphenoccipital tubercles, as this is also the position of the suture in other hadrosauroids (e.g., Sues and Averianov 2009: p. 2551; Prieto-Márquez 2010: p. 847; McDonald et al. 2012: pp. 16–17; Xing et al. 2017: pp.

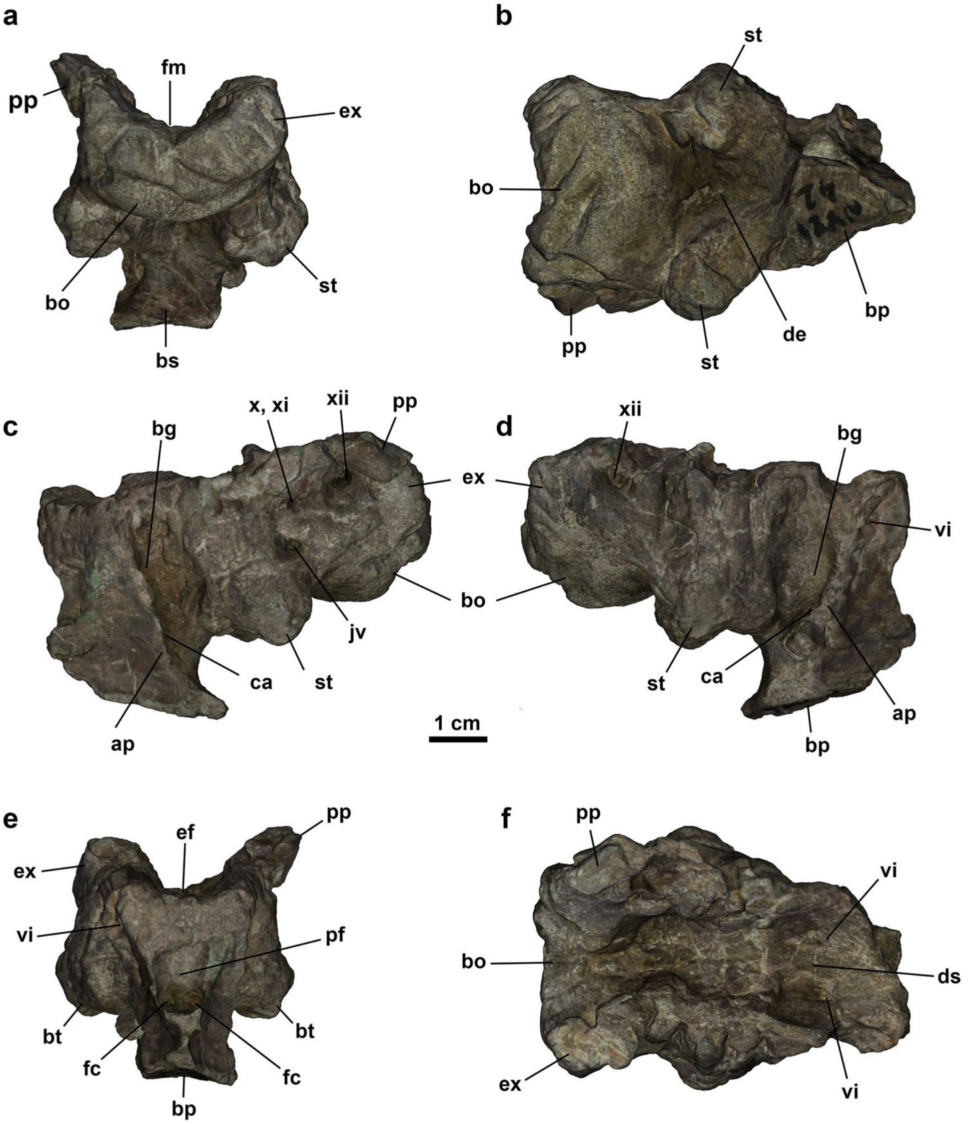

Fig. 2 Partial ornithopod basicranium, UBB NVZ1-42, here tentatively referred to the hadrosauroid dinosaur *Telmatosaurus transsylvanicus*, from the Upper Cretaceous of Nălaţ-Vad, Haţeg Basin. **a** Posterior view. **b** Ventral view. **c** Left lateral view. **d** Right lateral view. **e** Anterior view. **f** Dorsal view. All figures to the same scale. ap, alar process; bo, basioccipital; bg, groove on the lateral aspect of the basisphenoid; bp, basisphenoid platform on the ventral aspect of the basisphenoid; bs, basisphenoid–parasphenoid complex; ca, carotid artery; de, depression on the ventral aspect of the basicranium between the sphenoccipital tubercles; ds, dorsum sellae; ef, endocranial floor; ex, exoccipital; fc, foramen in the pituitary fossa connecting the carotid artery; fm, foramen magnum; jv, jugular vein; pf, pituitary fossa; pp, paroccipital process formed by the exoccipital–opisthotic complex; st, sphenoccipital tubercle; vi, cranial nerve six (abducens nerve); x, cranial nerve ten (vagus nerve); xi, cranial nerve eleven (accessory nerve); xii, cranial nerve twelve (hypoglossal nerve)

24–25). The basisphenoid, in turn, is completely fused to the parasphenoid anteriorly, forming the basisphenoid–parasphenoid complex. The sphenoccipital tubercles are connected to the antero-ventral part of basisphenoid through a ridge rising anteriorly and eventually merging with the antero-ventral part of basisphenoid. The antero-ventral part of the basisphenoid forms a transverse surface that mainly extends ventrally, approximately perpendicular to the long axis of the braincase. In ventral view, this antero-ventral part of the basisphenoid forms a slightly concave platform that is inclined antero-dorsally and would be connected to the missing basipterygoid processes.

In lateral view, there is a well-developed groove anterior to the sphenoccipital tubercles that extends antero-dorsally, is bordered by the alar process of the basisphenoid anteriorly and accommodates the latero-ventral entrance of the carotid artery in its lower half (Fig. 2c–d). The alar process is well preserved and forms a thin ridge extending mainly latero-posteriorly from the lateral side of the basisphenoid. Anterior to the alar process and near its upper margin is a small foramen, representing the opening for cranial nerve VI (abducens nerve). The anterior portion of the basisphenoid is incompletely preserved and wedge-shaped. In anterior view, a dorso-ventrally elongated pituitary fossa is visible (Fig. 2e), which exhibits two small foramina in its postero-ventral part that are likely connected to the latero-ventral entrance of the carotid artery (Xing et al. 2017: p. 25). The endocranial floor is completely visible in dorsal view (Fig. 2f) and is formed by the basioccipital and exoccipitals posteriorly and by the basisphenoid–parasphenoid complex anteriorly. The endocranial floor is relatively straight and has a constant width from the foramen magnum posteriorly to the anterior part of the preserved element. The dorsum sellae is located in the anterior part, more or less dorsally to the latero-ventral entrance of the carotid artery, and exhibits two foramina for the cranial nerve VI (abducens nerve). The lateral walls of the endocranial floor exhibit the suture between the basisphenoid–parasphenoid complex and the (missing) prootic.

Description of NHMUK R.3401A

The specimen NHMUK R.3401A comprises the basioccipital, both exoccipital–opisthotic complexes, the supraoccipital, and the anterior part of the basisphenoid–parasphenoid complex (Fig. 3). Aside from the missing parts, the specimen is relatively well-preserved. In posterior view, the occipital condyle is kidney-shaped and consists of the basioccipital ventrally and the exoccipitals dorso-laterally (Fig. 3a). On the right side of the occipital condyle, the suture between the basioccipital and the exoccipital is visible but slightly damaged. On the left side, the occipital condyle is weathered, obliterating the sutural contact between the basioccipital and the exoccipital. Both the basioccipital and the exoccipitals take part in the formation of the endocranial floor. The exoccipitals are completely fused to the opisthotics, forming the exoccipital–opisthotic complex (or paroccipital processes), which continues as an elongated and flat element from the triangular and bulbous ventral part that is forming the dorso-lateral corner of the occipital condyle.

The exoccipital–opisthotic complex is extending mainly dorsally and, to a much lesser degree, laterally, forming the lateral walls of the foramen magnum (Fig. 3a, b). In posterior view, the foramen magnum has a dorso-ventrally elongated, ellipsoidal shape. Dorsally, the exoccipital–opisthotic complex broadens and makes a postero-lateral curve (Fig. 3c–e). Medially, the dorsal part of the exoccipital–opisthotic complex is fused to the supraoccipital, the latter forming the dorsal margin of the foramen magnum. The supraoccipital is a roughly triangular to trapezoidal element in posterior view, wedged between the exoccipital–opisthotic complexes laterally. The dorsal part of the supraoccipital is relatively flat and extends antero-dorsally (Fig. 3f). The dorso-lateral and anterior parts of the exoccipital–opisthotic complexes as well as the anterior part of the supraoccipital are missing. However, the paroccipital processes clearly extend posteriorly beyond the level of the basioccipital and the exoccipitals in dorsal view, while the supraoccipital is lying anteriorly to the occipital condyle.

In ventral view, the basioccipital is rectangular in outline with a convex surface, although the left part of the basioccipital is missing and thus its morphology cannot be completely assessed (Fig. 3b). Directly anterior to the basioccipital, there are two bulbous processes on the ventral aspect of the braincase, the sphenoccipital tubercles (= basal tubera), which extend mainly ventro-laterally (Fig. 3e). The suture between the basioccipital and the basisphenoid is hardly visible but it probably runs across the sphenoccipital tubercles as indicated by a shallow, sinuous indentation on the right sphenoccipital tubercle; this is also the position of the suture between basioccipital and basisphenoid in other hadrosauroids (e.g., Sues and Averianov 2009: p. 2551; Prieto-Márquez 2010: p. 847; McDonald et al. 2012: pp. 16–17; Xing et al. 2017: pp. 24–25), as well as in NVZ1-42 discussed previously. Between the sphenoccipital tubercles, there is a deep depression. Anterior to the sphenoccipital tubercles, the basisphenoid rises markedly ventrally but the antero-ventral part of the basisphenoid is broken. The sphenoccipital tubercles are connected to the anterior and ventrally rising part of the basisphenoid through narrow ridges.

In lateral view, the occipital condyle formed by the basioccipital and the exoccipitals is slightly convex (Fig. 3c, d). A shallow depression is present anterior to the sphenoccipital tubercles that likely represents the dorsal part of the groove on the lateral side of the basisphenoid that is bordered by the alar process anteriorly (see above). The openings for the cranial nerves that are usually visible in lateral view (see above) are not discernible because the bone surface is imperfectly preserved and some missing parts, just dorsal of the exoccipitals, have been restored with plaster. The anterior part of the braincase is not preserved.

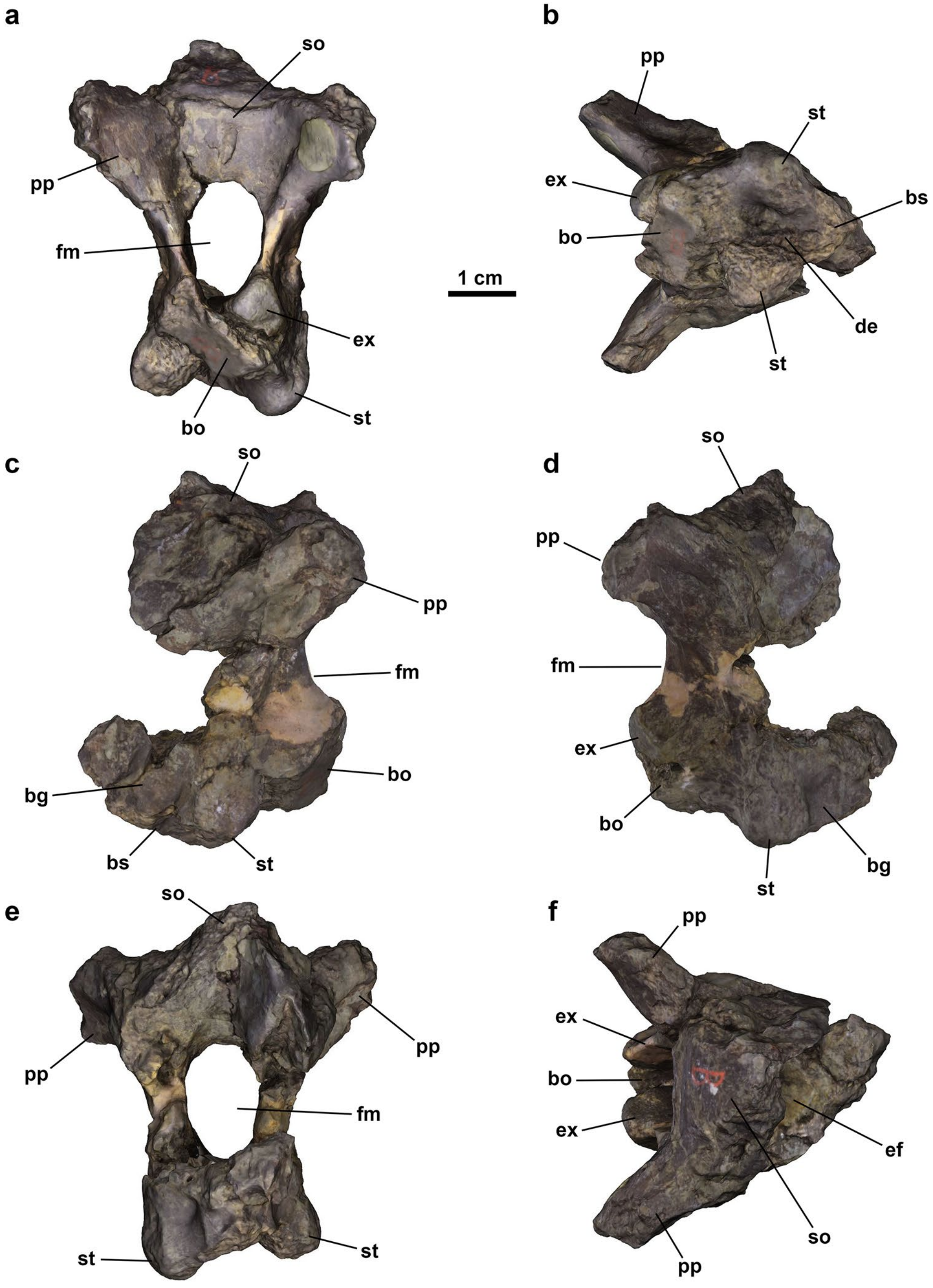

Fig. 3 Posterior part of an ornithopod skull, NHMUK R.3401A, here tentatively referred to the hadrosauroid dinosaur *Telmatosaurus transsylvanicus*, from the Upper Cretaceous Sînpetru Formation near Sânpetru, Haţeg Basin. **a** Posterior view. **b** Ventral view. **c** Left lateral view. **d** Right lateral view. **e** Anterior view. **f** Dorsal view. All figures to the same scale. bo, basioccipital; bg, groove on the lateral aspect of the basisphenoid; bs, basisphenoid–parasphenoid complex; de, depression on the ventral aspect of the basicranium between the sphenoccipital tubercles; ef, endocranial floor; ex, exoccipital; fm, foramen magnum; pp, paroccipital process formed by the exoccipital–opisthotic complex; st, sphenoccipital tubercle

Comparison

Both UBB NVZ1-42 and NHMUK R.3401A have been referred to the rhabdodontid dinosaur *Zalmoxes* in the past (Weishampel et al. 2003; Godefroit et al. 2009), although the latter specimen has originally been assigned to the hadrosauroid *Telmatosaurus* (Nopcsa 1904: tab. 1; Weishampel et al. 1993). Therefore, the following discussion focuses primarily on comparisons of these two specimens with other hadrosauroid and rhabdodontid basicrania from the Haţeg Basin. In addition, a short comparison to other hadrosauroids and basal iguanodontians is also provided.

Comparison with *Telmatosaurus* and other hadrosauroids

For *Telmatosaurus*, two undisputed basicrania are known, both of which come from the Sînpetru Formation of the Sibişel Valley section near Sânpetru, southern Haţeg Basin. One is part of the largely complete but crushed holotype skull NHMUK R.3386 (Fig. 4a) that was described and figured by Nopcsa (1900); it is noteworthy that this skull was explicitly mentioned as the basis for the erection of the genus (Nopcsa 1900: 559; *contra* Dalla Vecchia 2009a). The second, NHMUK R.3387 (Fig. 4b), is an isolated basicranium, comprising the basioccipital and the basisphenoid that was described and figured in the same publication as the holotype skull (Nopcsa 1900). Both of these basicrania described by Nopcsa (1900) are extremely similar to the specimens described here (UBB NVZ1-42 and NHMUK R.3401A)—in fact, they are nearly indistinguishable, aside from the different preservational states of the skulls and the different sizes. These similarities are most apparent in ventral view, also because this is the best-preserved part in all four specimens (Fig. 4). Both the holotype of *Telmatosaurus* (NHMUK R.3386) and the referred basicranium (NHMUK R.3387) described by Nopcsa (1900), strongly resemble the specimens described here (UBB NVZ1-42 and NHMUK R.3401A), as they have a short, convex basioccipital that is slightly rectangular in ventral view and directly connected to a pair of sphenoccipital tubercles (= basal tubera) anteriorly, which have a well-developed depression between them (Fig. 4; Nopcsa 1900: pl. 3). In addition, all four specimens share a medio-laterally narrow basisphenoid, which lies immediately anterior to the depression, is steeply rising ventrally, and is connected to the sphenoccipital tubercles through a narrow, antero-medially extending ridge. In the holotype of *Telmatosaurus* (NHMUK R.3386), the sphenoccipital tubercles are slightly more splayed and farther apart than in the other basicrania referred to *Telmatosaurus*, in which they are closer to each other. Moreover, the central depression between the sphenoccipital tubercles is narrower in NHMUK R.3387 as compared to the other specimens. In all specimens, the foramen magnum opens into a relatively straight endocranial floor.

The basicranium anatomy of hadrosauroids is well known and has been described for many different taxa. Overall, an antero-posteriorly short basioccipital, bulbous sphenoccipital tubercles lying immediately anterior to the basioccipital, and a depression between the sphenoccipital tubercles are typically present in basal hadrosauroids, including *Bactrosaurus johnsoni* (Gilmore 1933: Fig. 25), *Batyrosaurus rozhdestvenskyi* (Godefroit et al. 2012a: Fig. 20.2), *Eolambia caroljonesa* (McDonald et al. 2012: Fig. 20), *Gobihadros mongoliensis* (Tsogtbaatar et al. 2019: Fig. 8), *Levnesovia transoxiana* (Sues and Averianov 2009: Fig. 1), *Ouranosaurus nigeriensis* (Taquet 1976: Fig. 12), *Plesiohadros djadokhtaensis* (Tsogtbaatar et al. 2014: Fig. 7.8), *Proa valdearinnoensis* (pers. com. Fabien Knoll), *Sirindhorna khoratensis* (Shibata et al. 2015: Fig. 2), *Tanius sinensis* (Wiman 1929: pl. 5), and *Tethyshadros insularis* (Chiarenza et al. 2021: Fig. 2, p. 5). Additionally, the same general bauplan of the braincase is also seen in more derived hadrosaurids such as *Acristavus gagslarsoni* (Gates et al. 2011: Fig. 9), *Amurosaurus riabinini* (Godefroit et al. 2004: Fig. 7), *Arenysaurus ardevoli* (Pereda-Suberbiola et al. 2009; Fig. 3; Cruzado-Caballero et al. 2015: suppl. 1), *Brachylophosaurus canadensis* (Prieto-Márquez 2005: Fig. 6), *Edmontosaurus regalis* (Lull and Wright 1942: Fig. 4; Xing et al. 2017: Fig. 10), *Eotrachodon orientalis* (Prieto-Márquez et al. 2016: Fig. 16), *Gryposaurus notabilis* (Ostrom 1961: Fig. 11; Prieto-Márquez 2010: Fig. 4), *Gryposaurus monumentensis* (Gates and Sampson 2007: Fig. 11), *Hypacrosaurus altispinus* (Evans 2010: Figs. 10, 11), *Maiasaura peeblesorum* (McFeeters et al. 2021: Fig. 13), *Olorotitan arharensis* (Godefroit et al. 2012b: Fig. 4), *Ornatops incantatus* (McDonald et al. 2021: Fig. 7), *Parasaurolophus cyrtocristatus* (Gates et al. 2021: figs. 5, 9, 13), *Parasaurolophus tubicen* (Sullivan and Williamson 1999: Fig. 8), *Sahaliyania elunchunorum* (Godefroit et al. 2008: Fig. 3), and *Secernosaurus koerneri* (Prieto-Márquez and Salinas 2010: figs. 6, 7). Therefore, the basicranial morphology of these different hadrosauroids closely resembles that of the holotype and referred basicrania of *Telmatosaurus* (NHMUK R.3386 and NHMUK R.3387), but also that seen in the taxonomically contentious Romanian braincase specimens described above (UBB NVZ1-42 and NHMUK R.3401A).

Comparison with rhabdodontids and other basal iguanodontians

Four definitively identified rhabdodontid basicrania are currently reported from the Upper Cretaceous of the Haţeg Basin. The first two of these, NHMUK R.3408 and NHMUK R.3409, were excavated, apparently isolated according to Nopcsa (1904), more than a century ago in the stratotype

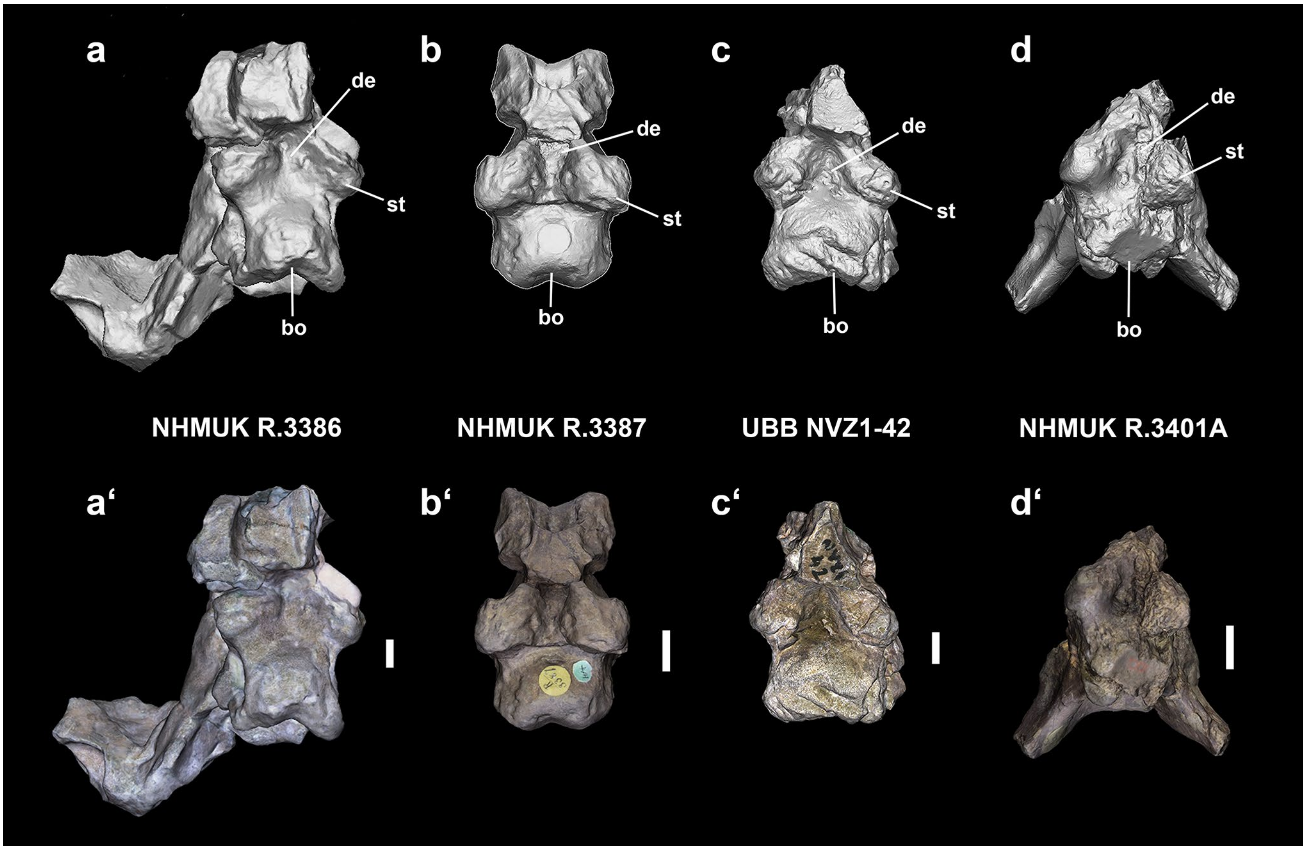

Fig. 4 Comparison of the ornithopod basicrania described herein (UBB NVZ1-42 and NHMUK R.3401A) with the holotype skull (NHMUK R.3386) and the referred isolated basicranium (NHMUK R.3387) of *Telmatosaurus transsylvanicus*, all from the Upper Cretaceous of the Haţeg Basin. All specimens are displayed in ventral view but are not to the same scale. **a** Surface model of the holotype skull of *Telmatosaurus*, NHMUK R.3386 from the Sînpetru Formation near Sânpetru, south-central Haţeg Basin. **a'** The same specimen as in A with texture. **b** Surface model of the isolated *Telmatosaurus* basicranium NHMUK R.3387 from the Sînpetru Formation near Sânpetru, south-central Haţeg Basin. **b'** The same specimen as in B with texture. **c** Surface model of the basicranium UBB NVZ1-42 from the Râul Mare River section, near Nălaţ-Vad, central Haţeg Basin. **c'** The same specimen as in C with texture. **d** Surface model of the posterior skull NHMUK R.3401A from the Sînpetru Formation near Sânpetru, south-central Haţeg Basin. **d'** The same specimen as in D with texture. Scales equal 1 cm. bo, basioccipital de, depression on the ventral aspect of the basicranium between the sphenoccipital tubercles; st, sphenoccipital tubercle

Sînpetru Formation along the Sibişel Valley, near Sânpetru. These specimens were described and figured by Nopcsa (1904) who referred them tentatively to the rhabdodontid *Mochlodon* (=*Zalmoxes*). NHMUK R.3408 (Fig. 5a) comprises the basioccipital and most of the basisphenoid, whereas NHMUK R.3409 (Fig. 5b) only preserves the region around the basal tubera. A third, relatively complete basicranium, LPB (FGGUB) R.1723, was recovered much later (2000) from the middle part of the Densuş-Ciula Formation at the Tuştea-Oltoane nesting site, in the northwestern part of the Haţeg Basin (see Botfalvai et al. 2017, for a recent review of the locality). It comprises the basioccipital and most of the basisphenoid and has been described and figured by Weishampel et al. (2003: Fig. 11). The last rhabdodontid basicranium specimen that was referred previously to the Rhabdodontidae, LPB (FGGUB) R.1629 (Fig. 5c), is also from the Tuştea locality, where it was found in 1998. The specimen was briefly mentioned by Weishampel et al. (2003: p. 78) and then was preliminarily illustrated in articulation with the matching left exoccipital LPB (FGGUB) R.1591 by Botfalvai et al. (2017: Fig. 8H), but it has never been thoroughly figured before nor described in detail.

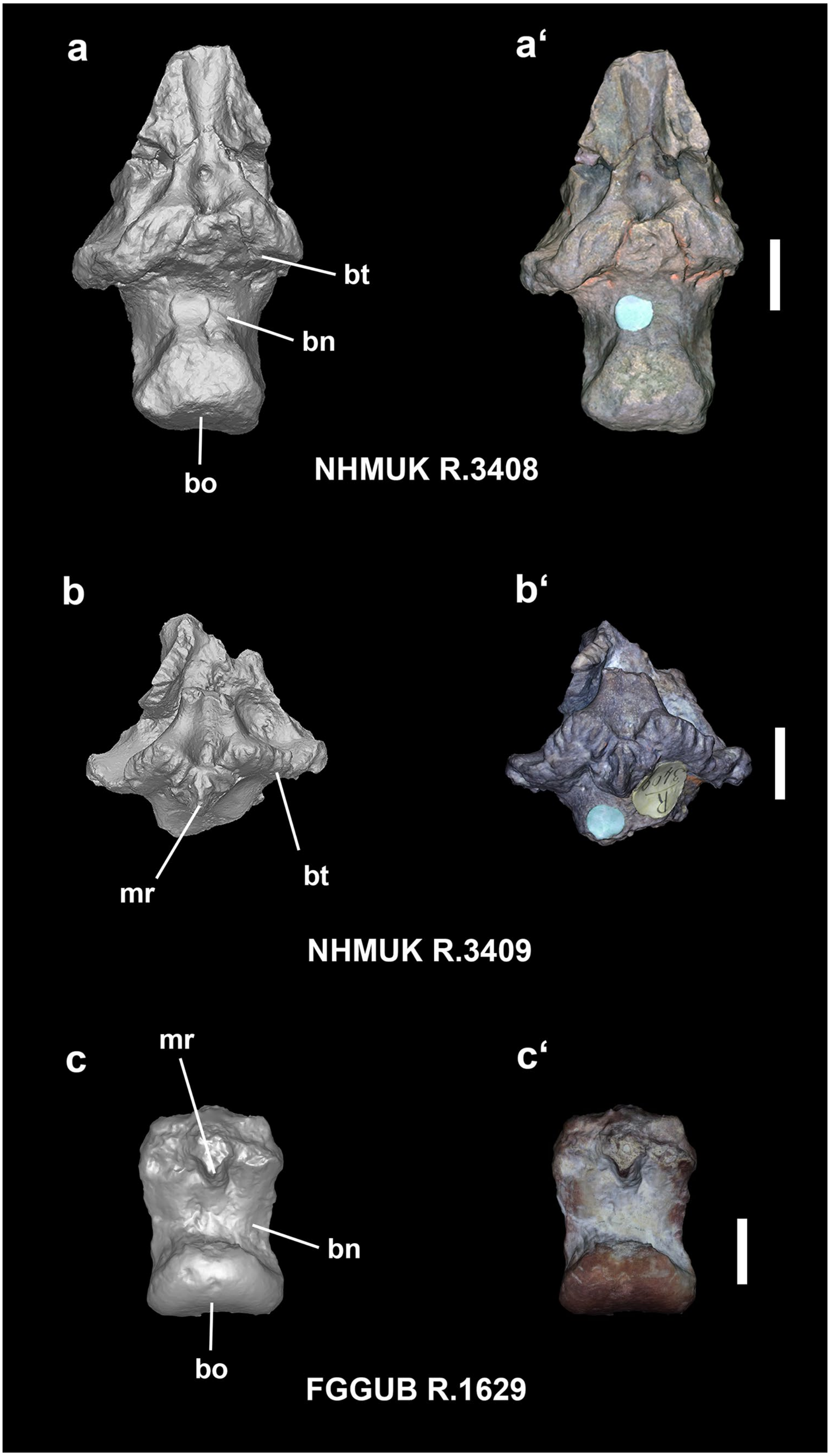

Fig. 5 Rhabdodontid basicrania from the Upper Cretaceous of the Haţeg Basin in ventral view. **a** Surface model of the isolated rhabdodontid basicranium NHMUK R.3408 from the Sînpetru Formation near Sânpetru, south-central Haţeg Basin. **a'** The same specimen as in A with texture. **b** Surface model of the isolated fragmentary rhabdodontid basicranium NHMUK R.3409 from the Sînpetru Formation near Sânpetru, south-central Haţeg Basin. **b'** The same specimen as in B with texture. **c** Surface model of the isolated rhabdodontid basicranium LPB (FGGUB) R.1629 from the Densuş-Ciula Formation near Tuştea, northwestern Haţeg Basin. **c'** The same specimen as in C with texture. Scales equal 1 cm. bn, basioccipital neck; bo, basioccipital; bt, basal tubera (=sphenoccipital tubercles); mr, midline ridge on the posterior part of the basisphenoid

All three rhabdodontid specimens comprising the complete basioccipital (NHMUK R.3408, LPB (FGGUB) R.1723 and R.1629), have a distinct, elongated and well-developed neck connecting the occipital condyle with the basal tubera anteriorly (Fig. 5a, c). Moreover, all the rhabdodontid basicrania from the Haţeg Basin lack bulbous sphenoccipital tubercles (= basal tubera) and a median depression on the ventral aspect of the braincase (Figs. 5, 6). Furthermore, the basal tubera join together medially to form a wide, medio-laterally extending ridge that has a wrinkled appearance on the posterior side with a prominent transverse midline ridge (Fig. 5). Therefore, these rhabdodontid basicrania from the Haţeg Basin differ markedly from the corresponding elements of *Telmatosaurus* described by Nopcsa (1900) (NHMUK R.3386 and NHMUK R.3387), as well as from the basicranial specimens described herein (UBB NVZ1-42 and NHMUK R.3401A). In fact, as already noted, specimens UBB NVZ1-42 and NHMUK R.3401, resemble the *Telmatosaurus basicrania* described by Nopcsa (1900), including the holotype of that genus, much more closely than those of rhabdodontids.

In contrast, the morphology of these rhabdodontid basicrania from the Haţeg Basin is quite similar to that of the rhabdodontid *Rhabdodon* from France (Chanthasit 2010: figs. 4.2, 4.3, the only other rhabdodontid for which some information is currently available, in features such as the possession of a distinct basioccipital neck supporting the occipital condyle, the lack of sphenoccipital tubercles, the lack a ventral median depression between these tubercles, and the presence of wide transversal ridge formed by the medially confluent basal tubera. In addition, these same features can be found in a wide variety of other basal iguanodontians, including *Anabisetia saldiviai* (Coria and Calvo 2002: Fig. 4), *Camptosaurus dispar* (Gilmore 1909: figs. 4, 5; Carpenter and Lamanna 2015: figs. 7, 8), *Cumnoria prestwichii* (Hulke 1880; Fig. 1; Galton and Powell 1980; Fig. 1), *Dakotadon lakotaensis* (Weishampel and Bjork 1989: figs. 4, 5; Boyd and Pagnac 2015: Fig. 8), *Dryosaurus altus* (Galton 1983: figs. 2, 3, 1989: pl. 2), *Dryosaurus elderae* (Carpenter and Galton 2018: Fig. 28), *Dysalotosaurus lettowvorbecki* (Galton 1989: pl. 1, 3; Hübner and Rauhut 2010: Fig. 7), *Iguanodon bernissartensis* (Norman 1980: figs. 5, 9), *Mantellisaurus atherfieldensis* (Norman 1986: figs. 7, 10, 18), *Owenodon* sp. (Galton 2009: Fig. 19), *Tenontosaurus tilletti* (Galton 1989: Fig. 4), *Tenontosaurus dossi* (Winkler et al. 1997: figs. 6, 7, 8), and an indeterminate iguanodontian from Australia (Bell et al. 2018: Fig. 8). The wide distribution of this type of basicranial morphology in basal iguanodontians, markedly different from that seen in both more basal and derived (i.e., hadrosaurid) hadrosauroids, suggests that it represents a plesiomorphic feature within the clade—as is also indicated by the presence of this type of basicranium morphology in basal ornithopods such as *Hypsilophodon foxii* (Galton 2001: figs. 7, 9, 17, 19), and *Convolosaurus marri* (Andrzejewski et al. 2019: Fig. 10), in basal neornithischians such as *Changchunsaurus parvus* (Liyong et al. 2010: Fig. 6), and *Thescelosaurus neglectus* (Galton 1989: pl. 4; Boyd 2014: Fig. 11), as well as in basal ornithischians such as *Heterodontosaurus tucki*, (Norman et al. 2011: figs. 3, 6, 13, 15), and *Lesothosaurus diagnosticus* (Porro et al. 2015: Fig. 9).

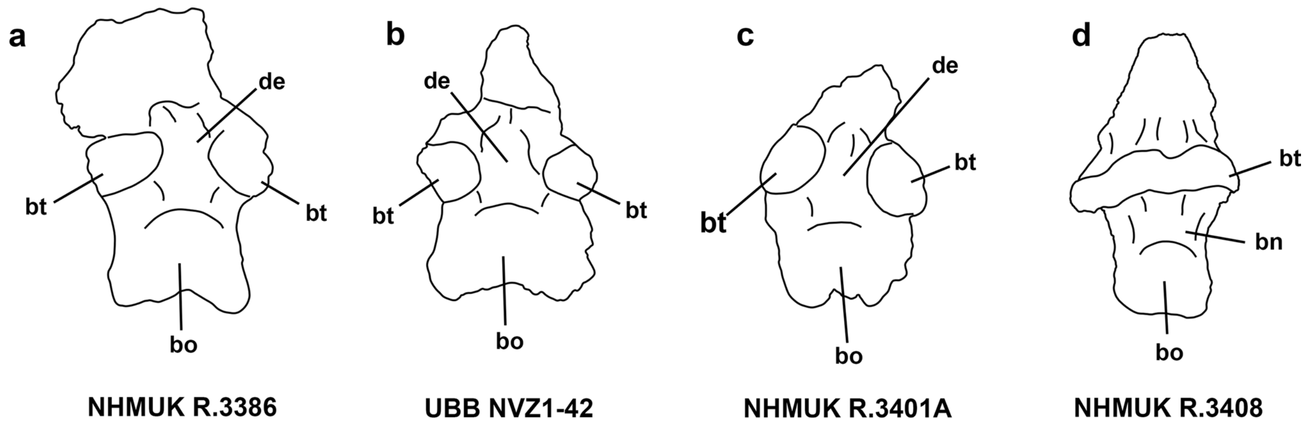

Fig. 6 Simplified drawing comparing the two basicranial specimens described here (UBB NVZ1-42 and NHMUK R.3401A) with the basicranium of the holotype skull of *Telmatosaurus transsylvanicus* (NHMUK R.3386) and the referred basicranium of *Zalmoxes robustus* (NHMUK R.3408) in ventral view. **a** Basicranium of the holotype skull of *Telmatosaurus transsylvanicus*, NHMUK R.3386. **b** Basicranium UBB NVZ1-42. **c** Basicranium of the partial skull NHMUK R.3401A. **d** Referred basicranium NHMUK R.3408 of *Zalmoxes robustus*. The drawings are not to the same scale. bn, basioccipital neck; bt, basal tubera (= sphenoccipital tubercles); de, depression between the sphenoccipital tubercles

Discussion and Conclusion

Based on the comparison presented above, we confidently identify both ornithopod basicrania from the Haţeg Basin described herein, UBB NVZ1-42 and NHMUK R.3401A, as hadrosauroid basicrania, and tentatively refer them to *Telmatosaurus transsylvanicus*, the only currently recognized hadrosauroid taxon from the Transylvanian area. In fact, both specimens are nearly indistinguishable from the holotype of that species (Fig. 4a, Nopcsa 1900: pl. 3). In addition, both UBB NVZ1-42 and NHMUK R.3401A exhibit several features that are only present in hadrosauroids and absent in more basal iguanodontian ornithopods. These features include: (i) an antero-posteriorly short basioccipital lacking a distinct neck; (ii) the presence of two well-developed bulbous processes, the sphenoccipital tubercles (= basal tubera) on the ventral aspect of the braincase that are directly positioned anterior to the basioccipital; and (iii) a deep depression on the ventral aspect of the braincase between the sphenoccipital tubercles. Conversely, characters that are typically present in rhabdodontids and other basal iguanodontians, including a distinct and elongated basioccipital neck and the basal tubera forming a medio-laterally extending wide ridge, are absent in UBB NVZ1-42 and NHMUK R.3401A.

The re-assignment of UBB NVZ1-42 to *Telmatosaurus* as advocated herein also requires a revision of the most recent diagnosis of *Zalmoxes shqiperorum* proposed by Godefroit et al. (2009) because it was partly based on features of UBB NVZ1-42—the only basicranium referred to this species to date. More specifically, one autapomorphy that has been proposed for *Zalmoxes shqiperorum*—i.e., an 'occipital condyle not separated from the sphenooccipital tubercles (= basal tubera) by a distinct neck' (Godefroit et al. 2009: p. 528)—has to be removed from the species diagnosis. Remarkably, these authors also noted that this character is not seen in any other basal iguanodontian (Godefroit et al. 2009: pp. 546–548) and that is in fact more similar to the morphology usually seen in hadrosaurids (Godefroit et al. 2009: p. 534), which would make this character highly derived within Rhabdodontidae. With the taxonomic re-interpretation of the basicranium UBB NVZ1-42 as proposed here, the diagnosis of *Z. shqiperorum* can be accordingly emended, and the autapomorphically derived basicranial morphology of this taxon that was previously suggested to differentiate it from its sympatric sister-species *Z. robustus*, can be rejected. As a consequence, the basicranial morphology of the genus *Zalmoxes* (currently only documented in *Z. robustus*) seems to be rather conservative, reminiscent to that seen in basal iguanodontians in general, and this plesiomorphic morphology appears to be typical of rhabdodontids as it also occurs in the closely related *Rhabdodon*.

Interestingly, several of the differences noted here between the hadrosauroid type of braincase morphology and that of more primitive iguanodontians were already pointed out by Nopcsa (1904), in his description of additional skull remains attributable to *Mochlodon* (= *Zalmoxes*). There, he compared the basicranium of '*Mochlodon*' with that of *Telmatosaurus*, and even figured basicrania referred to these genera (NHMUK R.3408 and NHMUK R.3387, respectively) in ventral view (Nopcsa 1904: figs. 1, 2), noting the much more elongated basioccipital of the rhabdodontid basicranium and the different morphology of the basal tubera, among other aspects (Nopcsa 1904: pp. 244–245).

Our re-assignment of the specimens UBB NVZ1-42 and NHMUK R.3401A to *Telmatosaurus transsylvanicus* doubles the number of known partial braincases for that genus but significantly reduces the number of previously reported rhabdodontid basicrania from the Haţeg Basin from six to only four. The comparisons provided herein also demonstrate the presence of several important morphological differences between the basicranium of hadrosauroids and that of rhabdodontids, which allows for the confident assignment of even isolated specimens in the future.

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THIRD PAPER

A NEW ORNITHOPOD DINOSAUR, *TRANSYLVANOSAURUS PLATYCEPHALUS* GEN. ET SP. NOV. (DINOSAURIA: ORNITHISCHIA), FROM THE UPPER CRETACEOUS OF THE HAŢEG BASIN, ROMANIA.

BY

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ARTICLE

A NEW ORNITHOPOD DINOSAUR, *TRANSYLVANOSAURUS PLATYCEPHALUS* GEN. ET SP. NOV. (DINOSAURIA: ORNITHISCHIA), FROM THE UPPER CRETACEOUS OF THE HAŢEG BASIN, ROMANIA

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ABSTRACT—Rhabdodontid dinosaurs were a group of medium-sized iguanodontian ornithopods from the Late Cretaceous of Europe. The uppermost Cretaceous continental deposits from the Haţeg Basin of western Romania yielded a very rich assemblage of vertebrates including abundant rhabdodontid remains, which have been exclusively referred to the genus *Zalmoxes* thus far. Here we describe a new rhabdodontid dinosaur, *Transylvanosaurus platycephalus* gen. et sp. nov., from the uppermost Cretaceous of the Haţeg Basin. The holotype of the new taxon was discovered in early–late Maastrichtian strata near Pui in the eastern part of the basin and comprises the articulated basicranium and both frontals. *Transylvanosaurus* differs from all previously reported rhabdodontids in having particularly wide and crested frontals, elongated and straight paroccipital processes that make only a gentle lateral curve and project mostly posterolaterally, prominent and massive prootic processes that extend mainly anterolaterally and ventrally, wide and crest-like basal tubera that meet the long axis of the braincase at a very flat angle, widely splayed basipterygoid processes that extend mainly ventrolaterally and slightly anteriorly, as well as a well-developed notch on the lateral side of the basicranium that is continuous, straight, and inclined anteroventrally. Phylogenetic analyses employing two different datasets consistently recovered the new taxon within the Rhabdodontidae, at the base of the iguanodontian radiation. Based on the morphological comparisons presented herein, we propose a particularly close relationship between *Transylvanosaurus* and *Rhabdodon* from southern France, which in turn provides evidence for a more complex biogeographic history of the Rhabdodontidae than previously thought.

http://zoobank.org/urn:lsid:zoobank.org:pub:57B462E5-E08E-42DC-B256-4E978DFBFCC7

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INTRODUCTION

The Late Cretaceous dinosaur faunas of Europe are characterized by a unique taxonomic composition, comprising coelurosaurian and ceratosaurian theropods, titanosaurian sauropods, nodosaurid ankylosaurs, as well as hadrosauroid and rhabdodontid ornithopods (for an overview, see Csiki-Sava et al., 2015). Among these, rhabdodontids are particularly remarkable, as they represent the most common medium-sized herbivores in the Upper Cretaceous deposits of Europe. Moreover, the family seems to have been endemic to Europe and all undisputed members of the clade are restricted to the Late Cretaceous (Bunzel, 1871; Nopcsa, 1902a; Weishampel et al., 2003; Ősi et al., 2012; Godefroit et al., 2017; Párraga and Prieto-Márquez, 2019). Recently, an unnamed iguanodontian from the Lower Cretaceous (Barremian–Aptian) of northern Spain, the 'Vegagete ornithopod,' has been suggested to represent the oldest member of the family (Dieudonné et al., 2016, 2020; Yang et al., 2020), although this referral has been questioned subsequently and it may instead represent a close outgroup of the Rhabdodontidae (Dieudonné et al., 2021). Phylogenetic analyses consistently recover the Rhabdodontidae as a group of basally branching iguanodontians, placed at the very base of the iguanodontian radiation (Weishampel et al., 2003; Butler et al., 2008; McDonald, 2012; Ősi et al., 2012; Boyd, 2015; Dieudonné et al., 2016, 2021; Madzia et al., 2018; Yang et al., 2020). Based on this phylogenetic placement and their exclusively Late Cretaceous fossil record, rhabdodontids are characterized by an exceptionally long ghost lineage.

As currently understood, the Rhabdodontidae includes eight species within five genera. The first named rhabdodontid was *Rhabdodon priscus* from the Upper Cretaceous of southern France (Matheron, 1869). In addition, the Upper Cretaceous (Campanian–Maastrichtian) of southern France has yielded a

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second species of *Rhabdodon*, *R. septimanicus* (Buffetaut and Le Loeuff, 1991; Chanthasit, 2010), as well as the recently described *Matheronodon provincialis* (Godefroit et al., 2017). The second report of a rhabdodontid was made by Bunzel (1871), who described '*Iguanodon*' *suessi* from the Upper Cretaceous (lower Campanian) of eastern Austria, which was subsequently placed in its own genus *Mochlodon* (Seeley, 1881). Another species of *Mochlodon*, *M. vorosi*, was erected much later for material from the Upper Cretaceous (Santonian) of western Hungary (Ősi et al., 2012). Rhabdodontids were also discovered in the Upper Cretaceous (Campanian–Maastrichtian) deposits of northern, central and eastern Spain, including material that was assigned to the genus *Rhabdodon* (Pereda-Suberbiola and Sanz, 1999) as well as a new genus and species, *Pareisactus evrostos* (Párraga and Prieto-Márquez, 2019).

One of the best records for rhabdodontids is known from the uppermost Cretaceous deposits of the Transylvanian area in western Romania, and chiefly of the Haţeg Basin (Fig. 1), where they represent the most abundant dinosaur group. Rhabdodontid material from the Upper Cretaceous of the Haţeg Basin was first reported by Nopcsa (1897), who then referred the material to the genus *Mochlodon*, as the new species *M. robustum* (Nopcsa, 1900:579, 1902a, 1904). Subsequently, Nopcsa synonymized the genera *Mochlodon* and *Rhabdodon* and, given the priority of the latter, re-assigned the rhabdodontid material from the Haţeg Basin to *Rhabdodon*, also synonymizing the species *M. robustum* with *R. priscum* (Nopcsa, 1915:4–5). A re-evaluation both of the original specimens studied by Nopcsa and of newly discovered material, mainly also from the Haţeg Basin, by Weishampel et al. (2003), led to the erection of the new genus *Zalmoxes* for all the rhabdodontid material from Romania, represented by two species, *Z. robustus* and *Z. shqiperorum*. Recent phylogenetic analyses indicate either a close relationship between *Zalmoxes* and *Mochlodon* from Austria and Hungary (Ősi et al., 2012; Dieudonné et al., 2021), or alternatively between *Zalmoxes* and *Rhabdodon* from France and Spain (Dieudonné et al., 2016). Until now, all the rhabdodontid material from the Haţeg Basin has been assigned indiscriminately to the genus *Zalmoxes*, most often without positive supportive evidence in the form of shared apomorphies.

In this study, we describe a new genus and species of rhabdodontid dinosaur, *Transylvanosaurus platycephalus*, from the uppermost Cretaceous of the eastern Haţeg Basin, near Pui. The holotype specimen LPB (FGGUB) R.2070 comprises the articulated basicranium, composed of the basioccipital, the exoccipital-opisthotic complexes, the basisphenoid-parasphenoid complex, the prootic, and the laterosphenoid, which was found associated with the articulated left and right frontals (Fig. 2). The holotype specimen represents one of the most complete clearly associated rhabdodontid skulls from the Haţeg Basin known so far. Remarkably, the morphological comparisons presented herein indicate a particularly close relationship of the new taxon with *Rhabdodon* from the uppermost Cretaceous of France, which in turn provides evidence for a much more complex biogeographic history of the Rhabdodontidae than previously thought.

Institutional Abbreviations—CM, Collection Méchin, Vitrolles, France; **LPB (FGGUB)**, Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; **MBFSZ**, Mining and Geological Survey of Hungary, Budapest, Hungary; **MC**, Musée de Cruzy, Cruzy, France; **MMIRS**, Ioan Raica Municipal Museum Sebeș, Sebeș-Alba, Romania; **NHMUK**, Natural History Museum, London, U.K.; **UBB**, Babeș-Bolyai University, Cluj-Napoca, Romania.

GEOLOGICAL SETTING

The type specimen described here was discovered in the intramontane Haţeg Basin, which is located in the southwestern Carpathians, western Romania (Fig. 1A). The Haţeg Basin comprises extensive continental deposits from the uppermost Cretaceous that crop out mainly in the northwestern, central, south-central, and eastern parts of the basin (Fig. 1B). The uppermost Cretaceous continental strata in the south-central part of the Haţeg Basin along the Sibişel Valley near Sânpetru host the great majority of the original Nopcsa localities and represent the stratotype section of the early to early late Maastrichtian-aged Sînpetru Formation that is composed mainly of reddish siliciclastic sediments (Grigorescu, 1983; Therrien, 2006; Therrien et al., 2009; Panaiotu and Panaiotu, 2010). The Upper Cretaceous deposits from the northwestern part of the basin have been assigned to the Densuş-Ciula Formation of early to late Maastrichtian age, which likewise comprises mainly reddish siliciclastic sedimentary rocks but with a higher content of volcanoclastic sediments (Grigorescu, 1992; Bojar et al., 2011; Csiki-Sava et al., 2016). The Upper Cretaceous continental rocks in the central part of the Haţeg Basin, which are exposed along the Râul Mare River section near Nălaţ-Vad and Totești, consist mostly of grayish siliciclastics that are likely 'middle' to late Maastrichtian in age, though it has been debated whether they belong to the Sînpetru Formation, the Densuş-Ciula Formation, or represent a separate lithostratigraphic unit (Codrea et al., 2002; Smith et al., 2002; Van Itterbeeck et al., 2004, 2005; Panaiotu et al., 2011; Csiki-Sava et al., 2016). The uppermost Cretaceous continental sedimentary rocks from the eastern part of the Haţeg Basin that crop out along the Bărbat River Valley section near Pui probably also belong to a distinct lithostratigraphic unit, presumably of 'middle' Maastrichtian age (see below).

These four, roughly coeval, lithostratigraphic units have yielded an extremely diverse array of fossil vertebrates. In fact, the continental uppermost Cretaceous deposits from the Haţeg Basin host one of the richest terrestrial vertebrate faunas known from the entire Upper Cretaceous of Europe (Nopcsa, 1923a; Grigorescu, 1983; Weishampel et al., 1991; Csiki-Sava et al., 2015, 2016). The latest Cretaceous vertebrate assemblages from the Haţeg Basin include fishes, amphibians, several species of kogaionid multituberculate mammals, at least two distinct turtles, squamates, at least four different crocodyliforms, azhdarchid pterosaurs, as well as nodosaurid ankylosaurs, rhabdodontid and hadrosauroid ornithopods, titanosaurian sauropods, non-avian coelurosaurian theropods, and birds (e.g., Nopcsa, 1900, 1902a, 1923b, 1928, 1929a; Huene, 1932; Rădulescu and Samson, 1986; Weishampel et al., 1993; Rădulescu and Samson, 1996; Buffetaut et al., 2002; Weishampel et al., 2003; Martin et al., 2006; Csiki et al., 2010a, 2010b; Martin et al., 2010; Wang et al., 2011; Vasile et al., 2013; Csiki-Sava et al., 2015, 2016; Venczel et al., 2016; Venczel and Codrea, 2016; Csiki-Sava et al., 2018; Vremir et al., 2018; Augustin et al., 2021). Generally, the vertebrate occurrences can be grouped into distinct taphonomic categories, ranging from isolated bones and teeth to associated and partly articulated remains, to microvertebrate accumulations, or else to small, mainly lenticular multitaxic bonebeds, the so-called 'fossil-pockets' (Nopcsa, 1902b; Grigorescu, 1983; Csiki et al., 2010c). Some of the bones show bioerosional trace fossils, documenting the feeding activity of insects and vertebrates (Csiki, 2006; Csiki et al., 2010c; Augustin et al., 2019).

The type specimen of *Transylvanosaurus platycephalus* gen. et sp. nov. has been recovered from the uppermost Cretaceous continental strata cropping out near Pui, in the eastern part of the Haţeg Basin, which are exposed along the Bărbat River Valley (Figs. 1B, 2). The stratigraphic relationships of these Bărbat River deposits have been rather controversial and in the past, they have been considered either as belonging to the Sînpetru Formation (Nopcsa, 1905; Mamulea, 1953;

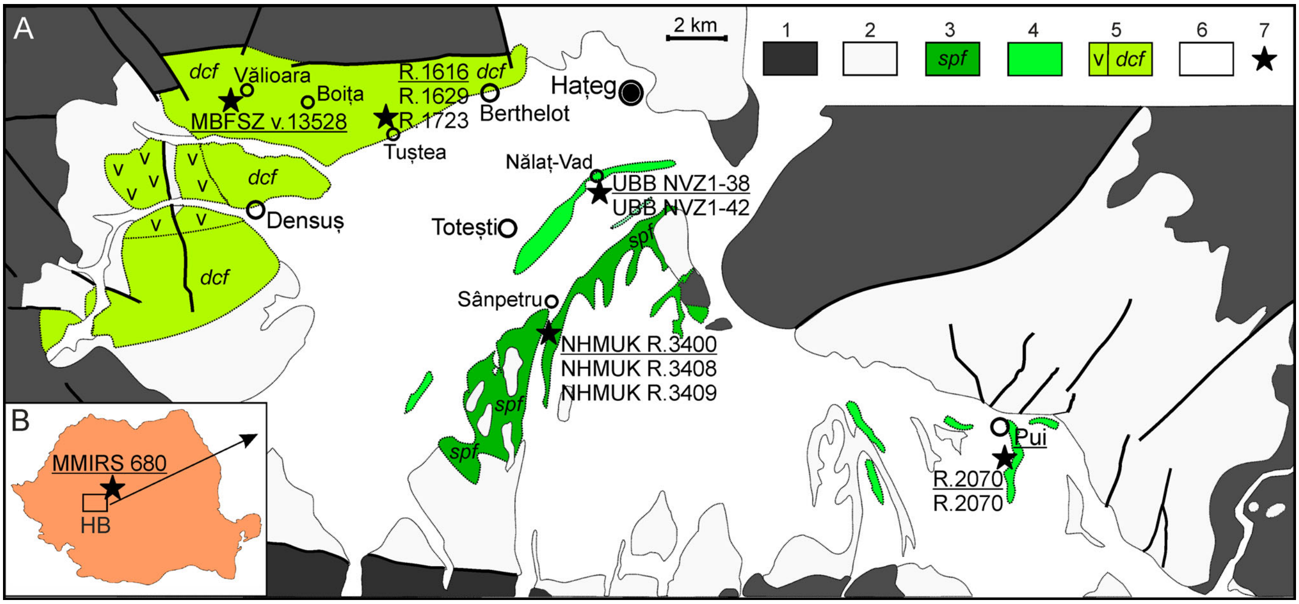

FIGURE 1. Locality information for the holotype of *Transylvanosaurus platycephalus* gen. et sp. nov. **A**, Location of the type locality of *Transylvanosaurus platycephalus* gen. et sp. nov. south of Pui, in the eastern Haţeg Basin, western Romania, alongside with that of other rhabdodontid posterior cranial remains (frontals and basicrania listed above, respectively below the horizontal line) discussed in the text; the holotype is LPB (FGGUB) R.2070, in bold (for details on specimen numbers, see text). Key: **1**, uplifted pre-Alpine crystalline basement rocks bordering the Haţeg Basin; **2**, pre-uppermost Cretaceous sedimentary units of the Haţeg Basin (mainly marine beds); 3–5, vertebrate-bearing uppermost Cretaceous (Maastrichtian) continental deposits: **3**, Sînpetru Formation (*spf*); **4**, Sînpetru Formation-correlative units ('Râul Mare Beds' in the central part of the basin, 'Pui Beds' in the eastern part); **5**, Densuş-Ciula Formation (*dcf*), with v—volcanoclastic 'lower member'; **6**, Cenozoic (mainly Quaternary) sedimentary cover; **7**, main fossiliferous localities with rhabdodontid posterior cranial material. **B**, Inset shows the position of the Haţeg Basin within Romania (rectangle), as well as the approximate location of the rhabdodontid frontal MMIRS 780 in the southwestern part of the Transylvanian Basin (star).

Grigorescu, 1992), or, more recently, as representing a distinct lithostratigraphic unit that has informally been referred to as the 'Bărbat Formation' (Therrien, 2005) or the 'Pui Beds' (Csiki-Sava et al., 2016, 2018). The sedimentary rocks that crop out along the Bărbat River Valley comprise mainly red pedogenic silty mudstones and gray-greenish conglomeratic channel sandstones with occasionally occurring dark-gray silty mudstone horizons, all of which were probably deposited within a meandering river floodplain under a seasonal and semi-arid climate (Van Itterbeeck et al., 2004; Bojar et al., 2005; Therrien, 2005; Csiki-Sava et al., 2016). The age of the 'Pui Beds' probably corresponds to the 'middle' Maastrichtian, being refined to around the early to late Maastrichtian boundary based on palynostratigraphy (Van Itterbeeck et al., 2005). The Bărbat River Valley section has yielded a rich assemblage of vertebrates including fishes, amphibians, kogaionid multituberculates, turtles, squamates, crocodyliforms, azhdarchid pterosaurs, rhabdodontids, hadrosauroids, titanosaurian sauropods, and diverse maniraptoran theropods (Grigorescu et al., 1985, 1999; Rădulescu and Samson, 1986; Csiki et al., 2005; Folie and Codrea, 2005; Vasile and Csiki, 2010; Codrea and Solomon, 2012; Smith and Codrea, 2015; Vremir et al., 2015; Solomon et al., 2016; Venczel and Codrea, 2016, 2019; Csiki-Sava et al., 2018; Vasile et al., 2019).

MATERIAL AND METHODS

The holotype specimen of *Transylvanosaurus platycephalus* gen. et sp. nov. described herein was found in 2007 at the Bărbat River Valley section near Pui in the eastern Haţeg Basin and comprises the articulated basicranium as well as the associated left and right frontals. It was prepared mechanically at the Laboratory of Paleontology of the Faculty of Geology and Geophysics, University of Bucharest, where it is also permanently stored under the catalog number LPB (FGGUB) R.2070. The specimen was digitalized using the photogrammetry technique detailed by Mallison and Wings (2014) as well as the software Agisoft Photoscan Professional, in order to create surface models. Subsequently, 3D prints were produced at the Centre of Visualisation, Digitisation and Replication at the University of Tübingen (VDR) based on the surface models, which are deposited in the Palaeontological Collection of the University of Tübingen.

In order to assess the phylogenetic relationships of the new Romanian taxon within Ornithopoda, we performed two sets of phylogenetic analyses. For the first analysis, we used the matrix of Dieudonné et al. (2021), which represents the most extensive and most recent dataset for basally branching ornithopod dinosaurs, and which is built on the previous datasets of Dieudonné et al. (2016) and Xu et al. (2006), respectively, with numerous revised character scorings. The dataset employed by Dieudonné et al. (2016), in its turn, combined the character-data matrices of McDonald et al. (2010), Ősi et al. (2012), and Brown et al. (2013). The resulting compound matrix of Dieudonné et al. (2021) comprises 342 characters scored for 72 taxa (i.e., 73 taxa with *Transylvanosaurus* included). In our analysis, we treated all characters as equally weighted and some multistate characters (i.e., 111, 151, 204, and 283) as ordered (following Dieudonné et al., 2021). *Herrerasaurus ischigualastensis* was treated as the operational outgroup taxon. The dataset was run in TNT v. 1.5 (Goloboff and Catalano, 2016), with traditional search and the tree bisection reconnection algorithm using 10,000 replications of Wagner trees and 10 trees saved per replication. A second round of tree bisection reconnection was applied to all trees retained in memory to recover all most

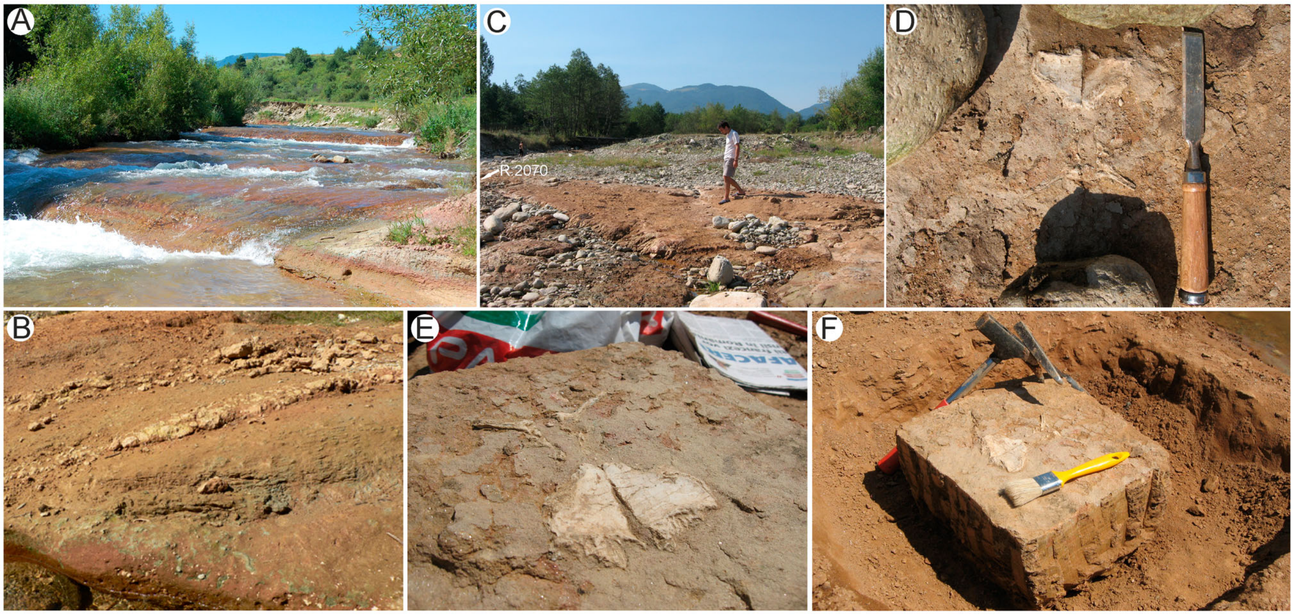

FIGURE 2. The type locality of *Transylvanosaurus platycephalus* gen. et sp. nov. at the Bărbat River Valley section, near Pui, eastern Haţeg Basin. **A**, General overview of the riverbed outcropping condition of the uppermost Cretaceous continental 'Pui Beds' along the Bărbat River, south of Pui; in the background, flat-lying coarse cobbly-sandy Quaternary deposits covering the reddish uppermost Cretaceous rocks. **B**, Details of the superposed greenish coarser-grained channel deposits and red fine-grained floodplain sediments with well-developed whitish pedogenic calcrete horizons, characteristic of the 'Pui Beds.' **C**, View of the 'Pui Beds' looking southward, with the type locality and bed (a red silty mudstone) of *Transylvanosaurus platycephalus* gen. et sp. nov. exposed in the middle ground; the type specimen, LPB (FGGUB) R.2070, was discovered near the left edge of the photograph (white arrow). **D**, Partial posterior cranium of *Transylvanosaurus platycephalus* gen. et sp. nov., specimen LPB (FGGUB) R.2070 (exposed paired frontals, above, and partly buried basicranium, below) in the moment of its discovery, July 2007; chisel for scale. **E**, Specimen LPB (FGGUB) R.2070 completely exposed during excavation. **F**, Block containing specimen LPB (FGGUB) R.2070 after completed excavation and before plaster jacketing.

parsimonious trees. We did not exclude or prune any taxon from the analysis.

Additionally, in order to test the results of the first analysis, we ran a second phylogenetic analysis with one of the two matrices used by Madzia et al. (2018). This dataset is a modified version of the matrix compiled by Boyd (2015), including some additional taxa and several revised character scorings (Madzia et al., 2018). The resulting matrix consists of 255 characters and 75 taxa (i.e., 76 taxa with *Transylvanosaurus* included). We treated all characters as equally weighted and unordered. *Marasuchus lilloensis* was treated as the operational outgroup taxon. The second analysis was again run in TNT v. 1.5 (Goloboff and Catalano, 2016), but using a different approach from the first analysis. This was done because, for the matrix (Madzia et al., 2018), we were not able to conclude the second round of tree bisection reconnection (run with the trees retained in memory), because it reached the maximum number of trees that can be saved by TNT. Therefore, we applied an alternative approach altogether, using TNT's "New Technology search" instead of the Traditional/heuristic search. For that, we selected the "Driven search" option for obtaining the trees, changing only the number of times the minimum length was found to 100 times ("Find minimum length 100 times"), and maintaining all other default parameters. For the search algorithms used, we enabled all four options: "Sectorial Search", "Ratchet", "Drift," and "Tree fusing". In the "Sectorial Search" settings, we only changed the number of drifting cycles used for selections of size above 75 (changing from 6 to 100), maintaining all other default parameters. In the "Ratchet" settings, we only changed the total number of iterations (changing from 10 to 100), maintaining all other default parameters. In the "Drift" settings, we only changed the number of cycles (changing from 10 to 100), maintaining all other default parameters. Finally, we did not alter the settings of the "Tree fusing" algorithm. We did not exclude or prune any taxon from the second analysis. For the results of both phylogenetic analyses, see below.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1888
ORNITHOPODA Marsh, 1881
IGUANODONTIA Sereno, 1986

RHABDODONTIDAE Weishampel, Jianu, Csiki, and Norman, 2003

TRANSYLVANOSAURUS gen. nov.

Type Species—*Transylvanosaurus platycephalus* sp. nov.

Etymology—'Trans' (Latin) meaning across, 'silva' (Latin) meaning forest, and 'sauros' (Greek σαύρος) meaning lizard ('Lizard from across the forest'). The genus is named after Transylvania, the historical region that includes the Haţeg Basin and the type locality of the genus.

Diagnosis—As for the type and only species.

TRANSYLVANOSAURUS PLATYCEPHALUS sp. nov.
Figs. 3–6

Holotype—LPB (FGGUB) R.2070, a fragmentary skull comprising the articulated basicranium composed of the

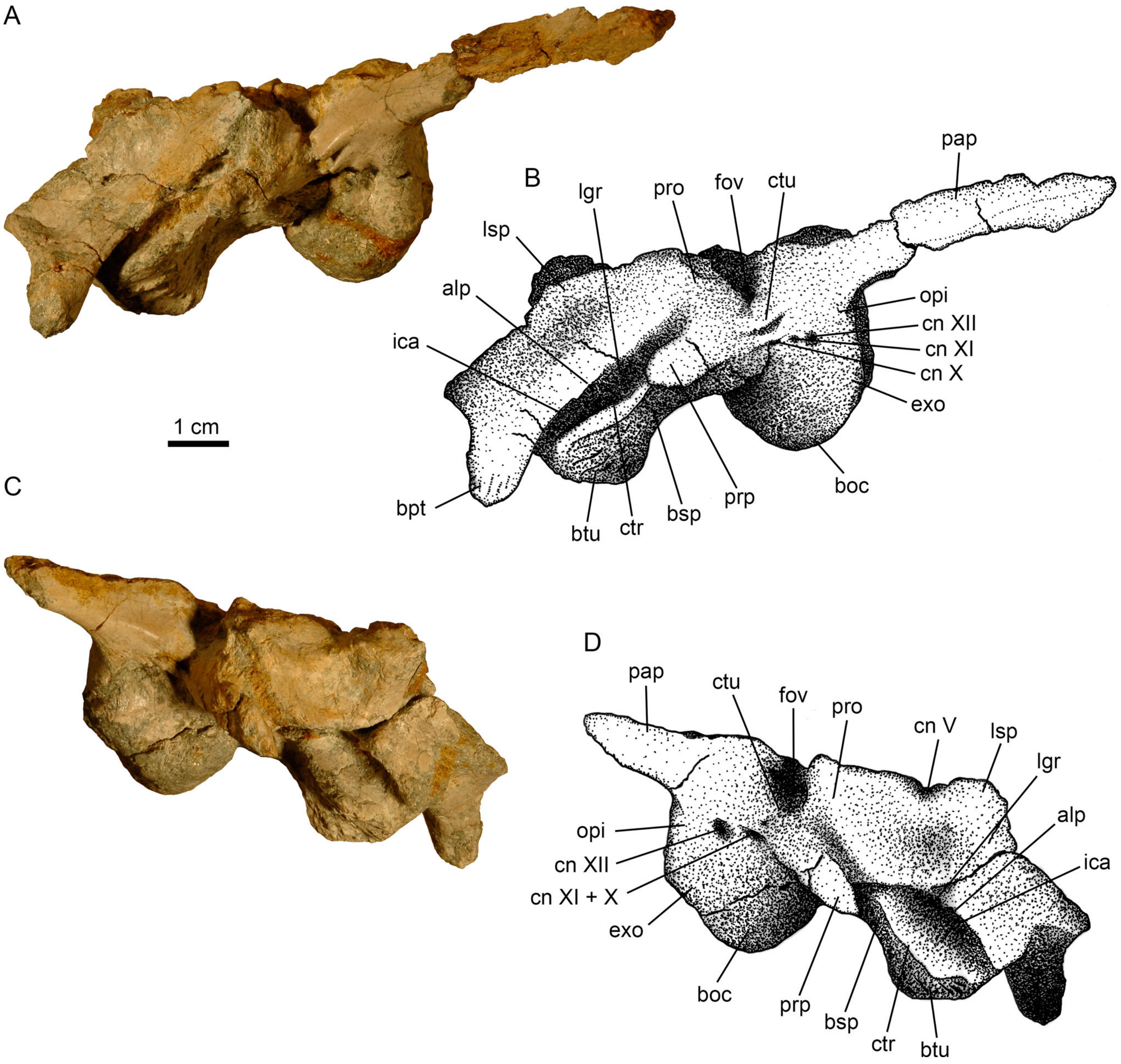

FIGURE 3. *Transylvanosaurus platycephalus* gen. et sp. nov., holotype basicranium, FGGUB (LPB) R.2070, in lateral view. **A**, photo and **B**, drawing of the basicranium in left lateral view. **C**, photo and **D**, drawing of the basicranium in right lateral view. **Abbreviations**: **alp**, alar process; **boc**, basioccipital; **bpt**, basipterygoid process; **bsp**, basisphenoid; **btu**, basal tubera; **cn**, cranial nerve; **ctr**, crista transversalis; **ctu**, crista tuberalis; **exo**, exoccipital; **fov**, foramen ovalis; **ica**, opening for the internal carotid artery; **lgr**, lateral groove; **lsp**, laterosphenoid; **opi**, opisthotic; **pap**, paroccipital process; **pro**, prootic; **prp**, prootic process.

basioccipital, the exoccipital-opisthotic complexes, the basisphenoid-parasphenoid complex, the prootic and the laterosphenoid, as well as the articulated left and right frontals.

Etymology—‘Platys’ (Greek πλατύς) meaning wide, and ‘cephalos’ (Greek κέφαλος) meaning head. The specific name refers to the exceptionally wide skull of the new dinosaur compared with that of other rhabdodontids.

Type Locality—The holotype material was found in the Bărbat River Valley section, near Pui, eastern Haţeg Basin, Hunedoara County, Romania. The bones of the basicranium and the paroccipital processes were found in articulation, directly below and behind the articulated frontals (Fig. 2).

Type Stratum—LPB (FGGUB) R.2070 was recovered in 2007 from the middle part of the uppermost Cretaceous continental succession from the Bărbat River Valley section, informally also referred to as the ‘Bărbat Formation’ (Therrien, 2005) or the ‘Pui Beds’ (Csiki-Sava et al., 2016). The ‘Pui Beds’ have been estimated to be ‘middle’ Maastrichtian in age, i.e., close to the early to late Maastrichtian boundary (Van Itterbeeck et al., 2005); the locality yielding specimen LPB (FGGUB) R.2070 is located slightly southwards of (i.e., stratigraphically above) the level sampled for palynology by Van Itterbeeck et al. (2005).

Diagnosis—A small- to medium-sized rhabdodontid ornithopod dinosaur characterized by the following autapomorphies: (1) proportionately wide frontals with an anteroposterior length to mediolateral width ratio of 1.38; (2) presence of a well-developed, anteriorly placed transverse frontal crest that

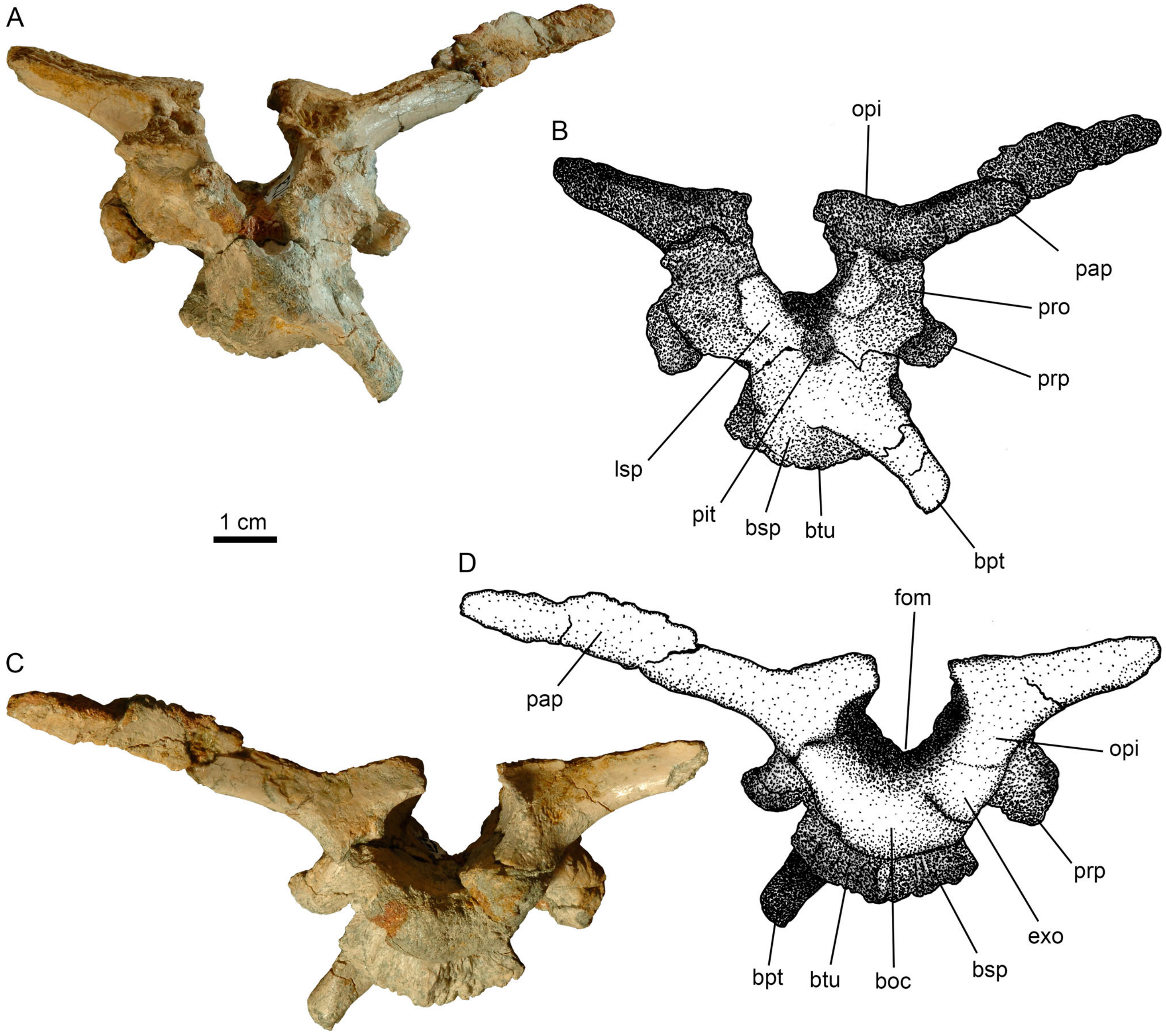

FIGURE 4. *Transylvanosaurus platycephalus* gen. et sp. nov., holotype basicranium, FGGUB (LPB) R.2070, in anterior and posterior view. **A**, photo and **B**, drawing in anterior view. **C**, photo and **D**, drawing in posterior view. **Abbreviations**: **boc**, basioccipital; **bpt**, basipterygoid process; **bsp**, basisphenoid; **btu**, basal tubera; **exo**, exoccipital; **fom**, foramen magnum; **lsp**, laterosphenoid; **opi**, opisthotic; **pap**, paroccipital process; **pit**, pituitary fossa; **pro**, prootic; **prp**, prootic process.

distally bounds the confluent nasal-prefrontal articulation facets; (3) very long, straight and thin paroccipital processes that make only a gentle lateral curve, and direct mostly posterolaterally and slightly dorsally; (4) very prominent and massive prootic processes that extend mainly anterolaterally and ventrally; (5) mediolaterally wide, crest-like basal tubera that meet the long axis of the braincase, which is parallel to the orientation of the endocranial floor, at a very flat angle of approximately 140°; (6) widely splayed basipterygoid processes that extend mainly ventrolaterally and slightly anteriorly, diverging approximately 25° from the sagittal plane; (7) a well-developed, anteroventrally inclined notch on the lateral side of the basicranium, just anterior to the basal tubera, that is continuous, straight, and semi-circular in cross section.

In addition, the taxon differs from all other rhabdodontids by the following unique combination of characters: a basioccipital condyle that is highly convex and trapezoidal in ventral view; a heart-shaped foramen magnum that is wider mediolaterally than it is high dorsoventrally; a flat and straight endocranial floor that constantly widens posteriorly; a weakly developed crista tuberalis; an anteroposteriorly elongated basisphenoid; a dorsoventrally deep basisphenoid-parasphenoid complex; a wrinkled posterior surface of the basal tubera with a prominent midline process that does not extend for the entire dorsoventral height of the basal tubera.

DESCRIPTION

The holotype specimen of *Transylvanosaurus platycephalus*, LPB (FGGUB) R.2070, comprises the articulated basicranium (Figs. 3, 4, 5) composed of the basioccipital, the exoccipital-opisthotic complexes, the basisphenoid-parasphenoid complex, the prootic, and the laterosphenoid, which were found in the field associated with the articulated left and right frontals (Fig. 6). Aside from the missing parts, the specimen is well-preserved

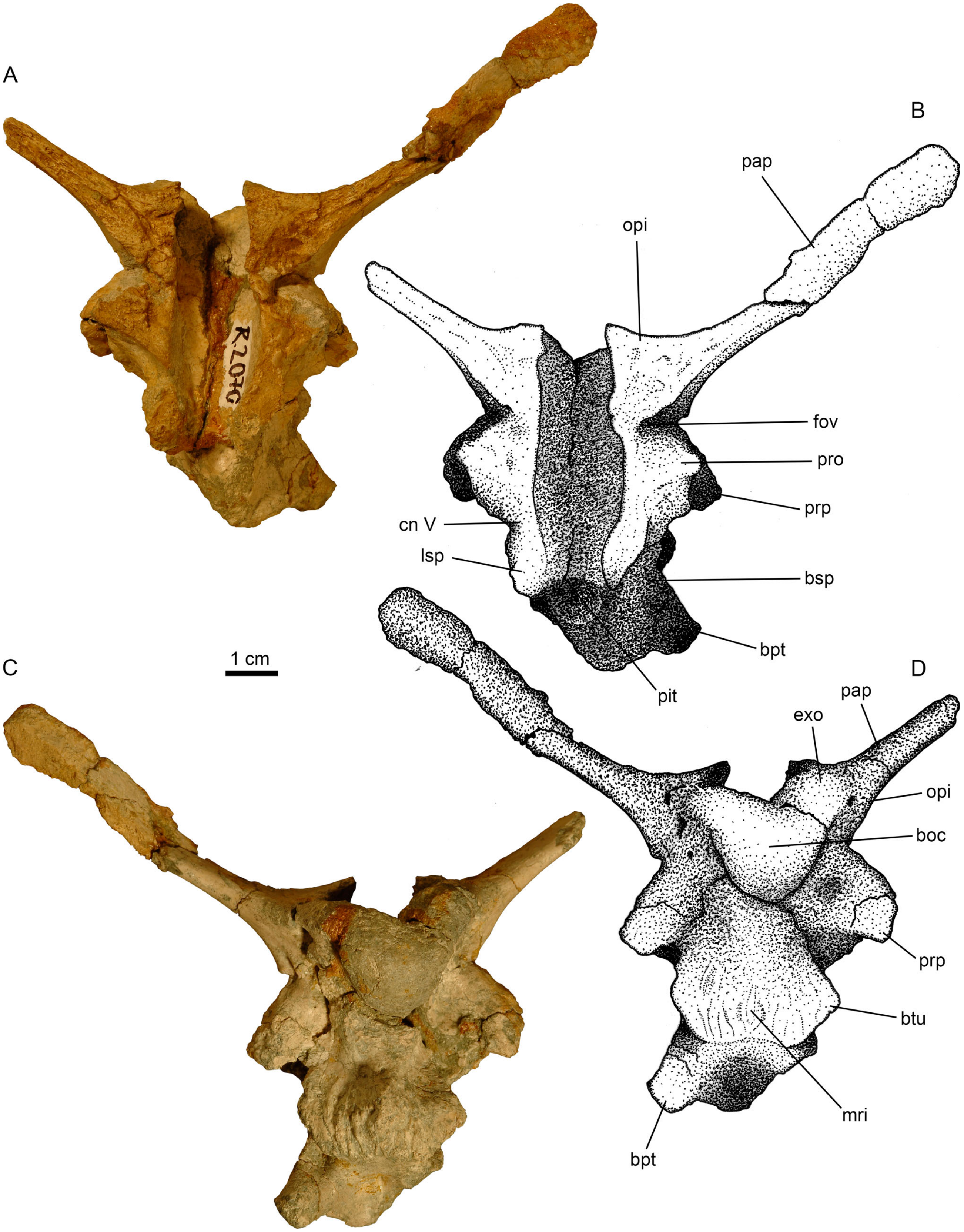

FIGURE 5. *Transylvanosaurus platycephalus* gen. et sp. nov., holotype basicranium, FGGUB (LPB) R.2070, in dorsal and ventral view. **A**, photo and **B**, drawing of the basicranium in dorsal view. **C**, photo and **D**, drawing of the basicranium in ventral view. **Abbreviations**: **boc**, basioccipital; **bpt**, basipterygoid process; **bsp**, basisphenoid; **btu**, basal tubera; **cn**, cranial nerve; **exo**, exoccipital; **fov**, foramen ovalis; **mri**, midline ridge on the basal tubera; **lsp**, laterosphenoid; **opi**, opisthotic; **pap**, paroccipital process; **pit**, pituitary fossa; **pro**, prootic; **prp**, prootic process.

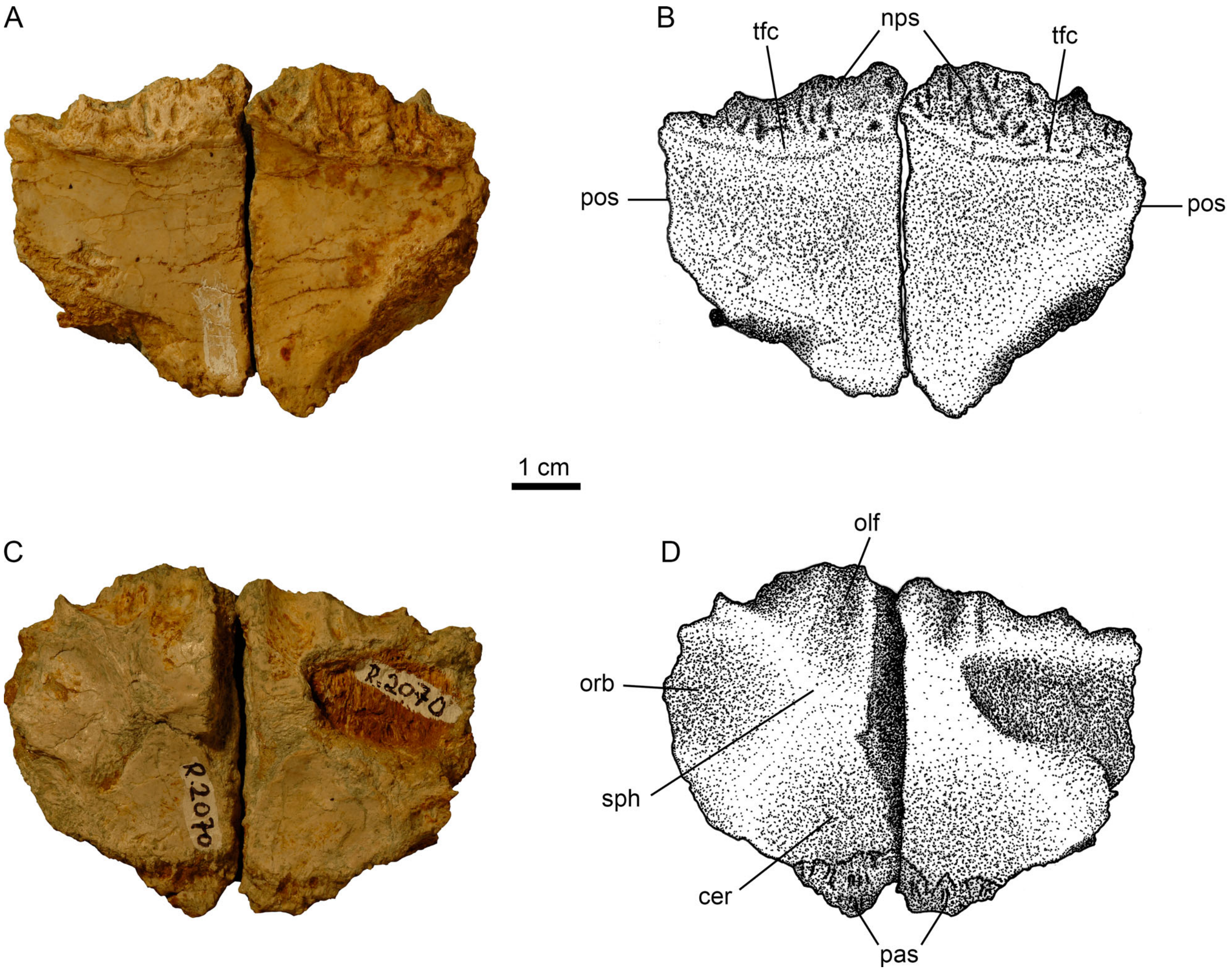

FIGURE 6. *Transylvanosaurus platycephalus* gen. et sp. nov., holotype frontals, FGGUB (LPB) R.2070. **A**, photo and **B**, drawing of the frontals in dorsal view. **C**, photo and **D**, drawing of the frontals in ventral view. Note that the ventral side of the left frontal is damaged and thus does not preserve the impressions of the orbital roof and the olfactory bulb. **Abbreviations**: **cer**, impression of the cerebrum; **nps**, confluent nasal-prefrontal suture; **olf**, impression of the olfactory bulb; **orb**, orbital roof; **pas**, parietal suture; **pos**, postorbital suture; **sph**, sutural contact with the sphenethmoid plate; **tfc**, transverse frontal crest.

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with small processes and foramina still present and largely undistorted. The frontals were found slightly above and anterior to the basicranium in their roughly correct anatomical position (Fig. 2D, E). No additional skull bones or remains thereof have been found between the basicranium and the frontals nor in their close proximity. This peculiar state of preservation indicates that originally, some soft tissues were probably still connecting the basicranium with the frontals when the specimen was embedded into the sediment. Also, the pattern of surface exposure of the specimen when identified in the field (Fig. 2D), together with the dorsally damaged margins of the basicranium as currently preserved, suggests that other parts of the occipital section of the skull may also have been preserved during burial, but were most probably removed by fluvial erosion in this very dynamic, actively eroding riverbed site, prior to the discovery of the specimen.

Basioccipital

The basioccipital contributes to the posterior and ventral parts of the braincase (Fig. 3A–D). It is kidney-shaped in posterior view, as well as trapezoidal and markedly convex in ventral view. The posterior articular surface for the atlas is slightly convex and directed posteroventrally. The dorsal aspect of the basioccipital is concave, forming the ventral part of the foramen magnum and the posterior part of the endocranial floor (Fig. 4A–D). A small part of the bone near the right posterolateral margin is missing. The basioccipital is fused to the exoccipitals dorsolaterally and to the basisphenoid-parasphenoid complex anteriorly (Fig. 5A–D). The suture between the basioccipital and the exoccipitals is hardly visible and only a faint suture is present on the left side, whereas a crack largely obliterates the sutural contact on the right side. In posterior view, the suture between the basioccipital and the exoccipitals extends dorsomedially. In lateral view, the suture between the basioccipital and the exoccipital extends anteriorly and to a lesser degree ventrally. Together, the basioccipital and the ventromedial extremities of the exoccipitals form the occipital condyle, although the former contributes to a much greater extent. In ventral view, the basioccipital is connected to the basisphenoid anteriorly through a short but distinct neck (Fig. 5C, D). The suture between the basioccipital and the basisphenoid is not discernible in ventral nor in dorsal view. On the ventral aspect of the basicranium, a large crack runs anterolaterally, extending almost for the entire diagonal width of the basicranium.

Exoccipital-Opisthotic Complex

The exoccipital-opisthotic complex contributes to the posterior and the lateral parts of the braincase (Fig. 3A–D). It is formed by the exoccipitals ventromedially and by the opisthotics dorsolaterally. The exoccipitals are roughly ellipsoidal and convex in posterior view, having a knob-like morphology. The posteroventral part participates in the formation of the occipital condyle, although to a much lesser degree than the basioccipital. Additionally, the exoccipitals form the ventrolateral margin of the foramen magnum (Fig. 4C, D). Ventrally, the exoccipitals are fused to the basioccipital and dorsally to the opisthotics along a well-discernible suture. The suture between the exoccipitals and opisthotics extends anteroventrally, subparallel to the suture between the basioccipital and the exoccipitals, but is inclined slightly more ventrally than the latter. In lateral view, three large foramina are visible that lie approximately on the suture between the exoccipital and the opisthotic (Fig. 3A, B). The posterior-most and largest of these represents the opening for cranial nerve XII or hypoglossal nerve. The two foramina that are located more anteriorly are much smaller and represent the openings for cranial nerve XI or accessory nerve, as well as the opening for cranial nerve X or vagus nerve, respectively.

The opisthotic forms the rod-like paroccipital process that extends mainly posterolaterally and dorsally (Figs. 3A–D, 4C, D). The paroccipital process is relatively thin both anteroposteriorly and dorsoventrally. It has a roughly ellipsoidal cross section being higher dorsoventrally than wide anteroposteriorly. In posterior view, the paroccipital process makes a gentle dorsolateral curve and meets the exoccipital at a wide angle. The distal parts of the paroccipital processes are missing. In addition to this dorsolateral and posterior development, the opisthotic also extends dorsomedially, forming the curved dorsolateral part of the foramen magnum. The dorsal and anterior faces of the paroccipital processes are slightly damaged but still exhibit the sutural contacts with the (not preserved) supraoccipital and squamosal, respectively. The foramen magnum is wide and slightly heart-shaped in posterior view, although the dorsal margin is unknown due to the missing supraoccipital, which would apparently be wedged in between the two opisthotics along a rather straight and vertical contact (Fig. 4C, D). From what is preserved, however, the foramen magnum seems to have been wider mediolaterally than high dorsoventrally. The anterolateral part of the opisthotic forms a weakly developed ridge or crest, the crista tuberalis, which connects to the prootic anteriorly and lies directly ventral to the fenestra ovalis (see below).

Basisphenoid-Parasphenoid Complex

The basisphenoid-parasphenoid complex contributes to the ventral part of the braincase (Figs. 3A–D, 5C, D). It is actually composed of two bones that, however, are seamlessly fused to each other. The basisphenoid-parasphenoid complex comprises the concave ventral part of the endocranial floor dorsally (Fig. 5A, B), as well as the prominent crest-like basal tubera and the large wing-like basipterygoid processes anteroventrally (Fig. 5C, D). The basisphenoid-parasphenoid complex is fused to the basioccipital posteriorly, as well as to the prootic and laterosphenoid dorsally. In dorsal view, the basisphenoid-parasphenoid complex forms the middle and anterior part of the endocranial floor. In general, the endocranial floor is completely straight and flat with a semi-circular cross section that progressively widens posteriorly. The dorsum sellae is located on the anterior portion of the endocranial floor and exhibits two small, hardly visible foramina, the openings for the paired cranial nerve VI or abducens nerve. Anterior to the dorsum sellae, the endocranial floor sharply slopes down ventrally. The basisphenoid-parasphenoid complex is broken anterior to this section, exposing the ellipsoidal pituitary fossa in anterior view that lies ventral to the endocranial floor and houses two canals for the paired internal carotid arteries (Fig. 4A, B).

In ventral view, the basisphenoid is connected to the basioccipital posteriorly through a distinct neck. The suture between the basisphenoid and the basioccipital is not discernible. The region between the basioccipital and the basisphenoid shows a large crack that continues anterodorsally through the basisphenoid-parasphenoid complex. Anterior to the basioccipital neck, are the prominent and well-developed basal tubera that project mainly anteroventrally and together form a wide, mediolaterally extending ridge with a crest-like morphology (Figs. 3A–D, 5C, D). The basal tubera meet the long axis of the braincase, which is parallel to the orientation of the endocranial floor, at an angle of about 140°, which is best seen in lateral view. The posterior face of the basal tubera has a wrinkled appearance, especially near its ventral margin. This surface likely was the attachment site for the m. rectus capitis ventralis (Weishampel et al., 2003). Moreover, the posterior surface of the basal tubera bears a prominent transverse midline process, which projects mainly posteriorly and is dorsoventrally elongated but does not extend for the entire dorsoventral height of the basal tubera.

In lateral view, a well-developed deep notch is located just anterodorsal to the basal tubera that extends anteroventrally at an angle of about 45° relative to the long axis of the braincase (Fig. 3A, B). This notch is bordered by the crest-like lateral expansion of the basal tubera (i.e., the crista transversalis) posteroventrally and by the alar process anterodorsally. It is relatively straight and completely continuous, ending in a semi-circular opening both dorsally and ventrally. In the ventral third of this notch lies the entrance for the carotid artery. On the right side of LPB (FGGUB) R.2070, the notch is slightly damaged by the large crack that runs through the basisphenoid-parasphenoid. The alar process is a thin ridge that extends posterolaterally and borders the deep notch on the lateral aspect of the basisphenoid. Ventrally, the alar process merges with the basipterygoid process that projects ventrolaterally, being inclined at an angle of about 25° relative to the sagittal plane, and also slightly anteriorly (Figs. 3A, B, 4A, B). The lateral part of the basipterygoid process is slightly rugose, likely indicating the (cartilaginous) contact with the pterygoid (Holliday and Witmer, 2008). Only the left basipterygoid process is preserved. The surface between the basipterygoid processes is roughly triangular in ventral view, smooth and slightly anterodorsally inclined. The lateral surface of the basisphenoid-parasphenoid complex, dorsal to the basipterygoid processes, is roughly triangular and dorsomedially inclined, parallel to the orientation of the basipterygoid processes, resulting in a wing-like morphology of this area. A slight depression in this area probably corresponds to the attachment site of the m. protractor pterygoideus (Holliday, 2009).

Prootic and Laterosphenoid

The prootic and the laterosphenoid bones contribute to the lateral parts of the braincase (Fig. 3A–D). The prootic is sutured to the exoccipital-opisthotic complex posteriorly, to the laterosphenoid anteriorly, and to the basisphenoid ventrally. The laterosphenoid, in its turn, is sutured to the prootic posteriorly, and to the basisphenoid-parasphenoid complex ventrally. The suture between the prootic and the laterosphenoid is not discernible in the holotype specimen, however, and thus they are here described as a single complex, unless indicated otherwise. In lateral view, the prootic-laterosphenoid complex is a roughly rectangular to trapezoidal block-like element. Between the opisthotic and the prootic, there is a large opening, the fenestra ovalis (Fig. 3A–D). Anterior to this opening, the prootic becomes markedly thicker mediolaterally and contributes to the dorsal part of the deep notch extending across the lateral side of the braincase, which is bordered by the basal tubera posteroventrally and the alar process anterodorsally (see above). A prominent ventral process of the prootic forms the posteroventral margin of this notch. This ventral prootic process has a knob-like morphology and extends mainly anterolaterally and also somewhat ventrally.

The suture between the prootic and the basisphenoid is situated on the ventral aspect of this prootic process and extends approximately anteroposteriorly. In ventral view, there is a large cleft between the prootic process and the basal tubera of the basisphenoid. Anterior to the deep notch, the prootic-laterosphenoid complex becomes thinner and curves slightly medially. A large indentation is located anterior to the conspicuous swelling of the prootic-laterosphenoid complex, probably representing the opening for cranial nerve V, or trigeminal nerve. The dorsal margin of the prootic-laterosphenoid complex is imperfectly preserved and it gently slopes down anteroventrally (Fig. 5A, B). The sutural contact with the supraoccipital is partly visible in the posterior part of the complex, although the supraoccipital itself is missing.

Frontals

The left and right frontals are well-preserved, undistorted, and almost complete (Fig. 6). They are nearly symmetrical, although the left frontal seems to have been somewhat larger. The frontals are not fused to each other but were found next to each other in articulation, separated by a narrow gap filled with sediment (Fig. 2D–F). Both frontals are relatively flat dorsoventrally and have a trapezoidal to sub-triangular outline in dorsal and ventral views, being only slightly longer anteroposteriorly than wide mediolaterally. The length to width ratio of the frontals is approximately 1.38, based on the dimensions of the slightly more complete left frontal. The width of the frontals is greatest near their anterior margin, and then it stays relatively constant for more than half of their length before becoming narrower posteriorly. The anterior width of the frontal bone is over four times larger than its posterior width near the parietal facet. The frontals are sutured to each other along midline, to the parietal posteriorly, to the postorbital laterally as well as to the nasal and prefrontal anteriorly. The suture between the frontals is relatively straight and extends anteroposteriorly.

Posteriorly, the frontals form a broad triangular projection medially that shows a well-developed sutural contact on its ventral aspect for articulation with the parietal, which they seem to have considerably overlapped. Along their lateral margins, the frontals show a suture with the postorbital that extends anteroposteriorly at the lateral segment of the frontal and anterolaterally at the posterolateral segment, respectively. The sutural contact with the cranial elements lying anterior to the frontal (the nasal medially and the prefrontal laterally) occurs along the mediolaterally oriented wide transversal anterior margin of the frontals (Fig. 6A, B). These two contacts cannot be identified as clearly separate facets and they appear to have been confluent within a joint naso-prefrontal-to-frontal sutural facet. This naso-prefrontal-frontal suture is extensive and coarsely ridged, covering the entire wide anterior margin of the frontals, and is visible primarily on their dorsal aspect, which seem to have been overlapped by the nasals and prefrontals accordingly. This joint suture is bordered posteriorly by a low but angular, clearly visible ridge that extends mainly mediolaterally. Similarly, a low ridge also borders the posterolateral margin of the frontals in dorsal view. The surface between these raised rims is markedly concave and in medial view, the anterior and posterior margins of the frontals are somewhat dorsally curved. Other than these ridge-like features, the dorsal surface of the frontals is very smooth.

The ventral aspect of the frontals is much better preserved in the right frontal than in the left one, in which this side is locally damaged. In ventral view, the frontal shows three distinct concave depressions (one anterior, one lateral, and one posterior), which are separated from one another by low ridges (Fig. 6C, D). The thickest part of the frontals is at the center of the bone, near the ventral ridge that separates the anterior depression from the posterior one. The anterior depression likely represents the impression of the olfactory bulb of the brain. It has a roughly triangular shape, with the tip directed posteromedially, and is bordered medially by an anteroposteriorly extending ridge, and laterally by an anterolaterally extending ridge. The lateral depression is round and represents the medial part of the roof of the orbit. It is separated from the posterior depression by a very shallow rim that extends in a posterolateral direction. The posterior depression is elliptical to subtriangular and represents the impression of the cerebral part of the endocranium. The ridge that separates the anterior depression of the olfactory bulb roof from the lateral depression of the orbital roof likely represents the sutural contact of the frontal with the sphenethmoid plate.

COMPARISONS

Transylvanosaurus platycephalus is clearly referable to the Rhabdodontidae, as it exhibits the characteristic basicranial morphology of the group, i.e., a distinct and well-developed neck connecting the occipital condyle with the basal tubera anteriorly, as well as a mediolaterally wide and crest-like basal tubera (for a discussion contrasting the basicranial morphology in rhabdodontids, other basally branching iguanodontians and hadrosauroids, see Augustin et al. in press). Furthermore, two sets of phylogenetic analyses performed by us also consistently recovered *Transylvanosaurus* as being firmly nested within Rhabdodontidae (see below). As such, in the following section, the holotype of *Transylvanosaurus platycephalus* is compared extensively to rhabdodontid cranial material previously reported from the Upper Cretaceous of the Transylvanian area, which until now has exclusively been referred to the genus *Zalmoxes*. In addition, we compare the holotype partial skull described herein with the only other rhabdodontid for which substantial parts of the braincase and the frontals had been described, i.e., the genus *Rhabdodon* from southern France. In order to make the comparisons with the currently existing rhabdodontid cranial material from Romania and France as clear and meaningful as possible, and because there have been uncertainties as to the taxonomic affinities of some specimens (Ősi et al., 2012), we specifically refer to individual specimens instead of simply referring to *Zalmoxes* and *Rhabdodon* in the case of the Romanian and, respectively, the French material.

An Overview of the Braincase Material referred previously to Rhabdodontidae

In total, four more or less complete rhabdodontid basicrania have been reported until now from the Upper Cretaceous of the Transylvanian area, all recovered from the Haţeg Basin (see also Augustin et al., in press). The first two of these, NHMUK R.3408 and NHMUK R.3409, were excavated more than a century ago from the stratotype Sînpetru Formation along the Sibişel Valley, in the south-central part of the basin (Fig. 1B). These specimens were described and figured by Nopcsa (1904), who referred them initially to the rhabdodontid *Mochlodon robustus*, later transferred to *Zalmoxes robustus* by

Weishampel et al. (2003). Specimen NHMUK R.3408 comprises the complete basioccipital and most of the basisphenoid (Nopcsa, 1904:fig. 2, pl. 1), whereas NHMUK R.3409 only preserves the anterior-most part of the basioccipital and the posterior-most part of the basisphenoid, i.e., the region around the basal tubera (Nopcsa, 1904:pl. 1). A third rhabdodontid basicranium, LPB (FGGUB) R.1629, was recovered much later, in 1998, from the middle part of the Densuş-Ciula Formation at the Tuştea-Oltoane nesting site, in the northwestern part of the Haţeg Basin (Fig. 1B). The specimen consists of a complete basioccipital that was mentioned by Weishampel et al. (2003:78), and was subsequently illustrated and briefly described by Augustin et al. (in press:fig. 5). A largely complete left exoccipital-opisthotic complex, LPB (FGGUB) R.1591, was found in close proximity to, and shows a perfect fit with, LPB (FGGUB) R.1629, and thus almost certainly belongs to the same individual (Botfalvai et al., 2017: fig. 8). The last known rhabdodontid basicranium from the Haţeg Basin, LPB (FGGUB) R.1723, was also found at the same Tuştea locality in 2000 (Fig. 1B). It comprises the complete basioccipital and most of the basisphenoid, and has been described and figured by Weishampel et al. (2003:fig. 11). Two other Transylvanian braincase specimens that have been referred to *Zalmoxes* in the past, UBB NVZ1-42 (Godefroit et al., 2009) from Nălaţ-Vad and NHMUK R.3401A (Weishampel et al., 2003) from Sânpetru (Fig. 1B), were recently re-assigned to the hadrosauroid dinosaur *Telmatosaurus* (Augustin et al. in press), and are thus not considered in our comparisons.

Several more or less well-preserved rhabdodontid frontals have been described in the past from the Upper Cretaceous deposits of Romania, the most complete ones of which are used in the comparisons below. The first specimen, NHMUK R.3400, has been recovered from the Sînpetru Formation of the Sibişel Valley section (Fig. 1B) and was originally described by Nopcsa (1904), who referred it to *Mochlodon* (= *Zalmoxes*). This specimen comprises the fused left and right frontals (Nopcsa, 1904:pl. 1). Later, Nopcsa (1929b:fig. 1) figured and described another pair of fused frontals, MBFSZ v.13528, from the Densuş-Ciula Formation near Vălioara (Fig. 1B), which he assigned to the hadrosauroid *Orthomerus* (= *Telmatosaurus*). Later, this specimen was first referred to an indeterminate arctometatarsalian theropod by Jianu and Weishampel (1997), before Weishampel et al. (2003) re-assigned it to *Zalmoxes robustus* (Weishampel et al., 2003:fig. 8). A nearly complete left frontal fused to the postorbital, LPB (FGGUB) R.1616, was recovered much later from the Tuştea-Oltoane site of the Densuş-Ciula Formation (Fig. 1B). The specimen was described and figured by Weishampel et al. (2003:fig. 10), who referred it to *Zalmoxes robustus.* A largely complete frontal from the Râul Mare River section near Nălaţ-Vad (Fig. 1B), UBB NVZ1-38, was figured and described by Godefroit et al. (2009:fig. 6). Based on its association within the same site with other, more diagnostic material, these authors referred UBB NVZ1-38 to *Zalmoxes shqiperorum* (Godefroit et al., 2009). Most recently, an almost complete left frontal from the lowermost part of the Maastrichtian Sebeș Formation cropping out at Petrești-Arini, in the southwestern Transylvanian Basin (and about 70 km to the northeast of the Haţeg Basin localities; Fig. 1A), MMIRS 680, was described and figured by Vremir et al. (2014:27–28, fig. 10), who referred it to *Zalmoxes* sp.

Four rhabdodontid braincase specimens have been described to date from the Upper Cretaceous of southern France and all have been assigned to the genus *Rhabdodon*. Two of these specimens, MC-M4 and MC-MN25, both from the Upper Cretaceous (upper Campanian–lower Maastrichtian; Buffetaut et al., 1999) of southern France near Cruzy (Languedoc), were described in detail by Pincemaille-Quillevere et al. (2006). MC-M4 comprises a largely complete braincase including the basioccipital, the exoccipital-opisthotic complex, the basisphenoid-parasphenoid complex, the prootic, the laterosphenoid, and the supraoccipital (Pincemaille-Quillevere et al., 2006:figs. 1–4), whereas MC-MN25 is more incompletely preserved and includes only the distorted posterior part of the braincase. Due to the poor preservation of MC-MN25, we mostly excluded it from the comparisons below. More recently, two additional rhabdodontid braincase specimens have been reported from the Upper Cretaceous of southern France, CM-669 from the late Campanian–early Maastrichtian locality Fox-Amphoux (Provence), and MC-M1575 also from Cruzy (Chanthasit, 2010). They both preserve the majority of the braincase, including the basioccipital, the exoccipital-opisthotic complex, the basisphenoid-parasphenoid complex, the prootic, the laterosphenoid, the supraoccipital, and the parietal (Chanthasit, 2010:45–49). Until now, no reasonably complete frontal has been described for the genus *Rhabdodon*; the only currently known referred specimen is an incomplete right frontal, MC-QR8, from the Upper Cretaceous of southern France (Chanthasit, 2010).

The holotype of *Transylvanosaurus platycephalus*, LPB (FGGUB) R.2070, is one of the most complete rhabdodontid skulls composed of associated elements that are undoubtedly referable to a single individual that has been reported so far from the Upper Cretaceous of Romania, despite previous claims of several associations of rhabdodontid cranial elements by Nopcsa (1904; see also Dumbravă et al., 2017). Notably, it is very similar in size to the other rhabdodontid basicrania from the Haţeg Basin, especially to LPB (FGGUB) R.1629 and R.1723, and is only slightly larger than NHMUK R.3408 and R.3409. The rhabdodontid braincases from the Upper Cretaceous of France show a larger variation in size, ranging from close in size to those from Romania (as in MC-M4), to somewhat larger (up to a third larger, as in CM-669, MC-M1575), and even to significantly (more than a third) larger, as in MC-MN25, in agreement with previous assessments regarding a similar amount of overall body size difference between the latest Cretaceous Romanian (*Zalmoxes*) and French (*Rhabdodon*) rhabdodontids (e.g., Weishampel et al., 2003). Although being of a roughly similar size, the basicranium morphology of *Transylvanosaurus* differs considerably from all other rhabdodontid basicrania of the Haţeg Basin as well as from those of southern France. The rhabdodontid frontals known from the Upper Cretaceous of Romania show a much higher size disparity than that noted for the basicrania, LPB (FGGUB) R.1616 and MMIRS 680 being at least one-third larger than *Transylvanosaurus.* Furthermore, just as for the braincase, the frontals of *Transylvanosaurus* also show several remarkable morphological differences from these other known Romanian rhabdodontid frontals.

Basioccipital and Endocranial Floor

The basioccipital is largely similar among the rhabdodontid basicrania from the Haţeg Basin and southern France, but some differences are nevertheless noteworthy. The basioccipital is reniform in posterior view, as well as trapezoidal and convex in ventral view in all these rhabdodontid specimens preserving the occipital condyle, although the ventral convexity is most pronounced in *Transylvanosaurus*, which has an almost round basioccipital in ventral view. Specimen LPB (FGGUB) R.1629 differs from *Transylvanosaurus* and the other rhabdodontid basicrania in that the occipital condyle is demarcated from the basioccipital neck anteriorly by a well-developed rim. In LPB (FGGUB) R.1723, a well-developed notch is present on the anterolateral part of the basioccipital, which is absent or at most weakly developed in *Transylvanosaurus*, LPB (FGGUB) R.1629, NHMUK R.3408, and all of the French specimens. Like the other rhabdodontids, *Transylvanosaurus* has a well-developed neck connecting the occipital condyle with the basisphenoid.

Notably, the holotype of *Transylvanosaurus* differs from all other Romanian rhabdodontid specimens in having a straight endocranial floor. In contrast, the endocranial floor in LPB (FGGUB) R.1723 curves slightly dorsally anterior to the foramen magnum reaching a dorsal peak in the anterior half of the basioccipital, before sloping sharply ventrally to a ventral peak approximately at the level of the opening for the internal carotid artery; anterior to this ventral peak, the endocranial floor curves dorsally again. In LPB (FGGUB) R.1629 and NHMUK R.3408, the endocranial floor is relatively straight posteriorly, up until mid-length of the basioccipital, and then curves down ventrally reaching the deepest point approximately at the level of the opening for the internal carotid artery. Therefore, the endocranial floor is markedly sinuous in LPB (FGGUB) R.1723, as well as, to a lesser extent, in LPB (FGGUB) R.1629 and NHMUK R.3408, as opposed to the completely straight endocranial floor in *Transylvanosaurus*. The orientation of the endocranial floor is not visible in the specimens from southern France as the endocranium is filled with sediment in CM-699, crushed in MC-MN25, or fully concealed by the braincase itself in MC-M4 and MC-M1575.

Exoccipital-Opisthotic Complex

The exoccipital-opisthotic complex of *Transylvanosaurus* differs markedly from that of LPB (FGGUB) R.1591, the only other reasonably complete element known from Transylvania, as well as from those preserved in specimens MC-M4, MC-M1575, and CM-699 from southern France. Generally, the ventromedial corner of the exoccipital in all of these basicrania is knob-like and participates in the formation of the occipital condyle in the form of a condylid, thus resembling the exoccipital of *Transylvanosaurus*. Additionally, in both LPB (FGGUB) R.1591 and MC-M4, the openings for cranial nerves X–XII are positioned on a relatively straight line extending roughly anteroposteriorly between the exoccipital condylid and the paroccipital process, just as in *Transylvanosaurus*.

However, the morphology of the paroccipital processes is completely different in *Transylvanosaurus* as compared with that of the other rhabdodontids. In *Transylvanosaurus*, the paroccipital process makes only a gentle dorsolateral curve proximally and is completely straight otherwise. In contrast, the paroccipital process of LPB (FGGUB) R.1591 makes a much sharper dorsolateral curve and its ventral margin is curved over the entire length of the process. In the specimens from southern France referred to *Rhabdodon*, the paroccipital process curves slightly dorsomedially before it turns sharply dorsolaterally and then extends only laterally at about the level of the skull roof. Consequently, the paroccipital processes in these French specimens resemble that of *Transylvanosaurus* in that they are relatively straight for most of their length, differing from the highly arched paroccipital process seen in LPB (FGGUB) R.1591 that laterally curves downward (i.e., ventrally). In general, however, the paroccipital processes of *Transylvanosaurus* extend much more laterally but less dorsally than do those of LPB (FGGUB) R.1591 as well as MC-M4, MC-M1575, and CM-699, therefore being overall straighter. Moreover, the paroccipital processes are also somewhat longer and considerably thinner dorsoventrally in *Transylvanosaurus* than in all other rhabdodontid specimens. Nevertheless, it more closely resembles specimens MC-M4, MC-M1575, and CM-699 in this regard, too, whereas LPB (FGGUB) R.1591 has much thicker paroccipital processes. Due to the highly arched paroccipital processes of LPB (FGGUB) R.1591 as well as to their greater dorsoventral thickness and shorter length, the skull of this animal seems to have been somewhat narrower but relatively higher than that of *Transylvanosaurus* and the French rhabdodontids.

The medial margin of the exoccipital-opisthotic process that forms the lateral wall of the foramen magnum is also dorsoventrally higher in LPB (FGGUB) R.1591, MC-M4, MC-M1575, and MN-25, compared with LPB (FGGUB) R.2070. Accordingly, the foramen magnum is higher dorsoventrally than wide mediolaterally in these specimens, whereas it is wider mediolaterally than high dorsoventrally in *Transylvanosaurus*. Furthermore, the crista tuberalis is only weakly developed in *Transylvanosaurus*, while it is much more pronounced in all the other known rhabdodontid braincases. Although the supraoccipital is missing in the holotype specimen of *Transylvanosaurus*, based on the morphology of the opisthotic, it must have been very narrow mediolaterally. Additionally, the suture between the opisthotic and the supraoccipital is nearly vertical (extending dorsoventrally) in *Transylvanosaurus*, whereas it is oblique (extending dorsolaterally) in LPB FGGUB) R.1591, CM-699, MC-M1575, and MC-M4.

Prootic

In *Transylvanosaurus*, the ventral part of the prootic forms a well-developed and massive process that extends mainly anterolaterally and to a lesser degree also ventrally. This process is completely absent in MC-M4 and MC-M1575, while this region is preserved neither in LPB (FGGUB) R.1723 and R.1629, nor in NHMUK R.3408 and R.3409. But even so, it is nonetheless highly probable that the prootic must have had a slightly different morphology in these specimens when compared with *Transylvanosaurus*. In *Transylvanosaurus*, the prootic process participates in the formation of the groove on the lateral side of the braincase that houses the entrance for the internal carotid artery, whereas in all the other rhabdodontid braincases, this groove ends in a small chamber dorsally on the lateral aspect of the basisphenoid-parasphenoid complex and thus cannot reach the prootic process (if present). A small crest-like extension of the prootic in CM-699 might correspond to the prootic process seen in *Transylvanosaurus*, although it is much more weakly developed and appears to represent more likely a continuation of the crista transversalis of the basal tubera. Consequently, it differs completely from the massive knob-like process seen in *Transylvanosaurus* that is almost completely separated from the crista transversalis.

Basisphenoid-Parasphenoid Complex

The basisphenoid-parasphenoid complex of *Transylvanosaurus* shows several significant differences from those of all other currently known rhabdodontid basicrania. Arguably, the most important difference is that the transverse, crest-like basal tubera meet the long axis of the braincase, which is parallel to the orientation of the endocranial floor, at an angle of approximately 140° in *Transylvanosaurus* as opposed to 120° in NHMUK R.3408 and R.3409, as well as LPB (FGGUB) R.1723, 125° in MC-699 as well as 130° in MC-M4 and MC-M1575. Consequently, *Transylvanosaurus* resembles more closely the rhabdodontid specimens from southern France in this regard. Partly due to the flat angle between the basal tubera and the long axis of the braincase, the basisphenoid is also much more elongated anteroposteriorly in *Transylvanosaurus* compared with the other rhabdodontid basicrania.

Moreover, the basal tubera display different morphologies in the different rhabdodontid braincase specimens. The dorsoventral extension (or height) of the basal tubera and of the entire basisphenoid-parasphenoid complex is much greater in *Transylvanosaurus*, in the different French rhabdodontid basicrania, and in LPB (FGGUB) R.1723, compared with the condition seen in NHMUK R.3408 and R.3409. In addition, the anterior part of the basisphenoid-parasphenoid complex (just anterior to the basal tubera) is anterodorsally inclined in *Transylvanosaurus*, the French rhabdodontid basicrania, and LPB (FGGUB) R.1723, while it is completely straight and extends only anteriorly in NHMUK R.3408 and R.3409. The two London specimens further differ from *Transylvanosaurus* in that the basal tubera extend not only anteroventrally but also laterally and thus encircle the ventral portion of the basicranium up until the level of the endocranial floor in a semicircular manner. Therefore, the basal tubera are very wide mediolaterally in NHMUK R.3408 and R.3409 and well visible in dorsal view, lateral to the endocranial floor. Although a similar condition can also be noted in MC-M4, MC-M1575, and CM-699, it is much more pronounced in NHMUK R.3408 and R.3409. In contrast, the basal tubera of LPB (FGGUB) R.1723 project mostly anteroventrally, just as in *Transylvanosaurus*. *Transylvanosaurus* differs, however, from LPB (FGGUB) R.1723 in having basal tubera that are much wider mediolaterally and thus visible in dorsal view as well. In all rhabdodontid basicrania from the Haţeg Basin, the posterior face of the basal tubera seems to have a slightly wrinkled appearance and a prominent midline ridge, albeit only a fractured surface marks its position in NHMUK R.3408. Both the wrinkles and the midline ridge are, however, much more strongly developed in *Transylvanosaurus* than in the other specimens. The French rhabdodontid basicrania lack both the wrinkled appearance on the posterior face of the basal tubera and the midline ridge.

Another striking difference between *Transylvanosaurus* and the other rhabdodontids concerns the morphology of the groove on the lateral aspect of the basisphenoid housing the entrance for the internal carotid artery. In all rhabdodontids except *Transylvanosaurus*, this groove is oriented roughly dorsoventrally and terminates in a rounded chamber, well below the level of the endocranial floor. In contrast, this groove displays a completely different morphology in *Transylvanosaurus*, where it is oriented anteroventrally and forms a continuous canal that extends above the level of the endocranial floor. The basipterygoid processes also have a unique morphology and orientation in *Transylvanosaurus*, differing markedly from the condition seen in LPB (FGGUB) R.1723, MC-M4, and MC-M1575. In *Transylvanosaurus*, these processes direct ventrolaterally and anteriorly, whereas they project ventrolaterally and posteriorly in the other rhabdodontid specimens. In addition, the basipterygoid processes diverge from the sagittal plane at a wider angle in *Transylvanosaurus* and their lateral surface is much broader anteroposteriorly, giving them a wing-like morphology. The ventral surface between the basipterygoid processes is narrower and somewhat more steeply inclined in LPB (FGGUB) R.1723 and MC-M1575 than in *Transylvanosaurus*. Unlike the condition seen in *Transylvanosaurus*, the region anterior to the basal tubera, on the ventral aspect of the basicranium, shows a straight and elongated groove extending anteroposteriorly in specimens NHMUK R.3408 and R.3409; in the first of these two specimens, two triangular fractured surfaces mark the position of the missing basipterygoid processes lateral to this groove. Although imperfectly preserved in *Transylvanosaurus*, the pituitary fossa is apparently much shorter dorsoventrally than in LPB (FGGUB) R.1723 and thus resembles the tube-like and round pituitary fossa present in NHMUK R.3409.

Frontals

Although the frontals of *Transylvanosaurus* generally resemble those that have been previously referred to the Rhabdodontidae from the Upper Cretaceous of Romania, some notable differences are present. Most importantly, the frontals of *Transylvanosaurus* are very wide mediolaterally, having an anteroposterior length to mediolateral width ratio of 1.38, which represents the lowest value recorded among the rhabdodontid frontals that have so far been described. This ratio can be reliably measured for three other frontals that are reasonably complete, all from the Haţeg Basin. Of these, MBFSZ v.13528 has a length to width ratio of 1.46 and thus is relatively close to the value seen in *Transylvanosaurus*. The other two frontals however, LPB (FGGUB) R.1616 and NHMUK R.3400, have much higher values of this ratio, of 1.69 and 1.93, respectively, more in line with the general diagnosis of the frontal of *Zalmoxes* as given by Weishampel et al. (2003). Moreover, the frontals remain relatively broad for almost their entire length in *Transylvanosaurus* and MBFSZ v.15328, whereas they evenly and markedly taper posteriorly in LPB (FGGUB) R.1616 and NHMUK 3400. Accordingly, the outline of the frontals is rather trapezoidal (short and broad) in *Transylvanosaurus* and MBFSZ v.13528, as opposed to the more triangular (long and narrow) outlines of LPB (FGGUB) R.1616 and NHMUK R.3400. Although imperfectly preserved, specimen MMIRS 680 from the southwestern Transylvanian Basin seems to have been relatively broad as well, with a length to width ratio of approximately 1.51, thus more closely resembling *Transylvanosaurus* in this regard. However, unlike *Transylvanosaurus*, this frontal also tapers posteriorly giving it a triangular outline, also seen in the frontal UBB NVZ1-38 from Nălaţ-Vad, the only such specimen referred to *Zalmoxes shqiperorum* by Godefroit et al. (2009). All of these ratios were calculated with measurements of the left frontal, which is more complete in both *Transylvanosaurus* and NHMUK R.3400, as well as being the only side preserved in LPB (FGGUB) R.1616 and MMIRS 680.

Aside from their variable overall outline and relative dimensions, the known rhabdodontid frontals also differ in other aspects of their general morphology. In *Transylvanosaurus*, the dorsal surface of the frontals is concave, just as in MMIRS 680 and MBFSZ v.13528, whereas it is rather flat or even slightly convex in NHMUK R.3400 and LPB (FGGUB) R.1616. Additionally, a well-developed transverse crest, placed closely behind and parallel to the unique naso-prefrontal suture of the frontal, is present in *Transylvanosaurus* and some other rhabdodontid frontals from Romania, including MMIRS 680 and MBFSZ v.13528, but it is absent in LPB (FGGUB) R.1616 (where a very slightly raised posterior margin of these two non-coalesced sutural facets is present, nevertheless) and in NHMUK R.3400. The unique naso-prefrontal suture extends primarily mediolaterally in *Transylvanosaurus*, MBFSZ v.13528, and MMIRS 680, and the frontals are overlain anteriorly by the nasals and prefrontals along their entire width (although the sutural contacts between the frontal and the nasal medially, respectively the prefrontal laterally, cannot be identified as clearly separate facets, see above). In contrast to this condition, the frontal-nasal and frontal-prefrontal sutures are clearly divided, posteriorly pointed triangular facets in NHMUK R.3400 and UBB NVZ1-38. Specimen LPB (FGGUB) R.1616 exhibits still another configuration of this sutural relationship, in which the two facets are partly confluent (as noted by Weishampel et al., 2003), although they are still clearly discernible, with a less posteriorly projected and smaller prefrontal facet laterally and a larger, more posteriorly extended nasal facet medially. Consequently, the fronto-nasal suture is somewhat oblique in LPB (FGGUB) R.1616, NHMUK R.3400, and UBB NVZ1-38 and the nasals overlie the frontals mostly in the medial part, giving the nasals a triangular shape in dorsal view with the posteriorly pointed tip inserted between the paired frontals. Interestingly, the frontal specimens in which a well-developed transverse frontal crest is present also seem to have a concave dorsal surface, a relatively wider overall shape and a roughly similar, confluent and transversely oriented frontal/nasal-prefrontal suture morphology. The general pattern presented by the ventral surface of the frontals, housing the impressions of the olfactory bulb and the cerebrum, as well as the orbital roof, is very similar in all rhabdodontid frontals.

PHYLOGENETIC ANALYSES

Two phylogenetic analyses were performed in order to assess the phylogenetic relationships of *Transylvanosaurus platycephalus* (for details on the two datasets and the settings used for the analysis, see above). We added *Transylvanosaurus* to the first dataset of Dieudonné et al. (2021) and, given the nature of its holotype, restricted to the partial posterior skull, were able to score a total of 18 characters (representing only 5% of the total dataset) for the new taxon (the complete data matrix can be found in the Supplementary material). The analysis recovered 2508 equally parsimonious trees with 1422 steps. Consistency (CI) and retention indices (RI) were calculated for the whole tree (CI = 0.296 and RI = 0.615) using the script available in TNT. Adding *Transylvanosaurus* to the matrix of Dieudonné et al. (2021) resulted in an overall much poorer resolution of the tree topology compared with the original analysis. In the strict consensus tree, *Transylvanosaurus* was recovered at the base of Iguanodontia in a polytomy with *Fostoria*, the 'Vegagete ornithopod,' as well as the *Rhabdodon*, *Mochlodon*, and *Zalmoxes* (Fig. 7).

In addition, we added *Transylvanosaurus* to the second matrix of Madzia et al. (2018) in order to test the results of the first analysis and were able to score 15 characters for it in total, representing about 6% of the dataset (the complete data matrix can be found in the Supplementary material). The second analysis recovered 362 equally parsimonious trees with 904 steps. Consistency (CI) and retention indices (RI) were again calculated for the whole tree (CI = 0.344 and RI = 0.640) using the script available in TNT. Just as in the case of the first analysis, adding *Transylvanosaurus* to the matrix of Madzia et al. (2018) resulted in an overall much poorer resolution of the tree topology compared with the original analysis, which was to be expected given the large amount of missing data for the new Romanian taxon. In the strict consensus tree of the second analysis, *Transylvanosaurus* was recovered at the base of Iguanodontia in a polytomy with *Mochlodon* and *Zalmoxes*, these taxa together forming the sister group to *Rhabdodon* (thus recovering a monophyletic Rhabdodontidae including all traditionally assigned genera as well as the new taxon from Pui), with *Muttaburrasaurus* placed in a more basal position (Fig. 8).

DISCUSSION

The holotype specimen of *Transylvanosaurus platycephalus* can be definitely referred to a rhabdodontid iguanodontian as it exhibits the typical basicranium morphology of the group (see Augustin et al. in press). Moreover, it was recovered as member of the (admittedly poorly resolved) Rhabdodontidae by both phylogenetic analyses performed herein. *Transylvanosaurus* is thus only the second rhabdodontid genus from the Upper Cretaceous deposits of the Haţeg Basin aside from *Zalmoxes.* Furthermore, the holotype of *Transylvanosaurus*, LPB (FGGUB) R.2070, represents one of the most complete (although still highly incomplete) rhabdodontid skulls reported so far from the Upper Cretaceous of eastern Europe, composed of different elements clearly referable to a single individual. Although the exact ontogenetic stage of LPB (FGGUB) R.2070 is difficult to assess, the holotype individual likely does not represent a juvenile as most bones of the posterior skull are clearly fused, such as the basioccipital with the basisphenoid and exoccipital, as well as the lateral wall of the braincase with the basisphenoid-parasphenoid complex (for details on the sequence of fusion of the braincase, see Hübner and Rauhut, 2010). On the other hand, based on the lack of fusion between some of the bones, such as between the frontals or between the opisthotic and the supraoccipital, it likely represents a subadult individual.

Phylogenetic Analyses

The new taxon, *Transylvanosaurus*, was recovered as a rhabdodontid by both phylogenetic analyses we performed herein with two different and largely independent data sets. The first analysis, for which we used the dataset of Dieudonné et al. (2021), placed *Transylvanosaurus* in a polytomy with the traditionally recognized Late Cretaceous rhabdodontids *Rhabdodon*, *Mochlodon*, and *Zalmoxes* as well as with the late Early Cretaceous *Fostoria* and the 'Vegagete ornithopod,' while *Muttaburrasaurus* was recovered in a more basal position lying outside of this grouping. The second analysis recovered *Transylvanosaurus* in a polytomy with *Zalmoxes* and *Mochlodon* together forming a sister group to *Rhabdodon*, with *Muttaburrasaurus* in a more basal position. Recently, Madzia et al. (2021) formally defined Rhabdodontidae as the smallest (most exclusive) clade containing *Rhabdodon priscus* and *Zalmoxes robustus*, which corresponds to the original intent of the same clade definition as was first proposed by Weishampel et al. (2003). The larger and more inclusive clade Rhabdodontomorpha was defined by Madzia et al. (2021) as the largest (most inclusive) clade containing *Rhabdodon priscus* but not *Hypsilophodon foxii* and *Iguanodon bernissartensis.* According to these formal definitions and to the results of our phylogenetic analyses, *Transylvanosaurus* is definitively a member of the Rhabdodontidae.

In several recent studies, *Muttaburrasaurus* is placed outside of the Rhabdodontidae as a basally branching rhabdodontomorph (Dieudonné et al., 2016, 2021; Bell et al., 2018; Madzia et al., 2018), although it has also been recovered as a member of the Rhabdodontidae (McDonald et al., 2010; McDonald, 2012) as well as in a more basal (Bell et al., 2019) or more derived (Boyd, 2015; Herne et al., 2019) position within Iguanodontia. *Fostoria* has been proposed to represent either a basally branching rhabdodontomorph (Dieudonné et al., 2021) or a more basally branching iguanodontian (Bell et al., 2019). The unnamed 'Vegagete ornithopod' was variably recovered as the earliest and basal-most rhabdodontid (Dieudonné et al., 2016), as a more derived member of the family and the sister taxon to *Mochlodon suessi* (Yang et al., 2020), or as the closest outgroup of the family within Rhabdodontomorpha (Dieudonné et al., 2021). On the other hand, the three latest Cretaceous European taxa *Rhabdodon*, *Mochlodon*, and *Zalmoxes* are unequivocally recovered as members of the Rhabdodontidae (Ősi et al., 2012; Dieudonné et al., 2016, 2021; Madzia et al., 2018; Bell et al., 2019). Notably, the support for the clade including *Transylvanosaurus* (i.e., Rhabdodontidae) is relatively low in both analyses (Bremer support value = 1), which is, however, unsurprising given the fragmentary nature of most of its members. Based on the results of our phylogenetic analyses alone, it is difficult to exclude the possibility of *Transylvanosaurus* representing a rhabdodontomorph related to *Fostoria* and the Vegagete ornithopod (neither of which is included in the second dataset we used), as no basicranial elements are known for these taxa. Morphologically however, *Transylvanosaurus* resembles *Rhabdodon* (see below) to a great extent, thus strengthening the case of it representing a rhabdodontid.

Adding *Transylvanosaurus* to the matrices used in our investigations results in a much poorer resolution of the tree topology compared with the original analyses performed by Dieudonné et al. (2021) and Madzia et al. (2018), respectively. The poor resolution within Rhabdodontidae in both cases is unsurprising given the incomplete nature of the holotype of *Transylvanosaurus* but also the comparatively poor representation of relevant posterior skull characters in the matrices used. Overall,

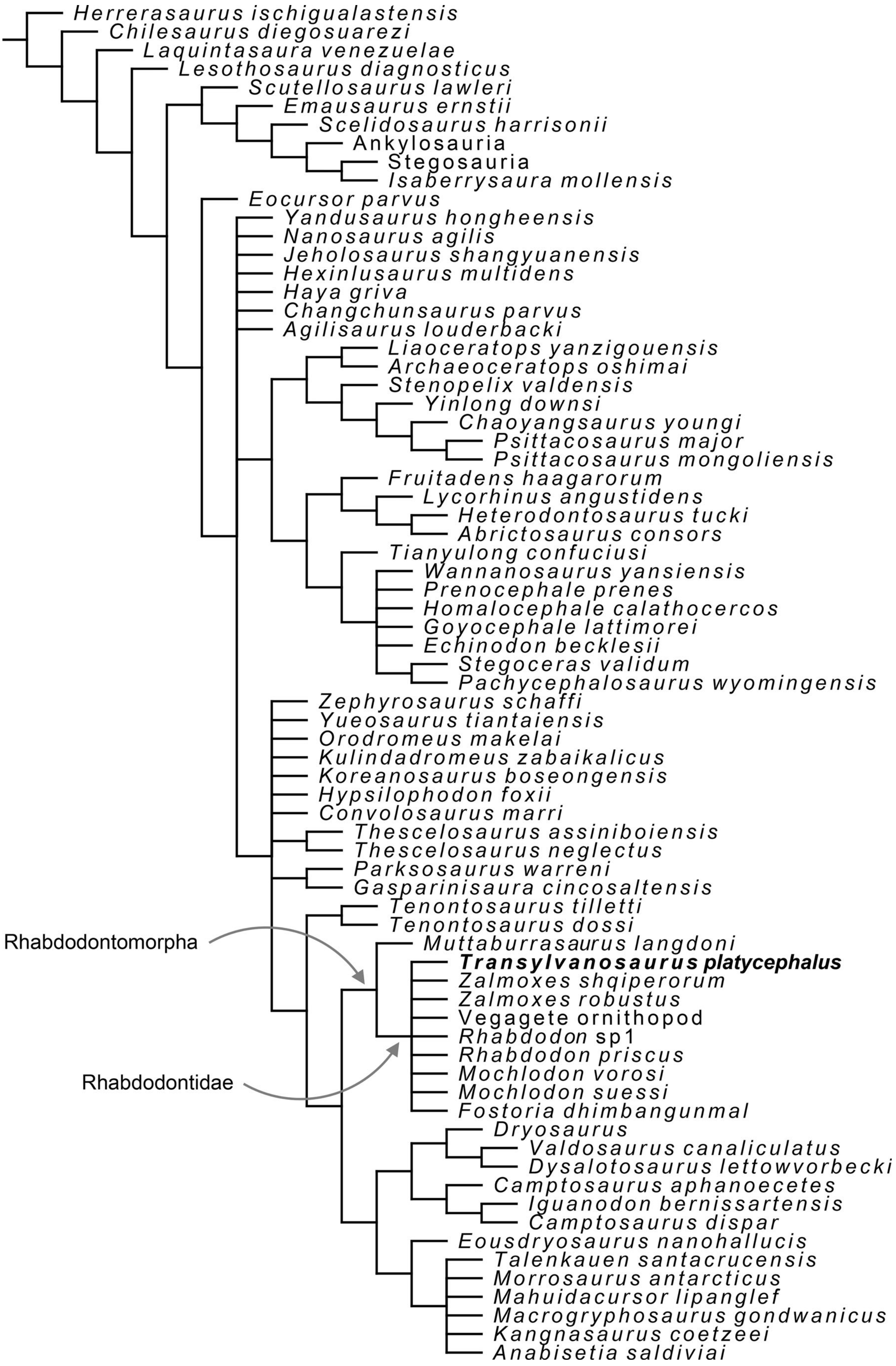

FIGURE 7. Strict consensus tree of the first phylogenetic analysis performed by us using the matrix of Dieudonné et al. (2021), showing the relationships of *Transylvanosaurus platycephalus* within Ornithischia and Ornithopoda.

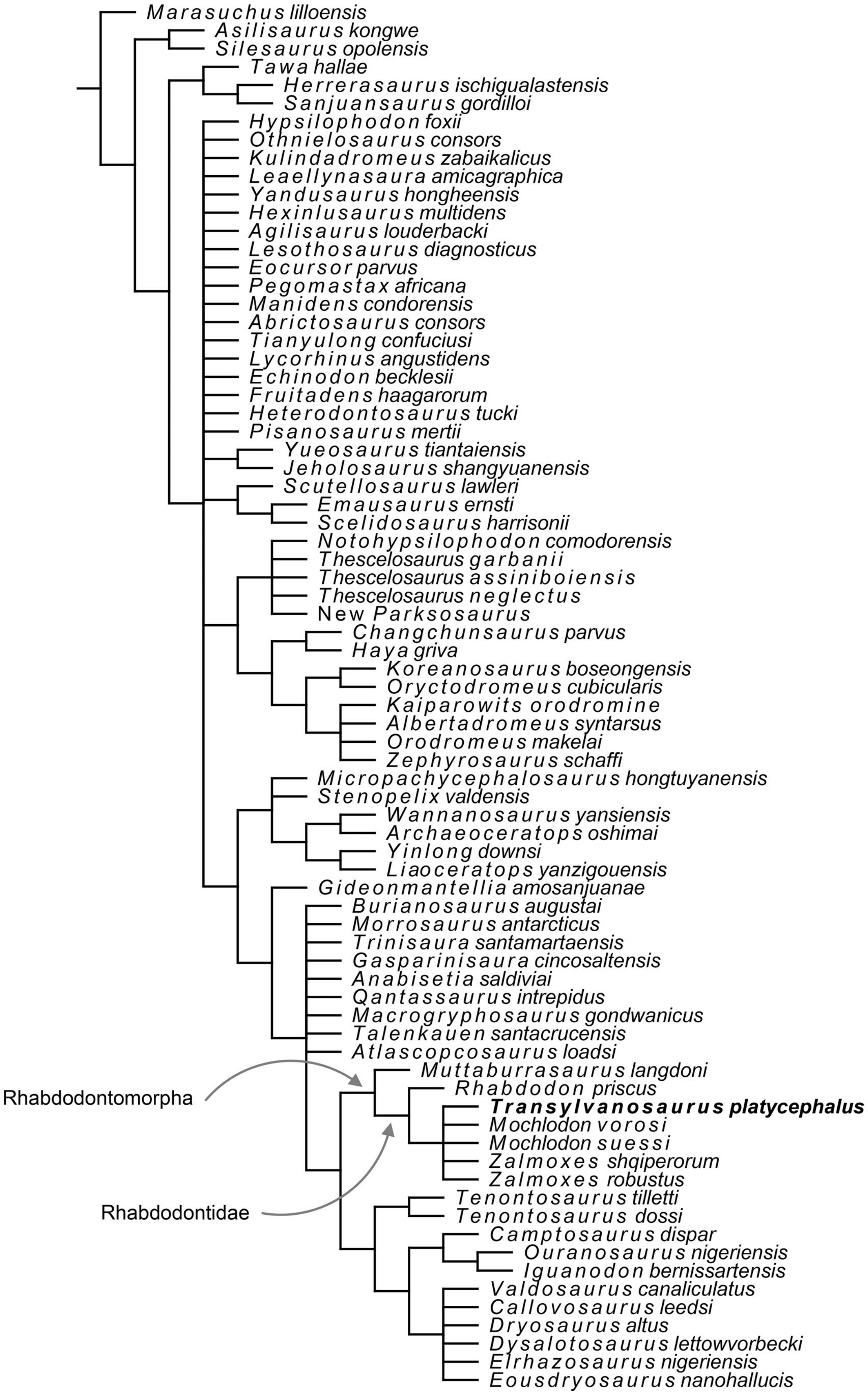

FIGURE 8. Strict consensus tree of the first phylogenetic analysis performed by us using the matrix of Madzia et al. (2018), showing the relationships of *Transylvanosaurus platycephalus* within Ornithischia and Ornithopoda. Notably, the phylogenetic relationships within Rhabdodontidae as shown herein differ from those reconstructed based on our thorough morphological comparisons (i.e., a particularly close relationship between *Transylvanosaurus* and *Rhabdodon*). Due to the scarcity of relevant braincase characters in the original dataset and the poor resolution of Rhabdodontidae, we regard the hypothesis derived from the morphological comparisons as more likely.

only 15 characters (6%) concern the basicranium and five characters (2%) the frontals, amounting to less than 8% of 255 total characters in the matrix we used from Madzia et al. (2018). Although with a quantitatively slightly higher contribution in the data matrix of Dieudonné et al. (2021), the relevant posterior skull characters are still severely underrepresented, with 22 characters (6.5%) derived from the basicranium and four characters (about 1%) from the frontals, thus only 7.5% out of the total 342 characters. Notably, specimen LPB (FGGUB) R.2070 can be scored for most of these relevant cranial characters, that is, for 75% of the entire set of basicranial and frontal characters from Dieudonné et al. (2021), and for 70% of that derived from Madzia et al. (2018), respectively.

Nonetheless, despite the small number of characters that can be scored for *Transylvanosaurus*, the results of both analyses clearly suggest that *Transylvanosaurus* represents a rhabdodontid iguanodontian, which is in accordance with the results of our morphological comparisons. These results are even more remarkable given that none of these frontal and basicranial characters were used to diagnose this clade by Weishampel et al. (2003). Accordingly, not only that the rhabdodontid status of the new Romanian taxon appears rather well supported, it (together with other rhabdodontid material from Romania, currently under study, e.g., Vremir et al., 2017, and from elsewhere) also offers the prospects of completing and improving the previously proposed diagnoses of this endemic European iguanodontian clade, as well as of better understanding the ingroup relationships between the different rhabdodontid taxa.

However, due to the currently existing poor phylogenetic resolution within Rhabdodontidae and the scarcity of braincase characters in both datasets used, for the moment the relationships of *Transylvanosaurus* with other rhabdodontids were assessed primarily based on morphological comparisons. Notably, the interpretation of the phylogenetic relationships of *Transylvanosaurus* within Rhabdodontidae as based on our morphological comparisons (see below) differs from the results of the second phylogenetic analysis (Fig. 8), which recovered *Transylvanosaurus* in a polytomy with *Zalmoxes* and *Mochlodon*, together forming the sister clade to *Rhabdodon*. It is important to note that the grouping of *Transylvanosaurus*, *Zalmoxes*, and *Mochlodon* in this second phylogenetic analysis is not supported by synapomorphies and that the reason for the position of *Rhabdodon* outside of this group lies in *Rhabdodon* showing several autapomorphic features, which are however not preserved in *Transylvanosaurus* and thus could not be coded (see Supplementary material). This demonstrates that a better understanding of the anatomy of *Transylvanosaurus* through the discovery of more complete material as well as the inclusion of additional braincase characters in the datasets used would probably result in a different tree topology, i.e., one showing a particularly close relationship between *Transylvanosaurus* and *Rhabdodon*.

Morphological Comparisons

Transylvanosaurus shares several features with previously described rhabdodontid cranial material from both western Romania and southern France. These include a reniform basioccipital that is connected by a distinct neck to the basisphenoid anteriorly, and well-developed crest-like basal tubera. Nevertheless, the holotype skull of *Transylvanosaurus* differs considerably from all previously known rhabdodontid skulls, both from France and from Romania, in several aspects including exceptionally wide and crested frontals with confluent nasal-prefrontal articulation facets (though no relevant comparative material is currently reported from western Europe), elongated and straight paroccipital processes that make only a gentle lateral curve and direct mostly posterolaterally and slightly dorsally, wide and crest-like basal tubera that meet the long axis of the braincase at a very flat angle, widely splayed basipterygoid processes that extend mainly ventrolaterally and slightly anteriorly, and a well-developed notch on the lateral side of the basicranium that is continuous, straight, and inclined anteroventrally.

However, based on comprehensive morphological comparisons with the rhabdodontid braincases reported so far, LPB (FGGUB) R.2070 is more similar to specimens from southern France, which were assigned previously to the genus *Rhabdodon* (Pincemaille-Quillevere et al., 2006; Chanthasit, 2010) than to those described from Romania. The features shared by LPB (FGGUB) R.2070 and the specimens from southern France primarily include dorsoventrally deep basal tubera that mostly project anteroventrally, an anterior portion of the basisphenoid-parasphenoid complex that is inclined anterodorsally, as well as paroccipital processes that extend mostly laterally and are relatively straight for most of their length. A particularly close relationship between *Transylvanosaurus* and *Rhabdodon*, as suggested tentatively herein, would establish the presence of a second, distinct lineage of rhabdodontids in the latest Cretaceous of Eastern Europe, besides the lineage comprising *Zalmoxes* and *Mochlodon* (see below).

Interestingly, a conjoined pair of frontals from the uppermost Cretaceous of the northwestern Haţeg Basin near Vălioara, MBFSZ v.13528, resembles *Transylvanosaurus* very closely. This is also true for a left frontal described from the uppermost Cretaceous of the southwestern Transylvanian Basin (MMIRS 680), which is however, not complete and thus comparisons to this element are somewhat limited. Given that the other previously known rhabdodontid frontals from the Haţeg Basin, i.e., LPB (FGGUB) R.1616 and NHMUK R.3400, are completely different in their overall morphology (see above), MBFSZ v.13528 might indeed be assignable to *Transylvanosaurus* or to a closely related taxon. The features shared by MBFSZ v.13528 and MMIRS 680 with LPB (FGGUB) R.2070 include a similar length to width ratio, the presence of a well-developed transverse crest near the anterior edge, a concave dorsal surface, and a large mediolaterally extending joint naso-prefrontal suture. It must be noted, however that neither MBFSZ v.13528 nor MMIRS 680 were associated with basicranial material, which considerably complicates a potential referral of these specimens to *Transylvanosaurus.*

Furthermore, as pointed out above, *Transylvanosaurus* might be phylogenetically closer to *Rhabdodon* than to its sympatric *Zalmoxes*, suggesting the presence of a second lineage of rhabdodontids in the Upper Cretaceous of Romania. Therefore, it is conceivable that the frontals in this second lineage, comprising *Transylvanosaurus* and *Rhabdodon*, have a different morphology when compared with those of the lineage that includes *Zalmoxes.* What complicates this issue even more is that no complete frontals have yet been described for the genus *Rhabdodon*. Moreover, based on the specimen MBFSZ v.13528 presence of a pronounced frontal crest has previously been suggested to be related to sexual dimorphism (at that moment, in the hadrosauroid *Orthomerus*), the larger crest presumably being associated with the male morphotype (Nopcsa, 1929b). More material is definitely needed before a conclusive assignment of MBFSZ v.13528 to *Transylvanosaurus* or another, maybe closely related, taxon can be established. Nonetheless, with the material at hand it is highly unlikely that MBFSZ v.13528 belongs to the genus *Zalmoxes.* Removal of this specimen from the list of those referable to *Zalmoxes* also prompts a revised diagnosis of that taxon, as one autapomorphy was clearly based on MBFSZ v.13528 and thus has to be removed from the genus diagnosis: 'a transverse frontal crest that may be sexually dimorphic' (Weishampel et al., 2003:69).

At this point, we would like to add an important side note concerning this iconic Romanian dinosaur. As more and more morphological differences between the specimens previously referred to *Zalmoxes* become apparent (such as in the case of the frontals discussed above), we propose that *Zalmoxes*, as originally erected, defined, and understood by Nopcsa, is probably properly typified (regarding the skull elements discussed herein) by the original Nopcsa specimens excavated by himself from Sînpetru, i.e., the basicrania NHMUK R.3408 and R.3409 as well as the two conjoined frontals NHMUK R.3400. Of these, at least the frontals are definitely known to originate from the type locality of this taxon (Quarry 1 or 'Nest 1'), i.e., the locality that yielded the designated holotype dentary (NHMUK R.3392) of '*Mochlodon*' (=*Zalmoxes*) *robustus* (Nopcsa, 1900:579, 1902a, 1904). Although not mentioned as explicitly as for the paired frontals NHMUK R.3400, the two basicrania NHMUK R.3408 and R.3409 probably originate from the type locality of *Zalmoxes robustus* as well (Nopcsa, 1904:230–231), or at least from the same local succession of the stratotype Sînpetru Formation, which places these both spatially and temporarily closely associated with the type material of this taxon. Even more importantly, Nopcsa (1904) listed NHMUK R.3400 as belonging to the same individual ('Individuum B'; Nopcsa, 1904: tab. 1, p. 237 and caption of pl. 1) as several other cranial elements including a dentary, NHMUK R.3401B (see also Dumbravă et al., 2017), and thus an element that can be directly compared with the type dentary of *Zalmoxes robustus* NHMUK R.3392 (Weishampel et al., 2003). Unfortunately, Nopcsa (1904) explicitly notes that the basicrania NHMUK R.3408 and R.3409 were found isolated and that neither of the two was found associated with other cranial bones (Nopcsa, 1904: tab. 1 and p. 239). From these suggestions, as well as from our novel recognition of a higher genus-level diversity of the Transylvanian rhabdodontids than that acknowledged before, it follows that direct comparisons between *Zalmoxes* and *Transylvanosaurus* (as well as other rhabdodontids) should be restricted to the type (and directly comparable and referable) material from the Sibişel Valley section at Sânpetru, unless rhabdodontid skeletal material from other localities can clearly be referred to *Zalmoxes* based on positively identified apomorphies.

Paleobiogeography

Previously, the presence of two distinct lineages of rhabdodontids has been suggested in the Late Cretaceous of Europe based on their respective areal distribution and phylogenetic position (Ősi et al., 2012). The first, western lineage included the different *Rhabdodon* spp. from southern France and northeastern Spain, while the second, eastern lineage consisted of *Mochlodon suessi* and *M. vorosi* from Austria and Hungary, respectively, as well as *Zalmoxes robustus* and *Z. shqiperorum* from Romania (Ősi et al., 2012; Csiki-Sava et al., 2015). The recently described *Pareisactus evrostos* from the uppermost Cretaceous of Spain was recovered in a sister-taxon relationship with *Rhabdodon priscus* and thus likely also belongs to the first, western lineage of rhabdodontids (Párraga and Prieto-Márquez, 2019). A similar dichotomous east-west distributional pattern has also been suggested for several other continental vertebrates, including turtles (Rabi et al., 2013; Csiki-Sava et al., 2015; Augustin et al., 2021), mammals (Csiki-Sava et al., 2015; Gheerbrant and Teodori, 2021), hadrosauroids (Csiki-Sava et al., 2015), and eusuchian crocodyliforms (Narváez et al., 2016; Blanco and Brochu, 2017; Blanco, 2021). In general, high degrees of regional faunal differences and endemism, including the east-west disjunct distribution pattern described above, have often been reported for the vertebrates living on the Late Cretaceous island archipelago of Europe and were usually linked to the geographic isolation of the different emergent landmasses (for an overview, see Csiki-Sava et al., 2015).

The results of our study challenge this concept of two distinct and geographically separated lineages of rhabdodontids inhabiting the eastern, respectively western parts of the Late Cretaceous European Archipelago. Based on our thorough morphological comparisons of *Transylvanosaurus platycephalus* with rhabdodontid material assigned to both *Rhabdodon* and *Zalmoxes*, representing the western and eastern rhabdodontid clades, respectively, we herein tentatively propose a particularly close relationship between the new taxon from the Maastrichtian of western Romania and *Rhabdodon* spp. from the uppermost Cretaceous of southern France. More specifically, *Transylvanosaurus* and *Rhabdodon* seem to share several basicranial characters that are not present in *Zalmoxes*. Although this conclusion is far from certain, it has potential implications for the biogeographic history of the Rhabdodontidae.

As pointed out by Ősi et al. (2012), the Santonian age of *Mochlodon vorosi* indicates that the split between the western clade that includes *Rhabdodon*, and the eastern clade, comprising *Mochlodon* and *Zalmoxes*, must have occurred before the Santonian, after which both lineages evolved independently, in relative isolation from each other. The presence of *Transylvanosaurus*, presumably a member of the 'western lineage,' in the uppermost Cretaceous (Maastrichtian) of Eastern Europe suggests a more complex biogeographic history of the Rhabdodontidae than previously thought. In this case, post-Coniacian allopatric speciation alone cannot account for the observed distribution pattern, indicating at least one dispersal event of the 'western' European rhabdodontid lineage. Such dispersal may have taken place either from west towards the eastern European realm (i.e., the Transylvanian area) or else westward, into the western European realm (i.e., the Ibero-Armorican area), depending on the place of origin for the Rhabdodontidae and its main lineages.

In the first of these scenarios, sympatric speciation must have taken place within the 'western lineage' of rhabdodontids after the pre-Santonian basal split of the clade identified by Ősi et al. (2012) followed by western isolation of the *Rhabdodon* lineage, but before the early Campanian, the moment of the first appearance of *Rhabdodon*-like rhabdodontids in southern France (Villeveyrac Basin; Buffetaut et al., 1996; Chanthasit, 2010). This western speciation event, which can be thus loosely constrained to the Santonian–earliest Campanian time interval, gave rise to the ancestors of both *Rhabdodon* and *Transylvanosaurus* on the Ibero-Armorican landmass. Subsequently, ancestors of *Transylvanosaurus* were able to spread towards eastern Europe, reaching the Transylvanian landmass, although the exact moment and path of this migration remains currently unknown. Such a scenario would be convincingly upheld by the discovery of *Transylvanosaurus*-like rhabdodontids in western Europe in pre-Maastrichtian beds, but would be contradicted by fossils referable to the western lineage found in pre-lower Campanian deposits of eastern Europe. Also, such a scenario does not impose any constraint on the geographic origin of Rhabdodontidae or else of its eastern, respectively western lineages, as long as an early (pre-Campanian) divergence and isolation of these main lineages did take place.

In the second dispersalist scenario, both the main basal split of Rhabdodontidae into eastern and western lineages, respectively the subsequent splits within these lineages (between *Mochlodon* and *Zalmoxes*, respectively between *Transylvanosaurus* and *Rhabdodon*) took place in eastern Europe, with a subsequent dispersal event towards western Europe of the ancestors of the *Rhabdodon* line. Based on the currently known spatiotemporal distribution of the rhabdodontids, such a scenario would require a pre-Santonian basal split within Rhabdodontidae, with both subsequent cladogenetic events in the resulting lineages constrained to the Santonian, with the westward dispersal taking place around the Santonian-Campanian at the latest. Unlike the first scenario discussed above, this second one puts severe constraints on the evolutionary history of the group, with its early stages (such as the origin of Rhabdodontidae and its main currently recognized cladogenetic events) being restricted to the eastern part of the Late Cretaceous European Archipelago. This scenario would be further supported by the discovery of fossils representing the western (*Transylvanosaurus*, *Rhabdodon*) lineage in Santonian-lowermost Campanian deposits from the eastern European areas (e.g., the Transylvanian or the Austro-Alpine landmasses), but would be weakened significantly (albeit not contradicted completely) through the identification of any rhabdodontids in Santonian (or pre-Santonian) beds of western Europe.

A possible alternative to this second dispersalist scenario would be represented by a variant in which ancestors of the western rhabdodontid lineage were spread across the entire southern European area after its split from its sister taxon, and the subsequent divergence between the Ibero-Armorican (or western) *Rhabdodon* line and the Transylvanian (or eastern) *Transylvanosaurus* line within this lineage occurred as a consequence of geographic isolation and resulting vicariant cladogenesis. Such an alternative scenario would not necessarily require dispersals between eastern and western Europe (although do not rule out completely such events from occurring, either) to explain the presence of members of the western lineage concomitantly in both eastern and western Europe during the latest Cretaceous (Campanian–Maastrichtian). Such a vicariant scenario would be supported by the recovery of (preferably stem) western lineage rhabdodontids in Santonian beds from both western and eastern Europe, but would be contradicted (at least in its purest vicariant version, with no dispersal involved at all) by the presence of *Transylvanosaurus*-like fossils in Ibero-Armorica and/or that of *Rhabdodon*-like fossils in eastern Europe in Campanian–Maastrichtian deposits.

It is worth emphasizing here that the recognition of the new rhabdodontid taxon *Transylvanosaurus*, identified as a potentially close relative of the Ibero-Armorican taxon *Rhabdodon*, in eastern Europe blurs the previously recognized distinctiveness of an exclusively western rhabdodontid lineage including *Rhabdodon* (and possibly also *Pareisactus*) as opposed to an exclusively eastern lineage composed of the different species of *Zalmoxes* and *Mochlodon*. Evaluation of such a clear-cut rhabdodontid provincialism is further complicated by the fact that the potential phylogenetic affinities of the sixth named rhabdodontid genus, *Matheronodon* from Provence in southern France (Godefroit et al., 2017), are currently unknown, and also by the limited amount (and often non-overlapping nature) of the skeletal material available for many rhabdodontids, including here *Transylvanosaurus* as well. The overall scarcity of the rhabdodontid fossils, and especially of those that allowed us to recognize a wider than previously acknowledged geographic distribution of the western lineage (frontals, braincase), makes testing of the different scenarios outlined above difficult at the moment, Nevertheless, the identification of *Transylvanosaurus* at Pui in the Haţeg Basin suggests that, at the least, the previously proposed term of 'western' rhabdodontid lineage may represent a misleading oversimplification, and that such a terminology, one that we admittedly also employed in our paleogeographic discussions, should be replaced with a less confusing one in the future as more rhabdodontid fossils and taxa will be described.

Finally we note that regardless of the specific details of the evolutionary scenarios outlined above, a ghost-lineage of several million years (up to as much as 10 to 14 My) separates the moment of this intra-'western lineage' split between the western *Rhabdodon*-line and the eastern *Transylvanosaurus*-line from the first (and currently only) known occurrence of *Transylvanosaurus* in the Haţeg Basin, suggesting the presence of a lengthy hidden evolutionary history of *Transylvanosaurus*-like rhabdodontids in the eastern European islands. More material of *Transylvanosaurus platycephalus* (and of other rhabdodontids), as well as better age constraints on their occurrences, are surely needed in order to explore in more detail the phylogenetic relationships within the Rhabdodontidae and thus to corroborate (or dismiss) any of the alternative paleobiogeographic hypotheses presented here.

Paleoecology

The family Rhabdodontidae is characterized by a comparatively high taxonomic diversity, especially at a low taxonomic level. In general, several of the known rhabdodontid species seem to have lived alongside at least one other sympatric rhabdodontid taxon. In the uppermost Cretaceous (Campanian–Maastrichtian) of northeastern Spain, *Rhabdodon* sp. co-occurs with *Pareisactus evrostos* (Pereda-Suberbiola and Sanz, 1999; Párraga and Prieto-Márquez, 2019), while the upper Campanian–lower Maastrichtian deposits of southern France have yielded the two species *Rhabdodon priscus* and *R. septimanicus* as well as *Matheronodon* (Buffetaut and Le Loeuff, 1991; Chanthasit, 2010; Godefroit et al., 2017). Similarly, in Romania, two species of rhabdodontids have been described from the uppermost Campanian–Maastrichtian deposits of the Haţeg and Transylvanian basins, *Zalmoxes robustus* and *Z. shqiperorum* (Weishampel et al., 2003). Meanwhile, only one species of rhabdodontid has been reported from the Upper Cretaceous strata of both Austria (lower Campanian) and Hungary (Santonian), represented by *Mochlodon suessi* and *M. vorosi*, respectively (Seeley, 1881; Ősi et al., 2012), and apparently only one rhabdodontid taxon, probably related to *Rhabdodon*, is known from the lower Campanian deposits from southern France (Buffetaut et al., 1996), as well. With the description of *Transylvanosaurus* from the 'middle' Maastrichtian of the Haţeg Basin, the diversity of rhabdodontids on the so-called 'Haţeg Island' (i.e., the Tisia Dacia block, representing roughly present-day Transylvania; Benton et al., 2010) appears to have been even higher than previously recognized and thus similar to the diversity observed from the Ibero-Armorican landmass (i.e., present-day northeastern Spain and southern France). Interestingly, rhabdodontids are absent or very rare in deposits younger than early Maastrichtian in western Europe, whereas in eastern Europe, the clade was present and remained abundant until the late Maastrichtian (Csiki-Sava et al., 2015; Vila et al., 2016).

Notably, the different sympatric rhabdodontids seem to have overlapped considerably in terms of body size, including *Rhabdodon* and *Pareisactus* in northern Spain (Párraga and Prieto-Márquez, 2019), *Rhabdodon* and *Matheronodon* in southern France (Chanthasit, 2010; Godefroit et al., 2017), as well as *Zalmoxes robustus* and *Z. shqiperorum* in the Transylvanian area (Weishampel et al., 2003; Ősi et al., 2012). Although *Transylvanosaurus* seems to have been roughly similar in size to the sympatric *Zalmoxes* based on the referred basicranium specimens (see above), the new taxon appears to have been very different in its cranial morphology. Perhaps the most apparent and remarkable differences between the two genera concern the markedly different proportions of the preserved cranial elements, certainly reflecting widely divergent skull shapes. While *Transylvanosaurus* seems to have been characterized by a rather wide and low skull, both at the level of the orbital region and across the occiput, as documented by the very wide frontals in *Transylvanosaurus* as well as the very long, thin and laterally extending paroccipital processes, *Zalmoxes* had a much narrower and higher skull. The taller and wider basal tubera and the widely splayed basipterygoid processes of *Transylvanosaurus* represent additional important differences that likely correspond to a different overall skull shape. While a direct relationship is difficult to establish (and we refrain here to discuss this issue in more depth), the wider skull of *Transylvanosaurus* likely correlates with different size and line of action of certain muscles related to the preserved cranial elements (e.g., a larger attachment site for m. rectus capitis ventralis and m. protractor pterygoideus in *Transylvanosaurus*, see above), and thus could ultimately reflect differences in feeding adaptations and corresponding dietary niche partitioning between the two sympatric rhabdodontid genera from the Haţeg Basin.

CONCLUSIONS

The uppermost Cretaceous continental deposits of the Haţeg Basin have yielded one of the richest and most diverse vertebrate assemblages from the entire Upper Cretaceous of Europe. Rhabdodontid dinosaurs are among the most abundant vertebrates recovered from these deposits, and previously all rhabdodontid remains have been referred to a single locally endemic genus, *Zalmoxes.* Here we describe a second genus of rhabdodontid dinosaurs, *Transylvanosaurus platycephalus*, from uppermost Cretaceous (around the lower–upper Maastrichtian boundary) strata near Pui, in the eastern part of the Haţeg Basin. The holotype specimen comprises the articulated basicranium (basioccipital, exoccipital-opisthotic complexes, basisphenoid-parasphenoid complex, prootic, and laterosphenoid), which was found associated with the articulated left and right frontals. *Transylvanosaurus platycephalus* is clearly referable to the Rhabdodontidae, as it exhibits the typical basicranial morphology of the group. In addition, two different phylogenetic analyses performed, both recovered *Transylvanosaurus* as being firmly nested within the Rhabdodontidae.

The holotype skull of *Transylvanosaurus* differs from all previously reported rhabdodontid skulls in several aspects including exceptionally wide frontals, elongated and straight paroccipital processes that make only a gentle lateral curve and direct mostly posterolaterally, prominent and massive prootic processes that extend mainly anterolaterally and ventrally, wide and crest-like basal tubera that meet the long axis of the braincase at a very flat angle, widely splayed basipterygoid processes that extend mainly ventrolaterally and slightly anteriorly, and a well-developed notch on the lateral side of the basicranium that is continuous, straight, and inclined anteroventrally. Based on detailed morphological comparisons with other rhabdodontid braincases reported so far, *Transylvanosaurus* seems to be more similar to specimens from southern France that were referred to the genus *Rhabdodon*. The features shared by these taxa include dorso-ventrally deep basal tubera that mostly project anteroventrally, an anterior portion of the basisphenoid-parasphenoid complex that is inclined anterodorsally, as well as paroccipital processes that extend mostly laterally and are relatively straight for most of their length. The identification of the new rhabdodontid taxon *Transylvanosaurus* in the Haţeg Basin, the first new dinosaur taxon to be described from here after more than a decade, documents a higher local taxonomic diversity of the clade than was previously acknowledged, mirroring to an extent the increasingly diverse fossil record of the same clade in the western European Ibero-Armorican landmass. Meanwhile it also demonstrates that the currently recognized diversity of the latest Cretaceous Transylvanian continental vertebrates may still represent an underestimate of the true paleobiodiversity of this ancient island ecosystem.

Previously, the presence of two distinct lineages of rhabdodontids in the Late Cretaceous of Europe has been proposed based on their respective paleogeographic distribution and phylogenetic position. The first lineage was considered to have been restricted to western Europe, including the different *Rhabdodon* species, as well as potentially other rhabdodontids such as *Pareisactus*, from southern France and northeastern Spain, while the second lineage consisting of species of *Mochlodon* from Austria and Hungary, as well as those of *Zalmoxes* from Romania, was considered to have been distributed across eastern Europe. The findings of the current study, identifying a new rhabdodontid taxon in western Romania that is apparently more closely related morphologically to western European taxa such as *Rhabdodon*, challenge this concept of two distinct and geographically separated lineages of rhabdodontids inhabiting the eastern and western parts of the Late Cretaceous European Archipelago and suggest more complex, although as yet incompletely understood patterns of the rhabdodontid evolutionary history.

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