A new ornithopod dinosaur, *Transylvanosaurus platycephalus* gen. et sp. nov. (Dinosauria: Ornithischia), from the Upper Cretaceous of the Haţeg Basin, Romania

Felix J. Augustin, Dylan Bastiaans, Mihai D. Dumbravă & Zoltán Csiki-Sava

ARTICLE

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

FELIX J. AUGUSTIN,[*,1] DYLAN BASTIAANS,[2,3] MIHAI D. DUMBRAVĂ,[4] and ZOLTÁN CSIKI-SAVA[*,5]

[1]Department of Geosciences, University of Tübingen, Hölderlinstraße 12, 72074 Tübingen, Germany; felix.augustin@uni-tuebingen.de;

[2]Palaeontological Institute and Museum, University of Zürich, Karl-Schmid-Strasse 4, 8006 Zürich, Switzerland; dylan.bastiaans@pim.uzh.ch;

[3]Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, the Netherlands;

[4]ZOIC PalaeoTech, Longburton, Sherborne, Dorset, U.K.; lilliensternus@gmail.com;

[5]Faculty of Geology and Geophysics, University of Bucharest, 1 Nicolae Bălcescu Avenue, 010041 Bucharest, Romania; zoltan.csiki@g.unibuc.ro

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.

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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 Hațeg Basin (Fig. 1), where they represent the most abundant dinosaur group. Rhabdodontid material from the Upper Cretaceous of the Hațeg 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 Hațeg 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 Hațeg 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 Hațeg 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 Hațeg 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 Hațeg 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 Hațeg Basin, which is located in the southwestern Carpathians, western Romania (Fig. 1A). The Hațeg 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 Hațeg Basin along the Sibișel 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 Densuș-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 Hațeg Basin, which are exposed along the Râul Mare River section near Nălaț-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 Densuș-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 Hațeg 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 Hațeg 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 Hațeg 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 Hațeg 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;
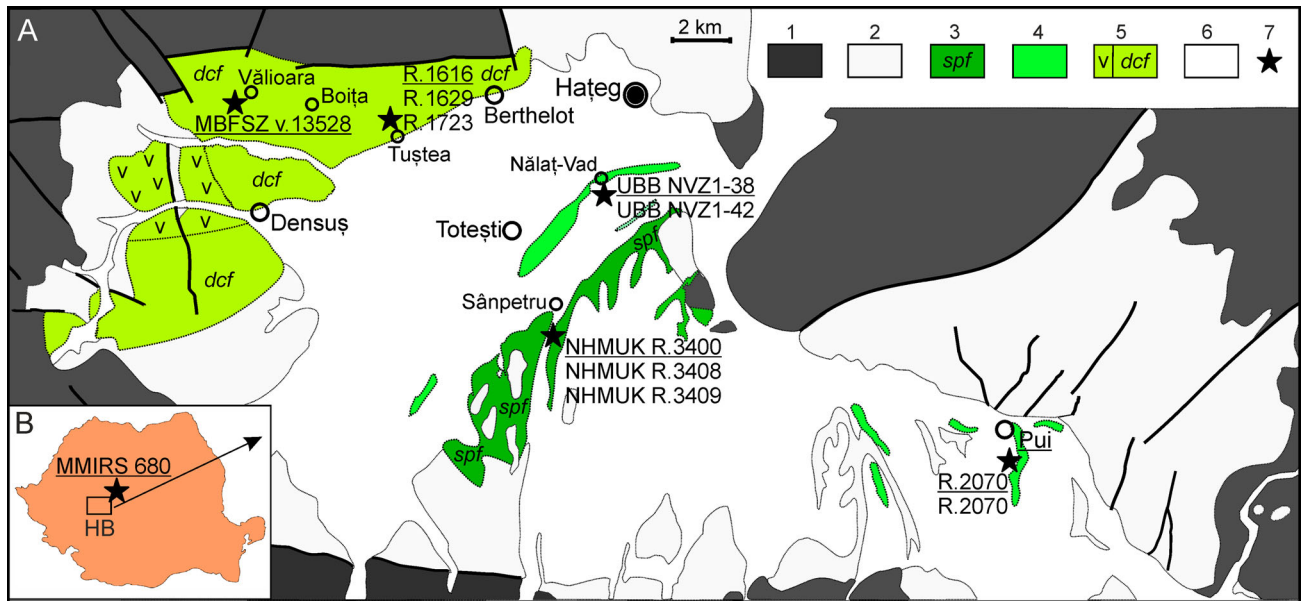
FIGURE 1. Locality information for the holotype of *Transylvanosaurus platycephalus* gen. et sp. nov. **A**, Location of the type locality of *Transylvanosaurus platycephalus* gen. et sp. nov. south of Pui, in the eastern Haţeg Basin, western Romania, alongside with that of other rhabdodontid posterior 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
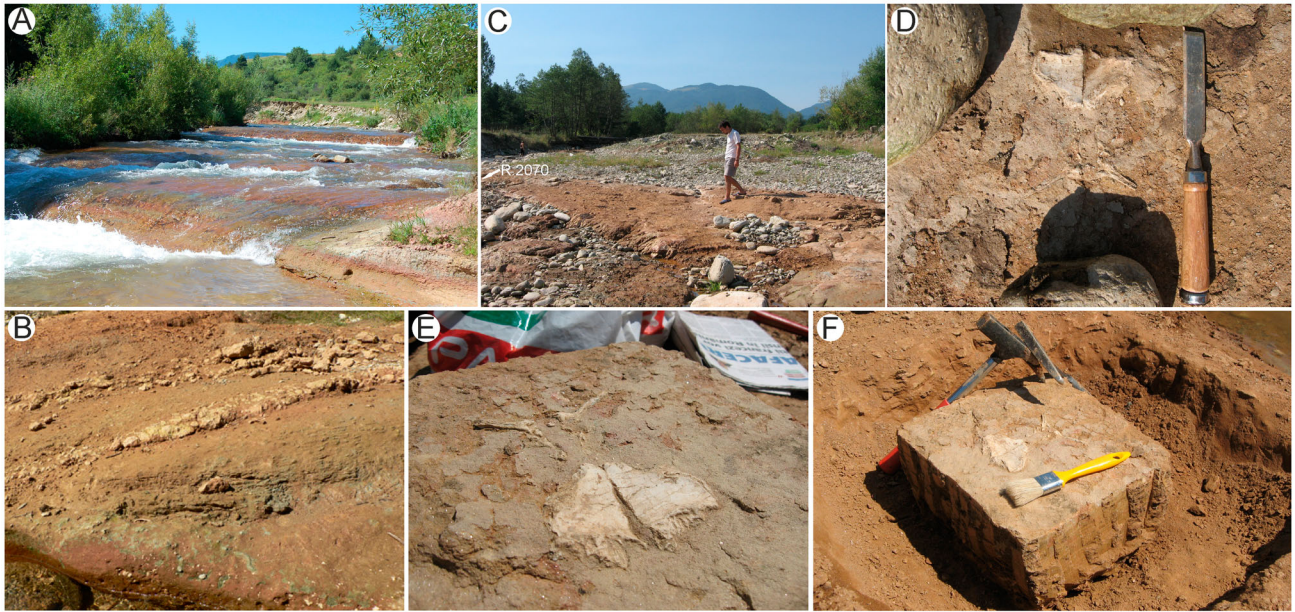
FIGURE 2. The type locality of *Transylvanosaurus platycephalus* gen. et sp. nov. at the Bărbat River Valley section, near Pui, eastern Haţeg Basin. **A**, General overview of the riverbed outcropping condition of the uppermost Cretaceous continental 'Pui Beds' along the Bărbat River, south of Pui; in 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
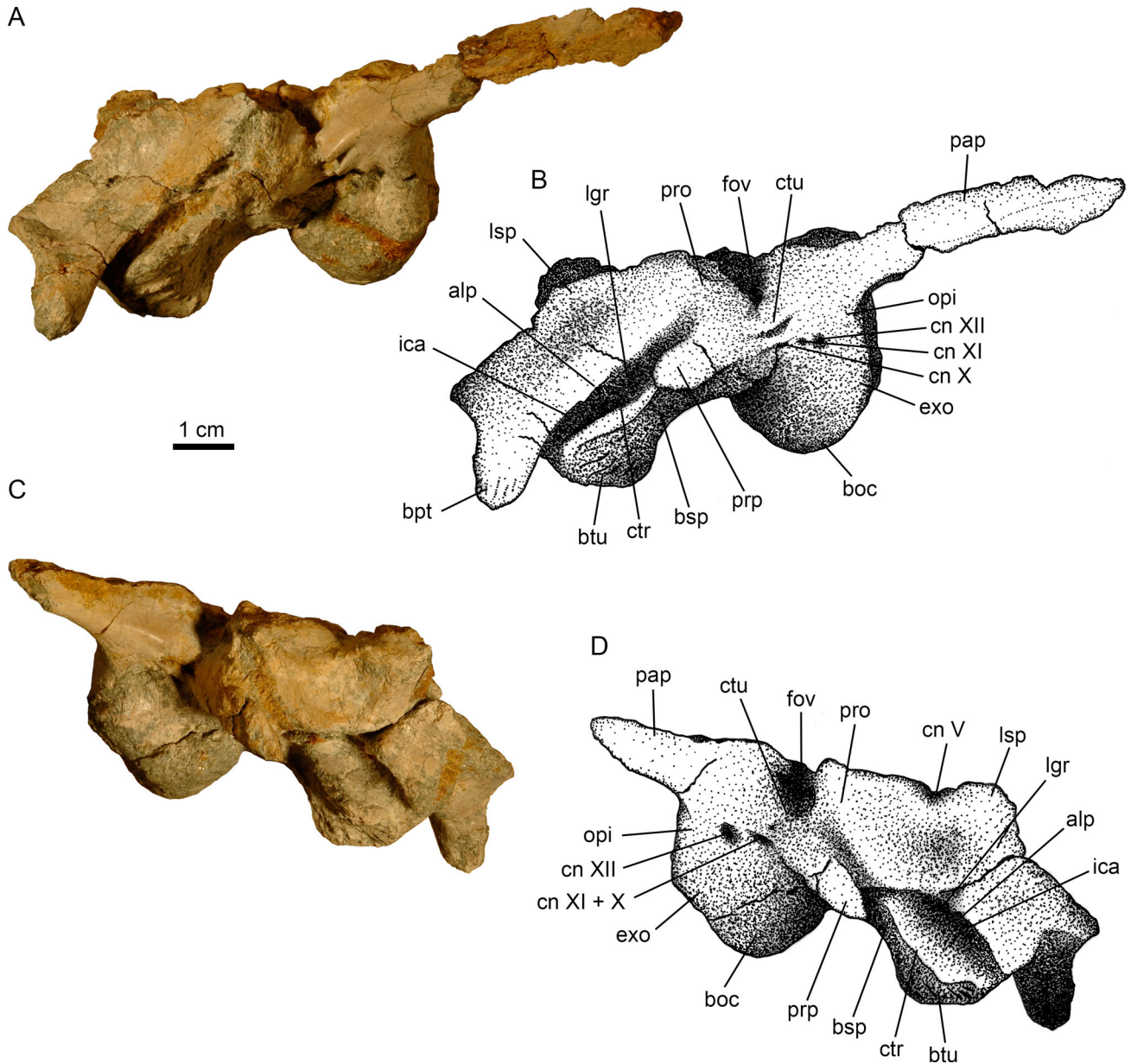
FIGURE 3. *Transylvanosaurus platycephalus* gen. et sp. nov., holotype basicranium, FGGUB (LPB) R.2070, in lateral view. **A**, photo and **B**, drawing of the basicranium in left lateral view. **C**, photo and **D**, drawing of the basicranium in right lateral view. **Abbreviations**: **alp**, alar 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
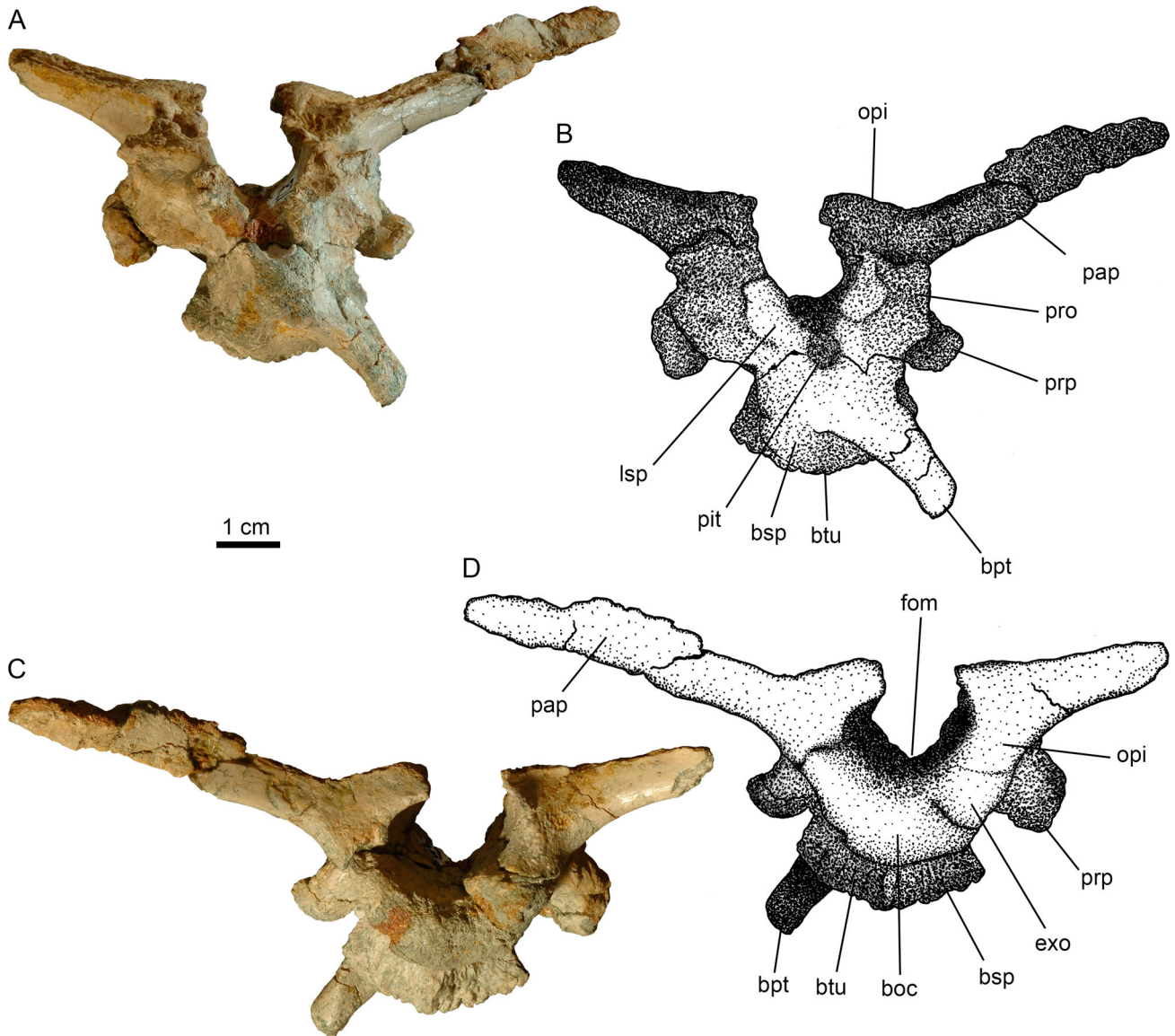
FIGURE 4. *Transylvanosaurus platycephalus* gen. et sp. nov., holotype basicranium, FGGUB (LPB) R.2070, in anterior and posterior view. **A**, photo and **B**, drawing in anterior view. **C**, photo and **D**, drawing in posterior view. **Abbreviations**: **boc**, basioccipital; **bpt**, basipterygoid 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
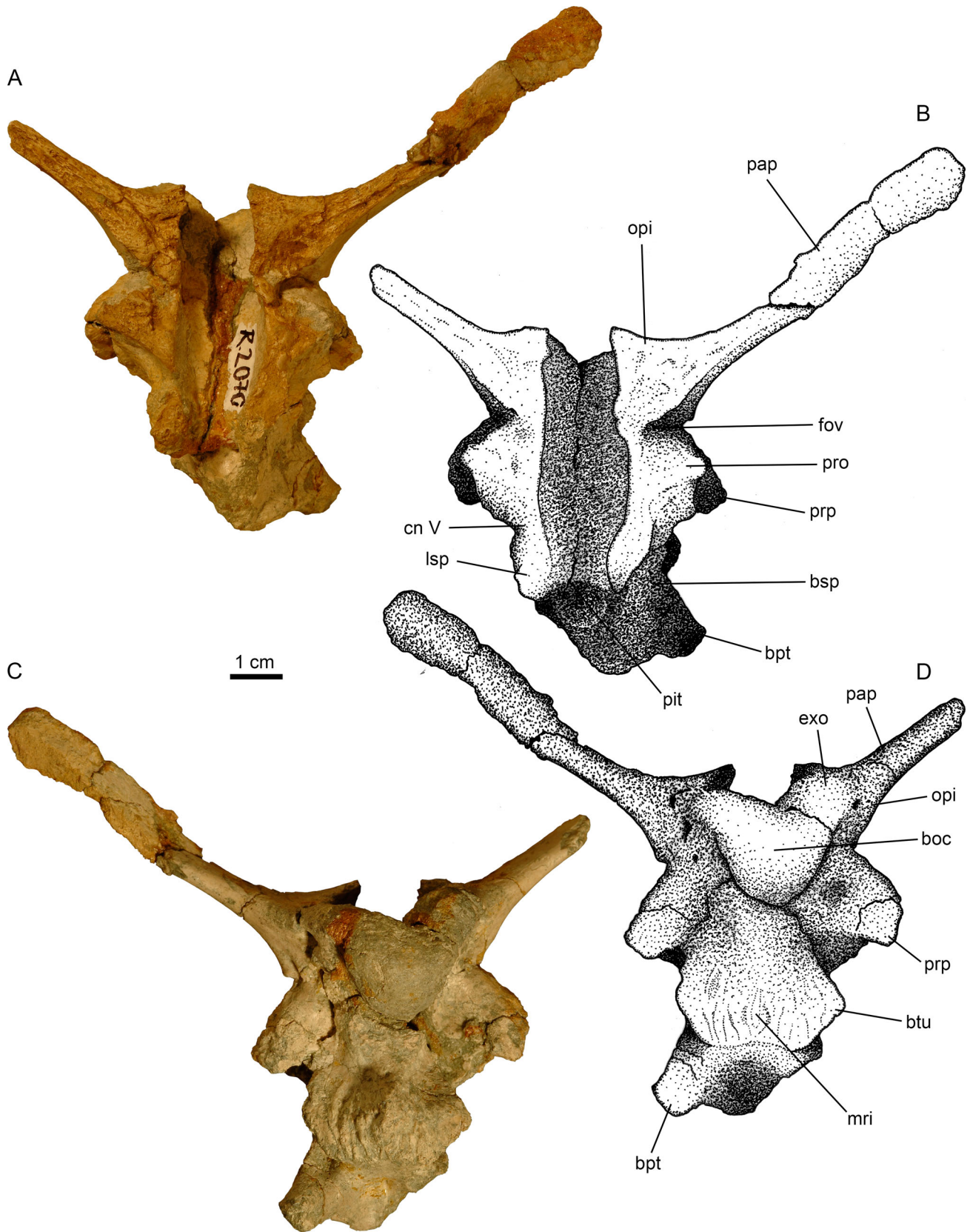
FIGURE 5. *Transylvanosaurus platycephalus* gen. et sp. nov., holotype basicranium, FGGUB (LPB) R.2070, in dorsal and ventral view. **A**, photo and **B**, drawing of the basicranium in dorsal view. **C**, photo and **D**, drawing of the basicranium in ventral view. **Abbreviations**: **boc**, basioccipital; **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.
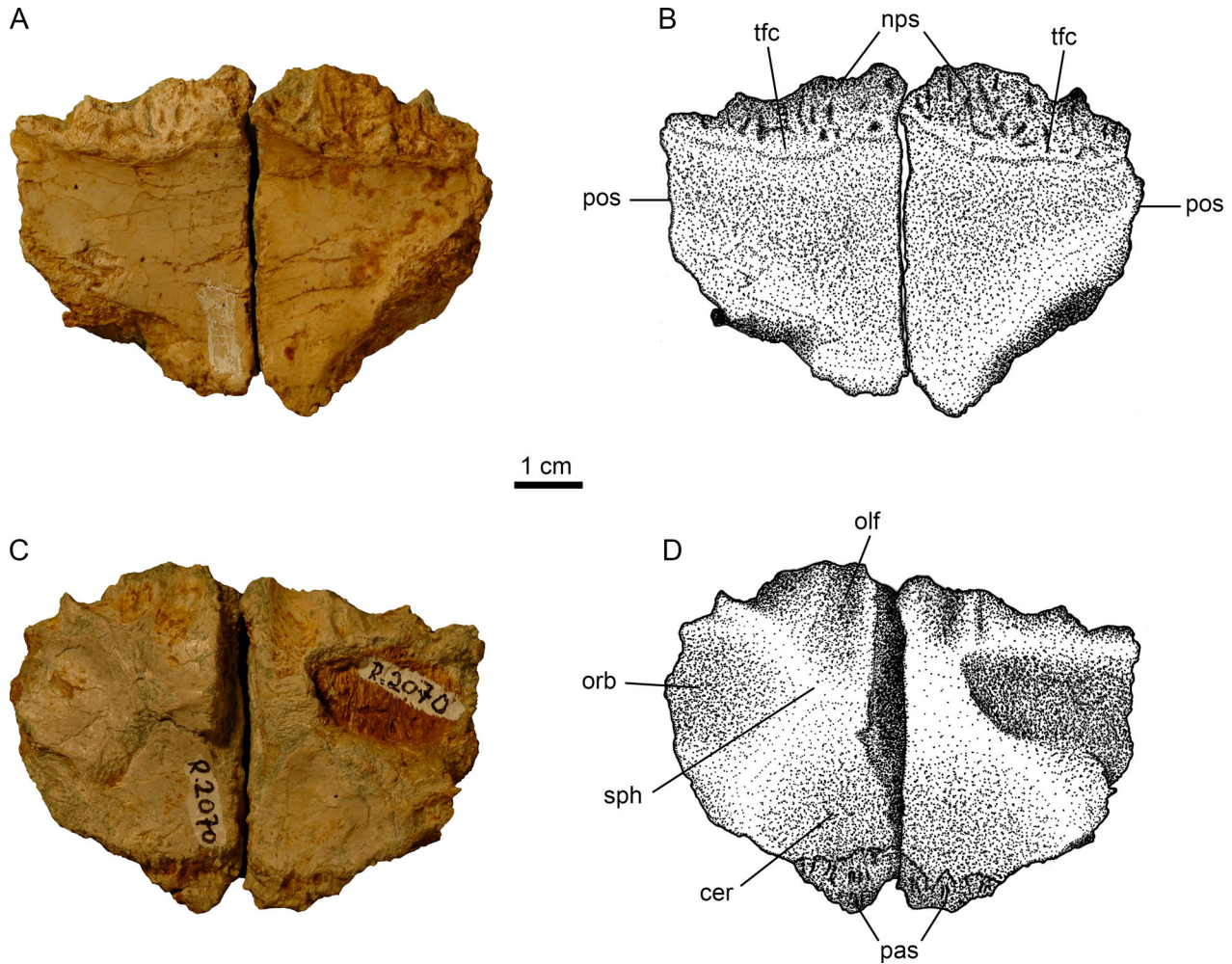
FIGURE 6. *Transylvanosaurus platycephalus* gen. et sp. nov., holotype frontals, FGGUB (LPB) R.2070. **A**, photo and **B**, drawing of the frontals in dorsal view. **C**, photo and **D**, drawing of the frontals in ventral view. Note that the ventral side of the left frontal is damaged and thus does 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.

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 exocipital-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 Sebeş Formation cropping out at Petreşti-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

exocipital-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 exocipital-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 antero-posteriorly 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 dorso-lateral 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 antero-laterally 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,
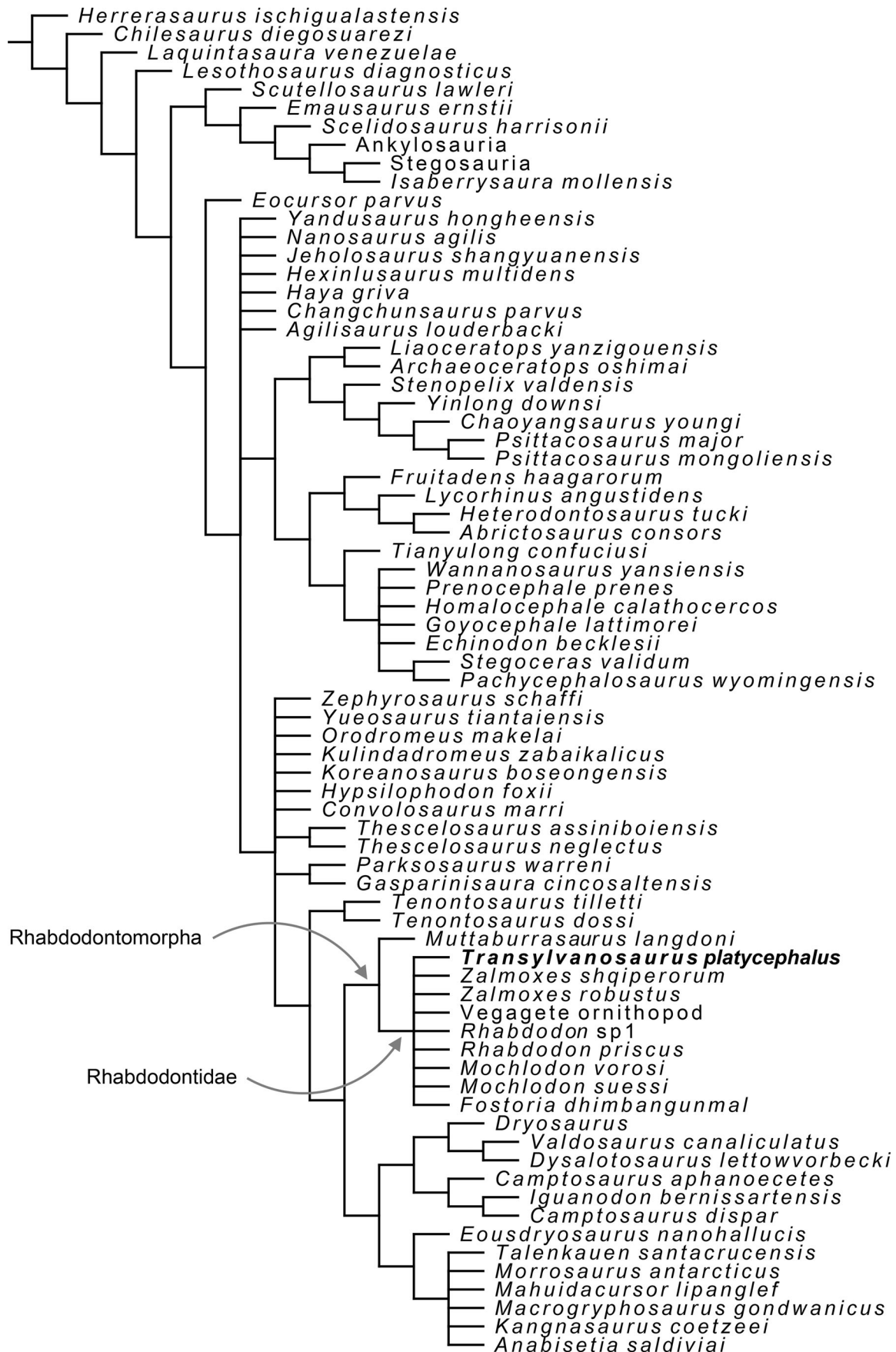
FIGURE 7. Strict consensus tree of the first phylogenetic analysis performed by us using the matrix of Dieudonné et al. (2021), showing the relation-ships of *Transylvanosaurus platycephalus* within Ornithischia and Ornithopoda.
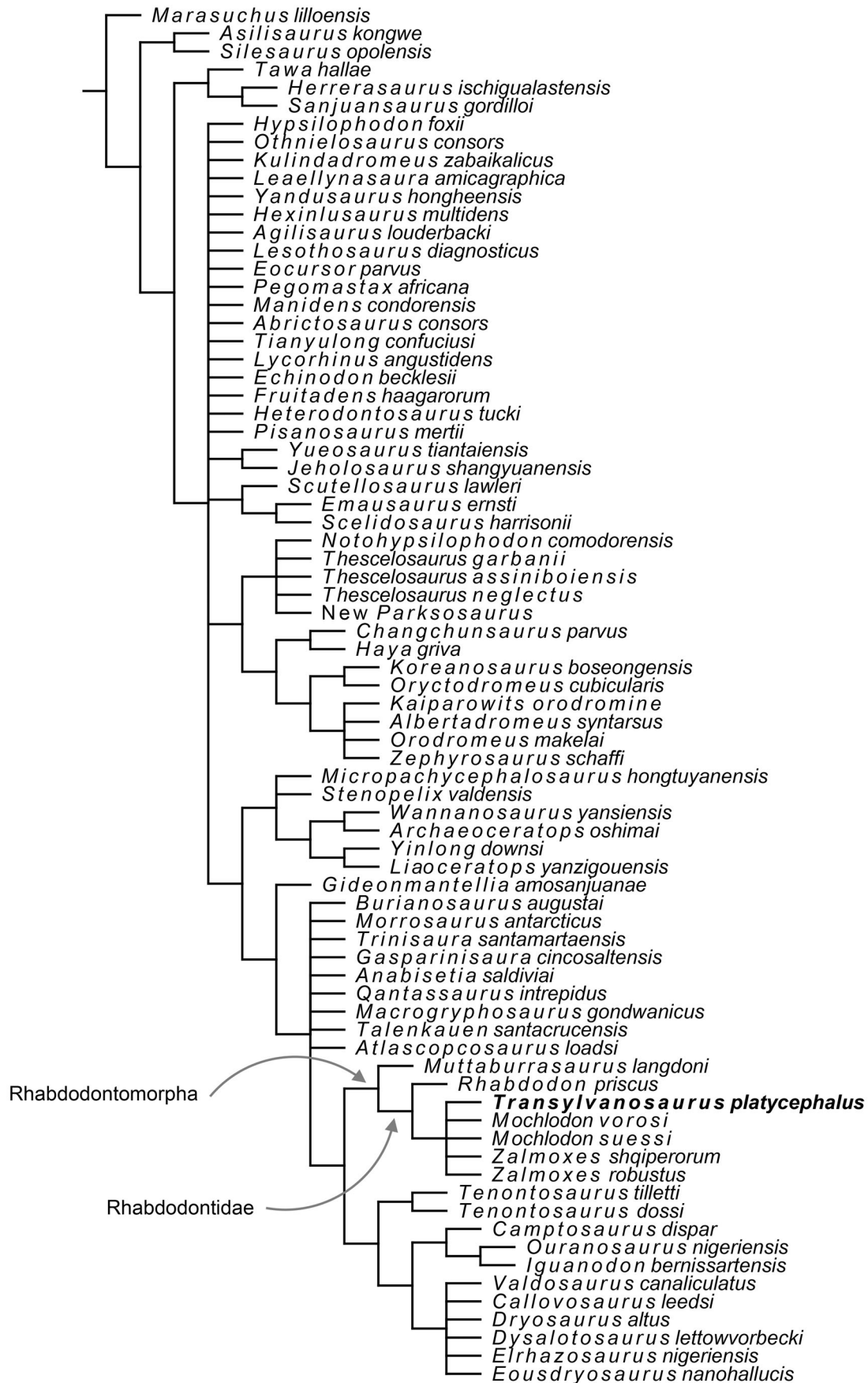
FIGURE 8. Strict consensus tree of the first phylogenetic analysis performed by us using the matrix of Madzia et al. (2018), showing the relationships of *Transylvanosaurus platycephalus* within Ornithischia and Ornithopoda. Notably, the phylogenetic relationships within Rhabdodontidae as shown herein 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 Hațeg 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 Hațeg 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 temporally 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 Sibișel 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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