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New early Maastrichtian ‘duck-billed’ dinosaur from Haţeg Basin (Densuş-Ciula Formation, Romania) documents an endemic clade of non-hadrosaurid hadrosauroids in the south-eastern Late Cretaceous European Archipelago

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We report the discovery of an associated incomplete hadrosauroid skeleton with cranial and postcranial elements from a new Maastrichtian (Upper Cretaceous) vertebrate site (Fântânele-3) north-west of Vălioara village in the westernmost part of the Haţeg Basin (Transylvania, Romania), from continental deposits of the Densuş-Ciula Formation. This hadrosauroid material is described here as a new taxon, *Kryptohadros kallaiae* gen. et sp. nov., based on one autapomorphic character of the dentary, two local autapomorphies of the surangular, as well as a unique combination of characters. It represents the second non-hadrosaurid hadrosauroid known from the Haţeg region besides *Telmatosaurus transsylvanicus*, a historical taxon for which we also provide a revised diagnosis and an updated list of securely referred specimens. The identification of *Kryptohadros* shows that basal hadrosauroids were more diverse during the latest Cretaceous in this area than previously thought. Furthermore, our phylogenetic analyses reveal particularly close relationships between all currently known Late Cretaceous south-eastern European hadrosauroids (*Telmatosaurus*, *Tethyshadros* and *Kryptohadros*) that belong to a newly recognized small endemic clade, Telmatosauridae. In addition, these analyses identify several different hadrosauroid evolutionary lineages present within the Late Cretaceous European Archipelago, and suggest that at least six other dispersal events took place between the Albian and the Maastrichtian from Asia towards North America and/or Europe, besides the arrival of the ancestors of Telmatosauridae before the Campanian. The absence of certain later-arriving European hadrosauroid lineages from the faunas of the south-eastern European islands supports earlier hypotheses that propose a direct migration route during the latest Cretaceous between Asia and the south-western European islands, circumventing south-eastern Europe.

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Keywords: anatomy; Hadrosauroidea; Haţeg Basin; Maastrichtian; palaeobiogeography; *Telmatosaurus*

Introduction

The first scientifically described dinosaur fossil from Transylvania is a quasi-completely preserved but crushed hadrosauroid skull (NHMUK R.3386), discovered by Ilona Nopcsa in 1895 along the Sibişel Valley near Săcel, in the central Haţeg Basin (Dalla Vecchia, 2006; Weishampel et al., 1993). Her brother, palaeontologist Ferenc Nopcsa, subsequently studied this specimen and published it as representing a new genus and species of duck-billed dinosaur – *Limnosaurus transsylvanicus* (Nopcsa, 1900). In that publication, the taxon had neither an unambiguously identified holotype nor a proper diagnosis, although the partial skull was mentioned as the basis for erecting the new taxon (Augustin et al., 2023). Later, the genus name was changed to *Telmatosaurus* (Nopcsa, 1903), as *Limnosaurus* had already been pre-occupied by a crocodylian (*Limnosaurus ziphodon* Marsh, 1872a). Subsequently, however, Nopcsa (1915) concluded that *Telmatosaurus* is actually a junior synonym of *Orthomerus* (Seeley, 1883) described from the Upper Cretaceous of Maastricht, based on his comparisons of the type material of this latter taxon with hadrosauroid femora from

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Vălioara, another fossiliferous area within Haţeg Basin. Nonetheless, *Orthomerus* is currently regarded a *nomen dubium* that is based on undiagnostic material (Brinkmann, 1988; Dalla Vecchia, 2006, 2014; Madzia et al., 2020; Weishampel & Horner, 2004).

Later, during the revision of Nopcsa's Transylvanian hadrosauroid, Weishampel et al. (1993) retained the name *Telmatosaurus*, and considered all hadrosauroid remains reported from the Transylvanian area (corresponding to an isolated landmass during the latest Cretaceous, often called the 'Haţeg Island'; e.g. Benton et al., 2010; Csiki-Sava et al., 2015) as belonging to the same species, that is, *T. transsylvanicus*. Subsequently, however, Dalla Vecchia (2006, 2009a, 2014, 2020) restudied the Transylvanian hadrosauroid fossil material referred to *Telmatosaurus* and suggested that only specimen NHMUK R.3386 (the lectotype skull) and possibly the vertebrae NHMUK R.3841 should be treated as belonging to this species. Dalla Vecchia (2006, 2009a, 2014) further stated that several of the diagnostic features of this taxon, as listed by Weishampel et al. (1993), are actually unsuitable for such a scope (see below). Finally, it was argued that the hadrosauroid fossils from Transylvania may conceivably represent more than one taxon, and it was noted that the previously referred material comes from at least five different lithostratigraphical units distributed across a large geographical area, each unit being several hundred metres thick, and together representing a broad stratigraphical range, recently shown to span the middle Campanian to late Maastrichtian time interval (e.g. Albert et al., 2025; Bălc et al., 2024; Csiki-Sava et al., 2016).

In 2019, our research team successfully set out to re-locate the historical uppermost Cretaceous Kadić dinosaur sites around Vălioara (Kadić, 1916), in the north-western Haţeg Basin, in order to thoroughly document their stratigraphical position and sedimentological setting (Botfalvai et al., 2021). During these fieldwork activities, further vertebrate accumulations were discovered near the former excavation sites, as were new fossiliferous sites, prompting the start of intensive investigations in this area from 2021 onward (see Albert et al., 2025). During the spring fieldwork of 2022, our team also examined the Fântânele microvertebrate bonebed (MvBB), which represents an important MvBB from Haţeg Basin (see details in Grigorescu et al., 1999; Vasile & Csiki, 2010). Unfortunately, access to the fossiliferous bed became difficult after 2016, and excavations at this site were discontinued (Csiki-Sava et al., 2023). Nevertheless, aided by a new road-cut encountered in the close vicinity of the Fântânele MvBB, new fossiliferous outcrops were identified – designated as Fântânele-3 – that apparently are correlated with the fossiliferous horizon of the Fântânele MvBB (Albert et al., 2025; Fig. 1).

Along with a very small number of other isolated macrovertebrate remains, Fântânele-3 yielded an associated incomplete hadrosauroid skeleton (LPB [FGGUB] R.2882 or the 'Jenna specimen') including both cranial and postcranial elements (see below). The hadrosauroid remains were situated in close proximity to each other and were collected from the same horizon of a single bonebed (Fig. 1C, D). The distal skeletal parts, including caudal vertebrae and chevrons, were discovered in the northern part of the excavation site, while the cranial and dental elements were located a few metres away within the southern side of the bonebed (Fig. 1C); the recovered limb bones, ribs and teeth were roughly uniformly distributed between these two more concentrated sets of elements.

Based primarily on features of the cranial elements, this hadrosauroid material can be differentiated from the previously known Transylvanian hadrosauroid *Telmatosaurus transsylvanicus* and belongs to a previously unknown taxon. The description of this material as a new hadrosauroid, *Kryptohadros kallaiae* gen. et sp. nov., supports earlier hypotheses suggesting that more than one hadrosauroid taxon was present in the ancient faunas of Haţeg Island. Furthermore, our phylogenetic analyses show that these Transylvanian hadrosauroids are closely related to the latest Cretaceous Italian hadrosauroid *Tethyshadros insularis* Dalla Vecchia, 2009b, together forming a newly separated small clade (Telmatosauridae), and we also explore here the evolutionary and palaeobiogeographical implications that derive from the recognition of this endemic south-eastern European clade.

Geological setting

The Haţeg Basin is an intermontane basin within the Southern Carpathians, connected to the larger Transylvanian Basin, both of them hosting discontinuous, but widely distributed, relatively thick successions of uppermost Cretaceous continental deposits, grouped into several quasi-synchronous lithostratigraphical units (e.g. Csiki-Sava et al., 2016; Fig. 1A). Such continental deposits from the central and south-eastern parts of Haţeg Basin belong to the Sînpetru Formation and tentatively correlative units, whereas other uppermost Cretaceous continental beds cropping out in the north-western part of the basin are grouped into the Densuş-Ciula Formation (e.g. Grigorescu, 1992). Within the Densuş-Ciula Formation, the Middle Member – representing probably the upper part of upper Campanian to lower part of upper Maastrichtian (Albert et al., 2025; Csiki-Sava et al., 2016) – is the most important fossil-

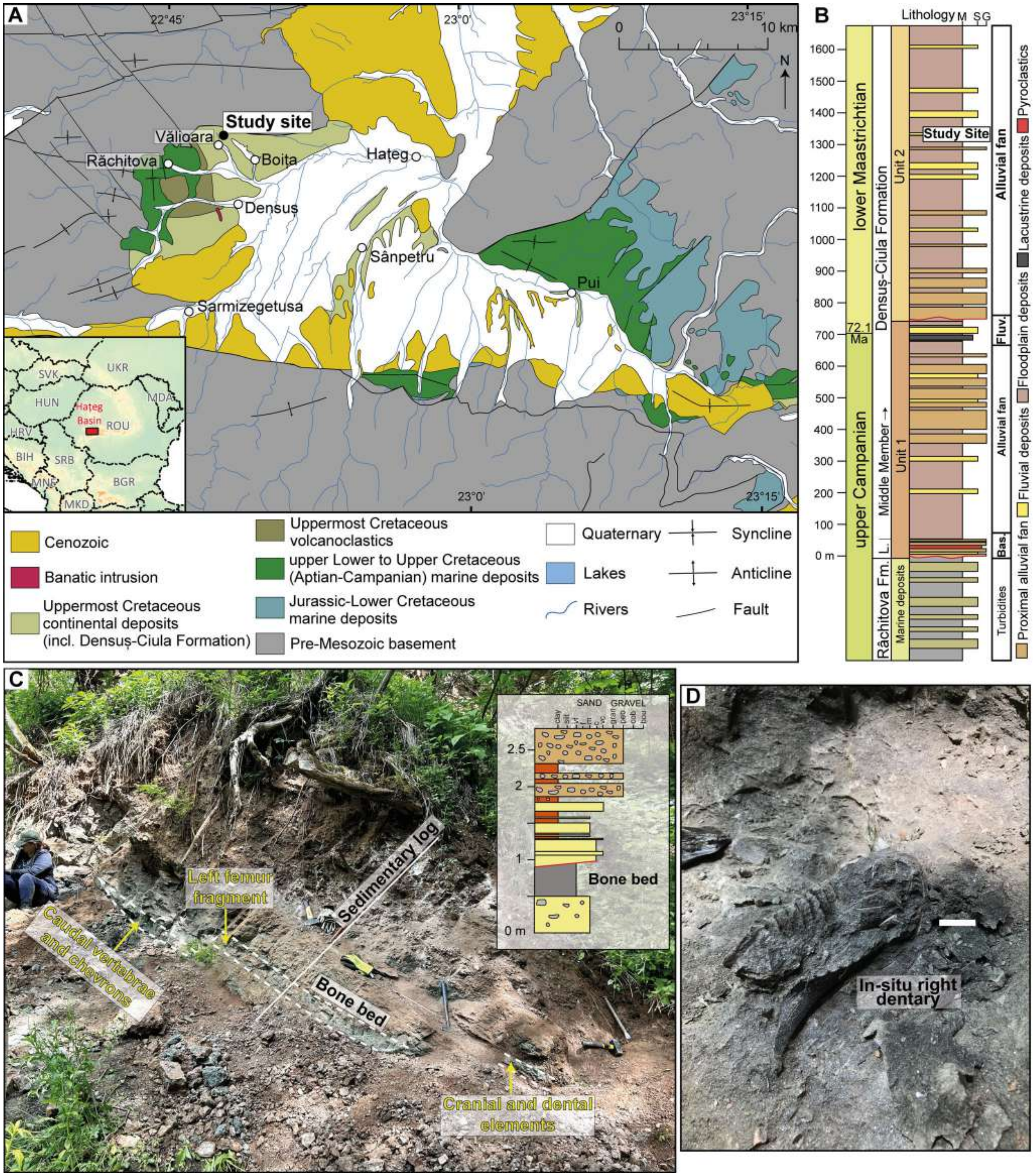


Figure 1. **A,** Geological map of Haţeg Basin, modified from Albert et al. (2025); **B,** Depositional units, sedimentological and palaeoenvironmental interpretation of the Densuş-Ciula Formation in the Vălioara area, indicating the position of site Fântânele-3 – type locality of the hadrosauroid *Kryptohadros kallaiae* gen. et sp. nov., modified from Albert et al. (2025); **C,** Position and sedimentological context of the bonebed within site Fântânele-3. Approximate position of the different hadrosauroid remains within the bonebed is indicated on the photo; **D,** *In situ* right dentary of *Kryptohadros kallaiae* gen. et sp. nov. Scale bar equals 1 cm.

yielding subunit, with several important localities reported (e.g. Botfalvai et al., 2017, 2021; Csiki-Sava et al., 2016; Kadić, 1916). Deposits belonging to the lower part of the Middle Member are exposed northwest of the village of Vălioara as well (Albert et al., 2025), including at site Fântânele-3 (Fig. 1B–D) that yielded the hadrosauroid material described herein (see also Csiki-Sava et al., 2023).

The basin-filling succession that corresponds to the locally outcropping interval of the Densuș-Ciula Formation is built up by two vertically superimposed fining upward cycles (*c.* 700 m and *c.* 950 m thick, respectively) representing continental, alluvial-fan deposition (Albert et al., 2025). The lower portion of each cycle is dominated by coarse, gravelly material that originated from the erosion of the subaerially exposed metamorphic basement and represents proximal fan environments, while the relative proportion of more finer-grained, floodplain and fluvial deposits gradually increases upward (Fig. 1B). According to Albert et al. (2025), the deposits cropping out at Fântânele-3 correspond to the upper portion of the second, upper sedimentary cycle.

The wider Vălioara area has already yielded a large number of macro- and microvertebrates during the last hundred years (e.g. Botfalvai et al., 2021; Csiki-Sava et al., 2016; Grigorescu et al., 1999; Kadić, 1916; Magyar et al., 2024), and an important microvertebrate site (the Fântânele MvBB; Grigorescu et al., 1999) has been known for decades in the close proximity of site Fântânele-3. One of the most productive MvBBs from the uppermost Cretaceous of the Transylvanian area overall (Csiki-Sava et al., 2023; Vasile & Csiki, 2010), Fântânele has yielded important fossils such as multituberculate teeth (Csiki & Grigorescu, 2000; Csiki-Sava, Lintz & Vasile, 2022; Csiki-Sava, Vremir et al., 2022), the holotype of the bombinatorine anuran *Hatzegobatrachus grigorescui* (Venczel & Csiki, 2003), remains of *Theriosuchus*-like neosuchians (Martin et al., 2014), and of ornithuran birds (X. Wang et al., 2011). In their overview of the local fossil record, Vasile & Csiki (2010) also noted the presence of characid and lepisosteid fishes, albanerpetontid amphibians, chelonians, squamates, other semi-aquatic and terrestrial crocodyliforms, and diverse dinosaurs (theropods, rhabdodontids and hadrosauroids) at Fântânele MvBB.

Sedimentological description and palaeoenvironmental interpretation of site Fântânele-3

Sediments at Fântânele-3 and its vicinity are dominated by intercalating wedge-shaped to tabular matrix-supported conglomerates and red to brownish red, sandy-gravelly mudstones, each of these attaining thicknesses that range from tens of centimetres to several metres. These sediments represent alternating debris flow and well-drained floodplain-dominated subenvironments, respectively, of a large alluvial fan system fed by the erosion of close-by subaerially exposed metamorphic basement (Albert et al., 2025). Besides these two dominant facies types, volumetrically less frequent but palaeontologically important, erosionally bounded, 10 cm to 1.5 m thick, lens-shaped sandy-gravelly sedimentary bodies were also observed at the site (Fig. 1C, D). These sediments are interpreted to represent ephemeral fluvial channel bodies formed during flooding events (Albert et al., 2025).

The grey, fine-grained, silty fossil-bearing bed represents the uppermost portion of a *c.* 10 m wide and 1 m thick fluvial channel body. The erosionally bounded channel thins and terminates towards the north-western part of the exposed local section. Its opposite termination cannot be observed, and thus its total width cannot be measured due to the strong tilt and high dip angle (35° to the east) of the deposits (Fig. 1C). Above the erosional basal surface, the sedimentary infill of the bone-bearing channel body starts with 0.5 m of pebbly, coarse grained, structureless sand at its thickest point, with the pebble content decreasing laterally with the thinning of the sedimentary body (Fig. 1C). This coarse basal part is overlain by a maximum 40 cm thick bone-bearing, grey, silty interval, which itself is overlain by floodplain mudstones or else its uppermost part is erosionally cut by a second, superimposed channel body. Based on its internal facies architecture, the fossiliferous channel body most likely formed during a flooding event, cutting down into the underlying muddy floodplain deposits and rapidly depositing structureless sand. The bone-bearing silty interval is interpreted as having been deposited in standing water in the abandoned fluvial channel during and after waning flood stages.

The relative spatial and geometric position of the fossil-bearing beds encountered at Fântânele-3 suggests that these could roughly represent a continuation of the fossiliferous horizon of the Fântânele MvBB. This latter was also interpreted as the infill of an abandoned channel or small floodplain depression (Csiki-Sava et al., 2023; Vasile & Csiki, 2010), although its sedimentary facies differs in certain details, since both the erosional base and the basal coarser grain size were not detectable at Fântânele MvBB. The two sites also differ in the nature and composition of their fossil assemblages. While the Fântânele MvBB is a typical high-diversity microvertebrate accumulation, with the largest part of the recovered fossil remains being isolated and less than 5 cm (most often even less than 1 cm) long, the new Fântânele-3 accumulation can be characterized as a high-diversity, mixed macrovertebrate-microvertebrate bonebed, with several macrovertebrate fossils excavated, including specimens that are definitely associated.

The preliminary faunal list assembled as the result of our excavations and screen-washing at Fântânele-3 was reported in Csiki-Sava et al. (2023) and Konecsni et al. (2024), and it includes isolated plant material (amber drops, seeds and coal fragments), remains of invertebrates (gastropod shells and termite coprolites), and vertebrates such as anurans, albanerpetontids, squamates, turtles (most likely the stem-testudine *Kallokibotion*), crocodyliforms (the larger *Allodaposuchus* as well as the smaller *Doratodon* and a *Theriosuchus*-like taxon), azhdarchid pterosaurs, theropods, rhabdodontids, titanosaurs and multituberculates. The most remarkable discovery at Fântânele-3 is represented, nonetheless, by the most probably associated, well-preserved cranial, axial and appendicular elements (Figs 2–12) of a hadrosauroid dinosaur individual, described in this publication.

Material and methods

Specimen collection and preparation

The associated incomplete skeleton of the hadrosauroid dinosaur reported here (LPB [FGGUB] R.2882) was collected from Fântânele-3, north-west of Vălioara village (north-western Haţeg Basin, south-western Transylvania, Romania; Fig. 1), a site excavated during several fieldwork sessions between 2022 and 2024. Besides this associated incomplete skeleton, the site yielded only a few macrovertebrate remains representing other taxa, such as isolated titanosaurian vertebrae, a cervical vertebra fragment and limb bone fragments of small-sized azhdarchid pterosaurs, crocodyliform osteoderms, and turtle plate fragments.

Although none of the hadrosauroid bones were found articulated, they are definitely associated and most probably represent one individual, since the bones come from an area of a few square metres of the same layer (Fig. 1C), match each other in size, have a similar state of preservation, and there are no duplicated elements among them. The fossils are mostly black or dark brown and generally well-preserved, with only some bones showing breaks with sharp edges or worn surfaces.

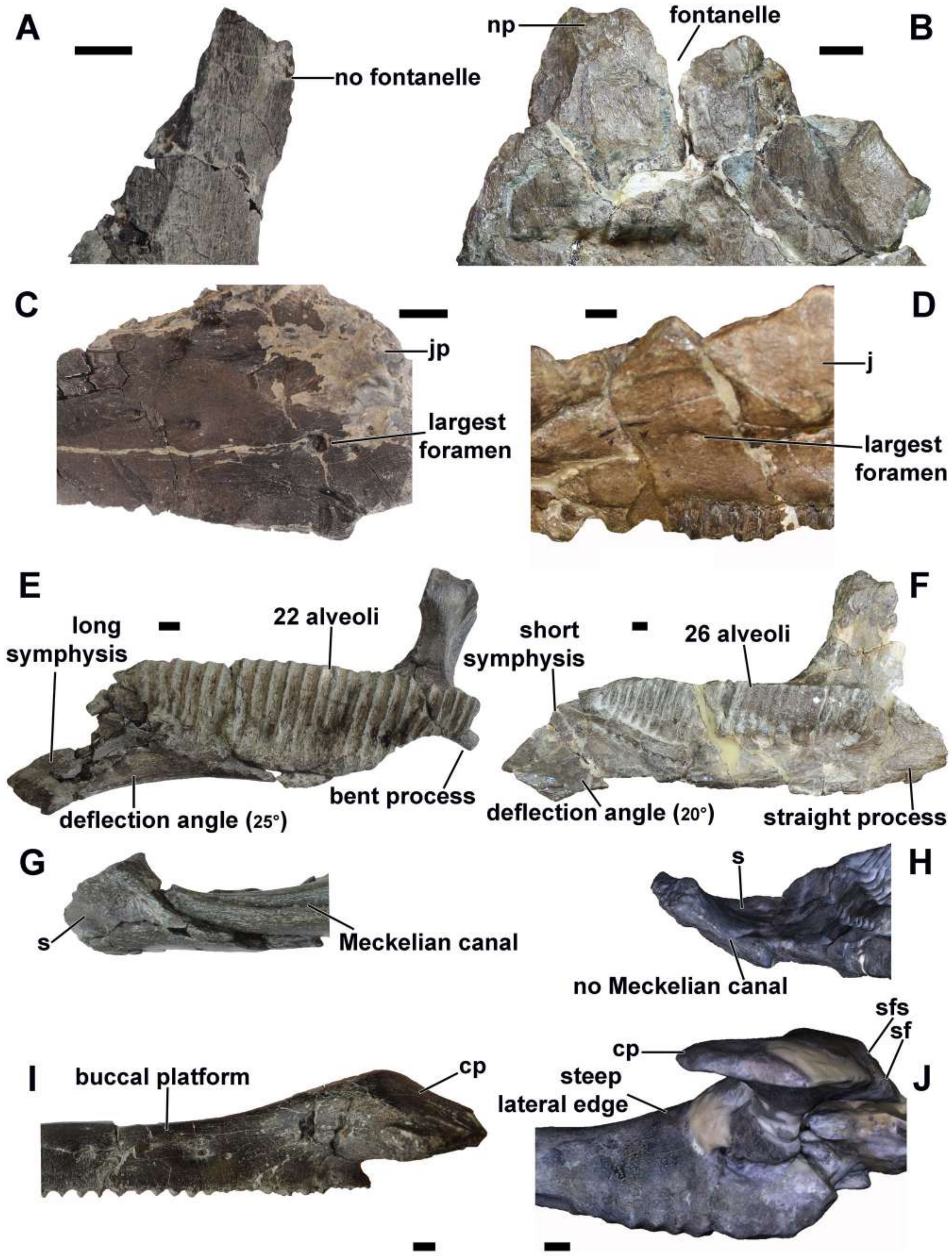
The recovered remains were prepared mechanically in the technical laboratory of the Department of Palaeontology of the Eötvös Loránd University (ELTE; Budapest, Hungary), using a Fiac Compact 106 oilless air compressor with W 224 pneumatic preparation head, Dremel engraver 290-02, and preparation needles. The bones were fixed by cyanoacrylic glue, and the dimensions of the specimens were measured with a ruler. Photos were taken with a Canon EOS 600D DS126311 camera. Subsequently, the prepared specimens were catalogued in the vertebrate palaeontology collections of the Faculty of Geology and Geophysics of the University of Bucharest (LPB [FGGUB]).

Phylogenetic analysis

To assess the phylogenetic relationships of the new hadrosauroid material from Fântânele-3, we performed a phylogenetic analysis using the character-taxon matrix of Longrich, Pereda-Suberbiola, et al. (2024). This is a modified version of the dataset from Longrich et al. (2021), with characters derived from Kobayashi et al. (2019) and Xing et al. (2014), and represents one of the most recent and most extensive datasets available for hadrosauroids.

We further updated and expanded the character-taxon matrix of Longrich, Pereda-Suberbiola, et al. (2024) – using Mesquite v.3.81 for editing – by adding four more operational taxonomic units: *Batyrosaurus rozhdestvenskyi* (Godefroit, Escuillié, et al., 2012), *Fylax thyrakolasus* (Prieto-Márquez & Carrera Farias, 2021), *Penelopognathus weishampeli* (Godefroit et al., 2005), and the new specimen from Fântânele-3. Furthermore, we changed the previously existing codings for the following characters in the case of *Telmatosaurus*, based on our observations of the lectotype: Character 6 (maximum number of ridges on the enamelled surface of the dentary tooth crown in lingual view) changed from 2 (two or three in total) to 3 (only one primary ridge); Character 144 (morphological feature of the rostral end of the nasal articulating with premaxillary caudodorsal process in lateral view) changed from ? to 0 (presence of a slender and wedge-shaped rostral end, gradually decreasing rostrally in width and depth); Character 146 (caudal-most apex of the external naris) changed from ? to 0 (consisting of nasal and premaxilla); Character 171 (participation of the prefrontal in the lateral border of the hollow supracranial crest) changed from ? to 0 (absent); Character 200 (nasal-frontal fontanelle on the dorsal surface of the braincase) changed from ? to 0 (present, the nasal-frontal fontanelle is still well developed and large in subadults or young adults); Character 356 (dentary, Meckelian groove) changed from ? to 1 (anterior end shifted ventrally, not visible more than halfway down the toothrow in medial view). The resulting matrix consists of 389 characters (of which 102 were ordered) scored for 93 taxa (Supporting data available through Zenodo (Magyar et al., 2025). *Iguanodon bernissartensis* was employed as the operational outgroup taxon.

Preceding the analyses, we increased the RAM to 1000 and maximized the available tree space for 99,999


A
no fontanelle
np
fontanelle
B
C
jp
largest foramen
D
j
largest foramen
E
long symphysis
22 alveoli
deflection angle (25°)
bent process
short symphysis
26 alveoli
F
deflection angle (20°)
straight process
G
s
Meckelian canal
s
H
no Meckelian canal
I
buccal platform
cp
cp
sfs
sf
steep lateral edge
J

trees. The traditional search was performed in TNT v. 1.6 (Goloboff & Morales, 2023) with the tree bisection reconnection algorithm using 10,000 replications of Wagner trees, with 10 trees saved per replication. The random seed was set to 1. We did not exclude or prune any taxon from the analysis, but characters 87 (morphological character of the caudal region of the premaxillary caudoventral process in adult individuals) and 367 (continental plate of the site) were excluded, as in Longrich, Pereda-Suberbiola, et al. (2024).

In order to test the results of the first analysis, we ran a second phylogenetic analysis using the character-taxon matrix dataset of Dai et al. (2025), which is a modified version of the matrix used by Xing et al. (2017). This dataset is very similar to the one used in our first analysis, but it contains fewer taxa and characters. Using Mesquite v.3.81 for editing, we added *Fylax thyrakolasus* and the Fântânele-3 specimen to the list of taxa, and modified several characters for *Telmatosaurus transsylvanicus*, as in the first analysis. As a result, the new character-taxon matrix consists of 346 unordered characters and 66 taxa (supporting data available through Zenodo; Magyar et al., 2025), with *Iguanodon bernissartensis* employed again as the outgroup. The settings in TNT v. 1.6 were the same as for the first analysis (RAM = 1000, available tree space = 99,999), except the random seed during the traditional search, which was set to 0 this time. During the traditional search, the tree bisection reconnection algorithm was used with 10,000 replications of Wagner trees, and 10 trees saved per replication, just as in our first analysis. Similar to the original analysis of Dai et al. (2025), we did not exclude or prune any taxon or character from the analysis. In both analyses, the consistency and retention indices, as well as the Bremer Support/Decay Index, were calculated using the scripts available in TNT.

Clade names used throughout this study follow the approach (and definitions) put forth by Madzia et al. (2021) in order to fully comply with the practices and requirements of the International Code of Phylogenetic Nomenclature (or PhyloCode; de Queiroz & Cantino, 2020).

Institutional abbreviations

AENM, Amur Natural History Museum of the Institute of Geology and Nature Management, Far Eastern Branch of the Russian Academy of Sciences, Blagoveschensk, Russia; **AMNH**, American Museum of Natural History, New York, NY, USA; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **DMNH**, Perot Museum of Nature and Science, Dallas, TX, USA; **IGM**, National Collection of Paleontology, Institute of Geology, National Autonomous University of Mexico, Mexico City, Mexico; **IMM**, Inner Mongolia Museum, Hohhot, Inner Mongolia, China; **IRSNB**, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **LPB (FGGUB)**, Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; **MNMKK-MTM**, Hungarian National Museum Public Collection Centre, Budapest – Hungarian Natural History Museum, Budapest, Hungary; **MPC**, Mongolian Palaeontological Center, Ulaanbaatar, Mongolia; **MPCN**, Patagonian Museum of Natural Sciences, General Roca, Río Negro Province, Argentina; **NHMUK**, Natural History Museum, London, UK; **ROM**, Royal Ontario Museum, Toronto, Canada; **SC**, Italian State collections, Italy; **SMU**, Southern Methodist University Shuller Museum of Paleontology, Dallas, TX, USA; **SXMG**, Shanxi Museum of Geology, Taiyuan, Shanxi, China; **SZTFH**, Collection of the Supervisory Authority for Regulatory Affairs (formerly the Geological Institute of Hungary – MAFI), Budapest, Hungary; **UCMP**, University of California Museum of Paleontology, Berkeley, CA, USA.

Results

Preliminary remarks on the status of *Telmatosaurus transsylvanicus*

Seconding the opinion of Dalla Vecchia (2006, 2009a, 2014, 2020), we also propose that the fossil material that definitely belongs to *T. transsylvanicus* should be restricted to the crushed skull described by Nopcsa

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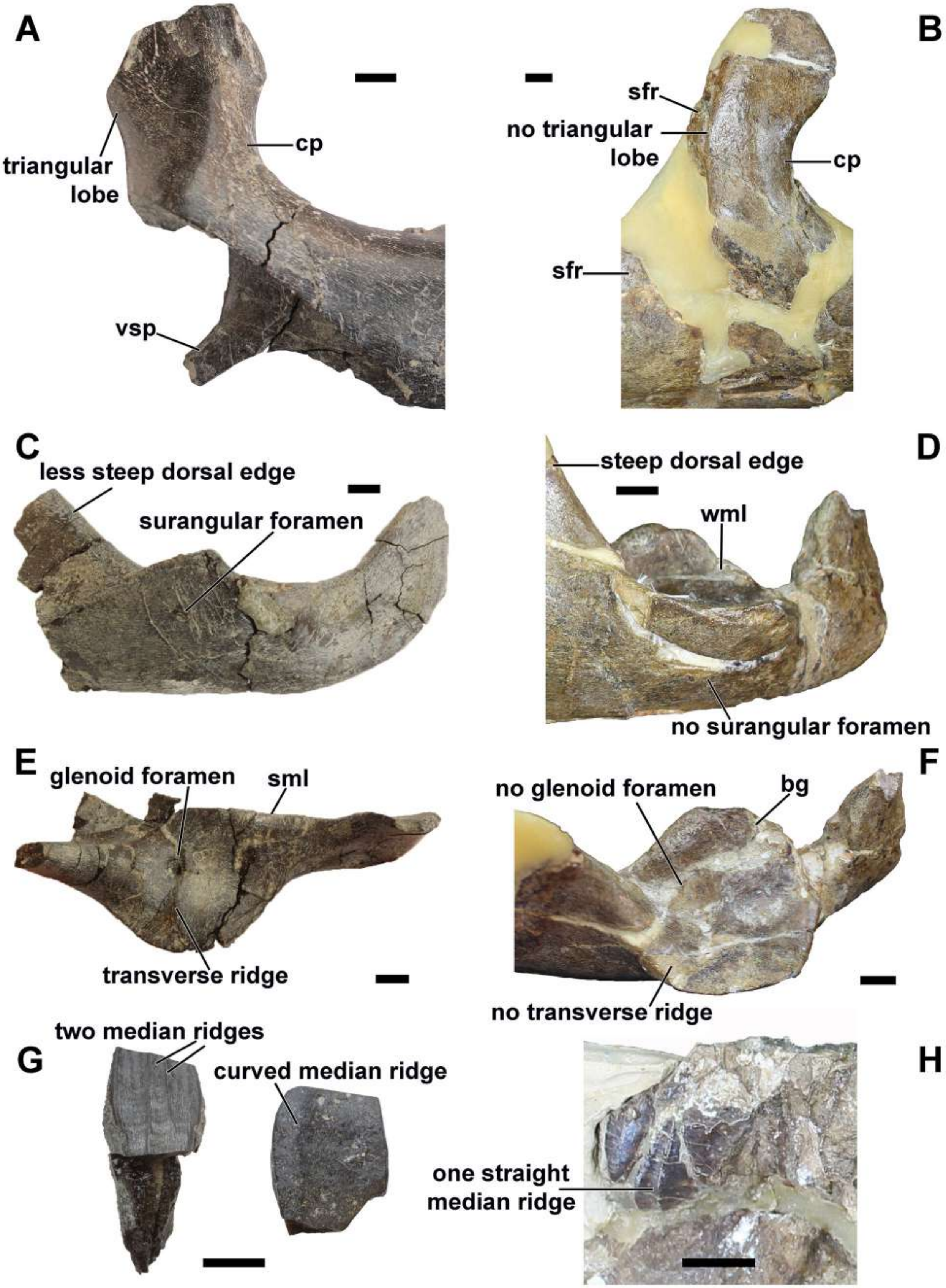
Figure 2. Comparison of cranial elements belonging to the holotype of *Kryptohadros kallaiae* gen. et sp. nov. (LPB [FGGUB] R.2882) and respectively, the lectotype of *Telmatosaurus transsylvanicus* (NHMUK R.3386). **A,** The posterior end of the right nasal of *K. kallaiae* gen. et sp. nov. (LPB [FGGUB] R.2882.8) in dorsal view; **B,** The nasal processes of the frontals of *T. transsylvanicus* in dorsal view; **C,** Left maxilla of *K. Kallaiae* gen. et sp. nov. (LPB [FGGUB] R.2882.1) in lateral view; **D,** Right maxilla of *Telmatosaurus* (reversed, for easier comparison) in lateral view; **E,** Right dentary of *K. kallaiae* gen. et sp. nov. (LPB [FGGUB] R.2882.2) in medial view; **F,** Left dentary of *T. transsylvanicus* (reversed, for easier comparison) in medial view; **G,** Symphyseal part of the right dentary of *K. kallaiae* gen. et sp. nov. in ventral view; **H,** Symphyseal part of the left dentary of *T. transsylvanicus* (reversed, for easier comparison) in ventral view (image from the 3D scan of the specimen); **I,** Right dentary of *K. kallaiae* gen. et sp. nov. in dorsal view; **J,** Right dentary of *T. transsylvanicus* in dorsal view (image from the 3D scan of the specimen). **Abbreviations: cp**, coronoid process; **j**, anterior part of the jugal; **jp**, jugal process; **np**, nasal process; **s,** symphysis; **sf**, surangular fragment; **sfs**, suture for surangular. Scale bars equal 1 cm.


A
triangular lobe
cp
vsp
B
sfr
no triangular lobe
cp
sfr
C
less steep dorsal edge
surangular foramen
D
steep dorsal edge
wml
no surangular foramen
E
glenoid foramen
sml
transverse ridge
F
no glenoid foramen
bg
no transverse ridge
G
two median ridges
curved median ridge
H
one straight median ridge

(1900) and the cervical, dorsal and caudal vertebrae that presumably belong to the same individual according to Nopcsa (1925). Additional referred specimens include other skull elements originating from the wider type locality area (i.e. Sibișel Valley, near Sânpetru), some of which were also mentioned by Nopcsa (1900) within the original description and definition of the taxon (the fragmentary left maxilla NHMUK R.3388 and the braincase NHMUK R.3387), as well as two maxillae (LPB [FGGUB] R.1010, NHMUK R.4911) that were used by Prieto-Márquez (2010c) to represent *T. transsylvanicus* in his cladistic analysis. These cranial elements overlap with the lectotype skull, are morphologically very similar to it, and were also collected from the Sînpetru Formation.

Comments on the currently existing diagnosis of *Telmatosaurus transsylvanicus*

As already noted by Dalla Vecchia (2006, 2009a, 2014), our recent detailed restudy of the material previously referred to this taxon has indeed demonstrated that several of the characters listed by Weishampel et al. (1993) as unique (=apomorphic) for *T. transsylvanicus* are unreliable, either because they are difficult to interpret/assess or else because the respective characters also occur in other taxa. Most importantly, however, as we emphasize and discuss in detail below, the diagnosis and re-description of this taxon by Weishampel et al. (1993) – even including one of its supposed diagnostic characters – is largely based on observations of specimens (see list in Weishampel et al., 1993, p. 362) that do not belong to the lectotype, are not directly comparable to it, and/or were collected from other localities, often belonging to lithostratigraphical units that are different from that hosting the type horizon of this taxon. All these recent observations, aligning with previous suggestions, show that the current status and diagnosis of this taxon needs to be updated, which we will do below.

The first category of these problematic issues concerning the diagnosis of *Telmatosaurus transsylvanicus* is represented by loosely defined and difficult-to-interpret characters such as 'a large ectopterygoid shelf', 'a relatively long post-metotic braincase', and 'relatively large basipterygoid processes' (Weishampel et al., 1993, p. 362–363), as the term 'relatively' does not have a clear standard of reference (Dalla Vecchia, 2006), and thus it is unclear what degree of development of the quoted anatomical features is considered to count as 'large'. Nonetheless, quantification of these characters may potentially help alleviate such issues, such as through characterizing the degree of development of the ectopterygoid shelf by a percentage-based numerical value (e.g. the length of the ectopterygoid shelf, more precisely, of the region lying behind the jugal process, given in relation to the total length of the maxilla).

The second category of these contentious issues groups problematic characters that are also now known to occur in other taxa. As increasingly more hadrosauroid species are recognized, features that were previously recorded in only one species may be subsequently identified in other newly described and often distantly related taxa. For example, Weishampel et al. (1993) identified the triangular rostral process of the jugal as one of the diagnostic features of *Telmatosaurus*, but Dalla Vecchia (2009a, 2014) pointed out that other taxa such as *Acristavus gagslarsoni*, *Aralosaurus tuberiferus*, *Brachylophosaurus canadensis*, *Maiasaura peeblesorum*, and even some subadults of *Edmontosaurus* also display a similar rostral process. Other characters such as 'small body size' or 'absent or very small diastema between the predentary and dentary' also seem to be common in at least some basal hadrosauroids (e.g. Dalla Vecchia, 2006, 2009b, 2014; Godefroit et al., 1998; Tsogtbaatar et al., 2019). These widely distributed characters should be thus removed as potential autapomorphies from the diagnosis of *T. transsylvanicus*, although some of them can be still useful within unique combinations of characters (see below).

The third category of problematic characters from the diagnosis includes those that are not actually observable on the lectotype. First, the presence of a 'scar for *m. protractor pterygoideus*' cannot be identified on the specimen, and nor is it mentioned by other authors for other hadrosauroids. Similarly, the exact place, size and orientation of the different foramina and neural canals

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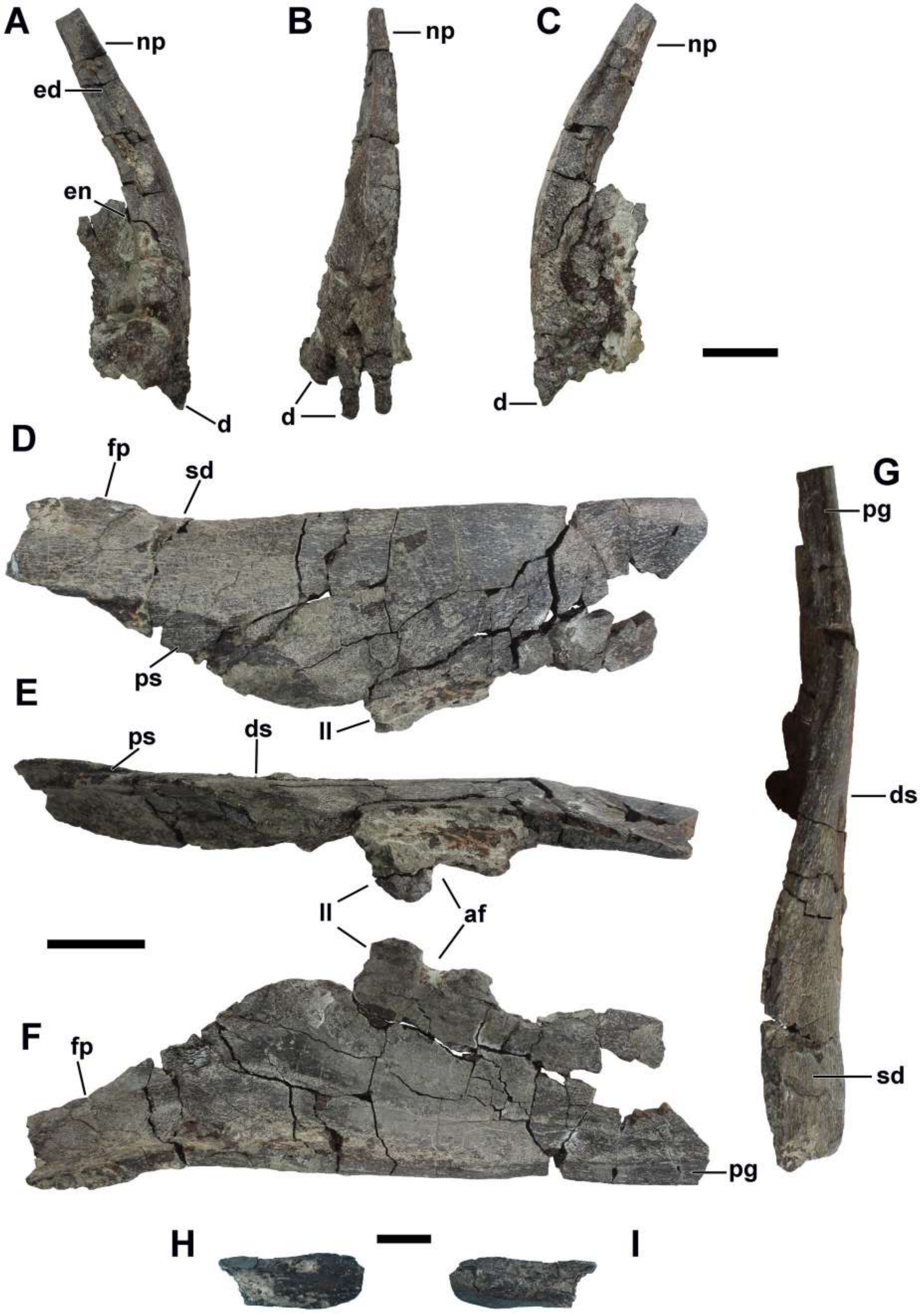
Figure 3. Comparison between the cranial elements of the holotype of *Kryptohadros kallaiae* gen. et sp. nov. (LPB [FGGUB] R.2882) and, respectively, the lectotype of *Telmatosaurus transsylvanicus* (NHMUK R.3386). **A,** Coronoid process of the right dentary (LPB [FGGUB] R.2882.2) of *K. kallaiae* gen. et sp. nov. in lateral view; **B,** Coronoid process of the right dentary of *T. transsylvanicus* in lateral view; **C,** Left surangular of *K. kallaiae* gen. et sp. nov. (LPB [FGGUB] R.2882.4) in lateral view; **D,** Right surangular of *T. transsylvanicus* (reversed, for easier comparison) in lateral view; **E,** Left surangular of *K. kallaiae* gen. et sp. nov. in dorsal view; **F,** Right surangular of *T. transsylvanicus* (reversed, for easier comparison) in dorsal view; **G,** Isolated dentary teeth of *K. kallaiae* gen. et sp. nov. (left: LPB (FGGUB) R.2882.17, right: R.2882.20); **H,** *In situ* anterior dentary teeth of *T. transsylvanicus*. **Abbreviations: bg**, bowl-shaped glenoid surface; **cp**, coronoid process; **sfr**, surangular fragment; **sml**, straight medial lobe; **vsp**, ventrolaterally and posteriorly oriented splenial process; **wml**, well-developed medial lobe. Scale bars equal 1 cm for A–F and H, and 0.5 cm for G.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on the basicranium are impossible to identify with certainty due to the poor preservation state of the braincase both in the lectotype and in specimen NHMUK R.4915 from an unidentified site near Vălioara that was also used by Weishampel et al. (1993) in their description of this element (but see comments below regarding this specimen).

Finally, as already indicated, characters based on specimens that do not belong/compare directly to the lectotype and thus cannot be confidently referred to the taxon were also included in the diagnosis, such as a ‘bowed femur’, considered to be a primitive feature common to basal iguanodontians by Norman (2004) and Dalla Vecchia (2014). Therefore, characters from this category also need to be removed from the diagnosis of *T. transsylvanicus*.

Systematic palaeontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1888
Ornithopoda Marsh, 1881
Iguanodontia Baur 1891, *sensu* Sereno, 1998
Ankylopollexia Sereno, 1986
Styracosterna Sereno, 1986
Hadrosauriformes Sereno, 1997
Hadrosauroidea *sensu* Sereno, 1998
Telmatosauridae novel clade name

Definition. The largest clade containing *Telmatosaurus transsylvanicus* (Nopcsa, 1900), but not *Gobihadros mongoliensis* Tsogtbaatar et al., 2019, *Hadrosaurus foulkii* Leidy, 1858 and *Claosaurus agilis* Marsh, 1872b. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Telmatosaurus transsylvanicus* [Nopcsa, 1900] ~ *Gobihadros mongoliensis* Tsogtbaatar et al., 2019 & *Hadrosaurus foulkii* Leidy, 1858 & *Claosaurus agilis* Marsh, 1872b).

Etymology. Derived from the generic name of the first identified member of this clade, *Telmatosaurus transsylvanicus*.

Reference phylogeny. Fig. 13B of this publication is treated here as the primary reference phylogeny. Additional reference phylogenies include fig. 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, Telmatosauridae comprises *Telmatosaurus transsylvanicus*, *Tethyshadros insularis* and *Kryptohadros kallaiae* gen. et sp. nov.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Diagnosis. Members of this clade share the following unique character combination: body length less than 6 m; presence of three denticles on the anteroventral edge of the premaxilla; >1.25 maxillary teeth/cm; saw-toothed or small mammilliform denticles along the ventral half of the maxillary crowns; and very short diastema on the anterior part of the dentary.

Furthermore, our first, main phylogenetic analysis also tentatively identified the following characters to be potentially shared by telmatosaurids, even if these are not known in all currently included taxa: the external and internal parts of the premaxilla not separated by a deep sulcus; ratio between the horizontal distance from the caudal margin of the coronoid process to the caudal-most end of the deflected ventral margin of the dentary and the horizontal distance from the caudal margin of the coronoid process to the rostral-most alveolus, is >0.78; maximum number of dentary teeth per alveolus in adults = 3; and occurrence of a posterior notch at the base of the anterior caudal neural spines.

Comment. Despite the poor to moderate (in the second and first phylogenetic analysis, respectively; see Material and methods section as well as supporting data - Magyar et al., 2025) support found by us for the newly introduced clade, as well as the only occasional recovery of its formerly known members within a distinct monophyletic grouping in previous analyses (see details below, Phylogenetic analysis section), we decided to name it nonetheless, based on the following supporting arguments: (1) albeit low, its support is still marginally higher (especially in the first, more comprehensive analysis) than that found for many other hadrosauroid clades, including historically well-established and widely accepted ones such as Brachylophosaurini, Kritosaurini or Parasaurolophini; (2) both its overall position within Hadrosauroidea as well as its intra-clade relationships are

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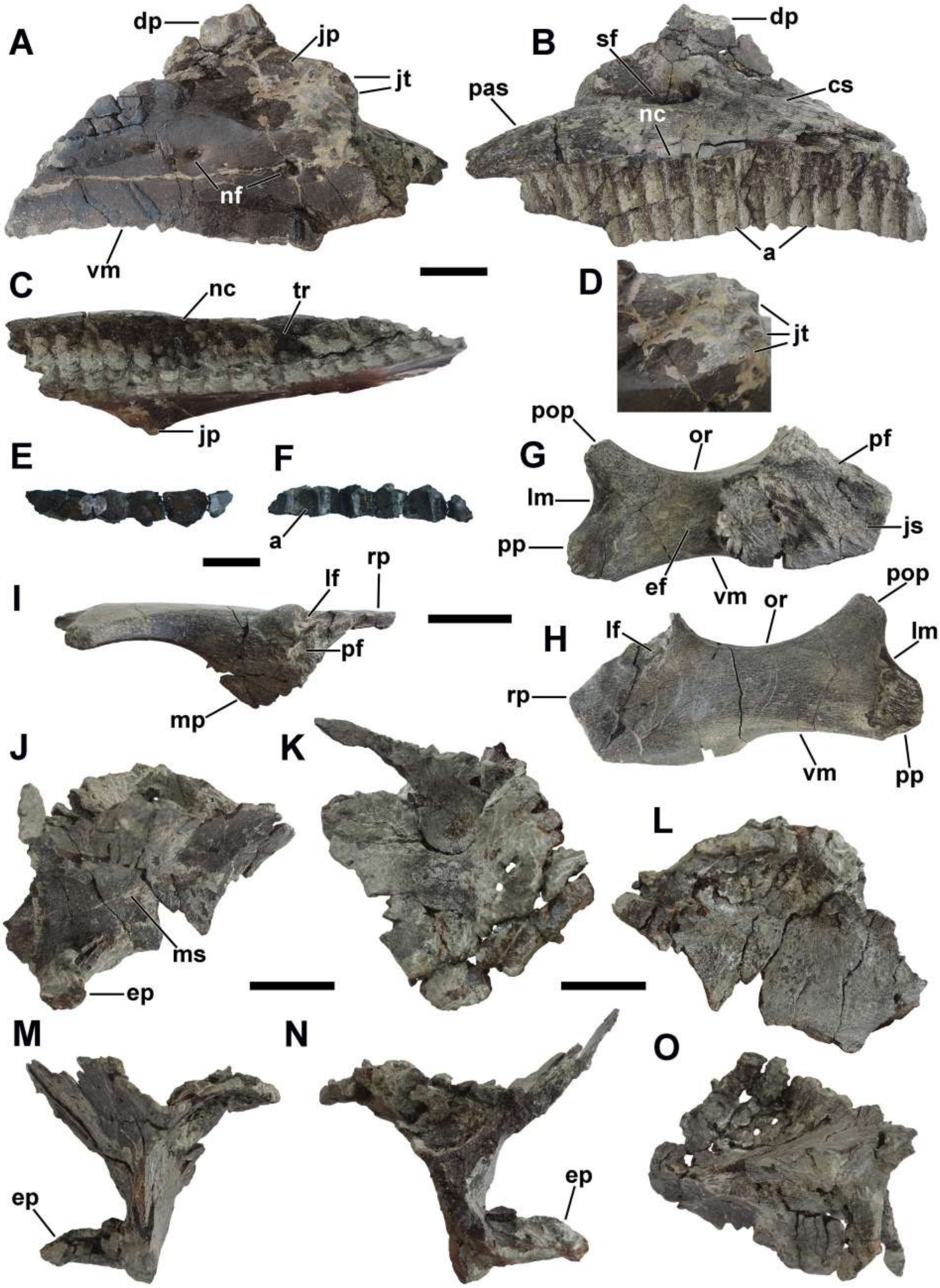
Figure 4. Cranial elements of *Kryptohadros kallaiae* gen. et sp. nov. from Fântânele-3, Vălioara, Haţeg Basin. **A–C,** Right premaxilla, LPB (FGGUB) R.2882.7, in **A,** lateral; **B,** anterior; and **C,** medial views. **D–G,** Right nasal, LPB (FGGUB) R.2882.8, in **D,** dorsal; **E,** lateral; **F,** ventral; and **G,** medial views. **H, I,** Fragment of the ventral premaxillar process of the maxilla (LPB [FGGUB] R.2882.1) in **H,** dorsal; and **I,** ventral views. **Abbreviations: af**, antorbital fenestra; **d**, denticula; **ds**, dorsal side; **ed**, elongated depression; **en**, external naris; **fp**, frontal process; **ll**, lateral lip; **np**, nasal process; **pg**, premaxillar groove; **ps**, prefrontal suture; **sd**, sagittal depression. Scale bars equal 2 cm for A–G, and 1 cm for H, I.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recovered consistently regardless of the analysis concerned, and the exact same topologies also occur within their maximum agreement subtrees, pointing to a remarkable robustness of the clade, at least based on the currently employed datasets; and (3) as currently defined, this spatially restricted and endemic European clade does appear to represent a distinct episode in the evolutionary and palaeobiogeographical history of Hadrosauroidea, in line with its assessed monophyletic status. We acknowledge, nonetheless, that future research, both in the form of new discoveries and that of further, updated and/or alternative phylogenetic analyses, is required to test the validity and robustness of this newly proposed clade, as well as its usefulness in deciphering the detailed patterns of hadrosauroid evolution.

Telmatosaurus Nopcsa, 1903

Telmatosaurus transsylvanicus Nopcsa, 1900

Lectotype. NHMUK R.3386, a crushed partial skull.

Referred material. NHMUK R.3841, ten cervical, five dorsal and four caudal vertebrae; NHMUK R.3387, basicranium; NHMUK R.3388, left maxilla; NHMUK R.4911, left and right maxillae; and LPB (FGGUB) R.1010, left maxilla.

Type locality. Lens (Bonebed) 1 of Nopcsa (1902), located along the Sibişel Valley near the village of Sânpetru, central Hațeg Basin, Hunedoara County, Transylvania, Romania.

Type horizon and age. Greyish continental sandstones from the lower part of the Sînpetru Formation stratotype section, cropping out along the Sibişel Valley near Sânpetru. The age of the type locality deposits can only be constrained to the interval extending from the early Maastrichtian to the early part of late Maastrichtian (later Late Cretaceous), and most probably falls in the older part of this time interval (see Csiki-Sava et al., 2016).

Revised diagnosis. A hadrosauroid ornithopod characterized by the following autapomorphies: (1) a medially extensive medial lobe of the surangular that is clearly separated from the medial edge of the retroarticular process and together with the attaching splenial forms a symmetrical bowl-shaped, rounded glenoid surface in dorsal view; and (2) caudal region of the maxilla (posterior to the jugal process) accounts for around 37% of its total length (currently the largest proportion recorded in any non-hadrosaurid hadrosauroid).

Besides these autapomorphies, *T. transsylvanicus* is also characterized by the following unique combination of characters: the anteroposterior length of the parietal roughly twice its lateromedial width; and well-developed, bulbous, ventrolaterally extended sphenoccipital tubercles (or basal tubera).

Remarks. Other specimens recently referred to *Telmatosaurus transsylvanicus* include a pair of tooth-bearing dentaries from a juvenile individual (LPB [FGGUB] R.1305; Dumbravă et al., 2016) and two isolated basicrania (UBB NVZ1-42 and NHMUK R.3401A; Augustin et al., 2023), mainly based on certain morphological similarities to the overlapping elements of the lectotype specimen. These specimens, however, also show some differences from the lectotype (see discussions in Augustin et al., 2023 and Dumbravă et al., 2016); furthermore, specimen NHMUK R.3401A is damaged, impeding in-depth comparisons regarding particular details of its morphology, whereas UBB NVZ1-42 was collected outside of the type locality and horizon of *Telmatosaurus*, coming from a different locality as well as a lithostratigraphical unit whose relationships to the Sînpetru Formation are contentious (see Csiki-Sava et al., 2016). Accordingly, we suggest here the temporary exclusion of all these elements from the list of referred specimens of *T. transsylvanicus* pending further, more in-depth investigations.

Kryptohadros gen. nov.

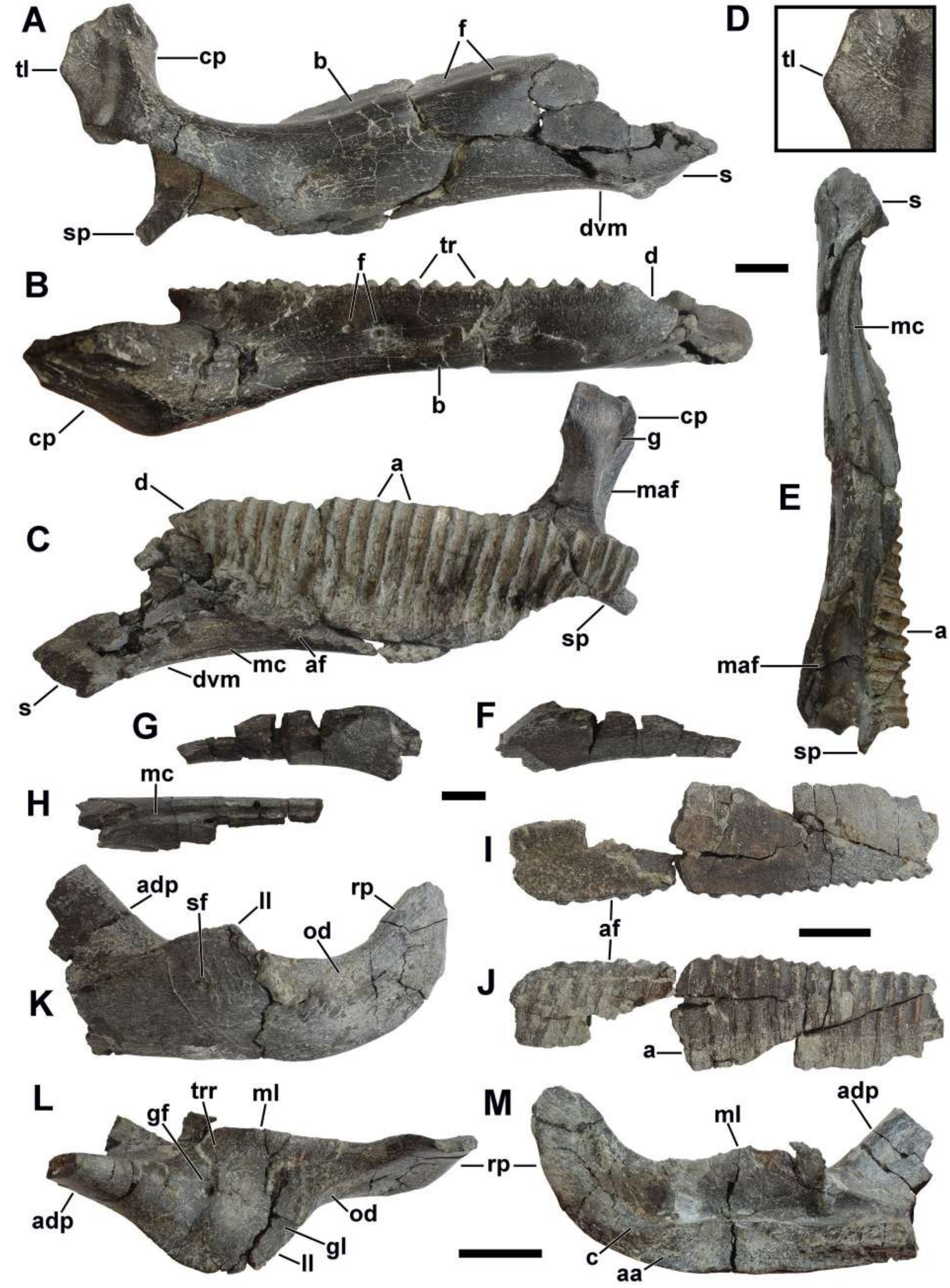
(Figs 2–12)

Type species. *Kryptohadros kallaiae.*

Diagnosis. As for the type and only species.

Etymology. *Kryptohadros*, from the Greek terms *krypto* (i.e. hidden) and *hadrós* (i.e. thick, bulky), the latter

Figure 5. Cranial elements of *Kryptohadros kallaiae* gen. et sp. nov. from Fântânele-3, Vălioara, Hațeg Basin. **A–D,** Left maxilla, LPB (FGGUB) R.2882.1, in **A,** lateral; **B,** medial; and **C,** ventral views. **D,** A closer look of the jugal process with the tuberculates in anterolateral view. **E, F,** Maxillary parapet fragment, LPB (FGGUB) R.2882.9, in **E,** external; and **F,** internal views. **G–I,** Left jugal, LPB (FGGUB) R.2882.5, in **G,** medial; **H,** lateral; and **I,** dorsal views. **J–O,** Right pterygoid, LPB (FGGUB) R.2882.6, in **J,** lateral; **K,** dorsal; **L,** medial; **M,** anterior; **N,** posterior; and **O,** ventral views. **Abbreviations: a**, alveolar sulci; **cs**, choanal shelf; **dp**, dorsal process; **ef**, ectopterygoid facet; **ep**, ectopterygoid process; **jp**, jugal process; **js**, jugal suture (for the maxilla); **jt**, jugal tubercles; **lf**, lacrimal facet; **lm**, margin of the laterotemporal fenestra; **mp**, maxillary process; **ms**, maxillary suture; **nc**, neurovascular canal; **nf**, neural foramina; **or**, orbital rim; **pf**, palatine facet; **pas**, articular region for the palatine; **pop**, postorbital process; **pp**, posterior process; **rp**, rostral process; **sf**, substantial foramen; **tr**, tooth row; **vm**, ventral margin. Scale bars equal 2 cm for A–C, 1 cm for E, F and 2 cm for G–O.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often used to name hadrosauroids, meaning ‘Hidden hadrosauroid’, with reference to the fact that the presence of a second hadrosauroid taxon in Haţeg Basin remained unacknowledged, i.e. ‘hidden’, for well over a century while all hadrosauroid remains were uncritically referred to the previously described *Telmatosaurus*. It also refers to the fact that the holotype lied hidden for decades in the immediate proximity of the previously intensively excavated Fântânele MvBB.

Kryptohadros kallaiae sp. nov.

Holotype. LPB (FGGUB) R.2882, an associated incomplete skeleton preserving elements of the skull, vertebral column and hind limbs. The recovered cranial elements include a right premaxilla fragment, the right nasal, the left maxilla, a left jugal fragment, two dental parapet fragments, the right pterygoid, the right dentary and a small fragment of the left dentary, the left surangular, as well as four isolated maxillary and six isolated dentary teeth. Postcranial elements include five dorsal rib fragments, eleven caudals, an isolated neural spine fragment, five chevrons, fragments of the left and right femora, the left tibia, and fragments of the left and right fibulae.

Etymology. The name *kallaiae* is in memory of †Csilla Kállai (1968–2003), mother of the first author, honouring her continuous and full-hearted support and encouragements for pursuing his studies in natural sciences.

Type locality. The holotype incomplete skeleton was found in site Fântânele-3, north-west of Vălioara, the westernmost part of Haţeg Basin, Hunedoara County, Transylvania, Romania (Fig. 1); its elements were discovered in close proximity over an area of a few square metres, within the same bed (Fig. 1C).

Type horizon and age. Greyish, fine-grained mudstones belonging to the lower part of the Middle Member of the uppermost Cretaceous Densuş-Ciula Formation. Most probably early part of early Maastrichtian in age (Albert et al., 2025; Fig. 1B).

Diagnosis. A hadrosauroid ornithopod characterized by one autapomorphy: posterior edge of the coronoid process presenting a well-developed triangular lobe that extends posteriorly. Furthermore, it also shows two ‘local’ autapomorphies (defined by Beeston et al., 2024, as ‘an apomorphy that is uniquely present in one taxon within a region of the tree, but that is also convergently present in phylogenetically distant taxa within the same higher-level clade’): presence of surangular and glenoid foramina on the surangular.

In addition, the new taxon displays the following unique character combination: dorsomedially placed longitudinal sagittal depression on the posterior part of the nasal (also present in *Jinzhousaurus yangi*); jugal process of the maxilla bearing five small jugal tubercles that gradually decrease in size from the most ventrally placed one to the most dorsal one; well-developed buccal shelf along the laterodorsal edge of the dentary; Meckelian canal reaching the anterior end of the symphysis on the ventral side of the dentary; ventrolaterally directed splenial process; apex of the long, posterodorsally elongated retroarticular process laterally inclined (as in *Amurosaurus riabinini*); and base of the mid caudal neural spine narrower than its apical part (similar to *Yunganglong datongensis*), due to the presence of a dorsoventrally elongated notch above the postzygapophyses.

In order to emphasize the morphological distinctiveness of *Kryptohadros* from its largely sympatric close relative *Telmatosaurus transsylvanicus*, we graphically document the main anatomical features distinguishing these taxa on Figs 2, 3.

Description and comparisons

The only known individual (i.e. incomplete holotype skeleton) of *Kryptohadros kallaiae* consists of cranial and postcranial elements that were found closely associated, albeit not articulated to each other. Several recovered elements show fractured or worn surfaces, but are only minimally distorted, any such instance being noted in the description.

Cranial elements.

Premaxilla. Specimen LPB (FGGUB) R.2882.7 (Fig. 4A–C) represents the anteromedial part of the right premaxilla, with an acute, sub-triangular profile of the anterior tip in lateral view. Similar to other derived

Figure 6. Lower jaw elements of *Kryptohadros kallaiae* gen. et sp. nov. from Fântânele-3, Vălioara, Haţeg Basin. **A-E,** Right dentary, LPB (FGGUB) R.2882.2, in **A,** lateral; **B,** dorsal; **C,** medial; and **D,** Closer look of the posterior triangular lobe in lateral view; **E,** ventral views. **F–H,** Left dentary fragment, LPB (FGGUB) R.2882.3, in **F,** lateral; **G,** medial; and **H,** ventral views. **I, J,** Dental parapet, LPB (FGGUB) R.2882.10, in **I,** external; and **J,** internal views. **K–M,** Left surangular, LPB (FGGUB) R.2882.4, in **K,** lateral; **L,** dorsal; and **M,** medial views. **Abbreviations: a**, alveolar sulci; **aa**, articular region for the angular; **adp**, ascending dorsal process; **af**, alveolar foramina; **b**, buccal shelf; **c**, canal; **cp**, coronoid process; **d**, diastema; **dvm**, deflected ventral margin; **f**, foramina; **g**, groove; **gf**, glenoid foramen; **gl**, glenoid; **ll**, lateral lip; **maf**, mandibular adductor fossa; **mc**, Meckelian canal; **ml**, medial lip; **od**, oval depression; **rp**, retroarticular process; **s**, symphysis; **sf**, surangular foramen; **sp**, splenial process; **tl**, triangular lobe; **tr**, tooth row; **trr**, transverse ridge. Scale bars equal 2 cm for A–C, E, 1 cm for F–H and 2 cm for I–M.

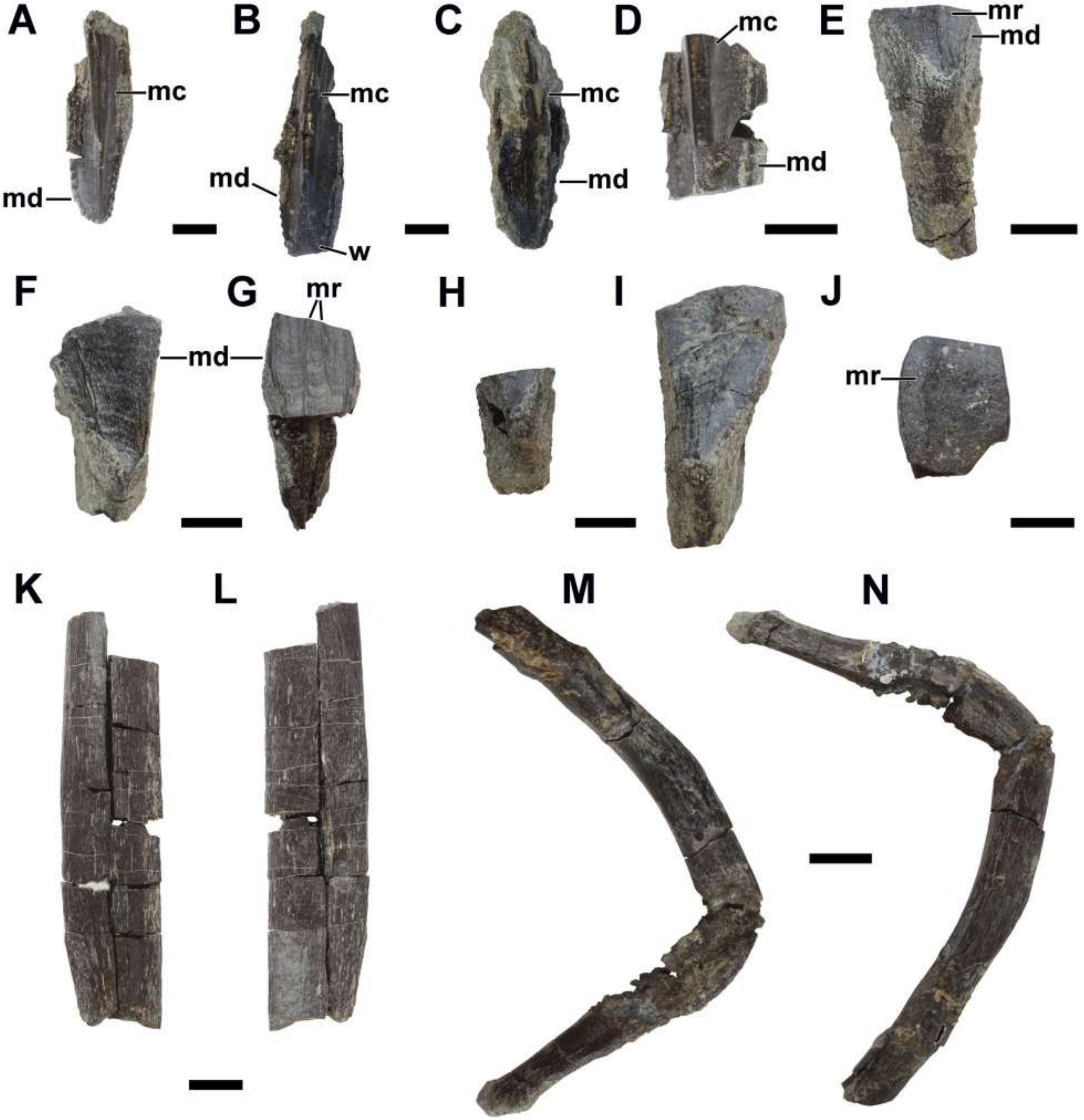
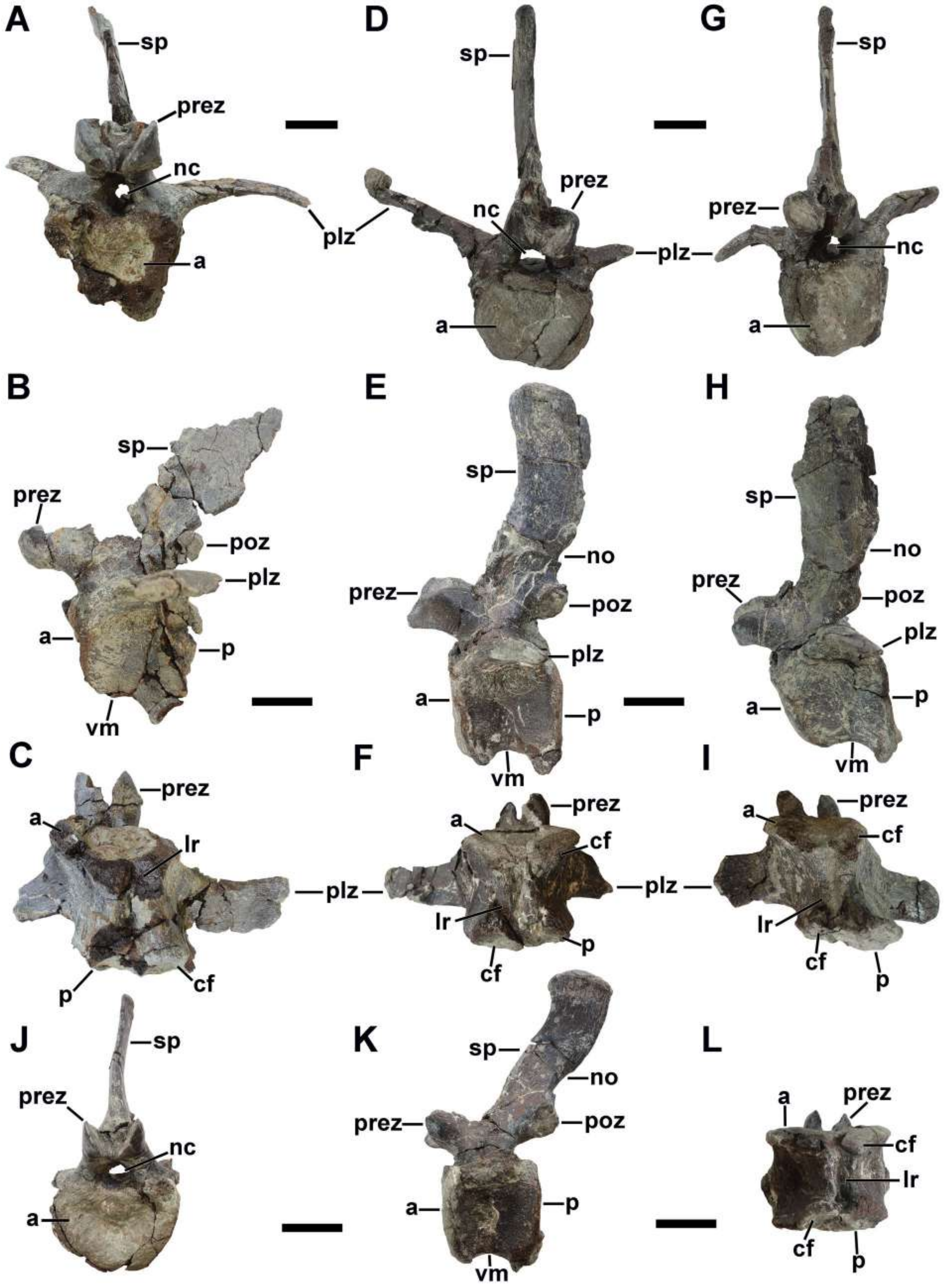


Figure 7. Isolated teeth and dorsal ribs of *Kryptohadros kallaiae* gen. et sp. nov. from Fântânele-3, Vălioara, Haţeg Basin. **A,** Maxillary tooth, LPB (FGGUB) R.2882.11, in lingual view; **B,** Maxillary tooth, LPB (FGGUB) R.2882.12, in lingual view; **C,** Maxillary tooth, LPB (FGGUB) R.2882.13, in lingual view; **D,** Maxillary tooth, LPB (FGGUB) R.2882.14, in lingual view; **E,** Dentary tooth, LPB (FGGUB) R.2882.15, in lingual view; **F,** Dentary tooth, LPB (FGGUB) R.2882.16, in lingual view; **G,** Dentary tooth, LPB (FGGUB) R.2882.17, in lingual view; **H,** Dentary tooth, LPB (FGGUB) R.2882.18, in lingual view; **I,** Dentary tooth, LPB (FGGUB) R.2882.19, in lingual view; **J,** Dentary tooth, LPB (FGGUB) R.2882.20, in lingual view. **K, L,** Dorsal rib, LPB (FGGUB) R.2882.21, in **K,** lateral; and **L,** medial views. **M, N,** Dorsal rib, LPB (FGGUB) R.2882.24, in **M,** lateral; and **N,** medial views. **Abbreviations: mc**, median carina; **md**, marginal denticles; **mr**, median ridge; **w**, wear facet. Scale bars equal 0.5 cm for A–J and 1 cm for K–N.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ornithopods, the premaxillary teeth are lost (Weishampel, 1984, 2004). The anterior edge of the oral margin bears three lateromedially flattened and sharp denticulae that are triangular in lateral view and ventrally pointed (Fig. 4A–C, d). These structures are similar to those seen in some other hadrosauriforms like *Iguanodon bernissartensis*, *Telmatosaurus transsylvanicus*, *Tethyshadros insularis*, *Lophorhothon atopus*, *Coahuilasaurus lipani* and, to some extent, *Eotrachodon orientalis* (Dalla Vecchia, 2009b; Gates & Lamb, 2021; Longrich, Ramirez Velasco, et al., 2024; Nopcsa, 1900; Norman, 1980; Prieto-Márquez et al., 2016a; Weishampel et al., 1993). Starting from the sagittal plane, the second denticle is somewhat longer ventrally than the first one, similar to the condition reported previously in specimen NHMUK R.3401A, referred to *Telmatosaurus* (probably erroneously, as R.3842) in Weishampel et al. (1993). Weishampel et al. (1993) also mentioned another premaxilla referred by them to *Telmatosaurus* (LPB [FGGUB] R.1015) that has only two denticulae, but this specimen is eroded anteromedially in the area where the third denticle is supposed to be (J. M. personal observation), and thus – based on the general morphology of the element – it most probably also had three denticulae originally. The corresponding denticulae of *Tethyshadros* are unique, because they are spike-like and directed anteriorly instead of ventrally (Dalla Vecchia, 2009b).

The lateromedially flattened nasal process of specimen LPB (FGGUB) R.2882.7 tapers posteriorly (Fig. 4A–C, np) and has a sharp ridge on the lateroventral surface; this ridge shifts laterally on the anterior section of the element and becomes the edge of the external naris (Fig. 4A, en). The laterodorsal surface bears an elongated depression (Fig. 4A, ed) marking the contact with the premaxillary process of the nasal.

Nasal. Specimen LPB (FGGUB) R.2882.8 is a partial right nasal (Fig. 4D–G). Its dorsal surface is slightly convex, while the ventral side is concave mediolaterally. Currently the only other hadrosauroid nasal known from the Transylvanian area is an anterior, somewhat more robust nasal fragment belonging to the lectotype of *T. transsylvanicus*, although it is too fragmentary to reconstruct its exact outline. Nevertheless, Weishampel et al. (1993) suggested that it probably had a gentle upward slope distally, based on the dorsal margin of the premaxilla. If so, the morphology of LPB (FGGUB) R.2882.8 differs somewhat from that assumed for *Telmatosaurus*, as while the anterior part is similarly dorsally curved, posteriorly this changes to a ventral curvature that is stronger along the medial side. This medial concavity forms an elongated sagittal depression (Fig. 4D, G, sd), reminiscent of that reported in *Jinzhosaurus yangi* (Barrett et al., 2009); nevertheless, given the poor preservation state of its lectotype, the presence of such a depression cannot be ruled out in *Telmatosaurus*, either. The nasal is also preserved in *Tethyshadros* and, according to Dalla Vecchia (2009b), it has a slightly curved dorsal margin. However, our observations indicate that both the holotype (SC 57021) and the referred specimen SC 57247 have sinuous nasal bones similar to that of *Kryptohadros*, although the resulting depression seems more posteriorly extended in *Tethyshadros*, being further accentuated by fractures.

On the lateral side of the nasal, posterior to the premaxillary groove (Fig. 4G, pg), there is a lateral lip (Fig. 4D–F, ll) representing the contact surface for the lacrimal. The lateral edge of this lip is strongly curved, suggesting that it could have formed the dorsal edge of the small antorbital fenestra (Fig. 4E, F, af). Based on the slightly rugose outer surface around this edge, the fenestra was probably completely covered laterally by the lacrimal and possibly the ventral process of the premaxilla, but the presence of a very small foramen at the suture between the lacrimal and the premaxilla cannot be excluded. The presence of a very small foramen or even a closed lateral depression occurs in some basal hadrosauroids (e.g. Gates et al., 2018; Wu & Godefroit, 2012; You, Ji, et al., 2003), and it seems that *Tethyshadros* and *Telmatosaurus* both lacked a laterally open antorbital fenestra, although in the case of *Tethyshadros* there is a shallow, oval depression on the lateral side of the maxilla (Dalla Vecchia, 2009b). Since the different *Tethyshadros* specimens are encased in rocky matrix, the medial side of their cranial elements is not visible. Nonetheless, the dorsal edge of the dorsal process of the maxilla of SC 57247 also shows a strong curvature, similar to *Kryptohadros*, and this could mark the ventral edge of a medially opened antorbital fenestra. In the case of *Telmatosaurus*, this region of the

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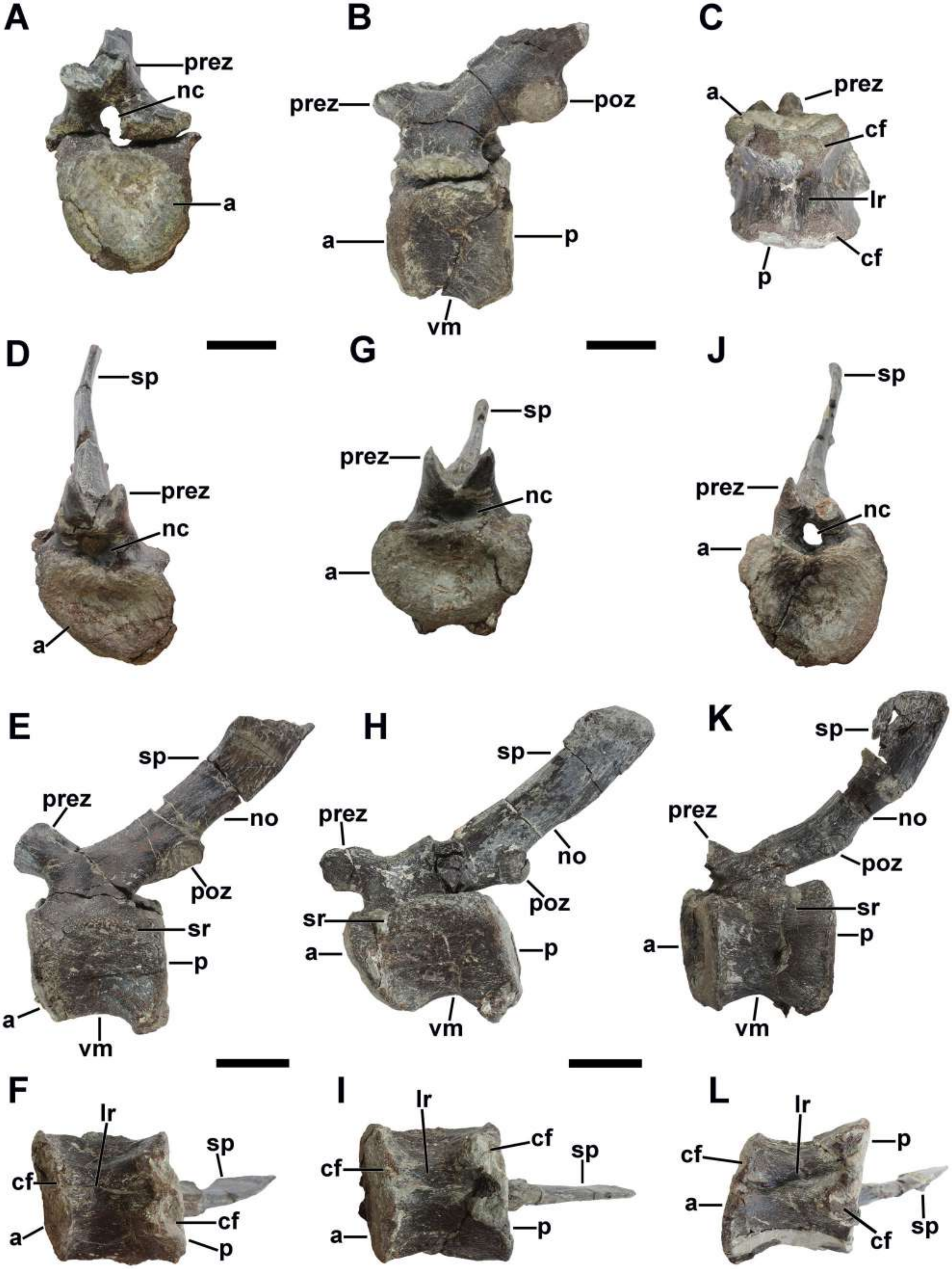
Figure 8. Caudal vertebrae of *Kryptohadros kallaiae* gen. et sp. nov. from Fântânele-3, Vălioara, Hațeg Basin. **A–C,** Anterior caudal vertebra, LPB (FGGUB) R.2882.25, in **A,** anterior; **B,** lateral; and **C,** ventral views. **D–F,** Anterior caudal vertebra, LPB (FGGUB) R.2882.26, in **D,** anterior; **E,** lateral; and **F,** ventral views. **G–I,** Anterior caudal vertebra, LPB (FGGUB) R.2882.27, in **G,** anterior; **H,** lateral; and **I,** ventral views. **J–L,** Mid caudal vertebra, LPB (FGGUB) R.2882.28, in **J,** anterior; **K,** lateral; and **L,** ventral views. **Abbreviations: a**, anterior surface; **cf**, chevron facet; **lr**, longitudinal ridge; **nc**, neural canal; **no**, notch; **p**, posterior surface; **prez**, prezygapophysis; **poz**, postzygapophysis; **plz**, pleurapophysis; **sp**, neural spine; **vm**, ventral margin. Scale bars equal 2 cm.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skull is too crushed to observe the medial sides of the nasal and maxilla.

The caudal end of the nasal, forming the contact region with the frontal (Fig. 4D, F, fp), is dorsoventrally very thin (about 1 mm) and not striated. This frontal process overlapped the nasal process of the frontal. Although the frontals were not recovered, the medial edge of the frontal process of the nasal is straight and shows the articulation area with its counterpart until the posterior end of the frontal process (Fig. 2A). This suggests that there was no fontanelle or fenestra at the junction of the nasals and frontals, unlike the case of *Telmatosaurus* where such a feature was present based on the slightly laterally bowed nasal process of the frontal (Fig. 2B, np). A frontonasal fontanelle or fenestra occurs in several basal hadrosauroids such as *Levnesovia*, *Bactrosaurus*, *Choyrodon* or *Gobihadros* (Gates et al., 2018; Sues & Averianov, 2009; Tsogtbaatar et al., 2019) as well as in some derived hadrosaurids, either saurolophines such as *Edmontosaurus* and *Lophorhothon* (Gates & Lamb, 2021; Langston, 1960; Maryańska & Osmólska, 1979), or basal lambeosaurines like *Amurosaurus* and *Aralosaurus* (Godefroit, Alifanov & Bolotsky, 2004; Godefroit, Bolotsky & Van Itterbeeck, 2004). The presence of the fontanelle seems to be more characteristic of young individuals, closing during ontogeny (Gates & Lamb, 2021; Langston, 1960; Maryańska & Osmólska, 1979), although a small fenestra may also persist in some adult hadrosauroids (Gates & Lamb, 2021; Rozhdestvensky, 1968). Apparently, just like the Fântânele-3 specimen, *Tethyshadros* also lacks this fontanelle (J. M., personal observation), so even if it may have been present at younger ages in this taxon, it was already closed by the earliest ontogenetic stage represented by the known specimens.

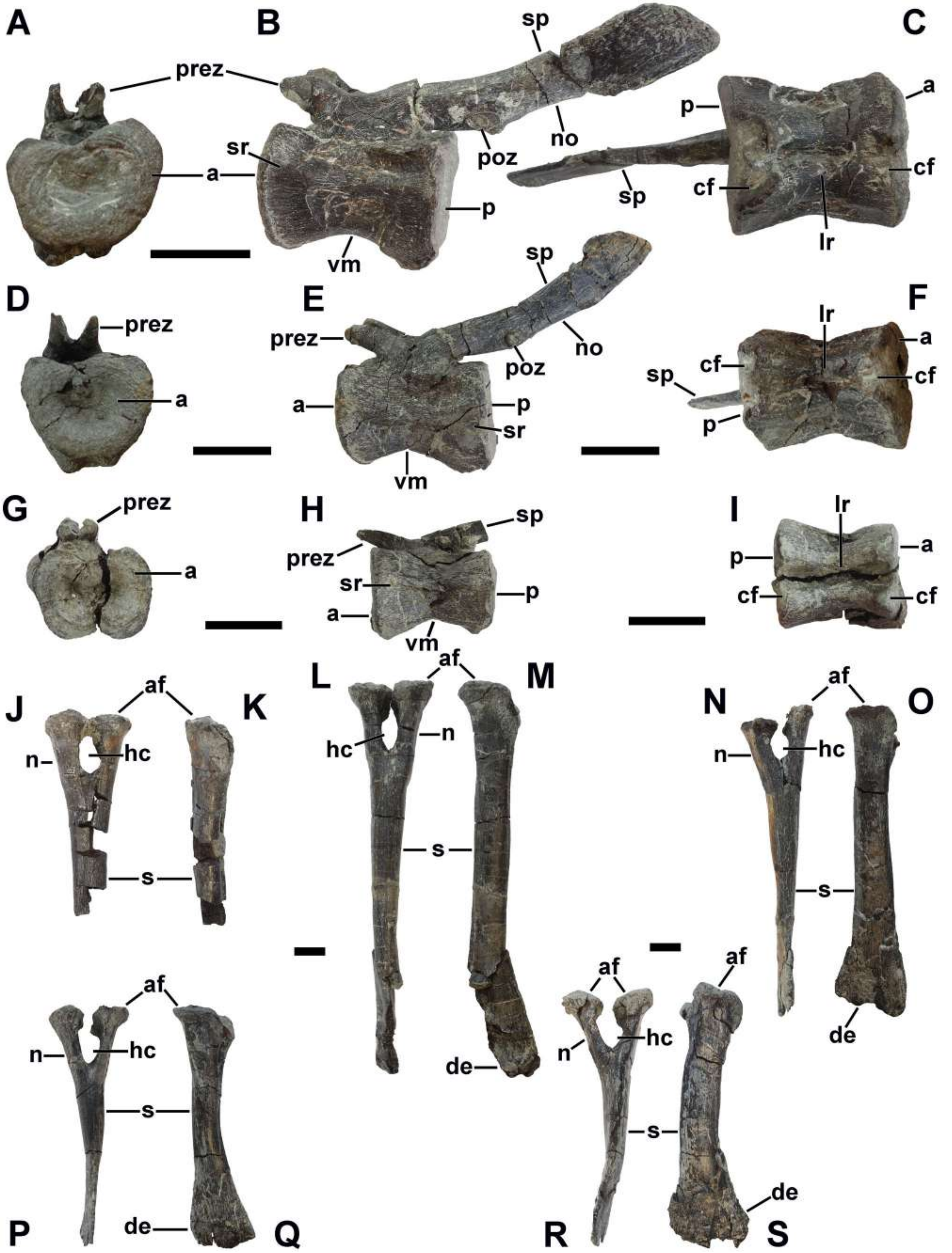
Maxilla. Specimen LPB (FGGUB) R.2882.1 is a middle fragment of the left maxilla (Fig. 5A–D) lacking *in situ* teeth. One dorsoventrally flattened, elongated and tongue-shaped bone fragment (Fig. 4H, I) was recovered near the maxilla; it could represent the anterior part of the ventral premaxillary process.

Posteroventral to the triangular dorsal process of the maxilla there is a dorsolaterally offset and ovoid jugal process (Fig. 5A, B, dp, jp), whose elevated posterior rim shows five small, spike-like jugal tubercles of different sizes (Fig. 5A, D, jt). The ventral-most of these is also the largest one, and the other tubercles gradually decrease in size up to the dorsal-most one. As preserved, the jugal process of the maxilla is covered by the jugal in both *Tethyshadros* and in the lectotype of *Telmatosaurus*, while in most referred maxillae of the latter taxon, this process is heavily eroded. As a result, the size and number of the tubercles are impossible to ascertain. However, in specimen LPB (FGGUB) R.1010 it can still be observed that the most ventrally placed tubercle was originally the largest. Similar sets of jugal tubercles, although of differing numbers and relative dimensions, have been observed in other basal hadrosauroids, including *Bactrosaurus johnsoni* (3 tubercles, of different sizes), *Gilmoreosaurus mongoliensis* (around 4, but at least 3 of these having the same size), *Gobihadros mongoliensis* (3, with at least 2 of these of similar size), and *Protohadros byrdi* (around 3, all of comparable size) (Head, 1998; Prieto-Márquez, 2011; Prieto-Márquez & Norell, 2010; Tsogtbaatar et al., 2019).

Several foramina are visible forming a straight line along the midline of the lateral surface of the maxilla (Fig. 5A, nf). Of these foramina four are relatively large, with 4–5 mm in diameter, and three are much smaller, only 1–2 mm in diameter, with the largest one located ventral and very slightly posterior to the jugal process (Fig. 2C). This condition differs from that reported in *Telmatosaurus* where, as noted by Weishampel et al. (1993), the largest foramen is placed beneath and slightly rostral to the articular surface of the jugal (Fig. 2D). The maxilla of *Tethyshadros* has only three foramina that are also placed anteroventral to the jugal articulation (Dalla Vecchia, 2009b). Although the number and disposition of the foramina in these taxa are somewhat different from the condition seen in the Fântânele-3 specimen, it is worth noting that these features usually vary to some extent even between individuals of the same taxon (e.g. Longrich et al., 2021; Prieto-Márquez & Guenther, 2018). Nevertheless, the location of maxillary neurovascular foramina is considered as an important feature for taxon identification in some cases (Longrich et al., 2021).

Twenty closely packed alveolar sulci are visible medially (Fig. 5B, a). These are long, narrow and upright,

Figure 9. Caudal vertebrae of *Kryptohadros kallaiae* gen. et sp. nov. from Fântânele-3, Vălioara, Hațeg Basin. **A–C,** Mid caudal vertebra, LPB (FGGUB) R.2882.29, in **A,** anterior; **B,** lateral; and **C,** ventral views. **D–F,** Mid caudal vertebra, LPB (FGGUB) R.2882.30, in **D,** anterior; **E,** lateral; and **F,** ventral views. **G–I,** Mid caudal vertebra, LPB (FGGUB) R.2882.31, in **G,** anterior; **H,** lateral; and **I,** ventral views. **J–L,** Mid caudal vertebra, LPB (FGGUB) R.2882.32, in **J,** anterior; **K,** lateral; and **L,** ventral views. **Abbreviations: a**, anterior surface; **cf**, chevron facet; **lr**, longitudinal ridge; **nc**, neural canal; **no**, notch; **p**, posterior surface; **prez**, prezygapophysis; **poz**, postzygapophysis; **sp**, neural spine; **sr**, sharp ridge; **vm**, ventral margin. Scale bars equal 2 cm.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with narrow edges that are parallel to each other. The articular region of the parapet, originally marking the neurovascular canal, is roughly straight and dorsally placed (Fig. 5B, C, nc). Dorsal to this articular edge, at the base of the dorsal process, there is a large substantial foramen on the posterior margin of the choanal shelf (Fig. 5B, sf, cs), a feature typical for hadrosaurids (e.g. Horner, 1992; Prieto-Márquez & Wagner, 2023). Posterior to this opening the striated bone surface represents the articular region for the palatine (Fig. 5B, pas). In ventral view, the tooth row is very slightly medially curved. In this regard LPB (FGGUB) R.2882.1 differs from the maxillae of *Telmatosaurus* in which the tooth row is mainly straight, slightly laterally curved posteriorly.

A small, anteroposteriorly elongated and lateromedially thin fragment (LPB [FGGUB] R.2882.9) is most probably the detached maxillary parapet. It shows seven, closely packed, narrow and upright alveoli with parallel and narrow edges on the internal side (Fig. 5E, F), while its external surface is smooth.

Jugal. The jugal LPB (FGGUB) R.2882.5 is a triradiate bone (Fig. 5G–I), with a roughly triangular rostral process (Fig. 5G–I, rp) and preserving the bases of the posterodorsally oriented postorbital and the posteroventrally oriented posterior processes, respectively (Fig. 5G, H, pop, pp). On the dorsal margin of the rostral process, there is an elongated articular facet for the lacrimal (Fig. 5H, I, lf). In dorsal view, the rostral process widens mediolaterally in its posterior part, forming the maxillary process (Fig. 5I, mp) that bears the anteroposteriorly elongated palatine facet (Fig. 5I, pf).

Posterior to the rostral process, the jugal shaft is dorsoventrally contracted and mediolaterally flattened; its ventral margin is rounded lateromedially, while the dorsal one is flat and smooth with angular lateral and medial edges, forming the ventral part of the rounded orbital rim (Fig. 5G, H, or). On the medial side, at about the middle of the shaft there is a very small facet for the contact with the ectopterygoid (Fig. 5G, ef) as also seen in several hadrosauriforms (e.g. Norman, 1980, 1986, 1998, 2002, 2004; Weishampel & Horner, 2004).

The general morphology of the jugal is most similar to that of specimens NHMUK R.4911 and NHMUK R.11545, earlier referred to *Telmatosaurus* by Weishampel et al. (1993), but currently regarded by us as indeterminate hadrosauroid jugals instead.

Pterygoid. Specimen LPB (FGGUB) R.2882.6 is a complex bone fragment (Fig. 5J–O) with very thin walls, showing similarities to hadrosauroid pterygoids (e.g. ROM 702; Evans, 2010, respectively MPC-D100/745; Tsogtbaatar et al., 2014). Based on these similarities, it may represent a right pterygoid fragment with flat and smooth lateral and medioventral surfaces, a smooth, cup-shaped dorsomedial surface, a short lateroventrally oriented ectopterygoid process on the ventrolateral side (Fig. 5J, M, N, ep), and an anteroposteriorly oriented, but dorsoventrally placed maxillary suture on the lateroventral side (Fig. 5J, ms). If the specimen is correctly identified, the ectopterygoid process would be more laterally directed than in the case of *Plesiohadros* or lambeosaurines, and the maxillary suture is laterally placed just as in *Plesiohadros*, albeit only reaching the most basal part of the ectopterygoid process (Evans, 2010; Heaton, 1972; Tsogtbaatar et al., 2014).

Dentary. A nearly completely preserved right dentary (LPB [FGGUB] R.2882.2) and a small anterior fragment of the left dentary (LPB [FGGUB] R.2882.3) were recovered from Fântânele-3 (Fig. 6A–H), thoroughly documenting the morphology of this element. The dentary is a dorsoventrally narrow but anteroposteriorly elongated bone, with a tall, dorsally expanded coronoid process and a straight tooth row, albeit without *in situ* preserved teeth.

The Transylvanian hadrosauroid dentaries previously referred to *Telmatosaurus* show variable proportions. This, together with the similarly variable *Tethyshadros* dentaries (see supplementary table 1 available in Magyar et al., 2025), shows that the taxonomic usefulness of the dentary proportions may be limited (e.g. Campione & Evans, 2011). Still, it is worth noting that despite the variability in the ratio of anteroposterior length to dorsoventral height seen among the hadrosauroid dentaries reported from the Sînpetru Formation,

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Figure 10. Caudal vertebrae and chevrons of *Kryptohadros kallaiae* gen. et sp. nov. from Fântânele-3, Vălioara, Hațeg Basin. **A–C,** Mid caudal vertebra, LPB (FGGUB) R.2882.33, in **A,** anterior; **B,** lateral; and **C,** ventral views. **D–F,** Mid caudal vertebra, LPB (FGGUB) R.2882.34, in **D,** anterior; **E,** lateral; and **F,** ventral views. **G–I,** Mid caudal vertebra, LPB (FGGUB) R.2882.35, in **G,** anterior; **H,** lateral; and **I,** ventral views. **J, K,** Anterior chevron, LPB (FGGUB) R.2882.36, in **J,** anterior; and **K,** lateral views. **L, M,** Anterior chevron, LPB (FGGUB) R.2882.37, in **L,** anterior; and **M,** lateral views. **N, O,** Mid chevron, LPB (FGGUB) R.2882.38, in **N,** anterior; and **O,** lateral view. **P, Q,** Mid chevron, LPB (FGGUB) R.2882.39, in **P,** anterior; and **Q,** lateral views. **R, S,** Mid chevron, LPB (FGGUB) R.2882.40, in **R,** anterior; and **S,** lateral views. **Abbreviations: a**, anterior surface; **af**, articular facets; **cf**, chevron facet; **de**, distal end; **hc**, haemal canal; **lr**, longitudinal ridge; **n**, neck; **no**, notch; **p**, posterior surface; **prez**, prezygapophysis; **poz**, postzygapophysis; **s**, shaft; **sp**, neural spine; **sr**, sharp ridge; **vm**, ventral margin. Scale bars equal 2 cm for A–I and 1 cm J–S.


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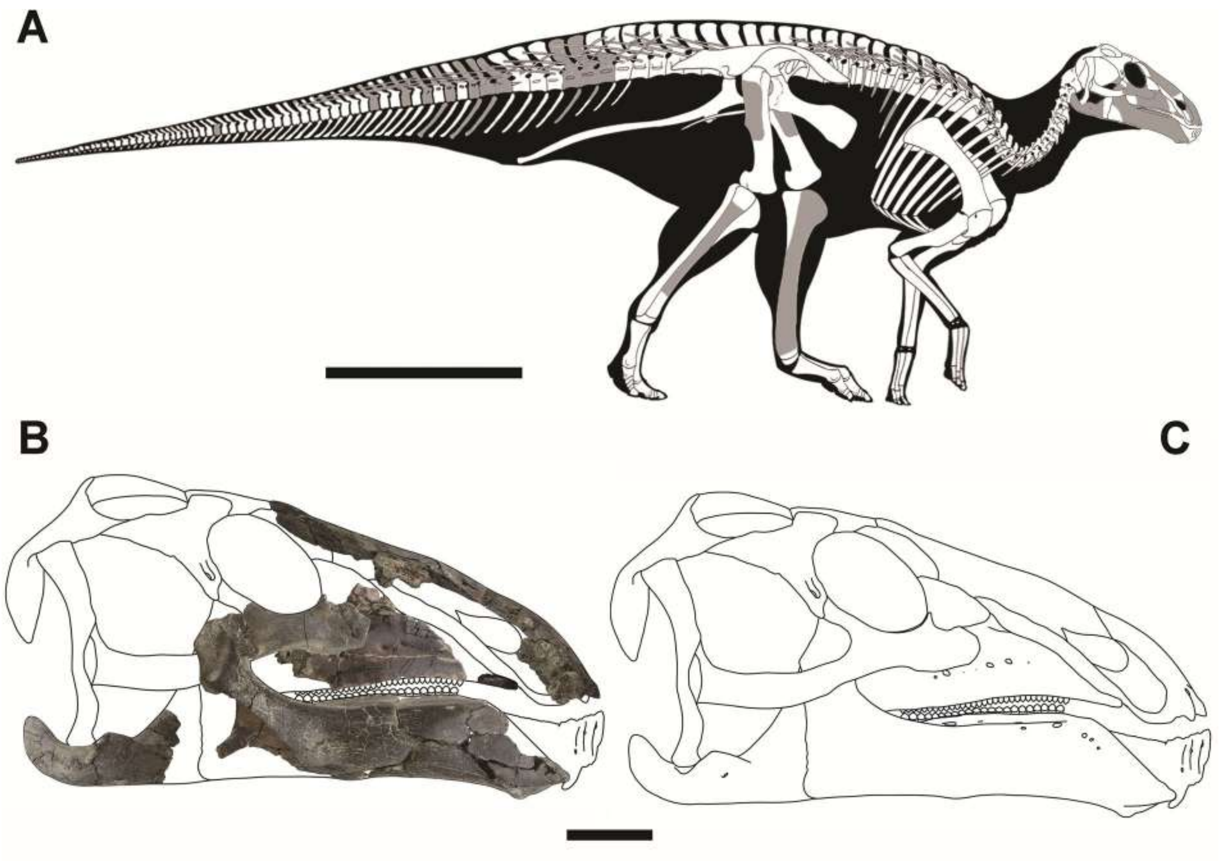

Figure 12. Reconstructions of *Kryptohadros kallaiae* gen. et sp. nov. **A,** Skeletal reconstruction of the holotype individual LPB (FGGUB) R.2882 (’Jenna’), based on a modified version of the skeletal reconstruction of *Tethyshadros insularis* from Chiarenza et al. (2021). recovered elements highlighted in grey shading; **B,** Cranial reconstruction of individual LPB (FGGUB) R.2882 showing the preserved cranial bones (elements from the opposite side are mirrored); **C,** Reconstruction of the skull outline, based on a modified version of the cranial reconstruction of *Tethyshadros insularis* from Dalla Vecchia (2009a). Scale bars equal 50 cm for A and 5 cm for B, C.

these are more similar to each other than to the Fântânele-3 specimen (see supplementary table 1 in Magyar, 2025).

The symphysis is downturned, similarly to that of *Telmatosaurus* and many other hadrosauroids such as *Brachylophosaurus canadensis* (Prieto-Márquez, 2005), *Eolambia caroljonesa* (McDonald, Bird, et al., 2012), *Eotrachodon orientalis* (Prieto-Márquez et al., 2016a), *Gonkoken nanoi* (Alarcón-Muñoz et al., 2023), *Gryposaurus orientalis* (Prieto-Márquez, 2010a), and *Edmontosaurus regalis* (Xing et al., 2017), but it differs in this respect from that of *Tethyshadros* where the rostral-most part of the dentary is not downturned. However, the downturned rostral part is somewhat longer relative to the anteroposterior length of the dentary compared to *Telmatosaurus* (see supplementary table 1 in Magyar et al., 2025). This downturned ventral margin forms an angle of about 25° with the horizontal dorsal

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Figure 11. Hind limb elements of *Kryptohadros kallaiae* gen. et sp. nov. from Fântânele-3, Vălioara, Hațeg Basin. **A, B,** Right femur fragment, LPB (FGGUB) R.2882.41, in **A,** lateral; and **B,** medial views. **C, D,** Left femur fragment, LPB (FGGUB) R.2882.42, in **C,** cranial; and **D,** caudal views. **E–H,** Left tibia, LPB (FGGUB) R.2882.43, in **E,** cranial; **F,** medial, **G,** caudal; and **H,** lateral views. **I, J,** Right fibula fragment, LPB (FGGUB) R.2882.45, in **I,** medial; and **J,** lateral views. **K, L,** Left fibula fragment, LPB (FGGUB) R.2882.44, in **K,** lateral; and **L,** medial views. **Abbreviations: af**, articular facet for the fibula; **ce**, caudal edge; **cf**, calcaneal facet; **cre**, cranial edge; **d**, depression; **ft**, fourth trochanter; **ir**, interosseous ridge; **lc**, lateral condyle; **le**, lateral edge; **ma**, muscle attachment site; **me**, medial edge; **pg**, popliteal groove; **pr**, posterior ridge; **s**, striated bone surface; **tf**, tibial facet; **tp**, thickened part. Scale bars equal 3 cm for A–D, 5 cm for E–H, and 3 cm for I–L.

margin of the medial wall of the dental battery (Fig. 2E; and Fig. 6C, a, s). The same angle is only 20° (Fig. 2F) in the left-side element of the *Telmatosaurus* lectotype (NHMUK R.3386), while the previously referred juvenile dentary specimens LPB (FGGUB) R.1305 are not downturned rostrally at all (see Dumbravă et al., 2016, fig. 1; supplemental figs 1, 4, 5).

The diastema is very short (Fig. 6B, C, d), just as in several other hadrosauroids such as *Telmatosaurus* (Dalla Vecchia, 2006, 2009a; Nopcsa, 1900; Weishampel et al., 1993), *Tethyshadros* (Dalla Vecchia, 2009b), *Bactrosaurus* (Godefroit et al., 1998) and *Gobihadros* (Tsogtbaatar et al., 2019).

The lateral surface of the element is smooth with eight relatively large foramina, and is dominated by a remarkably well-developed laterodorsal edge, forming a distinct buccal shelf that extends from the base of the coronoid process to the first alveolus (Fig. 6A, B, f, b). A similar shelf does not occur in the *Telmatosaurus* lectotype (Fig. 2J), nor in other hadrosauroid dentaries known from the Sânpetru area (NHMUK R. 3401A, NHMUK R. 3844, LPB [FGGUB] R.1305). Meanwhile, a somewhat more weakly developed shelf is present on fragmentary specimen SZTFH Ob.3107 referred previously to *Telmatosaurus* in Weishampel et al. (1993), but which comes from the deposits of the Densuș-Ciula Formation cropping out around Vălioara, just as LPB (FGGUB) R.2882. In *Tethyshadros* a comparable shelf exists, but it is weaker and anteroposteriorly shorter, ending near the mid-length of the dentary, except for specimen SC 57247 where there is no shelf at all.

The coronoid process is tall and laterally offset from the tooth row (Fig. 6B, cp, tr) as in other hadrosauroids (Weishampel & Horner, 2004); its top part, however, is not preserved. The long axis of the process is slightly lateromedially oriented, and its base is more laterally expanded than seen in *Telmatosaurus* and *Tethyshadros*. In lateral view, the basal part bends posteriorly, but the process is then redirected anteriorly around mid-length (Fig. 6A, cp), similarly to the condition seen in the lectotype of *Telmatosaurus transsylvanicus* (Fig. 3B, cp).

The anterior edge of the coronoid process is widely rounded lateromedially, while the posterior one is thin, with a triangular lobe extending posteriorly (Figs 3A, 6A, D, tl), which is well visible in lateral view. The presence and especially development of this triangular lobe is unique for *Kryptohadros kallaiae*. Although a less well developed, dorsoventrally elongated and somewhat rounded lobe appears in *Tethyshadros* as well (e.g. specimens SC 57026, SC 57247), here it is more medially placed and not visible in lateral view, unlike in the Fântânele-3 hadrosauroid. An even smaller, ridge-like thickening in this area is present in *Datonglong* (SXMG V 00005; Xu et al., 2016), whereas a small, rounded posterior lobe with a posteromedial direction occurs in both *Penelopognathus* (IMM 2002-BYGB-1; Godefroit et al., 2005) and *Protohadros* (SMU 74582; Head, 1998). Meanwhile, a more dorsally placed and tongue-shaped process occurs in *Ouranosaurus*, *Sirindhorna* and *Mantellisaurus*, but that process is formed by the medial surface of the coronoid process (Hooley, 1925; Shibata et al., 2015; Taquet, 1976).

On the medial side of the coronoid process, there is a dorsoventrally oriented groove (Fig. 6C, g); remarkably, a similar feature is also present in the isolated coronoid process SZTFH Ob.3068. This latter specimen, also coming from the Vălioara area, was originally identified as rhabdodontid (Weishampel et al., 2003), and was therefore treated as such in Magyar et al. (2024: Fig. 2G, H). However, closer inspection showed that this specimen is dorsoventrally tall, curved into the anterior direction length-wise, has an evenly semi-circular posterior edge in lateral view, and widens anteroposteriorly at its dorsal extremity, all features reminiscent of the coronoid process of the *T. transsylvanicus* lectotype. Accordingly, this specimen is here re-assigned to an indeterminate hadrosauroid.

The coronoid process borders the large mandibular adductor fossa from which the Meckelian canal extends along the ventral side of the dentary to reach the symphysis (Fig. 2G; and Fig. 6C, E, maf, mc). The Meckelian canal does not reach the symphyseal region in the lectotype of *T. transsylvanicus* (Fig. 2H), and neither does in other specimens from the Sînpetru Formation referred to this taxon by Weishampel et al. (1993), whereas in *Tethyshadros*, the Meckelian canal does not occur on the ventral side of the dentary (J. M. personal observation).

A total of 22 dental alveoli can be counted in medial view; these are separated from each other by sheet-like and parallel septa. The anterior alveoli are pointing slightly posteriorly, while the more posterior ones are more upright (Fig. 6C, a). Although in hadrosauroids the number of tooth positions is considered to increase to some extent during ontogeny (Weishampel & Horner, 2004), it is worth noting that the new specimen has fewer alveoli compared to the otherwise larger lectotype of *T. transsylvanicus*, stated to amount to 30 by Weishampel et al. (1993), but which has only 26 tooth positions (Fig. 2F) (Dumbravă et al., 2016). In the even larger *Tethyshadros* dentaries, Dalla Vecchia (2009b) identified 25 alveoli.

The last alveolus is somewhat more posteriorly placed (Fig. 2E) relative to the coronoid process than in the case of *Telmatosaurus* (Fig. 2F). Posterior to the last alveolus, the splenial process is pointed posteroventrally and very slightly laterally, with a triangular cross-section (Figs 2E, 3A, vsp; and Fig. 6A, C, E, sp), similar to the condition seen in *Gryposaurus latidens* (AMNH 5465; Prieto-Márquez & Gutarra, 2016), *Kundurosaurus nagornyi* (AENM 2/846; Godefroit, Bolotsky & Lauters, 2012) and *Kelumapusaura machi* (MPCN-PV-807; Rozadilla et al., 2022). This process is straight, posteriorly oriented and lateromedially strongly flattened in the lectotype of *T. transsylvanicus* (Fig. 2F).

Specimen LPB (FGGUB) R.2882.10 is probably a fragment of the alveolar parapet of the dentary, found in two pieces (Fig. 6I, J). The anteriorly placed alveoli it preserves point slightly posteriorly, while the more posteriorly placed alveoli are upright. All of them are long and narrow with lateromedially shallow edges. Around 22 alveoli can be counted on the specimen (Fig. 6J, a) just as in the case of the complete dentary (LPB [FGGUB] R.2882.2). The external surface is smooth, with tapered ends both anteriorly and posteriorly.

Surangular. The rather well-preserved left surangular (LPB [FGGUB] R.2882.4) is a curved, crescent-shaped element (Figs 3C, 6K–M). Only the base of the lateromedially narrow ascending dorsal process is preserved (Fig. 6K–M, adp), therefore it is not possible to determine whether there was a surangular accessory foramen at the surangular-dentary joint; this foramen is absent in both *Telmatosaurus* and *Tethyshadros* (Dalla Vecchia, 2006, 2009b; Nopcsa, 1900; Weishampel et al., 1993). The dorsal edge of this process is less steep compared to the condition seen in *Telmatosaurus* (Fig. 3C, D). Based on the size of the adductor fossa on the coronoid process of LPB (FGGUB) R.2882.2, the articulation with the surangular presumably extended up to the tip of the coronoid process, similarly to the condition seen in the type specimens of *T. transsylvanicus* and *Tethyshadros insularis* (Dalla Vecchia, 2006, 2009b; Nopcsa, 1900; Weishampel et al., 1993). This type of articulation seems to be more typical for basal hadrosauriforms than to derived hadrosaurids (Tsogtbaatar et al., 2019).

Posterior to the ascending dorsal process, there is the slightly depressed and asymmetrical glenoid with a large, semicircular lateral lip and a much smaller medial lip that has a nearly straight medial edge (Fig. 3E, sml; and Fig. 6K–M, gl, ll, ml). This structure seems to differ from that seen in the lectotype of *Telmatosaurus transsylvanicus*, where the medial lip is more extensive medially, is separated from the medial edge of the retroarticular process and, together with the presumably attached splenial, presents a more symmetrical bowl-shaped, rounded glenoid surface in dorsal view (Fig. 3D–F, bg, wml). In the case of *Tethyshadros*, these lips are also asymmetrical, as the medial lip is somewhat smaller and placed more anteriorly compared to the lateral one. Meanwhile, in *Tethyshadros* the glenoid surface is more anteroposteriorly elongated than in either of these Transylvanian surangulars.

Between the lateral and medial lips, there is a transverse ridge, with a glenoid foramen (Figs 3E, 6L, trr, gf) in the middle. This foramen clearly differentiates LPB (FGGUB) R.2882.4 from other closely related taxa, as its presence has so far only been observed in *Batyrosaurus rozhdestvenskyi*, where it was selected as one of the diagnostic features of this species (Godefroit, Escuillié, et al., 2012). However, at least some *Edmontosaurus* surangulars (CMN 2289; Cuthbertson et al., 2012; Xing et al., 2017; DMNH 2014-12-456; Takasaki et al., 2020; UCMP 235859; Wosik et al., 2019) also have a glenoid foramen. As this foramen is also known to be present in other, distantly related hadrosauroid taxa, its presence cannot be considered as uniquely diagnostic for *Batyrosaurus* any longer.

At about the centre of the lateral surface of the lateral lip sits the surangular foramen (Figs 3C, 6K, sf). This foramen usually occurs in basal hadrosauriforms, including *Iguanodon*, *Ouranosaurus*, *Altirhinus*, *Equijubus*, *Protohadros* and *Batyrosaurus* (Godefroit, Escuillié, et al., 2012; Head, 1998; Norman, 1980, 1986, 1998; Taquet, 1976; You, Luo, et al., 2003). However, it does not seem to be present in either *Tethyshadros* (Dalla Vecchia, 2009b) or *Telmatosaurus* (Nopcsa, 1900; Weishampel et al., 1993). Remarkably, the right and left surangulars of specimen SZTFH Ob. 3123 from the Vălioara area also present the surangular foramen, while this foramen could not be observed on the surangular pair NHMUK R.4911, collected from the Sînpetru Formation. All of these relatively poorly preserved specimens were referred to *Telmatosaurus* in Weishampel et al. (1993), but further studies are needed to determine their taxonomic affinities more precisely; nonetheless, based on presence of a surangular foramen we suggest that SZTFH Ob. 3123 can be safely excluded from *Telmatosaurus*, while it notably shares this feature with *Kryptohadros* coming from the same locality and horizon.

The retroarticular process is semicircular, strongly dorsally curved (Fig. 3C; and Fig. 6K–M, rp), being different in this respect from that of the lectotype of *T. transsylvanicus*, as in the latter, the dorsal bend of the (albeit fractured) retroarticular process seems to initiate immediately behind the glenoid (Fig. 3D). In this regard, the retroarticular process of *Kryptohadros* is more similar to that of *Tethyshadros*, although in lateral view its base is dorsoventrally thicker than its tip, unlike in the latter taxon. Furthermore, the anterodorsal surface of the process is flat in *Tethyshadros*, while it is mediolaterally rounded in *Kryptohadros*. In caudal view, the retroarticular process is lateromedially flattened and medially curved, although its tip is laterally deflected as in *Amurosaurus riabinini* (Godefroit, Bolotsky & Van Itterbeeck, 2004). Laterally, the base of the retroarticular process bears a small oval depression with a rugose surface (Fig. 6K, L, od); this depression extends along the entire lateral surface in the holotype of *Tethyshadros insularis*.

As in several other hadrosauroids (e.g. *Batyrosaurus*; Godefroit, Escuillié, et al., 2012; *Edmontosaurus*; Takasaki et al., 2020; *Eolambia*; McDonald, Bird, et al., 2012), one rostrocaudally oriented, deep canal dominates the medial side of the surangular (Fig. 6M, c), extending horizontally along its midline. When the canal reaches the retroarticular process, it follows the curved shape of the latter all the way to the apex, although it becomes much shallower here.

Teeth. Only a few isolated maxillary teeth have been collected at Fântânele-3 (LPB [FGGUB] R.2882.11–14). These are tall, mesiodistally narrower than the dentary teeth (see below) and have an asymmetrically placed strong median carina (Fig. 7A–D, mc), due to which they are wider lateromedially than mesiodistally. The completely preserved specimens (LPB [FGGUB] R.2882.11, R.2882.13) are conical in medial view with rounded tips and densely packed marginal denticles (Fig. 7A–C, md), of which there are slightly more on the distal margin (see supplementary table 2 in Magyar et al., 2025). These denticles are small and rounded at the base of the crown, but become more elongated at its tip. Specimens LPB (FGGUB) R.2882.12 and R.2882.14 show wear facets across their entire tip, and in LPB (FGGUB) R.2882.12 the wear facet extends labially even to the median carina (Fig. 7B, w).

The general morphology of the maxillary teeth of *K. kallaiae* is very similar to that of *Tethyshadros*, but due to the slightly asymmetrical placed median carina, it is even more reminiscent of that seen in *Telmatosaurus* (Dalla Vecchia 2006, 2009a, 2009b; Weishampel et al., 1993).

Several isolated, heavily worn dentary teeth with lenticular cross-section had also been recovered from Fântânele-3 (LPB [FGGUB] R.2882.15–20). The preserved fragments suggest a diamond-shaped crown morphology in lateral view (Figs 3G, 7E–J). Specimen LPB (FGGUB) R.2882.17 has two nearly straight, shallow median ridges (Fig. 3G; and Fig. 7G, mr), while specimen LPB (FGGUB) R.2882.20 bears only one that is slightly curved and offset mesially (Figs 3G, 7J, mr). Similarly, previously collected Transylvanian hadrosauroid teeth also vary in the development pattern of these primary ridges. The anterior replacement teeth preserved *in situ* in the right dentary of the lectotype of *T. transsylvanicus* show only one straight median ridge (Fig. 3H), while some isolated teeth (e.g. LPB [FGGUB] [5]) bear two slightly curved ones (Dalla Vecchia, 2009a; Weishampel et al., 1993). Meanwhile, the teeth sitting in the dentary fragment SZTFH Ob.3107 from Vălioara (the other catalogue number of this specimen: SZTFH v.13499) and in the above-mentioned juvenile dentary pair (LPB [FGGUB] R.1305) from the Sînpetru Formation have only one mesially offset median ridge (Dumbravă et al., 2016; J. M. personal observation), but this ridge is slightly curved only in the case of the former specimen. The teeth of *Tethyshadros* are also variable in this respect. The anterior teeth have only one straight median carina, while the more distally placed ones show a slightly sigmoid median carina accompanied by two subsidiary ridges; meanwhile, some lower replacement teeth lack subsidiary ridges altogether (Dalla Vecchia, 2009b).

Very small, knob-like marginal denticles are observed on the preserved mesial and distal margins of the Fântânele-3 dentary tooth specimens (Fig. 7E–G, md). In the case of *Telmatosaurus* and *Tethyshadros* this part of the crown is not denticulated (Dalla Vecchia, 2009a, 2009b; Weishampel et al., 1993), whereas the teeth of the juvenile dentaries (LPB [FGGUB] R.1305) as well as two posteriorly placed teeth of specimen SZTFH Ob.3107 show very slight denticulation on this region of the crown (Dumbravă et al., 2016; J. M. personal observation).

In conclusion, the pattern (i.e. number and development) of the primary ridges and denticles seen on the dentary teeth recovered from site Fântânele-3 differs from that of most previously known *in situ* hadrosauroid dentary teeth from Hațeg Basin.

Axial skeleton.

Ribs. A small number of relatively short, craniocaudally thin dorsal rib fragments (LPB [FGGUB] R.2882.21–24, R.2882.47; Fig. 7K–N) were recovered in the close proximity of other elements of the skeleton. They are slightly bowed medially and have a lateromedially flattened, crescent-like shape in cross-section. The bone surface is smooth, with rounded cranial and caudal edges.

Caudal vertebrae. Eleven nearly completely preserved caudals (LPB [FGGUB] R.2882.25–35) and one distal neural spine fragment (LPB [FGGUB] R.2882.46) were collected from Fântânele-3 (Figs 8, 9, 10A–I). All vertebrae display typical hadrosauroid features such as the hexagonal cranial or caudal outline of the centra, with a laterally compressed middle part and a horizontal dorsal surface (Weishampel & Horner, 2004). Three specimens (LPB [FGGUB] R.2882.25–27) are anterior caudals, while the rest are anterior-mid or mid caudals.

The centra are amphicoelous and longer anteroposteriorly than high dorsoventrally, although in the case of the anterior and anterior-mid caudals this difference is minimal, amounting to only a few millimetres. The relative elongation of the centra increases distally (see supplementary table 2 in Magyar et al., 2025), but it remains smaller than that reported in *Tethyshadros* (Dalla Vecchia, 2009b).

The ventral side of the centra is concave longitudinally, bears a longitudinal groove in the sagittal plane bounded laterally by transversely rounded ridges that bear chevron facets both anteriorly and posteriorly (Figs 8, 9, C, F, I, L, and 10, C, F, I, lr, cf), with the posterior facets being more prominent than the anterior ones. The dorsoventrally flattened pleurapophyses of the anterior caudals are well developed (Fig. 8A–I, plz) and, unlike in *Tethyshadros*, always longer lateromedially than wide anteroposteriorly. The mid caudals only display anteroposteriorly elongated, sharp ridges on their lateral sides (Figs 9E, H, K, 10B, E, H, sr) instead of pleurapophyses. The well-developed neural arches are centrally placed on the dorsal side, and bear anterodorsally oriented prezygapophyses and posterodorsally oriented postzygapophyses, both with smooth and oval articular surfaces, as well as tall, laterally flattened neural spines (Figs 8, 9; Fig. 10A–H, prez, poz, sp). The neural arches enclose a relatively small neural canal that is either rounded or slightly dorsally flattened oval in section (parts A, D, G, J of Figs 8, 9, nc). The size of the zygapophyses decreases in the more posteriorly positioned vertebrae, and these become more horizontally oriented.

The neural spines of the anterior caudals are generally vertical, strongly laterally compressed, and taller than the height of the centrum. The basal part of the spine is posterodorsally leaning, but its apical part is redirected anterodorsally. At the base of the neural spine, above the postzygapophyses, there is a 'notch' or 'neck' (Fig. 8E, H, no), causing the basal part of the spine to be anteroposteriorly thinner than its apical part, a feature that is also commonly present in both *Tethyshadros* and in several Transylvanian caudals (e.g. NHMUK R.4915, NHMUK R.4973) previously referred to *Telmatosaurus* (Dalla Vecchia, 2006, 2009a, 2009b, 2020); a similar condition has also been reported in *Qianjiangsaurus changshengi* (Dai et al., 2025). These notches are, however, more dorsoventrally expanded in the Transylvanian specimens than in *Tethyshadros* (Dalla Vecchia, 2020), being more similar in this respect to the condition found in *Qianjiangsaurus*. The apex of the neural spine is slightly expanded in lateral view, with a rounded dorsal edge, highly reminiscent of specimen NHMUK R.4915 from Haţeg Basin, but different from the hatchet-shaped, apically strongly widened spines of *Tethyshadros* (Chiarenza et al., 2021; Dalla Vecchia, 2009b).

The neural spines of the mid caudals differ from those of the anterior ones as they are posteriorly bent, less anteroposteriorly widened and mediolaterally flattened, although they remain longer than the anteroposterior length of their corresponding centra; their apex is either also rounded (LPB [FGGUB] R.2882.28, R.2882.31) or slopes into the anterior direction (LPB [FGGUB] R.2882.33–34). The posterior basal notches of these neural spines are even more proximodistally expanded than seen in the anterior caudals (Figs 9E, H, K, 10B, E, no); the presence of similar notches are also reported in *Yunganglong datongensis* (R.-F. Wang et al., 2013) and maybe also in *Ahshislesaurus wimani* (Dalman et al., 2025), but even in these taxa, the notches are less well developed than in *Kryptohadros*. None of the middle caudals referred to *Telmatosaurus* by Weishampel et al. (1993) preserves the neural spine, hindering any detailed comparison with the Fântânele-3 material in this respect. The mid caudal neural spines of *Tethyshadros*, on the other hand, are very different from those seen in the vertebrae of *Kryptohadros*, as they are shorter dorsoventrally than the anteroposterior length of their respective centra, are completely lateromedially flattened, almost evenly wide anteroposteriorly, and lacking a notch above the postzygapophyses (Dalla Vecchia, 2009b, 2020).

Chevrons. Five chevrons (LPB [FGGUB] R.2882.36–40) were recovered at Fântânele-3 (Fig. 10J–S), from the proximity of the caudal vertebrae. All specimens are 'Y'-shaped in anterior or posterior view like in other hadrosauroids, but similarly to the condition in *Tethyshadros* and *Gobihadros* they vary greatly in shape along the vertebral series (Dalla Vecchia, 2009b, 2020; Tsogtbaatar et al., 2019).

The articular facets of the anterior chevrons (LPB [FGGUB] R.2882.36–37) are closely appressed, but not fused together, while more posteriorly they are set further apart (Fig. 10J, L, N, P, R, af). These articular surfaces are rounded and slope posteriorly in lateral view (Fig. 10K, M, O, Q, S, af), although this posterior leaning becomes less significant in the more posteriorly placed chevrons (LPB [FGGUB] R.2882.38–40). The lateromedially slightly flattened neck of the articular surfaces forms the borders of the oval haemal canal (Fig. 10J, L, N, P, R, hc) that is relatively short compared to the total length of the chevron; these proportions also change along the tail, as the more posteriorly placed chevrons have dorsoventrally relatively shorter haemal spines.

The proximal part of the spine is straight, rod-shaped and sub-circular in cross-section. Its distal part, at least in the more anteriorly placed specimen LPB (FGGUB) R.2882.37, becomes slightly laterally compressed without widening anteroposteriorly (Fig. 10L, M, de). The spine of LPB (FGGUB) R.2882.38 is also straight, but is more laterally compressed, and its distal end is anteroposteriorly slightly expanded (Fig. 10N, O, de), similarly to the 6th chevron of the holotype of *Tethyshadros insularis* (Dalla Vecchia, 2009b, 2020). The last two chevron specimens coming from the distal part of the series (LPB [FGGUB] R.2882.39–40) show an even more transversely flattened oval cross-section. They are straight in anterior view, but slightly posteriorly curved in lateral view, and their distal ends are also more anteroposteriorly expanded (Fig. 10P–S, de), to a degree similar to that seen in the 8th and 9th chevrons of *Tethyshadros* (Dalla Vecchia, 2009b, 2020).

Appendicular skeleton.

Femur. Both femora (LPB [FGGUB] R.2882.41–42) are fragmentary (Fig. 11A–D), missing both epiphyses. Specimen LPB (FGGUB) R.2882.41 is a caudally curved shaft fragment of the right femur. Based on the proximally placed fourth trochanter (Fig. 11A, B, ft), it represents the craniocaudally slightly flattened mediocaudal part of the element. The fourth trochanter is depressed craniomedially with a striated surface for the attachment of the *m. caudofemoralis* (Fig. 11A, ma), but its caudolateral side is smooth and flat, similarly to the condition seen in the completely preserved hadrosauroid femur SZTFH Ob.3119, reported as MAFI v.10338 in Weishampel et al. (1993; also in Grigorescu & Csiki, 2006), and in another, undescribed femoral shaft fragment (SZTFH v.13533), both from Vălioara. The thickness of the bone wall differs between the craniomedial (1 cm) and caudolateral (0.5 cm) parts.

Specimen LPB (FGGUB) R.2882.42 is a straight shaft fragment with an oval cross-section, probably of the left femur, close to its proximal end. The bone surface is smooth and rounded craniomedially and flattened caudomedially in cross-section. The bone wall is on average 1 cm wide. It has a thickened oval part proximally (Fig. 11C, D, tp) with an eroded surface, which is medially offset, and bordered by a slightly proximodistally elongated depression both cranially and caudally (Fig. 11C, D, d). This suggests that the thickening could mark the base of the femoral head; otherwise, the specimen does not bear any noteworthy feature.

Tibia. Only a fragmentary but almost complete left tibia (LPB [FGGUB] R.2882.43) has been recovered from the site (Fig. 11E–H). The bone is long, slender, slightly sigmoidal in lateral view and typically twisted along its long axis.

In the proximal articular region, only the lateroventral and dorsal parts of the rounded lateral condyle as well as the shallow and relatively narrow popliteal groove are preserved (Fig. 11E, G, H, lc, pg). More distally, the shaft is straight, roughly lateromedially flattened and oval in cross-section, albeit missing the anterior surface. Towards the distal end of the tibia, the shaft widens lateromedially and flattens craniocaudally, and is furthermore slightly curved into the cranial direction. The rounded medial edge is also curved medially in this region. The distal end with the malleoli is missing. Only the proximal end of the prominent posterior ridge is preserved medially to the articular facet for the fibula (Fig. 11G, pr, af). A shallow depression with a striated surface on the anterior side represents the proximal part of the calcaneal facet (Fig. 11E, cf).

Due to the fact that its type material does not include limb bones, Weishampel et al. (1993) tentatively reconstructed the tibia of *Telmatosaurus transsylvanicus* based on four isolated fragments: SZTFH Ob.3129 (consisting of two tibiae), MNMKK-MTM v.60.1708 and MNMKK-MTM v.60.1709; all of these, however, discovered from the Densuș-Ciula Formation in the neighbourhood of Vălioara instead of the type locality-hosting Sînpetru Formation. Furthermore, it should be pointed out that the last one of these specimens was originally part of the type material of the titanosaur '*Magyarosaurus transsylvanicus*' (Huene, 1932; now considered a *nomen nudum*, Díez Díaz et al., 2025), and we also suggest this specimen to be a titanosaurian fibula instead.

These partial hadrosauroid tibiae (SZTFH Ob.3129, MNMKK-MTM v.60.1708) have a straight and narrow tibial shaft, similar to the Fântânele-3 specimen, but the proximal widening starts within the proximal third of the tibia length, instead of around shaft mid-length.

Meanwhile, the tibiae of *Tethyshadros*, although similarly straight and flaring craniocaudally only near their proximal end, have a mediolaterally relatively wider shaft compared to their dorsoventral height, unlike the condition seen in the Transylvanian specimens. In addition, in this taxon only the distal end of the tibia bends cranially (Dalla Vecchia, 2009b; J. M. personal observation).

The general morphology of the tibia, with the proximal expansion starting near the middle of the shaft makes specimen LPB (FGGUB) R.2882.43 more similar to the tibiae of several more distantly related Hadrosauriformes, among others, that of the iguanodontian *Iguanodon bernissartensis* (IRSNB. 1534; Norman, 1980), the hadrosauroid *Gobihadros mongoliensis*

(MPC-D100/746; Tsogtbaatar et al., 2019), and the lambeosaurines *Olorotitan arharensis* (AEHM 2/845; Godefroit, Bolotsky & Bolotsky, 2012), *Amurosaurus riabinini* (AEHM 1/969; Godefroit, Bolotsky & Van Itterbeeck, 2004) and *Latirhinus uitslani* (IGM 6583; Ramírez-Velasco et al., 2021).

Fibula. Two fragmentary specimens represent most probably left (LPB [FGGUB] R.2882.44), respectively right (LPB [FGGUB] R.2882.45) fibular shaft fragments (Fig. 11I–L). Both are preserved without their proximal and distal ends. These fragments are proximodistally elongated and craniocaudally slender elements, straight in lateral view but slightly medially bowed in cranial view, with a mainly smooth bone surface. The proximal part of LPB (FGGUB) R.2882.44 is concave medially and convex laterally, due to the deep and wide, distally narrowing sub-triangular proximal tibial facet (Fig. 11L, tf) on its medial side. The cranial and caudal edges of this area are evenly rounded. Distal to this depression there is a small, proximodistally oriented and longitudinally striated bone surface, the interosseous ridge (Fig. 11L, ir). Distal to this ridge, the cross-section of the shaft is lateromedially flattened oval. Specimen LPB (FGGUB) R.2882.45 preserves the shaft starting from a point distal to this area, thus not overlapping with specimen LPB (FGGUB) R.2882.44. Based on this second specimen, the distal part of the fibula is spindle-like and winding in the medial direction. On the cranial edge, there is an elongated ridge with striated bone surface (Fig. 11I, s). Distal to this ridge, the cross-section turns into lateromedially flattened oval with sharp cranial and caudal edges (Fig. 11I, J, ce, cre).

According to Weishampel et al. (1993) and Dalla Vecchia (2006), no hadrosauroid fibulae are known from Transylvania; nonetheless, several such specimens were collected from the Tuștea nesting locality, in Oltoane Hill near Tuștea (see Botfalvai et al., 2017), including LPB (FGGUB) R.1712, R.1850, and R.0247 (the latter two specimens representing hatchlings) as well as from Vălioara (SZTFH Ob.3282); of these, the adult elements are largely identical to the Fântânele-3 specimens as well as to the fibulae of *Tethyshadros*.

Phylogenetic results

In the first analysis (see Material and methods) we were able to score a total of 123 characters for the new taxon, representing about 32% of the total dataset. The analysis recovered 12,390 equally parsimonious shortest trees with 1558 steps, with a consistency index (CI) of 0.352 and a retention index (RI) of 0.818; for the detailed results, including the Bremer support/decay index (see supplementary fig. 1 of Magyar et al., 2025).

In the strict consensus of the most parsimonious trees, *Kryptohadros kallaiae* was recovered as a non-hadrosaurid hadrosauroid, closely related to *Tethyshadros* and *Telmatosaurus* (Fig. 13A; supplementary fig. 2 in Magyar et al., 2025). These three closely related genera form a distinct clade based mainly on the following unambiguous characters: more than 1.25 teeth/cm of the maxilla (Character 17, character state 1); saw-toothed or small mammilliform denticles along the ventral half of the maxillary crowns (Character 23, character state 0, although this character is polymorphic and also codes as 2 in *K. kallaiae*); and their occurrence in Europe (Character 374, character state 0). Additional characters may also represent potential shared apomorphies for this clade, but these are currently unknown in one or more of its members. These characters include: (i) bamboo leaf-like denticles along the dorsal half of the dentary crown (Character 11, character state 0, unknown in *K. kallaiae*); (ii) ratio between horizontal distance from the caudal margin of the coronoid process to the caudal-most end of the deflected ventral margin of the dentary and horizontal distance from the caudal margin of the coronoid process to the rostral-most alveolus, greater than 0.78 (Character 42, character state 0, but unknown in *Tethyshadros*); (iii) absent double layered premaxillary oral margin (i.e. the external and internal parts of the bone not separated by a sulcus; Character 79, character state 0, not known in *K. kallaiae*); (iv) ratio between the distance from the apex of the maxillary lateral surface rostroventral to jugal articular surface to the rostral end of the maxilla and the rostrocaudal length of the maxilla, between 0.35 and 0.46 (Character 100, character state 0, but unknown in *K. kallaiae*); and, finally, (v) ratio between the length of the ectopterygoid shelf and the rostrocaudal length of the maxillary dental battery greater than 0.35 (Character 111, character state 0, again, not known in *K. kallaiae*). Remarkably, within this clade the new taxon is more closely related to *Tethyshadros* than to *Telmatosaurus* based on the shared presence of a slightly curved primary ridge on the dentary teeth (Character 8, character state 1, instead of 0 in the case of the latter taxon).

This clade formed by the three latest Cretaceous eastern European taxa is recovered in a basal position within Hadrosauroidea, outside of the derived hadrosaurids (Fig. 13). Here, it appears in a wide polytomy with other, mainly Asian and North-American hadrosauromorphs such as *Gilmoreosaurus*, *Bactrosaurus*, *Hadrosaurus*, *Eotrachodon*, *Tanius* and *Claosaurus*. The only known Western European non-hadrosaurid hadrosauroid, *Fylax*, considered by Prieto-Márquez & Carrera

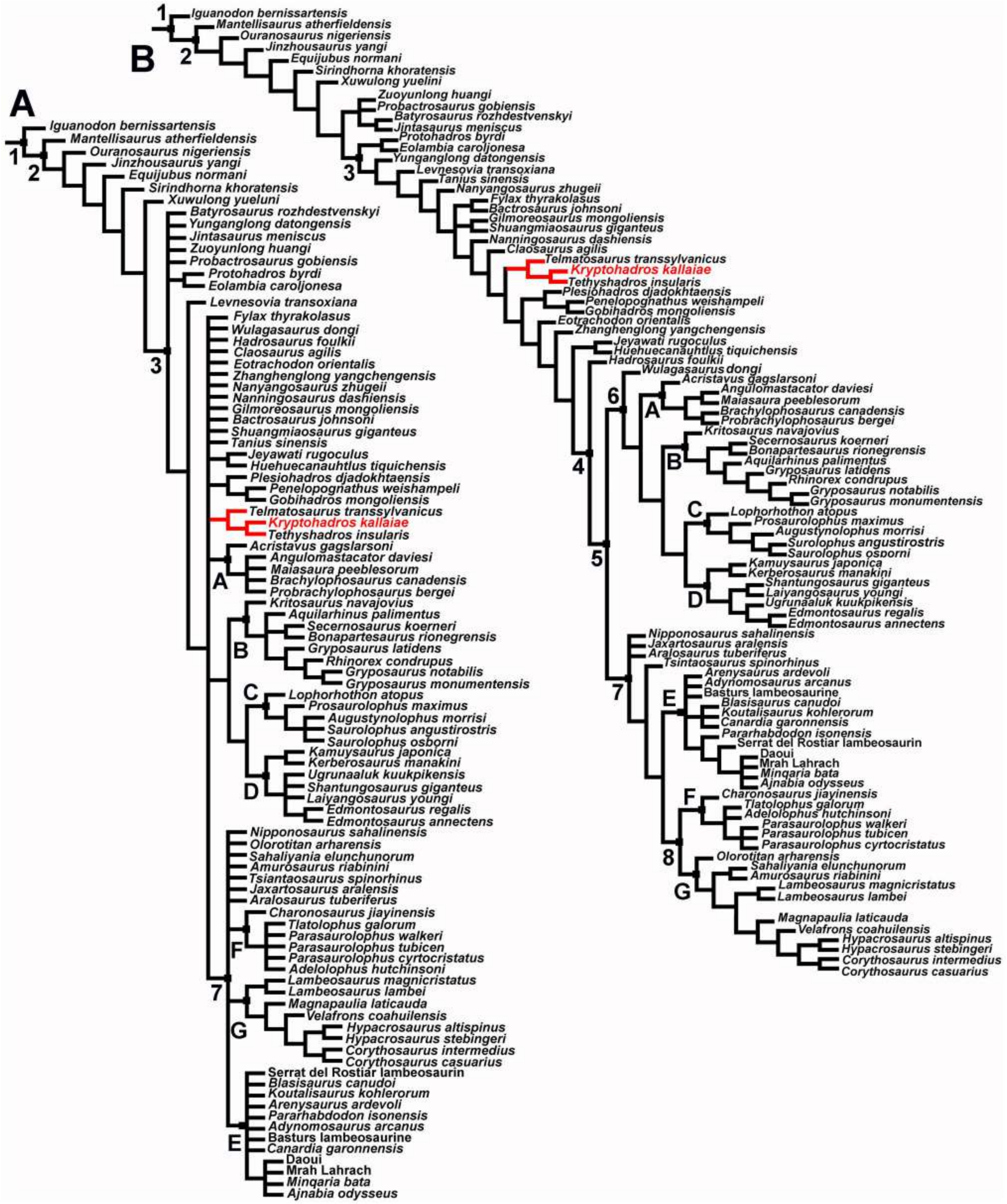


Figure 13. Results of the first phylogenetic analysis, using the updated dataset of Longrich, Pereda-Suberbiola, et al. (2024). **A,** Strict consensus tree; **B,** Majority rule consensus tree. The newly introduced taxa, Telmatosauridae and the name of *Kryptohadros kallaiae* gen. et sp. nov., are highlighted in red. Legend: 1, Hadrosauriformes; 2, Hadrosauroidea; 3, Hadrosauromorpha; 4, Hadrosauridae; 5, Euhadrosauria; 6, Saurolophinae; 7, Lambeosaurinae; 8, Corythosauria; A, Brachylophosaurini; B, Kritosaurini; C, Saurolophini; D, Edmontosaurini; E, Arenysaurini; F, Parasaurolophini; G, Lambeosaurini.

Farias (2021) to be the closest relative of *Tethyshadros*, is instead recovered outside of the clade containing the latter taxon in our analysis, although also within the large polytomy with the taxa listed above.

Interestingly, there is no separate Hadrosauridae recovered in the strict consensus tree; instead, each of the two large classical groupings of hadrosaurids, the Saurolophinae and Lambeosaurinae, cluster separately within the same large polytomy mentioned earlier. In addition, the Saurolophinae is split up, with taxa such as *Acristavus*, *Maiasaura*, *Angulomastacator*, *Probrachylophosaurus* and *Brachylophosaurus* (all members of tribe Brachylophosaurini) being placed into a clade separate from that uniting all the other members of Saurolophinae. Nevertheless, we also note that relationships between the taxa clustered into this large polytomy are much better resolved in the majority rule consensus tree (Fig. 13B; supplementary fig. 3 in Magyar et al., 2025). As expected, the majority rule tree recovers the same cluster formed by the new taxon, *Telmatosaurus* and *Tethyshadros*, whereas *Fylax* is shifted far more basally within Hadrosauroidea, on a common branch with *Bactrosaurus*. Furthermore, the majority rule consensus tree recovers both a monophyletic Hadrosauridae as well as a similarly monophyletic Saurolophinae within it, mirroring long-established relationships within these most derived hadrosauroids (e.g. Prieto-Márquez, 2010b,c). Finally, we also derived both the maximum agreement subtree (see supplementary fig. 4 in Magyar et al., 2025 for the results, including 68 taxa) and the implied weighting trees using a concavity constant of $K = 12$ (the resulted strict consensus and majority rule consensus trees of the 580 most parsimonious trees are shown in supplementary figs 5, 6 in Magyar et al., 2025). The results of these analyses, similarly to the majority rule consensus tree from the unweighted parsimony analysis (Fig. 13B) mentioned above, are better resolved than the strict consensus tree from the original analysis (Fig. 13A), and largely replicate the topology of that majority rule consensus tree, including the same position and ingroup relationships for Telmatosauridae, as well as the monophyly of both Hadrosauridae and Saurolophinae.

In the second analysis using the Dai et al. (2025) matrix we were able to score a total of 104 characters for *Kryptohadros* in the character–taxon matrix, representing about 30.1% of the total dataset. The analysis recovered 12 equally parsimonious shortest trees with 1116 steps. Both the consistency ($CI = 0.443$) and the retention index ($RI = 0.845$) values are higher than in the first analysis (for the Bremer support/decay index values, see supplementary fig. 7 in Magyar et al., 2025).

In both the strict consensus and the majority-rule consensus trees, similar to the first analysis, *K. kallaiae* was recovered as a non-hadrosaurid hadrosauroid, closely related to the other members of Telmatosauridae (Fig. 14; supplementary figs 8, 9 in Magyar et al., 2025), and *Tethyshadros* is again identified as the closest relative of the new taxon. This topology is primarily supported by the same characters as in the first analysis (characters 11, 17, 23, 42, and 79 for Telmatosauridae, and 8 for the *Kryptohadros*-*Tethyshadros* cluster, respectively). However, this new analysis also identified a potential additional common character of Telmatosauridae: maximum number of teeth per alveolus in the adult dentary (character 3, character state 1, albeit unknown in *Kryptohadros*).

As in the first analysis, Telmatosauridae is located among other Asian and North American basal hadrosauroids. Interestingly, however, *Gobihadros* and *Plesiohadros* now occupy more basal positions, with the latter forming a clade with *Qianjiangsaurus*. In contrast, *Fylax* appears to be more derived than Telmatosauridae and is recovered as the sister taxon of a monophyletic Hadrosauridae (Fig. 14).

Discussion

Ontogenetic stage of the Fântânele-3 hadrosauroid and relevance to its taxonomic status

Both its seemingly somewhat smaller absolute body size and the smaller number of tooth families within the dentary, as well as the unfused nature of the cranial elements, may indicate that the Fântânele-3 hadrosauroid represents a younger individual compared to the lectotype specimen of *Telmatosaurus transsylvanicus* or the larger specimen of *Tethyshadros* (SC 57247) (e.g. Griffin et al., 2021; Prieto-Márquez, 2014). Nevertheless, given the advanced degree of fusion of the caudal neural arches to their respective centra, this individual was no longer a juvenile, or at least was close to the end of that ontogenetic stage at the time of its death.

This rough ontogenetic stage assessment is also supported by the dimensions of its skeletal elements. The term ‘juvenile stage’ is usually used in the case of hadrosauroid specimens that have reached 50% or less of the estimated maximum skull or body length recorded for that species (Horner et al., 2000; Prieto-Márquez, 2014). Although *Kryptohadros* can only be compared with individuals of closely related taxa, it is worth emphasizing that the dentary of the holotype individual (LPB [FGGUB] R.2882) is only 4 cm shorter than that of the lectotype of *T. transsylvanicus*, and presumably

Figure 14. Results of the second phylogenetic analysis, using the updated dataset of Dai et al. (2025). In our results the strict consensus and the majority rule consensus trees show the same topology. The newly introduced taxa, Telmatosauridae and the name of *Kryptohadros kallaiae* gen. et sp. nov., are highlighted in red. Legend: 1, Hadrosauriformes; 2, Hadrosauroidea; 3, Hadrosauromorpha; 4, Hadrosauridae; 5, Euhadrosauria; 6, Saurolophinae; 7, Lambeosaurinae; 8, Corythosauria; A, Brachylophosaurini; B, Kritosaurini; C, Saurolophini; D, Edmontosaurini; E, Arenysaurini; F, Parasaurolophini; and G, Lambeosaurini.

about 8 cm shorter than those belonging to *Tethyshadros* (see supplementary table 2 in Magyar et al., 2025). As such, the length of the holotype dentary of *Kryptohadros kallaiae* is about 82.2% of that of the *T. transsylvanicus* lectotype, and 72.8% of the *Tethyshadros* specimens. These comparisons also suggest that the Fântânele-3 specimen most probably already reached at least the subadult stage.

Therefore, ontogenetically variable features, such as the number of tooth families in the dental battery or the ventral inclination of the symphysis, are expected to have changed to only a minor extent by the time the individual would have reached fully adult stage. The ontogenetically variable ventral inclination of the symphysis, with the degree of inclination increasing during growth, was reported in hadrosauroids like *Edmontosaurus* and possibly *Telmatosaurus* (Dumbravă et al., 2016; Prieto-Márquez, 2014; Wosik et al., 2019). Since the inclination of the symphysis is already greater in the Fântânele-3 individual than in the larger-bodied lectotype individual of *T. transsylvanicus*, the former cannot represent a younger ontogenetic stage of the latter; actually, this observation further reinforces the proposed taxonomic distinctiveness of the new Fântânele-3 hadrosauroid.

Although the degree of fusion of the neural arches and that of the cranial elements may be poorly informative in determining the ontogenetic stage of an individual (e.g. Bailleul et al., 2016; Griffin et al., 2021), the presence of a closed frontonasal fontanelle in LPB (FGGUB) R.2882 may provide further supportive evidence indicating that it does not simply represent an ontogenetically earlier growth stage of *T. transsylvanicus*. Indeed, while the lectotype individual of *T. transsylvanicus* may had been older given its somewhat larger body size, it still possessed an open fontanelle.

Examination of the limb bone surfaces reveals a high degree of porosity in certain areas. Limb bones with porous surfaces often indicate that the subperiosteal bone was still actively growing (e.g. Galton, 2010; Griffin et al., 2021; McGowan, 1994). However, in the case of the Fântânele-3 individual the underlying subperiosteal tissues visible in such patches were more probably exposed by taphonomic processes, and do not appear to reflect still ongoing growth.

Finally, the morphological differences noted between the different known Transylvanian hadrosauroid tibiae cannot be accounted for, either, by ontogenetic stage differences, as the absolute size of LPB (FGGUB) R.2882.43 (see supplementary table 2 in Magyar et al., 2025) does not differ significantly from that of the largest tibiae otherwise known from Transylvania (Grigorescu & Csiki, 2006). In addition, a preliminary investigation (Grigorescu & Csiki, 2006) of the ontogenetic development of *T. transsylvanicus* – still considered by those authors to include all the Transylvanian hadrosauroid material – has shown that there are no major morphological or proportional changes between tibiae that represent the very early (i.e. hatchling) and, respectively, the adult ontogenetic stages, excepting the increased relative size of the cnemial crest. This feature is, however, unfortunately not preserved and thus cannot be assessed in the Fântânele-3 individual.

To conclude, the potentially somewhat younger ontogenetic stage of the Fântânele-3 hadrosauroid compared to other loosely sympatric Transylvanian hadrosauroids of larger absolute dimensions (including the lectotype of *Telmatosaurus*) does not appear to account for the morphological and morphometric differences noted in the description and comparisons. Thus, these differences are most likely due to the taxonomic distinctiveness of *K. kallaiae* from *T. transsylvanicus*, the only previously described hadrosauroid taxon from Hațeg Island. Furthermore, since the tibia of *Kryptohadros* is more similar in morphology to that of several distantly related hadrosauroid taxa instead of its closest relatives, as discussed above, its distinctive anatomy most likely may also reflect some sort of special (albeit as yet undetermined) habitat-related adaptations that would have strongly impacted the architecture of the appendicular skeleton. Such a possibility appears to be supported by the occurrence of an unusual appendicular anatomy in its close relative *Tethyshadros*, as well, one that presumably arose as an adaptation to movement within a rough karstic environment that characterized the Adriatic-Dinaric Landmass of the Late Cretaceous European Archipelago (Dalla Vecchia, 2009b).

Phylogenetic position of *Kryptohadros kallaiae*

Our phylogenetic analyses clearly recovered the new taxon within Hadrosauroidea, as member of a distinct clade here named Telmatosauridae together with two other monospecific genera, *Telmatosaurus* and *Tethyshadros*, and lying outside of the derived Hadrosauridae. Within this clade, the new species appears to be more closely related to *Tethyshadros* than to *Telmatosaurus*, although this position is based only on a single shared character state of character 8, i.e. the slightly curved shape of the primary ridge of the dentary tooth crown. However, it should be noted that the lectotype dentary of *Telmatosaurus transsylvanicus* contains only three anterior replacement dentary teeth, *Kryptohadros kallaiae* is only represented by isolated and heavily worn dentary teeth, while the teeth of the holotype of *Tethyshadros insularis* are mainly observable in labial view, and their description is therefore mainly based on another tooth-bearing dentary fragment (SC 57026). All of these circumstances make reliable scoring of this character difficult. If this somewhat problematic character is disregarded, the three taxa collapse into a polytomy within their clade, one that nevertheless remains rather well supported by a large number of shared characters (see above, Phylogenetic Analysis, as well as supplementary figs 10–13 in Magyar et al., 2025). In our first analysis, the Bremer support value for Telmatosauridae is actually higher (3) than that found for most of the historically well-supported hadrosauroid clades such as Kritosaurini (1), Parasaurolophini (1), or Lambeosaurini (1) (see supplementary fig. 1 in Magyar et al., 2025), although the same index is somewhat lower (1) in our second analysis (see supplementary fig. 7 in Magyar et al., 2025).

Within its parent clade, *Kryptohadros* displays a mix of characters present in either *Telmatosaurus* or *Tethyshadros*, but not both. These include, for example, the ventrally deflected dentary symphysis (in which regard it is more similar to *Telmatosaurus*) and, respectively, a closed frontonasal fenestra (also found in *Tethyshadros*, but most probably not present in *Telmatosaurus*). It also possesses several autapomorphic features within this clade (i.e. ‘local autapomorphies’, according to Beeston et al., 2024), such as the presence of the surangular foramen, considered a characteristic of more basal hadrosauroid taxa. Since the most closely related species that definitely display a surangular foramen are the more basally placed *Eolambia caroljonesa* and *Batyrosaurus rozhdestvenskyi* (Godefroit, Escuillié, et al., 2012; McDonald, Bird et al., 2012), the presence of this feature in *K. kallaiae* would potentially indicate a more basal position for it than that of its sister taxa, and unlike the position recovered by our phylogenetic analyses. However, it is more likely that the presence of this foramen in *K. kallaiae* represents an autapomorphic reversal to the ancestral character state. The presence of a glenoid foramen on the surangular is also worth highlighting among the unique characters of the new taxon within Telmatosauridae, as this feature is – yet again – otherwise also found only in certain more distantly related taxa, and thus must represent an independently acquired convergent feature of *K. kallaiae* (see above, Description and comparisons).

Since the holotype skeleton of *K. kallaiae* does not display any uniquely shared diagnostic character that would place it unambiguously within any one of the previously described closely related genera (i.e. *Telmatosaurus* and *Tethyshadros*), and furthermore also presents several autapomorphies compared to these taxa, its assignment to a new genus and species – *Kryptohadros kallaiae* – is warranted, representing the second formally described non-hadrosaurid hadrosauroid from the latest Cretaceous Hațeg Island.

Notably, our phylogenetic analyses also support close relationships between the formerly erected latest Cretaceous south-eastern European non-hadrosaurid hadrosauroids *Telmatosaurus* and *Tethyshadros*, a relationship already recovered previously by several authors (e.g. Chiarenza et al., 2021; Dalla Vecchia, 2009b; Kobayashi et al., 2019; Longrich et al., 2021; Longrich, Pereda-Suberbiola, et al., 2024; McDonald et al., 2021; Xing et al., 2014). In this regard, however, they clearly depart from the results of other analyses that failed to find any close phylogenetic connections between these two taxa. Nonetheless, it is worth noting that these different analyses themselves yielded conflicting and sometimes widely divergent outcomes concerning the position of these two latest Cretaceous south-eastern European hadrosauroids, as some of them identified *Tethyshadros* as the more derived taxon (e.g. Prieto-Márquez et al., 2013, 2016b; Prieto-Márquez & Carrera Farias, 2021; Tsogtbaatar et al., 2014), whereas others found support for a reversed position, with *Telmatosaurus* lying closer to the base of Hadrosauridae (e.g. Bertozzo et al., 2017; McDonald, Bird, et al., 2012; McDonald, Espílez, et al., 2012; Prieto-Márquez & Wagner, 2023; Shibata et al., 2015; Tsogtbaatar et al., 2019); in both instances, the two taxa were usually placed outside of any of the less inclusive clades separated in the respective analyses. An even more intriguing result is that of McDonald, Espílez et al. (2012), which placed *Telmatosaurus* within Hadrosauridae, although in some other, related studies (e.g. McDonald, Bird, et al., 2012; McDonald et al., 2014) it still falls outside the crown group as the sister taxon of Hadrosauridae; meanwhile, *Tethyshadros* is constantly more basally placed in all these phylogenetic analyses. Conversely, while *Telmatosaurus* was still identified as the sister-taxon of Hadrosauridae in Prieto-Márquez & Wagner (2023), *Tethyshadros* was found by these authors to be a member of that clade, together with some other, Asian hadrosauroids such as *Penelopognathus weishampeli*, *Plesiohadros djadokhtaensis* and *Gobihadros mongoliensis*, all of which are usually recovered outside Hadrosauridae (e.g. Tsogtbaatar et al., 2014, 2019), just as they were in our study.

Furthermore, one or the other of these formerly erected latest Cretaceous European hadrosauroids was occasionally even grouped together with taxa of markedly different palaeogeographical distributions. *Telmatosaurus*, for example, was recovered within the same clade with, and basal to, a close-knit group of Late Cretaceous Eastern and Central Asian taxa such as *Bactrosaurus johnsoni*, *Levnesovia transoxiana* and *Tanius sinensis* by Tsogtbaatar et al. (2014), or else joined with the Asian *Penelopognathus weishampeli* and the North American *Lophorhothon atopus* by Prieto-Márquez & Carrera Farias (2021).

Similarly, *Tethyshadros* was found to be closely related to the latest Early Cretaceous *Jintasaurus meniscus* from western China (You & Li, 2009) by Ramírez-Velasco et al. (2012); in the final rendering of their phylogenetic analysis, however, *Telmatosaurus*, together with other hadrosauroids, was removed in order to improve resolution within the resulting tree. Still other analyses allied the Italian hadrosauroid with the Asian *Nanyangosaurus zhugeii* and *Gilmoreosaurus mongoliensis* as well as with the North American *Jeyawati rugoculus* and *Protohadros byrdi* (McDonald, Bird, et al., 2012), or else found it nested within a large polytomy with mostly Asian hadrosauroids (*Shuangmiaosaurus gilmorei*, *Levnesovia transoxiana*, *Gilmoreosaurus mongoliensis*, *Bactrosaurus johnsoni*, *Gobihadros mongoliensis*) besides *Claosaurus agilis*, and still lying outside Hadrosauridae (Tsogtbaatar et al., 2019).

Finally, Prieto-Márquez & Carrera Farias (2021) identified a novel sister-taxon relationship between *Tethyshadros* and their newly described *Fylax thyrakolasus* from the uppermost Cretaceous of northern Spain, whereas *Telmatosaurus* was placed in a somewhat more basal position, closely related to the latest Early Cretaceous (Albian) *Penelopognathus weishampeli* reported from Inner Mongolia by Godefroit et al. (2005). Our results depart markedly, albeit in different ways in the two analyses, from those of Prieto-Márquez

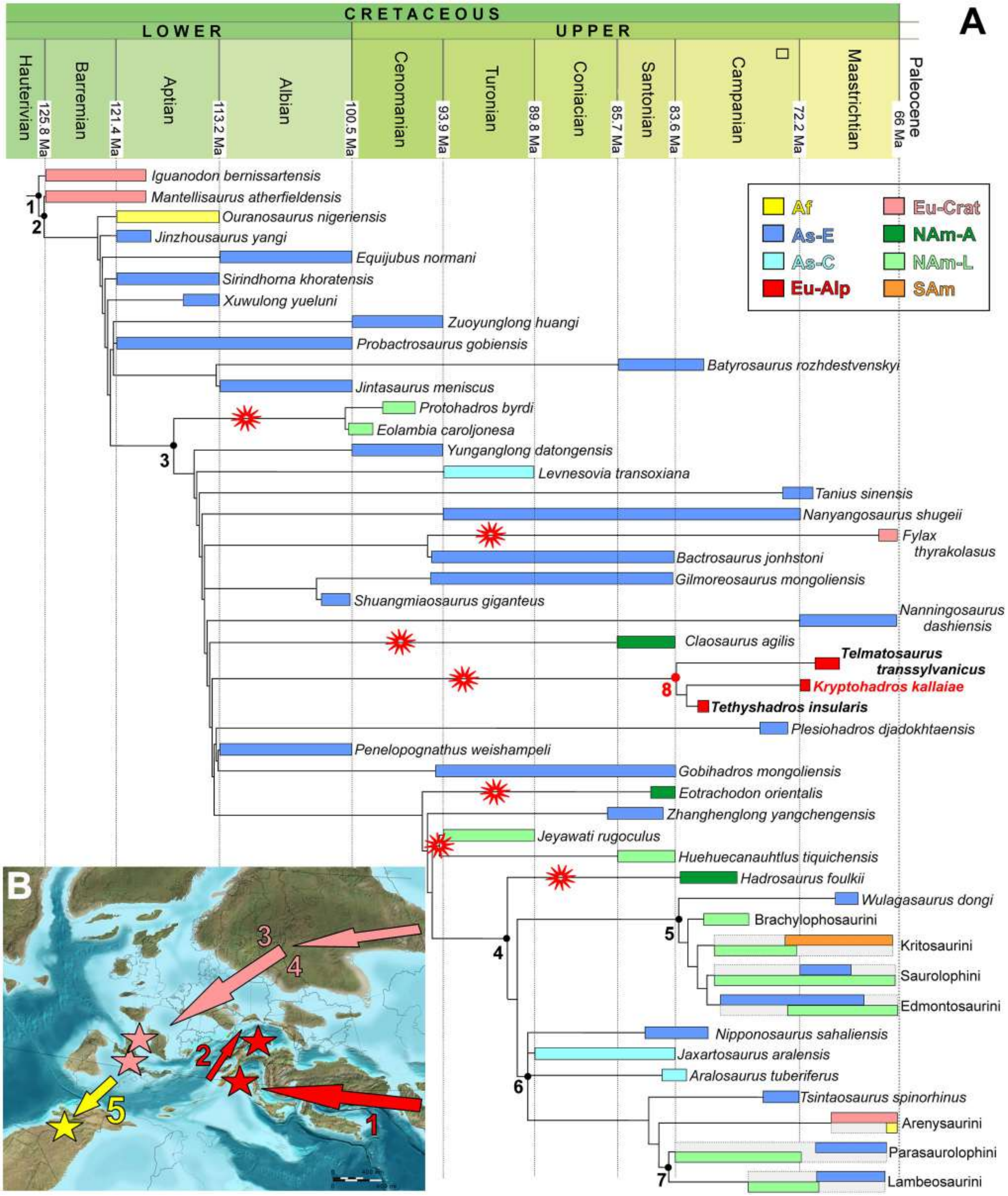
& Carrera Farias (2021). Indeed, *Fylax* appears in a more basal position than any of the other previously mentioned hadrosauroids in the first phylogenetic analysis (mirroring in this particular respect the original assessment of Prieto-Márquez & Carrera Farias, 2021, regarding the evolutionary grade of this taxon), and is definitively not closely related to any of the telmatosaurids, thus refuting the hypothesis of a close-knit *Fylax–Tethyshadros* grouping recovered by those authors. On the other hand, the Spanish hadrosauroid is retrieved in a significantly more derived position than that proposed by Prieto-Márquez & Carrera Farias (2021) in our second phylogenetic analysis, where it clusters within Hadrosauridae as the sister-taxon of Euhadrosauria (*sensu* Madzia et al., 2021), and again showing no close ties to Telmatosauridae.

Furthermore, in our results several of the other non-hadrosaurid hadrosauroid taxa mentioned above are recovered as members of exclusively eastern European (*Tethyshadros*, *Telmatosaurus* – our Telmatosauridae) and, respectively, exclusively eastern Asian (*Penelopognathus*, together with the early Late Cretaceous *Gobihadros* and the latest Cretaceous *Plesiohadros*) clades. Intriguingly, McDonald et al. (2021) even found a sister-group relationship between this eastern European hadrosauroid clade and an eastern Asian one made up by *Plesiohadros* alongside the latest Early Cretaceous *Shuangmiaosaurus gilmorei* (You, Ji, et al., 2003) and the middle Late Cretaceous *Zhanghenglong yangchengensis* (Xing et al., 2014). All these different positions and relationships identified for the same taxa both by previous as well as by our own analyses suggest that the phylogeny of non-hadrosaurid hadrosauroids is still in a flux, and that identification of new taxa may shift and rearrange previously proposed topologies in novel and often unexpected ways.

In conclusion, our identification of the second hadrosauroid taxon from the latest Cretaceous Haţeg Island, found to be closely related to both *Telmatosaurus* and *Tethyshadros*, revives the hypothesis of a relatively derived, endemic south-eastern European clade of non-hadrosaurid hadrosauroids (here named Telmatosauridae) present in this area of Alpine Europe in the latest Cretaceous (see Csiki-Sava et al., 2015). This grouping is here recognized as comprising all currently nominally erected taxa from this area, and is supported primarily by a series of dental features (see above). Meanwhile, most other putative hadrosauroid remains reported from this wider region are either represented exclusively by postcranial remains (e.g. Godefroit & Motchurova-Dekova, 2010; Lopatin et al., 2018; Nikolov et al., 2024) and thus their potential membership within Telmatosauridae cannot be ascertained in the present, or else were recently shown to fall outside Hadrosauroidea (e.g. *Riabininohadros weberae*; Lopatin & Averianov, 2020). Nonetheless, it is possible that at least some of these other south-eastern European hadrosauroids (although probably not those from Crimea, whose place of occurrence on the cratonic parts of the Late Cretaceous European Archipelago was palaeogeographically segregated from that of the island-dwelling hadrosauroids of southern and south-eastern Europe; see Csiki-Sava et al., 2015) may turn out to be further representatives of this clade (see below, Palaeobiogeographical implications).

Palaeobiogeographical implications

Recognition of a latest Cretaceous endemic south-eastern European non-hadrosaurid hadrosauroid clade, with its updated membership now including *Kryptohadros kallaiae* as well, also invites a reassessment of the evolutionary and palaeobiogeographical significance of its members. According to our results, the three southern and south-eastern European basal hadrosauroids form a closely related group with a common evolutionary origin – i.e. Telmatosauridae – lying close to, but not very near, the base of Hadrosauridae, within a plexus of mainly Asian taxa with a sprinkling of Appalachian and southern Laramidian ones. Although the strict consensus tree of the first analysis using the updated version of the Longrich, Pereda-Suberbiola, et al. (2024) dataset (Fig. 13A) recovered most of these taxa (including the clade of south-eastern European hadrosauroids) within a wide polytomy, the resulting majority rule consensus tree (Fig. 13B), further supported both by the maximum agreement subtree as well as by the implied weighting analysis (supporting data figs 4–6 in Magyar et al., 2025), and convergently also by the results of our second analysis (Fig. 14) based on the matrix of Dai et al. (2025), is somewhat better resolved in this part of the phylogeny, revealing a pectinate palaeogeographical distribution of the different basal hadrosauroids investigated – a pattern that suggests several different episodes of faunal interchange between the various northern, Laurasian landmasses (Fig. 15). Given that details of the majority rule consensus tree topology differ between our two analyses (compare Fig. 13B and Fig. 14), the following palaeobiogeographical evolution assessment is based largely on the results of the first, more comprehensive analysis with a wider taxonomic and palaeogeographical coverage (Fig. 15). Nonetheless, we acknowledge that certain aspects of the outlined scenario (such as the number and precise timing of the intercontinental dispersal episodes) may be altered in the future by discovery of new taxa as well as by new, more in-depth analyses, especially using quantitative


A
CRETACEOUS
LOWER
UPPER
Hauterivian
125.8 Ma
Barremian
121.4 Ma
Aptian
113.2 Ma
Albian
100.5 Ma
Cenomanian
93.9 Ma
Turonian
89.8 Ma
Coniacian
85.7 Ma
Santonian
83.6 Ma
Campanian
72.2 Ma
Maastrichtian
66 Ma
Paleocene
Af
Eu-Crat
As-E
NAm-A
As-C
NAm-L
Eu-Alp
SAm
1
2
Iguanodon bernissartensis
Mantellisaurus atherfieldensis
Ouranosaurus nigeriensis
Jinzhousaurus yangi
Equijubus normani
Sirindhorna khoratensis
Xuwulong yueluni
Zuoyunglong huangi
Probactrosaurus gobiensis
Batyrosaurus rozhdestvenskyi
Jintasaurus meniscus
Protohadros byrdi
Eolambia caroljonesa
3
Yunganglong datongensis
Levnesovia transoxiana
Tanius sinensis
Nanyangosaurus shugeii
Fylax thyrakolasus
Bactrosaurus jonhstoni
Gilmoreosaurus mongoliensis
Shuangmiaosaurus giganteus
Nanningosaurus dashiensis
Claosaurus agilis
Telmatosaurus transsylvanicus
8
Kryptohadros kallaiae
Tethyshadros insularis
Plesiohadros djadokhtaensis
Penelopognathus weishampeli
Gobihadros mongoliensis
Eotrachodon orientalis
Zhanghenglong yangchengensis
Jeyawati rugoculus
Huehuecanauhtlus tiquichensis
Hadrosaurus foulkii
Wulagasaurus dongi
5
Brachylophosaurini
Kritosaurini
Saurolophini
Edmontosaurini
4
Nipponosaurus sahaliensis
Jaxartosaurus aralensis
Aralosaurus tuberiferus
6
Tsintaosaurus spinorhinus
Arenysaurini
Parasaurolophini
7
Lambeosaurini
B
1
2
3
4
5

palaeobiogeographical methods. Be that as it may, we contend that its main conclusions (the significance of the newly recovered endemic Telmatosauridae, or the occurrence of several waves of out-of-Asia faunal dispersal events along distinct migration pathways) are rather robust and worth reporting.

It has been often assumed that the origin of these eastern European non-hadrosaurid hadrosauroids lies in a more basal stock of Asian hadrosauroids, as Asia was identified since long as the potential area of origin of the hadrosauroids (e.g. Godefroit et al., 2005; R.-F. Wang et al., 2017; Shibata et al., 2015; You & Li, 2009; You, Luo, et al., 2003). Consequently, in order to accommodate the complex palaeobiogeographical distribution pattern of higher hadrosauroids, several subsequent dispersal events were suggested to occur outward of Asia either between this landmass and western North America (Laramidia; e.g. Bolotsky & Godefroit, 2004; McDonald, Bird, et al., 2012; Ramírez-Velasco et al., 2012; Sues & Averianov, 2009; Tsogtbaatar et al., 2019), or else towards Europe (e.g. Chiarenza et al., 2021; Csiki-Sava et al., 2015; Dalla Vecchia, 2009b; Longrich et al., 2021; Longrich, Pereda-Suberbiola, et al., 2024; Prieto-Márquez & Carrera Farias, 2021; Sues & Averianov, 2009). The latter area was also regarded as eventually representing a mid-journey stop within a far-reaching dispersal event towards eastern North America (Appalachia; Brownstein, 2021; Prieto-Márquez & Carrera Farias, 2021), and our phylogenetic results are consistent with such a general scenario.

Indeed, the pectinate pattern displayed by the palaeogeographical distribution of the different non-hadrosauroid hadrosaurids in our first analysis (Fig. 15A) suggests the potential occurrence of at least another six different out-of-Asia dispersal events ranging in age from the Albian-Cenomanian to the Campanian, besides that of the ancestors of the eastern European Telmatosauridae. These are required to explain the presence of such different non-Asian lineages as the Ibero-Armorican *Fylax*, the Appalachian *Claosaurus* and *Eotrachodon*, as well as two small southern Laramidian groupings, the earlier (mid-Cretaceous) and more basal *Protohadros*-*Eolambia* clade, respectively the later-occurring (mid Late Cretaceous) and more derived *Jeyawati*-*Huehuecanauhtlus* clade, and finally the Appalachian basal-most hadrosaurid *Hadrosaurus*.

Meanwhile, having recovered all better-known south-eastern European Late Cretaceous hadrosauroids within one clade, our phylogenetic results also alleviate the need to hypothesize distinct dispersal events to account for the presence of both *Tethyshadros* and *Telmatosaurus* in this area (as required, e.g., by the palaeobiogeographical results of Prieto-Márquez & Carrera Farias, 2021). Indeed, these indicate that one single, pre-Campanian dispersal from Asia may have been responsible for the introduction of the ancestor(s) of Telmatosauridae into the south-eastern, Alpine part of the Late Cretaceous European Archipelago (Fig. 15B). Our results also raise the possibility of a second, distinct immigration episode of Asian origin into south-western Europe (i.e. Ibero-Armorican Landmass) implicating other hadrosauroids that gave rise to the very late-surviving *Fylax* in the western sector of the Late Cretaceous European Archipelago (Fig. 15B). Given that these two latest Cretaceous European hadrosauroid lineages appear not to be closely related, the route taken by this second dispersal event must have circumvented the more palaeogeographically-tectonically dynamic Alpine sector of the European archipelago, and connected Asia directly to its cratonic western part in order to account for the presence of *Fylax* – a dispersal route whose existence and functioning was suggested previously by Csiki-Sava et al. (2015) in the case of basal lambeosaurines and zhelestid eutherians.

In this regard, it is also worth noting that at least some recent phylogenetic analyses (including our own,

Figure 15. **A,** Simplified and time-calibrated phylogram of Hadrosauriformes, based on the results of the first phylogenetic analysis (see Fig. 13B for details; clade definitions mainly follow Madzia et al., 2021), highlighting the biogeographical distribution of the different taxa (colour legend in inset); data derived from references cited throughout the text. Red stars mark probable out-of-Asia dispersal events up to the origin of Hadrosauridae. Chronostratigraphical scale after Cohen et al. (2013, updated 2024). Legend for clades: 1, Hadrosauriformes; 2, Hadrosauroidea; 3, Hadrosauromorpha; 4, Hadrosauridae; 5, Saurolophinae; 6, Lambeosaurinae; 7, Corythosauria; 8, Telmatosauridae new clade (highlighted in red). **Abbreviations of biogeographical subdivisions: Af**, Africa; **As-E**, Eastern Asia; **As-C**, Central Asia; **Eu-Alp**, Alpine areas of the Late Cretaceous European Archipelago (south-eastern Europe); **Eu-Crat**, cratonic areas of the Late Cretaceous European Archipelago (south-western, western, northern and eastern Europe); **NAm-A**, Appalachia (eastern North America); **NAm-L**, Laramidia (western North America); **SAm**, South America (Patagonia). **B,** Campanian palaeogeographical map of Europe, showing the distribution of latest Cretaceous hadrosauroids, as well as hypothesized dispersal events and routes (numbered arrows) into Europe (see text and Fig. 15A for details). Legend: 1, dispersal of ancestral Telmatosauridae into Eu-Alp, before the earliest Campanian; 2, dispersal of Telmatosauridae within Eu-Alp, before the latest Campanian; 3, and 4, dispersal of the ancestors of *Fylax thyrakolasus*, respectively of Arenysaurini into Eu-Crat, before the later part of early Maastrichtian; 5, dispersal of Arenysaurini into north-western Africa, before the latest Maastrichtian (palaeogeographical map, courtesy of R. Blakey).

see Figs 13, 14) recovered one comprehensive clade of Ibero-Armorican (and subsequently north-western African) basal lambeosaurines, the Arenysaurini (e.g. Longrich et al., 2021; Longrich, Pereda-Suberbiola, et al., 2024). This clade is supposed to include all derived Maastrichtian hadrosauroids from this area, unlike the results of previous research that identified the presence of several different, both basal and derived, lambeosaurine lineages in the Ibero-Armorican assemblages (e.g. Cruzado-Caballero et al., 2013; Prieto-Márquez et al., 2013; Prieto-Márquez & Wagner, 2009). Such a topology would imply, similar to the case of Telmatosauridae, just one immigration event of Asian origin that occurred during the early Maastrichtian at the latest (Fig. 15B), and was followed by *in situ* diversification in Ibero-Armorica. This would explain the presence of all these western European lambeosaurines parsimoniously, in contrast to earlier, more complex scenarios that called for the synchronous introduction of several distinct lambeosaurine lineages of both Asian and Laramidian origin (e.g. Csiki-Sava et al., 2015 and references therein). Given that, just as in the case of *Fylax* discussed previously, neither did this second Asia-sourced latest Cretaceous dispersal event leave any trace in the south-eastern part of the European Archipelago, it probably also followed a similar northern, cratonic route as the one used by the hadrosauroids ancestral to the former taxon. It is furthermore also conceivable that these two range expansions took place more or less at the same time, during the early-middle part of the Maastrichtian, as both the more basal hadrosauroid *Fylax* and the different arenysaurins show up in the fossil record roughly concomitantly in upper Maastrichtian beds of southern France, Spain and Morocco (Fig. 15).

Returning to the close relationships of the south-east European basal hadrosauroids found in our analyses, one must assume the presence of a palaeogeographical connection between the Adriatic-Dinaric Carbonate Platform, hosting the lower Campanian north-eastern Italian site of Villaggio del Pescatore from where *Tethyshadros* originates (Chiarenza et al., 2021; Dalla Vecchia, 2009b), and the Maastrichtian hadrosauroid-bearing localities of the Tisia-Dacia Block (or Haţeg Island). It follows that, while arriving in the eastern part of the Late Cretaceous European Archipelago, basal hadrosauroids of most probably Asian origin (see above) reached the Adriatic–Dinaric Carbonate Platform and gave rise to *Tethyshadros* by the early Campanian at the latest. Afterwards, by the latest Campanian, representatives of Telmatosauridae also reached Haţeg Island (e.g. Ebner et al., 2025). The path of this northward range expansion may even be tracked by fossil remains discovered in two uppermost Cretaceous vertebrate localities of the northern Balkan Peninsula. The first of these occurrences, yielding mainly isolated, but well-preserved teeth, is reported from an upper Campanian-Maastrichtian locality near Kozina, Slovenia (Debeljak et al., 1999, 2002); among these teeth, referred previously to Hadrosauridae and Iguanodontidae, morphotypes 1 and 2 described in Debeljak et al. (2002) have very similar morphology to the teeth of *Tethyshadros*. More recently, indeterminate hadrosauroid remains that can potentially track this northward expansion of Telmatosauridae were also reported from the Vrabchov Dol locality near Tran, in western Bulgaria (of latest Santonian to early Campanian in age; Nikolov et al., 2025). Such a scenario of possible palaeobiogeographical connections between these areas (Villagio del Pescatore, Kozina, Vrabchov Dol, and the Transylvanian area) appears to be further supported by the shared presence of eusuchian crocodyliforms reminiscent of the genus *Acynodon* (Botfalvai et al., 2021; Csiki-Sava et al., 2016; Debeljak et al., 2002; Delfino et al., 2008; Martin et al., 2006; Muscioni et al., 2024; Nikolov et al., 2025).

Since our phylogenies suggest that *Kryptohadros* is more closely related to *Tethyshadros* than to its sympatric relative *Telmatosaurus*, it seems that the two Transylvanian taxa represent lineages that diverged well before they reached Haţeg Island and colonized it independently. This scenario of independent colonizing lineages may be also supported by the slight morphological differences between the earliest known (latest Campanian) Transylvanian hadrosauroid fossil (the isolated humerus EME 318 from Petreşti) and the hadrosauroid humeri (SZTFH Ob.3112 and Ob.3126) from the Vălioara area, combined with the closer similarity of EME 318 to humeri from the Sînpetru Formation (NHMUK R.3842, R.3845 and R.3847), as also indicated by Ebner et al. (2025).

Regardless of the precise details of this chain of colonization events, the presence of closely related telmatosaurid hadrosauroids on the Adriatic-Dinaric Carbonate Platform and Haţeg Island, respectively, clearly indicates opportunities for such biotic interchanges to take place during the latest Cretaceous between these landmasses. It thus suggests at least occasionally ongoing active and dynamic faunal connections between different parts of the archipelago, despite their palaeogeographically isolated nature and largely endemic local faunal assemblages (e.g. Csiki-Sava et al., 2015). Indeed, latest Cretaceous faunal connections between Haţeg Island and other European landmasses were already documented recently by Augustin et al. (2022) who pointed out potentially closer relationships of the newly described rhabdodontid *Transylvanosaurus* from Hațeg Basin to taxa from southern France instead of its sympatric relative *Zalmoxes*, indicating potential eastern–western palaeobiogeographical connections. Similar inter-island connections are supported even more poignantly by the results of Díez Díaz et al. (2025) who identified several immigration waves of distinct, not closely related titanosaur lineages onto Hațeg Island during the latest Campanian to Maastrichtian time interval.

On the other hand, our identification of a distinct south-eastern European non-hadrosaurid hadrosauroid lineage (Telmatosauridae), as opposed to the presence of another, distinct hadrosauroid lineage alongside an endemic western European lambeosaurine clade (the arenysaurins of Longrich et al., 2021) on the Ibero-Armorican Landmass replicates more overarching palaeobiogeographical patterns identified within the Late Cretaceous European Archipelago by Csiki-Sava et al. (2015). In that work, the authors recognized an important biogeographical divide between the tectonically active south-eastern Alpine sector of the archipelago and its western and northern, cratonic one. The presence of an endemic Telmatosauridae in south-eastern Europe thus reinforces the previously suggested pattern of Alpine versus cratonic palaeofaunistic distinction, and mirrors recently identified dissimilarities between latest Cretaceous eastern and western European titanosaur assemblages, mainly comprising members of not closely related phyletic lineages (Díez Díaz et al., 2025).

Hadrosauroid faunal differentiation and provincialism within Hațeg Island

The faunal assemblages recovered from the Densuș-Ciula and Sînpetru formations of Hațeg Basin had been historically considered to be largely identical at both higher and lower taxonomic levels. These earlier works thus often referred subsequently discovered fossil remains in an uncritical manner to already established species- or genus-level taxa (e.g. Codrea et al., 2010; Grigorescu, 1983, 1992, 2005; Nopcsa, 1915, 1923; Vremir et al., 2015; Weishampel et al., 1991, 1993, 2003, and references cited therein); on their turn, such perceived close faunal similarities were cited to support close chronostratigraphical correspondence between these rock units (e.g. Grigorescu, 1992; Nopcsa, 1905, 1923). More recent and detailed investigations, based on more precise chronostratigraphical constraints combined with apomorphy-focused taxonomic approaches, have suggested nonetheless that these different faunal assemblages reported from across the Transylvanian area are not entirely time-correlative (e.g. Csiki-Sava et al., 2016), and furthermore they may display regional differences both in their higher-level taxonomic composition (e.g. Treiber et al., 2025; Vremir et al., 2014) as well as in representation at the genus and/or species level (e.g. Augustin et al., 2022; Csiki-Sava, Vremir, et al., 2022; Díez Díaz et al., 2025; Magyar et al., 2024).

These observations that noted recurrent lower-level taxonomic differences between different lithostratigraphical units of Hațeg Basin are consistent with our identification of a new hadrosauroid taxon from site Fântânele-3 at Vălioara, north-western Hațeg Basin. The type locality of *Kryptohadros kallaiae* belongs to the lower part of the Middle Member of the Densuș-Ciula Formation, whereas the lectotype of *Telmatosaurus transsylvanicus* originates from Nopcsa's 'Nest 1' site (whose exact position is unclear, though it most probably lies within the lower Sînpetru Formation) at Sânpetru locality, central Hațeg Basin. The presence of the new hadrosauroid taxon at Vălioara further emphasizes the taxonomic distinctiveness reported previously between the different local faunal assemblages of Hațeg Basin for rhabdodontids (e.g. Augustin et al., 2022; Magyar, 2023; Magyar et al., 2024), titanosaurs (e.g. Csiki, Codrea, et al., 2010; Díez Díaz et al., 2025) and multituberculates (e.g. Codrea et al., 2017; Csiki-Sava, Vremir, et al., 2022), and begets an in-depth investigation as to whether such faunal differences are driven by spatial (provincialism, geographical isolation), temporal (partial diachronism of the hosting deposits) or ecological (habitat preferences, special resource requirements) causes, or else a combination thereof. Such an endeavour is beyond the scope of our present study as it requires thorough re-description and re-diagnosis of the historical taxa as well as completion of the detailed taxonomic assessment of older or more recently discovered important specimens and fossil assemblages, a work that is currently underway (e.g. Augustin et al., 2025; Botfalvai et al., 2021, 2025; Díez Díaz et al., 2025). Nonetheless, currently available data may already offer some interesting insights in this respect.

As already noted, the exact place of origin cannot be ascertained for the lectotype specimen of *Telmatosaurus transsylvanicus*, as only very limited and vague information (in the form of brief general mentions) is available about the position of Nopcsa's 'nest 1' (e.g. Nopcsa, 1900). However, according to these original notes, the site should be located somewhere in the middle part of the Sibișel Valley outcropping section of the Sînpetru Formation (see also comments in Dumbravă et al., 2016: supplementary material 1). If so, it would fall in the middle to upper part of the informal lower subdivision of the Sînpetru Formation (see Csiki-Sava et al., 2016; Grigorescu, 1983, 1992; Therrien, 2006), loosely putting its age into the later part of the early Maastrichtian to early part of the late Maastrichtian time interval. Meanwhile, recently acquired biostratigraphical and radiometric age constraints from the Vălioara study area (Albert et al., 2025) narrow down the age of the fossiliferous deposits at Fântânele-3 – and thus also that of *K. kallaiae* – to the early part of the early Maastrichtian, making *Kryptohadros* most probably somewhat older than the lectotype of *T. transsylvanicus*. Currently available evidence would thus indicate a slight diachronism between *Kryptohadros* and *Telmatosaurus*, suggesting that their taxonomic distinctiveness may be at least in part due to them being members of not strictly contemporary palaeo-communities. Nevertheless, it should be emphasized that age constraints are rather poor for the entire Sibișel Valley section of the Sînpetru Formation, seriously limiting the precision in estimating the potential age of the latter taxon.

Based on the available geological and sedimentological observations, the deposits cropping out at Fântânele-3 indicate a dominantly wet, proximal wetland-type accumulation characterized by swampy, ponding waters preserved within abandoned fluvial channels; these were formed in a distal alluvial fan setting under conditions of a relatively low sedimentation rate (Albert et al., 2025). Coalified fragments representing woody plant parts were also collected from the fossiliferous layer containing the partial skeleton of *Kryptohadros*, while small fragments of dark orange coloured amber drops and black, hexagonal termite coprolites were recovered from the screen-washed rock matrix; together with the recently reported palynological data (Albert et al., 2025), all these organic remains testify for the presence of a forested setting around the original depositional area. Meanwhile, palaeoenvironmental reconstructions of the lower subunit of the Sînpetru Formation suggest the presence of a shifting mosaic of wetlands, seasonal wetlands and moderately well-drained floodplains within a low-sinuosity braided river environment (Therrien, 2006; Therrien et al., 2009). Despite small differences between the palaeoenvironments reconstructed for the type localities of the two Transylvanian hadrosauroids, both indicate rather water-logged environments inhabited by the Haţeg telmatosaurids. Their palaeoenvironmentally biased distribution stands in contrast, however, with earlier conclusions by Csiki, Grigorescu, et al. (2010) who identified no obvious habitat preferences for hadrosauroids given the wide distribution of their fossil remains in the different lithofacies/sedimentary environments represented in Haţeg Basin, and also departs from the tentative suggestion of Ebner et al. (2025) who noted that the appearance of the currently known earliest Haţeg Island hadrosauroid remains seems to correlate with a palaeoenvironmental shift from wetter coastal plain environments to more better-drained alluvial floodplains. Establishing the presence (or absence) of potential palaeoenvironmental preferences of the different Transylvanian hadrosauroids, and whether such preferences influenced their geographical distribution, requires a more in-depth study of their taxonomic identity and spatial distribution patterns.

Finally, it must also be noted that some isolated hadrosauroid fossils that also originate from the Vălioara area – such as the above-mentioned coronoid process (SZTFH Ob.3068) with a convex posterior edge lacking a triangular posterior lobe, as well as a pair of frontals (NHMUK R.4915) mentioned by Weishampel et al. (1993), with a probably open fontanelle – presumably do not belong to *Kryptohadros kallaiae* (work in progress). If such preliminary assessments will be upheld by future studies, the presence of these fossils may suggest some degree of sympatry between *Kryptohadros* and a second hadrosauroid taxon that appears to show affinities to those known from the Sînpetru Formation. It should be emphasized here, nonetheless, that such cases of sympatric occurrences of closely related dinosaur taxa within the same lithostratigraphical unit are not uncommon in Haţeg Basin, having been reported previously for the two currently known species of the rhabdodontid *Zalmoxes* both in the Sînpetru Formation (Godefroit et al., 2009; Magyar et al., 2024) and in the ‘Râul Mare Beds’ (Brusatte et al., 2017). Ongoing investigations indicate that two different rhabdodontid taxa may be represented at the Tuștea nesting site in the upper part of the Middle Member of the Densuș-Ciula Formation, as well (e.g. Augustin et al., 2025).

Even more remarkable in this respect is the recent suggestion that two different (albeit not yet formally recognized) rhabdodontid taxa co-occur at Vălioara (Magyar et al., 2024), while loosely constrained sympatry of different titanosaur taxa (some nominal, others not diagnostic enough to be recognized as such, despite their clear morphological distinctiveness) had also been identified recently by Díez Díaz et al. (2025) in the same area. Both of these cases of sympatry occur within the lower Densuș-Ciula Formation, thus within the same subunit that also yielded the remains of *Kryptohadros* as well as those of the second potential hadrosauroid taxon mentioned above. It appears then that the latest Cretaceous continental ecosystems of Haţeg Basin were characterized both by relatively high local diversity (at least in the Vălioara area, during the early Maastrichtian), as well as by some degree of regional faunal provincialism of the herbivorous dinosaur assemblages, inclusively in the case of the hadrosauroids.

Conclusions

The discovery and investigation of a partial associated skeleton of a hadrosauroid dinosaur at Vălioara, in north-western Hațeg Basin, has prompted a critical re-evaluation of the sole previously known representative of this group from the Transylvanian area – *Telmatosaurus transsylvanicus*. Stemming from this reassessment, here we provide a revised and updated diagnosis of *T. transsylvanicus* based on the lectotype skull (NHMUK R.3386), highlighting a newly recognized unique combination of characters that diagnose this taxon. Furthermore, we propose restricting the list of specimens that can currently be reliably assigned to *T. transsylvanicus*. Pending a more thorough revision of the material formerly referred to this taxon, we refer to it solely elements that are overlapping with, and directly comparable to, the lectotype, and in the same time originate from the type area of this taxon.

In addition, we erect and describe here a new genus and species of non-hadrosaurid hadrosauroid, *Kryptohadros kallaiae* gen. et sp. nov., based on the above-mentioned incomplete skeleton that includes both cranial and postcranial elements. This individual (LPB [FGGUB] R.2882) comes from the newly discovered Fântânele-3 site near Vălioara representing the deposits of the lower part of the Middle Member of the Densuș-Ciula Formation. The dimensions of the recovered elements, as well as the degree of fusion of the neural arches to the caudal centra, suggest that the holotype individual was likely at least subadult. Identification of this new taxon shows that the Late Cretaceous hadrosauroid fauna of south-eastern Europe was more taxonomically diverse, as well as geographically and chronologically wider-ranging than previously thought.

Our phylogenetic analyses including *K. kallaiae* show that this taxon is a close relative of *Telmatosaurus transsylvanicus* and of *Tethyshadros insularis*, and together they form a distinct clade (here named Telmatosauridae) outside the derived hadrosaurids. Diagnostic apomorphies of this clade are derived mainly from their jaws and dentition. In addition, the presence of a notch in the posterobasal part of the anterior caudal neural spines may also support close relationships between these taxa. In turn, *Kryptohadros* shows several autapomorphic features within this clade, and furthermore it also possesses an apomorphic combination of characters, but also some features that are present in one or the other of its two close relatives.

This small, endemic telmatosaurid clade with an Asian origin appears to have reached the south-eastern sector of the European Archipelago before the major latest Cretaceous diversification of the derived hadrosaurids. Besides the migration involving the ancestors of Telmatosauridae, phylogenetic relationships between the other different hadrosauroid evolutionary lineages recognized in our phylogenetic analyses suggest that at least six other dispersal events took place from the Albian to the Maastrichtian from Asia towards Europe and/or North America; however, detailed assessment of these faunal exchanges requires further, preferably qualitative investigations.

Finally, the identification of *Kryptohadros* also documents faunal differentiation of the hadrosauroids between the different Upper Cretaceous continental formations of Hațeg Basin, one that mirrors similar patterns identified before for other vertebrates, and suggests potentially more complicated palaeoenvironmental affinities of these animals on Hațeg Island. Furthermore, an at least partial sympatry in the Vălioara area between the new taxon and a second hadrosauroid cannot be excluded, either, replicating patterns reported previously for rhabdodontids and titanosaurs, and indicating a relatively high diversity of these dinosaurian megaherbivores in the local fauna.

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Author contributions

JM and GB conceptualized the research and collected the material, with support from SB for sedimentological investigations. JM, ZCSS, ŐA, SB and GB interpreted the results and wrote the first version of the manuscript. GB and ZCSS provided financial support and project administration. All authors critically edited the manuscript.

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Data availability statement

All data supporting the findings of this study are openly available through Zenodo at https://doi.org/10.5281/zenodo.17550540 (Magyar et al., 2025).

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