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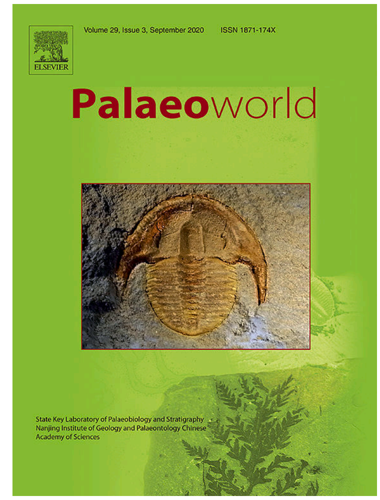

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First hadrosauroid record from Petreşti-Arini (Transylvanian Basin, Romania; Upper Cretaceous) and its implications for the evolution of the Haţeg Island vertebrate faunas

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Abstract

The uppermost Cretaceous continental deposits of Transylvania (western Romania) represent one of the most iconic sources for fossil vertebrates from the Late Cretaceous European Archipelago. Among the numerous uppermost Cretaceous sites known from the Transylvanian Basin, Petreşti-Arini is one of the most important, due to its geological age and preservation of an unusual transitional near-shore environment. Current knowledge of the local vertebrate assemblage included many of the groups typically present in the Upper Cretaceous of Romania but not the hadrosauroids or titanosaurs. In this report, we describe a right humerus of a hadrosauroid discovered at Petreşti-Arini in the lower part of the Sebeş Formation. The humerus can be confidently assigned to a basal hadrosauroid based on its long and robust deltopectoral crest (45% of the humeral length) that is nevertheless shorter than in derived members of the clade (in which the deltopectoral crest is > 55% of humeral length). The specimen represents the first record of hadrosauroids from Petreşti-Arini, dated to around the latest Campanian, making it not only the stratigraphically oldest record of hadrosauroids in the Transylvanian Basin but also one of their earliest well-constrained occurrences across Haţeg Island overall. The specimen refines previous scenarios and gives a better age constraint on the arrival of hadrosauroids to Haţeg Island, documenting their introduction to this area before the end of the Campanian. Additionally, it might imply some sort of paleoenvironmental control over hadrosauroid distribution on Haţeg Island.

Keywords: Hadrosauroidea; Haţeg Island; Late Cretaceous European Archipelago; Transylvanian Basin; Late Cretaceous; paleobiogeography

1. Introduction

Transylvania in western Romania represents one of the most iconic regions for dinosaur discoveries in Europe, and during the Late Cretaceous, this area was part of the famous Haţeg Island (e.g., Codrea et al., 2010; Csiki-Sava et al., 2015). Nowadays, the sedimentary rocks that were formed on this island crop out mainly in the Haţeg and Transylvanian basins (e.g., Codrea et al., 2010; Csiki-Sava et al., 2016). Vertebrate discoveries in the continental uppermost Cretaceous deposits of Transylvania were initiated more than 120 years ago, beginning with the work of Ferenc Nopcsa, one of the most renowned vertebrate paleontologists of the 20th century (e.g., Nopcsa, 1900). Among the numerous uppermost Cretaceous Transylvanian localities, the relatively recently discovered locality Petreşti-Arini stands out due to its old geological age and preservation of an unusual near-shore environment (Vremir et al., 2014; Csiki-Sava et al., 2016; Bălc et al., 2024). As currently known, the local paleofauna at Petreşti-Arini includes many of the groups typically present in the Upper Cretaceous of Romania including dortokid turtles, diverse crocodyliforms like the eusuchian *Allodaposuchus*, common rhabdodontid ornithopods, ankylosaurs, theropods, azhdarchid pterosaurs, and kogaionid mammals (Vremir, 2010; Vremir et al., 2014, 2015; Vasile et al., 2021; Csiki-Sava et al., 2022). However, other typical and elsewhere abundant taxa were undocumented from here until now, including the more terrestrial kallokibotionine turtles, as well as titanosaurs and hadrosauroids (Vremir et al., 2014; Bălc et al., 2024).

In this study, we describe an isolated humerus from Petreşti-Arini, representing the first evidence of hadrosauroids from this locality. Deposition of the continental units within which the hadrosauroid humerus was discovered started during the late Campanian, which makes this specimen one of the oldest hadrosauroid records from Romania (Vremir et al., 2014; Csiki-Sava et al., 2016). As such, its occurrence sheds further light on previously formulated hypotheses about the composition and evolution of the Haţeg Island vertebrate faunas.

Institutional abbreviations: EME, Transylvanian Museum Society, Cluj-Napoca, Romania; **IPS**, Institut de Paleontologia Dr. M. Crusafont, Sabadell, Barcelona, Spain; **LPB (FGGUB)**, Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; **MCD**, Museu de la Conca Dellà, Isona, Spain; **MDE**, Musée des Dinosaures, Espéraza, France; **MTM**, Magyar Természettudományi Múzeum, Budapest, Hungary; **NHMUK**, Natural History Museum, London, UK; **SC**, Italian State collections, deposited at the Museo Civico di Storia Naturale, Trieste, Italy; **SZTFH**, Collection of the Supervisory Authority for Regulatory Affairs (formerly the Geological Institute of Hungary (MAFI)), Budapest, Hungary.

Anatomical abbreviations: dpc, deltopectoral crest; **gtb**, greater tuberosity; **hh**, humeral head; **icg**, intercondylar groove; **ltb**, lesser tuberosity; **pm**, proximal margin; **rc**, radial condyle; **uc**, ulnar condyle.

2. Geological setting

The humerus specimen EME 318 was discovered in the Sebeş Formation at Petreşti-Arini (southwestern Transylvanian Basin, western Romania). The Transylvanian Basin, surrounded by the Carpathians to the east and south, and by the Apuseni Mountains to the west, hosts extensive uppermost Cretaceous continental sedimentary rocks cropping out mainly along its western margin (e.g., Codrea et al., 2010; Csiki-Sava et al., 2016). The richest and most important outcrops with vertebrate fossils are located in the southwestern part of the Transylvanian Basin (Fig. 1). These deposits are dominated by red siliciclastics that range from conglomerates to mudstones, deposited by meandering or braided river systems surrounded by mainly well-drained floodplains (Codrea et al., 2010; Vremir, 2010; Csiki-Sava et al., 2016). During the Late Cretaceous, the Transylvanian Basin, together with the neighboring and more famous Haţeg Basin, were situated on the subtropical Haţeg Island, which was part of the Late Cretaceous European Archipelago (e.g., Csiki-Sava et al., 2015, 2016).

At Petreşti-Arini, the transition from a marine (Bozeş Formation) to a terrestrial environment (Sebeş Formation) is recorded, which makes the locality noteworthy within the continental Upper Cretaceous of Romania for preserving this rather unusual environmental setting (Vremir et al., 2014; Bălc et al., 2024). While the uppermost Bozeş Formation consists of brownish-gray to dark-gray silty marl- and mudstones with rare sandstone interbeds, the Sebeş Formation comprises mostly red claystones with interbedded conglomerate and sandstone layers (Vremir et al., 2014). The base of the Sebeş Formation is marked by a thick dark-gray sandstone that represents the first fully fluvial intercalation within a section that records the gradual facies change from a shallow marine to a fully terrestrial environment (Vremir et al., 2014). The overlying sedimentary rocks of the basal Sebeş Formation document the transition from poorly-drained marshy wetlands in the lower part to well-drained overbank-dominated environments in the upper part (Vremir et al., 2014). Recently, calcareous nannofossils, foraminifera and palynomorphs were used to date the top Bozeş Formation to the middle late Campanian (Bălc et al., 2024). Furthermore, deposition of the continental sediments of the overlying Sebeş Formation began during the late Campanian, making the local succession one of the oldest, if not the oldest, within the entire vertebrate-bearing continental uppermost Cretaceous of Romania (Vremir et al., 2014; Csiki-Sava et al., 2016).

Vertebrate remains are common in the uppermost Cretaceous continental beds of the Transylvanian Basin, and several different groups have already been reported from Petreşti-Arini as well (see 1. Introduction). The level yielding the new specimen is situated in the basal part of the locally red Sebeş succession, overlying gray beds interpreted as transitional to wetland; it corresponds largely to a previously reported fossil level identified as Level L1a by Vremir et al. (2014: fig. 4). Despite the absence of any biostratigraphic markers or absolute age data from this part of the local section, Vremir et al (2014) originally placed this fossiliferous level tentatively into the 'lowermost Maastrichtian/?uppermost Campanian' interval, based on the identification of biostratigraphically loosely constrained upper Campanian marine beds about 40 m lower in the outcropping section, leading Csiki-Sava et al. (2016) to include the corresponding vertebrate occurrences into their Tier 1 (uppermost Campanian to lowermost Maastrichtian) chrono-biostratigraphic subdivision of the Haţeg Island faunal assemblage successions. Subsequently, more comprehensive and multi-proxy biostratigraphic sampling at the Petreşti locality, supplemented by detrital zircon U-Pb geochronology data, has demonstrated that the upper (but not uppermost) Campanian also encompasses the lowermost part of the continental Sebeş Formation, up to the uppermost sampled layer that lies less than 20 m below the fossil-bearing L1a bed (Bălc et al., 2024: fig. 2). Although biostratigraphic markers are yet to be identified from this critical but apparently largely barren (in terms of micropaleontology) 20-m interval, the relative stratigraphic position of the fossiliferous level L1 so close to reliably dated upper Campanian deposits (possibly as old as 76 Ma) strongly — albeit not entirely conclusively — indicates that specimen EME 318 probably comes from the uppermost Campanian as well.

3. Description

Specimen EME 318 is a right humerus that is nearly undistorted, virtually complete except for some slight damage to the radial condyle and the greater tuberosity, and, aside from small cracks, well preserved (Fig. 2). Overall, the surface of the bone is more or less smooth, with just the distal and proximal ends and the deltopectoral crest showing roughened surfaces. It is elongated and expands mediolaterally at its ends, with a maximum proximodistal length of 229 mm. In cranial and caudal views, its medial margin is strongly curved medially at the proximal end, while the lateral margin extends in a relatively straight to slightly concave line (proximodistally) until it reaches the mid-section of the shaft (Fig. 2A–D). Further distally, the lateral margin slants medially before curving laterally again near the distal end. The medial and lateral margins are slightly divergent in the distal half of the bone, curving first medially and then laterally (in cranial view).

The proximal end has a roughly D-shaped cross-section with the convex side facing caudally (Fig. 2I, J). It is the mediolaterally widest part of the humerus, and is craniocaudally compressed. The maximum mediolateral width of the proximal end is 76 mm and the maximum craniocaudal breadth is 31 mm (measured across the humeral head). The proximal end shows a large protuberance (= hh) in the midline and two smaller tubercles on the medial and lateral sides. The humeral head extends mainly caudally and, to a lesser degree, proximally. It has a nearly oval shape in caudal view, being proximodistally elongated and mediolaterally slightly compressed (Fig. 2C, D; hh). Additionally, it narrows distally and merges with the shaft after few centimeters. In cranial view, the humeral head is almost indiscernible except for a slight proximal elevation (Fig. 2A, B; hh). The medial tubercle (= ltb) forms the proximomedial corner of the bone. It is only slightly thickened craniocaudally and extends mainly medially, being much smaller and less well developed than the humeral head and the lateral tubercle. The lesser tuberosity narrows down towards the distal end and merges with the medial margin of the shaft in the proximal third of the bone. The proximal margin of the humerus between the humeral head and the lesser tuberosity slopes gently distally towards the latter (Fig. 2A–D; pm).

The caudoproximally slightly damaged lateral tubercle (= gtb) is robust, craniocaudally thickened, and curves cranially towards the lateral margin. The proximal margin between the humeral head and the greater tuberosity is distally bowed and saddle-shaped (Fig. 2A, B, I, J; pm). The cranial and caudal surface of the proximal end of the humerus, between the humeral head and the greater tuberosity, is concave. In cranial view, the lateral margin below the greater tuberosity thickens distally forming a well-developed deltopectoral crest that extends until mid-shaft along the craniolateral margin of the bone, having a proximodistal length of about 104 mm (Fig. 2A, B, G, H; dpc). The crest reaches its maximum craniocaudal thickness near its distal end, i.e., just above the mid-section of the specimen.

Unlike the generally smooth surface of the shaft, the deltopectoral crest shows a slightly roughened surface that extends over the entire length of the process and ends a few centimeters below the proximal end. Proximally, the cranial surface of the bone is broadly concave (craniocaudally), being bound laterally by the deltopectoral crest, whereas the caudal aspect is slightly convex. Accordingly, the humerus has an L-shaped cross-section in proximal view. The concave cranial surface continues distally until around mid-length.

From around mid-section towards the distal end, the element rapidly decreases in mediolateral width, and at the same time its craniocaudal width increases. As a result, the shaft reaches an oval to almost round cross-section just slightly distal to mid-length. Towards the distal end, the element widens again mediolaterally and, to a lesser degree craniocaudally (on the medial and lateral margins). The maximum mediolateral width of the distal end is 50 mm and the maximum craniocaudal thickness is 39 mm. The distal end of the bone develops into two condyles, the ulnar condyle medially and the somewhat smaller radial condyle laterally, although this is difficult to ascertain because the latter is damaged (Fig. 2A–H, K, L; rc, uc). The ulnar condyle extends slightly below (i.e., distal to) the level of the radial condyle. Caudally, a shallow but wide U-shaped depression, the caudal intercondylar groove, separates the ulnar and radial condyles (Fig. 2C, D, K, L; icg). The cranial surface of the distal end, between the two condyles, is relatively flat to slightly concave (Fig. 2A, B, K, L). The distal surface between the two condyles is concave and saddle-shaped (Fig. 2K, L). Additionally, the whole joint is slightly rotated caudolaterally and shows an hour-glass-shaped cross-section. On its caudal aspect and a few centimeters above the distal end is the only visible distortion of the humerus; here, the shaft is slightly compressed (Fig. 2C, D).

4. Comparisons

The humerus EME 318 can be confidently assigned to a hadrosauroid dinosaur as it displays the typical humeral morphology of the group. Specifically, the humerus has a robust and long deltopectoral crest that extends from the proximal end of the humerus to around mid-shaft humerus (amounting to 45% of the total length of the humerus), which is a feature distinctive for hadrosauroids (Horner et al., 2004: p. 454). In addition, it can be excluded from any of the other dinosaur groups present in the uppermost Cretaceous of Romania due to their completely divergent humeral morphologies (Fig. 3). Hadrosauroids have (in addition to the particularly long deltopectoral crest) an s-shaped humerus with a mediolaterally narrow distal end (Fig. 3A), whereas (i) titanosaurs have an overall straighter and more robust humerus with a wider distal end (Fig. 3B), (ii) ankylosaurs have a humerus with much widely expanded proximal and distal ends (Fig. 3C), and (iii) rhabdodontids have a humerus that is bowed laterally and have a more angular, knob-like (instead of crest-like) dpc (Fig. 3D).

In the following section, EME 318 is compared with other reasonably complete hadrosauroid humeri from Europe that have been described thus far (Fig. 4). From the uppermost Cretaceous continental deposits of Transylvania, several specimens have been recovered from the Haţeg Basin previously (e.g., Nopcsa, 1915; Weishampel et al., 1993); a number of these elements belong to hatchling individuals (e.g., Botfalvai et al., 2017) and are therefore excluded from the present comparisons.

The post-hatchling sample includes four humeri from the Densuş-Ciula Formation near Vălioara: a largely complete left humerus that is slightly damaged on its proximal end (SZTFH Ob.3126), a rather incomplete and slightly distorted left humerus, missing the proximal and distal ends (SZTFH Ob.3112), a fragmentary right humerus with only the distal third being preserved (SZTFH Ob.3127), and another rather incomplete left humerus that is missing the proximal and distal ends, being also heavily damaged medially and laterally on its proximal half (NHMUK R.4914). Of these, only specimen SZTFH Ob.3126 has been figured so far (Nopcsa, 1915: pl. 2; Weishampel et al., 1993: fig. 5; Grigorescu and Csiki, 2006: pl. 1), while the other specimens are unpublished. Additionally, four hadrosauroid humeri have been recovered from the Sînpetru Formation, near Sânpetru: a mostly complete right humerus that is missing the proximolateral as well as disto-medial and disto-lateral parts (NHMUK R.3842; listed in Weishampel et al., 1993), a largely complete right humerus missing its proximal end (NHMUK R.3845; listed in Weishampel et al., 1993), an unpublished fragmentary right humerus missing its proximal and distal end as well as a portion of the deltopectoral crest (LPB (FGGUB) R.1599), and the proximal third of a right humerus (NHMUK R.3847; listed in Weishampel et al., 1993). Furthermore, the distal half of a right humerus (NHMUK R.11112; listed in Weishampel et al., 1993) has been recovered from an unknown location from the Upper Cretaceous of Transylvania. Overall, many of these Transylvanian humeri have a roughly similar size to the humerus from Petreşti-Arini (e.g., SZTFH Ob.3112 and Ob.3126, NHMUK R.3842 and R.3847); two individuals are notably larger (SZTFH Ob.3127, NHMUK R.4914), while one specimen is slightly larger (NHMUK R.3845), and one specimen is slightly smaller (NHMUK R.11112).

Most of these elements are not only roughly comparable in size but also very similar morphologically. Only two specimens show minor morphological differences: (i) in SZTFH Ob.3112, the medial margin seems to be slightly straighter in its proximal half (extending more or less proximodistally) than in EME 318; and (ii) in Ob.3126, the deltopectoral crest becomes markedly narrower towards its distal end, with its medio-lateral thickness greatest in the proximal half, whereas that of EME 318 is widest close to its distal end and narrows proximally. The remaining specimens are nearly identical in their morphology to EME 318.

Aside from Romania, hadrosauroid humeri have also been described from the more westerly Ibero-Armorican Domain (Spain and southern France) and Italy, including an almost complete one (damaged at the proximal end and deltopectoral crest) from the Maastrichtian of northern Spain assigned to *Pararhabdodon isonensis* (Fig. 4H) (Casanovas et al., 1999), a complete humerus from the Maastrichtian of northern Spain referred to hadrosaurid gen. et sp. indet. (Fondevilla et al., 2018) (Fig. 4I), a complete humerus (MDE-Ma3-20) from the upper Maastrichtian of southern France and assigned to *Canardia garonnensis* (not figured herein; see Prieto-Márquez et al., 2013: fig. 9), and a nearly complete humerus (damaged at the ltb and uc) from the lower Campanian of northern Italy belonging to *Tethyshadros insularis* (Fig. 4J) (Dalla Vecchia, 2009). The two humeri from Spain (*Pararhabdodon isonensis* and hadrosaurid gen. et sp. indet.) and the humerus from southern France (*Canardia garonnensis*) differ from EME 318 in their relatively longer deltopectoral crest, which is more than half the length of the humerus (i.e., a dpc length/total length ratio of greater than 0.5), and thus they fall within the range of the more derived hadrosauroids, in good agreement with their currently accepted hadrosaurid affinities (e.g., Chiarenza et al., 2021; Longrich et al., 2024). Furthermore, the relative width of the deltopectoral crest (defined as the "ratio between the width of the humerus across the distal fourth of the deltopectoral crest and the width of the distal shaft at the point of maximum curvature", Prieto-Márquez, 2010: p. 494) has values over 1.65 for the humeri of *Pararhabdodon isonensis* and *Canardia garonnensis* (Prieto-Márquez et al., 2013: suppl. information S2), again differing markedly in this respect from EME 318 that has a rather low value of 1.56 and thus more closely resembles derived non-hadrosaurid hadrosauroids (see 5. Discussions). The humerus of *Tethyshadros insularis* closely resembles EME 318 (and the other hadrosauroid humeri reported from Transylvania, see above, same section), in having a relatively short (dpc length/total length ratio is less than 0.5) and narrow (relative width less than 1.65, see Prieto-Márquez et al., 2013: suppl. information S2) deltopectoral crest, and thus displays the typical condition seen in more basal (non-hadrosaurid) hadrosauroids (see 5. Discussions).

5. Discussions

As noted in 4. Comparisons, the humeri of hadrosauroids are distinctive in having a strongly developed deltopectoral crest that extends to around mid-shaft (Horner et al., 2004: p. 454). More basally within hadrosauroids the deltopectoral crest is relatively shorter compared with derived hadrosaurs (i.e., members of Saurolophidae), the latter being characterized by a deltopectoral crest comprising more than 55% of the proximodistal length of the humerus (e.g., Prieto-Márquez, 2008: fig. H.15; Prieto-Márquez, 2010: p. 461 and appendix, character 220). The deltopectoral crest of EME 318 (with a length amounting to 45% of the humeral length) exhibits this basal condition of a relatively short deltopectoral crest. The relative width of the humerus across the deltopectoral crest (Prieto-Márquez, 2010; see 4. Comparisons) is also known to vary between basal and more derived hadrosauroids (Prieto-Márquez, 2008: fig. H.16; Prieto-Márquez, 2010: p. 494 and appendix, character 220), with the latter exhibiting values of typically more than 1.65 (though a few exceptions are present). Again, EME 318 shows a value (1.56) that is rather low and lies in the range typically seen in more basal hadrosauroids. Consequently, based on these two features, EME 318 can confidently be assigned to a basal (i.e., non-hadrosaurid) hadrosauroid. Basal hadrosauroids have long been recognized as a typical paleofaunal component in the uppermost Cretaceous of Romania (e.g., Nopcsa, 1915; Grigorescu, 1983; Weishampel et al., 1993), and, in fact, the first named taxon from here — *Telmatosaurus transsylvanicus* (Nopcsa,

1900) — was a member of this group. Comparisons with previously discovered hadrosauroid humeri from these deposits reveal an overall high degree of morphological similarity between the different specimens. The slight morphological variation noted between some of the humeri (see 4. Comparisons) concerns only proportional differences and no discrete features. Although these differences may be due to taxonomy, they are so minor that they may well fall within the expected range of intraspecific variability.

So far, all hadrosauroid specimens from the Transylvanian uppermost Cretaceous identified to a lower taxonomic level have been uncritically assigned to the non-hadrosaurid hadrosauroid *Telmatosaurus* (Nopcsa, 1915; Weishampel et al., 1993). Notably, however, the holotype of *Telmatosaurus* comprises only a largely complete skull with associated cervical, dorsal and caudal vertebrae but no appendicular elements (Nopcsa, 1900, 1925; Augustin et al., 2023a) and, so far, association between appendicular and (diagnostic) cranial material has never been demonstrated reliably for this taxon. Therefore, most postcranial remains, at least for the moment, cannot be reliably assigned to *Telmatosaurus*, and previously referred postcranial material (e.g., Weishampel et al., 1993) has been only assigned on the basis that it was supposedly the only hadrosauroid from Transylvania, a practice similar to the case of the rhabdodontid *Zalmoxes* (Brusatte et al., 2017; Augustin et al., 2022, 2023b).

However, it cannot be excluded that the local diversity of the group was actually higher than currently recognized, and more than one hadrosauroid taxon inhabited Haţeg Island during the latest Cretaceous, as already hinted at by Dalla Vecchia (2006) and Magyar et al. (2024). A comparable situation was demonstrated recently for rhabdodontid ornithopods (Augustin et al., 2022). Intriguingly, the uppermost Cretaceous (Maastrichtian) deposits of western Europe (Spain and southern France) representing the Ibero-Armorican Island yielded at least six different hadrosauroid genera, some of which were even largely sympatric (e.g., Cruzado-Caballero et al., 2014; Prieto-Márquez and Carrera Farias, 2021); this demonstrates that at least some islands of the Late Cretaceous European Archipelago were inhabited by more than one hadrosauroid taxon. Given all these uncertainties, EME 318 cannot be reliably identified at the genus/species level and is referred here to hadrosauroid gen. et sp. indet.

Nonetheless, it is important to note that the occurrence of hadrosauroids at Petreşti-Arini, as demonstrated by EME 318, has wider implications for understanding the evolution of the Haţeg Island vertebrate faunas. As noted in 2. Geological setting, Petreşti-Arini is remarkable in being one of the geologically oldest vertebrate localities from the entire continental uppermost Cretaceous of Romania and in preserving a rather unusual near-shore depositional environment (Vremir et al., 2014). In addition, the composition of the local vertebrate assemblage is exceptional in that several typical and otherwise abundant taxa were undocumented from here, including the hadrosauroids until now. Such a biased local paleofaunal composition has been previously hypothesized to be linked to the old age and/or unusual environmental setting of the locality; more specifically, it was suggested that the taxa missing from the local assemblage were uncommon or absent in the coastal habitats recorded at Petreşti-Arini and/or that the taxonomic composition of the Haţeg Island paleofauna changed throughout the latest Cretaceous, with the potential immigration of certain taxa such as hadrosauroids occurring only during later times (Vremir et al., 2014; Csiki-Sava et al., 2016; Bălc et al., 2024).

The newly recognized occurrence of hadrosauroids at Petreşti-Arini allows better constraints regarding these previous hypotheses, and refines current scenarios according to which hadrosauroids were apparently introduced to Haţeg Island around the beginning of the Maastrichtian or very slightly afterwards (Bălc et al., 2024). The age of the specimen reported here is fairly well constrained, with current data suggesting that it may be from the uppermost Campanian. Indeed, the fossiliferous site yielding it sits only slightly above a level at the base of the Sebeș Formation dated as late Campanian (Bălc et al., 2024), which makes it not only the stratigraphically oldest record of hadrosauroids in the Transylvanian Basin (given the relative position of this locality compared to other ones — Fig. 1; Csiki-Sava et al., 2016) but also one of the earliest well-constrained occurrences of hadrosauroids on Haţeg Island overall. Therefore, EME 318 documents the arrival of hadrosauroids slightly earlier than proposed by Bălc et al. (2024) — i.e., most probably before the end of the Campanian — and may indeed represent one of the first members of its clade on this island. It also reinforces previous observations that only non-hadrosaurid hadrosauroids were present in Transylvania, unlike Ibero-Armorica, where most hadrosauroids are more or less derived hadrosaurids, and furthermore appear significantly later in the fossil record (e.g., Vila et al., 2016; but see Pereda-Suberbiola et al., 2015).

Finally, it is interesting to note that this oldest Transylvanian hadrosauroid occurrence correlates with the switch from grayish, more wetland-type beds of the lowermost Sebeş Formation to red floodplain deposits farther up-section, so potentially some sort of paleoenvironmental affinity might have controlled their distribution, at least locally. Rhabdodontids, by contrast, are found throughout the brackish to the wetland-type beds and up to the red floodplain beds at Petreşti-Arini (Vremir et al., 2014). Accordingly, EME 318 is not only one of the earliest well-constrained hadrosauroid occurrences across Haţeg Island but also implies that their distribution may have been shaped partly by habitat preferences.

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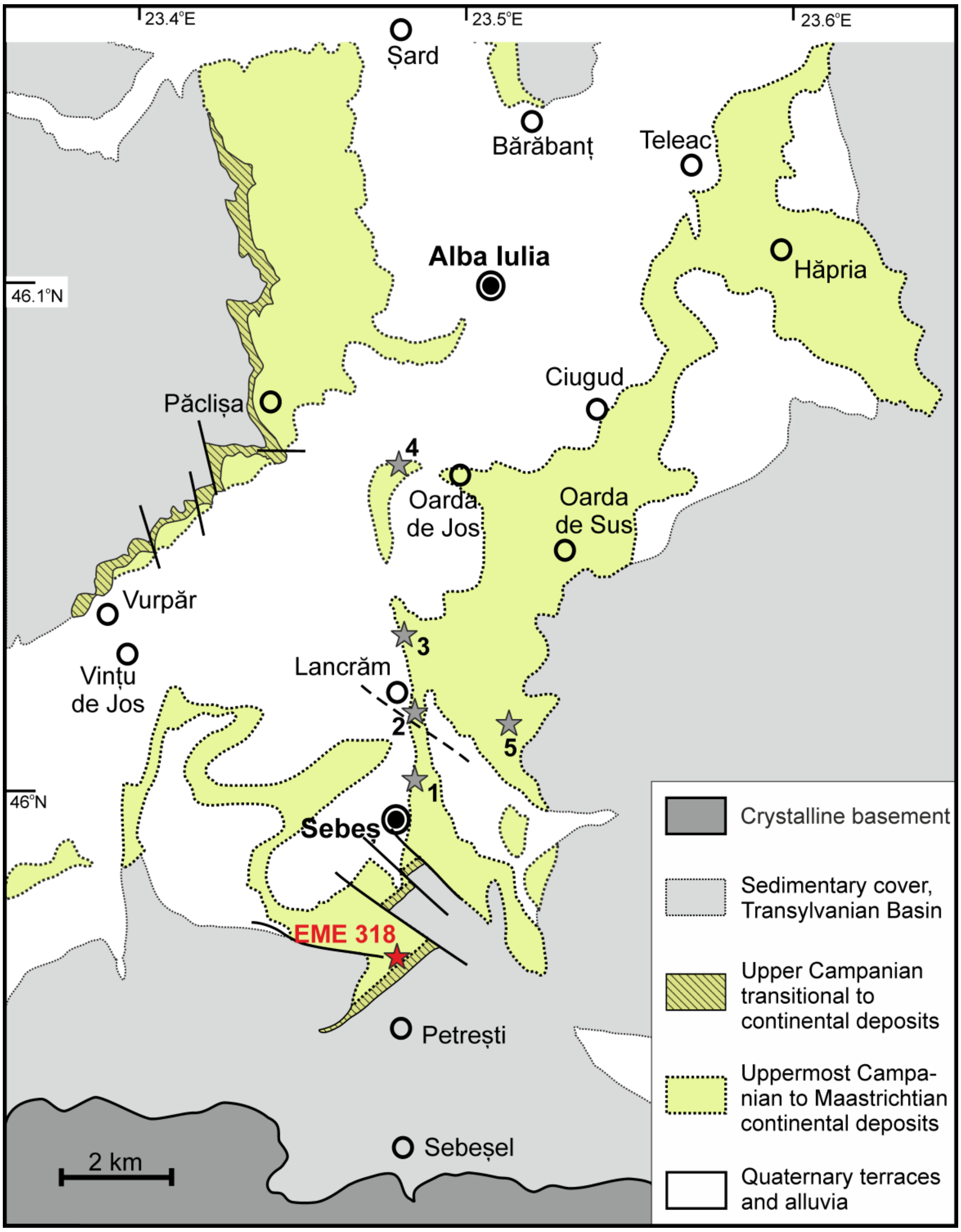
Figure captions

Fig. 1. Simplified geological map of the southwestern Transylvanian Basin with the locations of uppermost Cretaceous hadrosauroid occurrences (see Vremir et al., 2015), arrayed from oldest (1) to youngest (5). Legend: 1 – Sebeș-Glod locality; 2 – Secaș-Feții Hill locality; 3 – Lancrăm locality; 4 – Oarda de Jos locality; and 5 – Râpa Roșie locality.

Fig. 2. Right humerus of an indeterminate hadrosauroid (EME 318), Upper Cretaceous (most probably uppermost Campanian), Sebeş Formation, Petrești-Arini. (A, B) Anterior view; (C, D) posterior view; (E, F) lateral view; (G, H) medial view; (I, J) proximal view; (K, L) distal view.

Fig. 3. Simplified line drawing comparing the herein described specimen (EME 318) with the humeri of other common dinosaur groups of the uppermost Cretaceous deposits of Romania. (A) Specimen EME 318, referable to a hadrosauroid (see text for explanations). (B) Humerus of the titanosaur *Magyarosaurus dacus* (LPB (FGGUB) R.1047) drawn after Csiki-Sava et al. (2015). (C) Humerus of the ankylosaur cf. *Struthiosaurus* sp. (MTM PAL 2012.30.1) drawn after Ősi and Prondvai (2013). (D) Humerus of a rhabdodontid from the Sânpetru Formation of the Haţeg Basin (NHMUK R.1000). All humeri are shown in cranial view. The drawings are not to the same scale. The drawings of (B) and (D) were mirrored.

Fig. 4. Simplified line drawing comparing the herein described specimen (EME 318) with other reasonably complete hadrosauroid humeri from Romania (A–G) and other European regions (H–J). (A) Hadrosaurid gen. et sp. indet. (EME 318); (B) hadrosaurid gen. et sp. indet. (SZTFH Ob.3126); (C) hadrosaurid gen. et sp. indet. (NHMUK R.3842); (D) hadrosaurid gen. et sp. indet. (NHMUK R.3845); (E) hadrosaurid gen. et sp. indet. (NHMUK R.4914); (F) hadrosaurid gen. et sp. indet. (SZTFH Ob.3112); (G) hadrosaurid gen. et sp. indet. (LPB (FGGUB) R.1599); (H) *Tethyshadros insularis* (SC 57021) drawn after Dalla Vecchia (2009); (I) hadrosaurid gen. et sp. indet. (MCD-5009) drawn after Fondevilla et al. (2018); (J) *Pararhabdodon isonensis* (IPS SRA-15) drawn after Casanovas et al. (1999). All humeri are shown in cranial view. The drawings are not to the same scale. The drawings of specimens (B), (E), (F), (H), (I) and (J) were mirrored.



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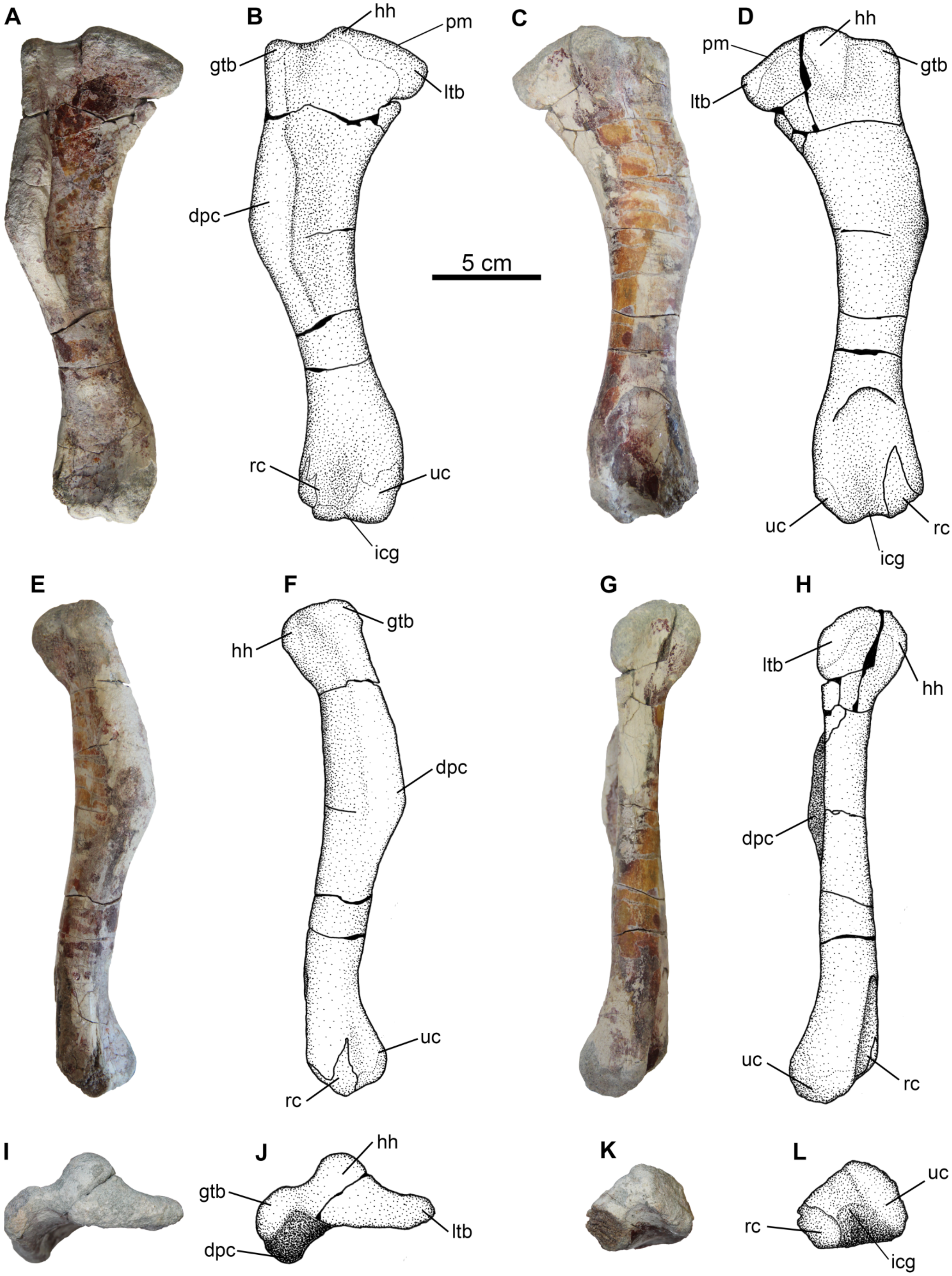
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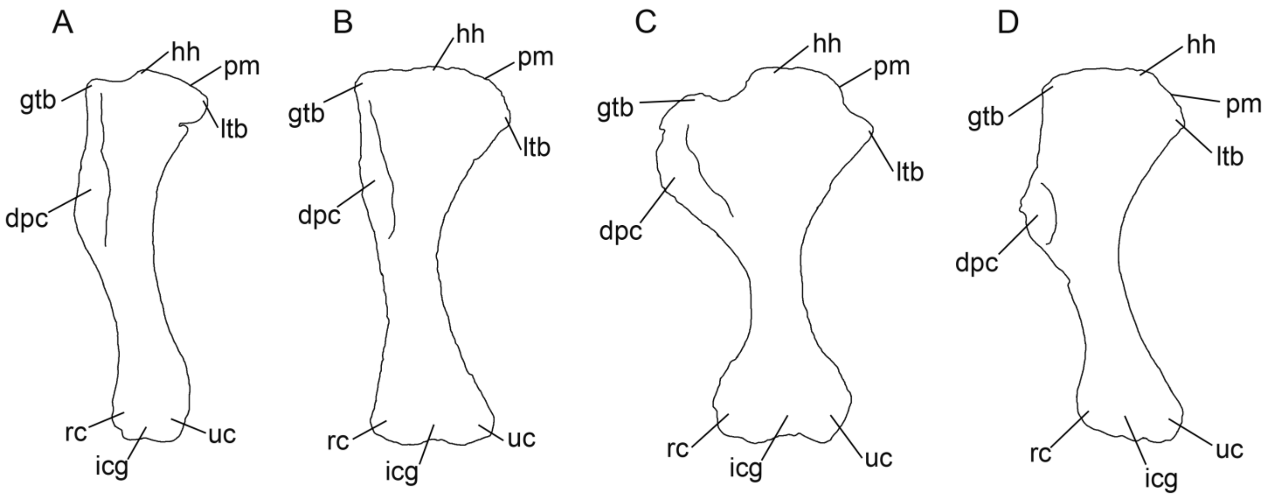
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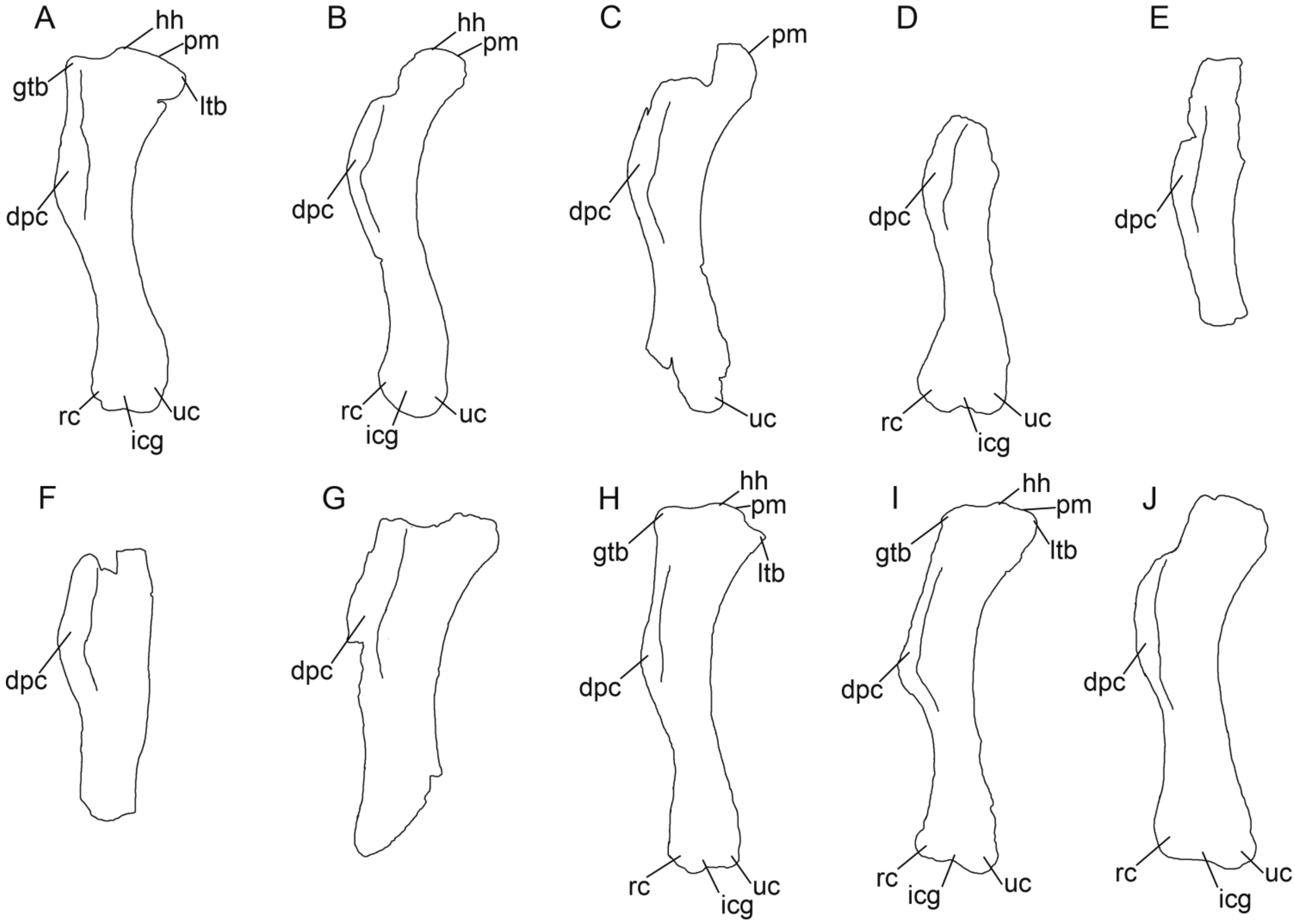
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