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New report of Late Cretaceous struthiosaurids from the Haţeg Basin, with an overview of the Transylvanian ankylosaur fossil record

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Abstract

Ankylosaurs are a widespread but rare constituent of the latest Cretaceous dinosaur faunas of Europe. In the famous Upper Cretaceous continental deposits of the Haţeg Basin (Romania), ankylosaurs were first reported over 100 years ago and since then have been found in various localities across the wider Transylvanian area; nevertheless, they still represent an uncommon faunal component. We report here the first evidence of the group from the fossil-rich Maastrichtian 'Pui Beds' of the eastern Haţeg Basin. The specimen, an isolated scapula, can be confidently assigned to *Struthiosaurus* sp. based on thorough morphological comparisons. Among the scapulae referred to *Struthiosaurus* from France, Austria and Romania, the Pui scapula is most similar to *S. transylvanicus* from roughly coeval strata of the central Haţeg Basin. Besides reporting this new specimen, we provide a detailed overview of the ankylosaur fossil record from Transylvania and discuss its implications for the palaeoecology and evolution of ankylosaurs in the eastern part of the Late Cretaceous European Archipelago. Contrary to previous hypotheses, ankylosaurs do not seem to have been environmentally segregated from the more common sympatric herbivorous dinosaur clades (rhabdodontids, titanosaurs, hadrosauroids) on Haţeg Island, but instead were widely distributed albeit numerically subordinate members of the palaeofauna(s). According to our updated overview, ankylosaurs first appeared in the Transylvanian Basin and only later show up in the Haţeg Basin. Finally, in stark contrast to the situation in the western Ibero-Armorican Landmass, ankylosaurs were present throughout the entire Maastrichtian in the Transylvanian area.

Keywords Ankylosauria · Haţeg Island · Late Cretaceous · Struthiosauridae · *Struthiosaurus*

Introduction

During the latest Cretaceous, Europe was home to a unique dinosaur fauna that is remarkable for not only displaying a high degree of endemism but also repeated, albeit regionally restricted, faunal exchanges with its neighbouring landmasses (Weishampel et al. 2010; Csiki-Sava et al. 2015). Perhaps one of the most notable features of this fauna is the presence of dwarfed dinosaurs, which were first reported over a century ago by Franz Nopcsa in eastern Europe from Maastrichtian deposits in Transylvania (e.g. Nopcsa 1897, 1900, 1915). The historical region of Transylvania in western Romania has since yielded a rich uppermost Cretaceous continental fossil record, allowing for the reconstruction of the famous "Haţeg Island" palaeoecosystem at the southeastern periphery of the Late Cretaceous European Archipelago (Benton et al. 2010; Csiki-Sava et al. 2015, 2016). These discoveries led to the recognition of a characteristic rhabdodontid-titanosaur-hadrosauroid-struthiosaurid dinosaurian faunal assemblage,

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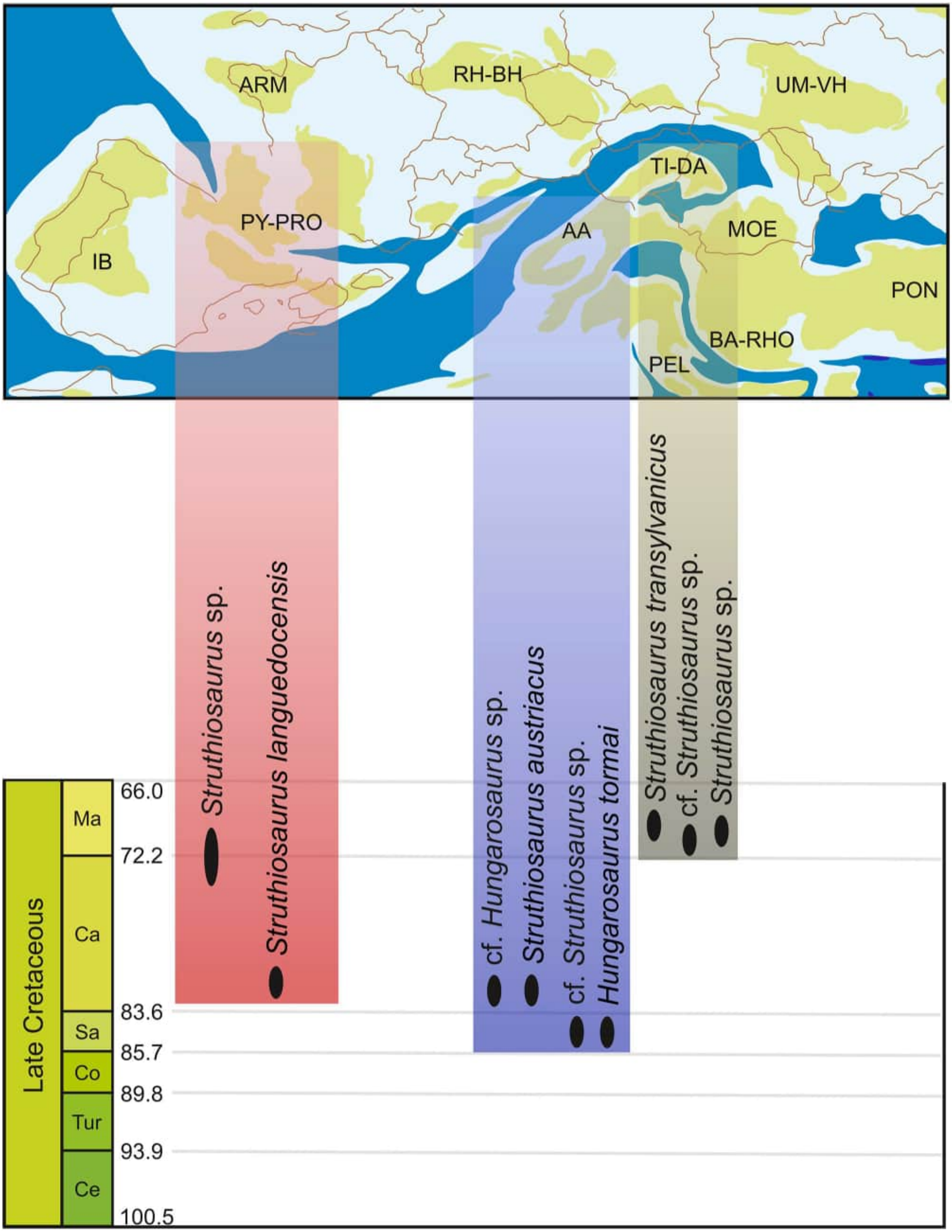

ARM
RH-BH
UM-VH
IB
PY-PRO
TI-DA
AA
MOE
PON
BA-RHO
PEL
Struthiosaurus sp.
Struthiosaurus languedocensis
cf. Hungarosaurus sp.
Struthiosaurus austriacus
cf. Struthiosaurus sp.
Hungarosaurus tormai
Struthiosaurus transylvanicus
cf. Struthiosaurus sp.
Struthiosaurus sp.
Late Cretaceous
Ma
Ca
Sa
Co
Tur
Ce
66.0
72.2
83.6
85.7
89.8
93.9
100.5

◂**Fig. 1** Palaeogeographic distribution (map depicts late Campanian, ~ 75 Mya) and chronostratigraphic range of confidently identified occurrences of Late Cretaceous European struthiosaurid ankylosaurs (occurrences of uncertain or indeterminate taxonomic affinities were omitted; for a complete overview of the Transylvanian record see Table 1). Modified and updated from Ősi and Prondvai (2013: fig. 3); modified base map for the late Campanian by R. Blakey (https://deeptimemaps.com/). Absolute ages for stage boundaries follow Cohen et al. 2013, updated v2024/12. Abbreviations: *AA* Austroalpine Domain (i.e. Austria, Hungary); *ARM* Armorican Massif (i.e. France); *BA-RHO*, Balkans-Rhodope Orogen; *IB* Iberian Landmass (i.e. Portugal, Spain); *MOE* Moesian Platform; *PEL* Pelagonian Domain; *PON* Pontides Orogen; *PY-PRO* Pyrenean-Provencal Landmass (i.e. France, Spain); *RH-BH* Rhenish-Bohemian High; *TI-DA* Tisia-Dacia Block (i.e. Haţeg Island, Romania); *UM-VH* Ukrainian Massif-Voronezh High

which has been widely reported from the Maastrichtian of “Haţeg Island”, chiefly from localities in the Haţeg and Transylvanian basins (Nopcsa 1915; Grigorescu 1983; Weishampel et al. 1991; Codrea et al. 2010b; Csiki-Sava et al. 2015, 2016). This assemblage groups the Transylvanian palaeoisland into a larger Late Cretaceous European bioprovince characterised, in part, by the co-occurrence of rhabdodontid ornithopods, titanosaurian sauropods and basal, struthiosaurid ankylosaurs, while still retaining a high degree of local endemism at the species and genus levels (Weishampel et al. 2010; Csiki-Sava et al. 2015, 2016). Yet while rhabdodontid and titanosaur (as well as hadrosauroid) remains are rather abundant in the uppermost Cretaceous of Romania, those of struthiosaurids have remained comparatively rare (Grigorescu 1983; Csiki et al. 2010; Csiki-Sava et al. 2016; Ősi et al. 2014) just as they are throughout most of the European Upper Cretaceous (Pereda-Suberbiola 1992; Ősi et al. 2014; Csiki-Sava et al. 2015; Vila et al. 2016), although they are fairly common in the Santonian of Hungary (Ősi et al. 2019).

Presently, only two valid and formally defined genera of struthiosaurid ankylosaurs are recognised from the Upper Cretaceous of Europe (Fig. 1). *Hungarosaurus tormai* from the Santonian Csehbánya Formation of the Iharkút locality in western Hungary is known from six partial skeletons alongside hundreds of isolated bones, making it the most complete and well preserved Late Cretaceous European ankylosaur (Ősi 2005; Ősi and Makádi 2009; Ősi et al. 2014, 2019). The second genus is *Struthiosaurus*, first described from the lower Campanian Grünbach Formation of Muthmannsdorf, eastern Austria, based on the type species *S. austriacus*, represented by at least three individuals (Bunzel 1871; Seeley 1881; Pereda-Suberbiola 1992; Csiki-Sava et al. 2015). A second species was described later by Nopcsa (1915) as *S. transylvanicus,* from the Maastrichtian Sînpetru Formation of the south-central Haţeg Basin, western Romania (see also Nopcsa 1929). Most recently, a third species, *S. languedocensis* was erected by Garcia and Suberbiola (2003) from the lower Campanian of the Villeveyrac-Mèze Basin at Villeveyrac, southern France. Additional material referred to *Struthiosaurus* sp. from southern France and Spain further emphasises the supposedly wide palaeogeographical and stratigraphical range of this genus (Pereda-Suberbiola 1992; Ősi et al. 2014; Ősi 2015). Furthermore, isolated ankylosaurian material from Iharkút, western Hungary, stemming from the same horizon as *H. tormai,* has been assigned to *cf. Struthiosaurus* sp., showing that a taxon closely related to *Struthiosaurus* co-existed with *H. tormai* during the Santonian (Ősi and Prondvai 2013; Ősi et al. 2019; Fig. 1), while also indicating an even wider temporal range for *Struthiosaurus* (Santonian to Maastrichtian). Such a co-occurrence of two struthiosaurid ankylosaur species was also suggested for Muthmannsdorf by Ősi et al. (2019), who reported that a large conical spike, previously referred to *S. austriacus*, is strikingly similar to material known from *H. tormai* (that alternative identification is listed as “cf. *Hungarosaurus* sp.” in Fig. 1). Additionally, three isolated ankylosaur teeth, distinct from those of species of *Struthiosaurus* and *H. tormai,* and reported from three different localities in the Haţeg Basin (Sânpetru-Cărare, Toteşti and Crăguiş: see below), might hint at a higher, as yet unrecognised taxonomic diversity among Late Cretaceous ankylosaurs in Europe (Ősi et al. 2014; Csiki-Sava et al. 2016).

In Romania, besides the holotype of *Struthiosaurus transylvanicus*—consisting of the posterior part of the skull, a cervical, as well as dorsal and caudal vertebrae, rib fragments, a complete right scapula with the sutured coracoid and osteoderms (Nopcsa, 1915, 1929)—and two partial skeletons described by Ősi et al. (2014), the ankylosaur fossil record reported from Upper Cretaceous deposits of Transylvania is currently restricted to a small number of isolated and fragmentary fossils only diagnostic at the family level (Ősi et al. 2014: table 1; Ősi 2015; Csiki-Sava et al. 2016; Figs. 1, 2; Table 1). Here we report the occurrence of, and describe, an ankylosaurian scapula from Pui in the southeastern part of the Haţeg Basin, which extends the known distribution of these characteristic Late Cretaceous European dinosaurs into the ‘middle’ Maastrichtian ‘Pui Beds’, also informally known as the ‘Bărbat Formation’ (Therrien 2005), and marks the first record of the group in that lithostratigraphic unit. Additionally, we also review the currently known fossil record of ankylosaurs from the uppermost Cretaceous of Transylvania and discuss some of its wider implications.

Geological setting

The herein described specimen was recovered from the Maastrichtian ‘Pui Beds’ of the Haţeg Basin in western Romania (Fig. 2). Located within the southwestern Carpathian Mountains, the Haţeg Basin represents an

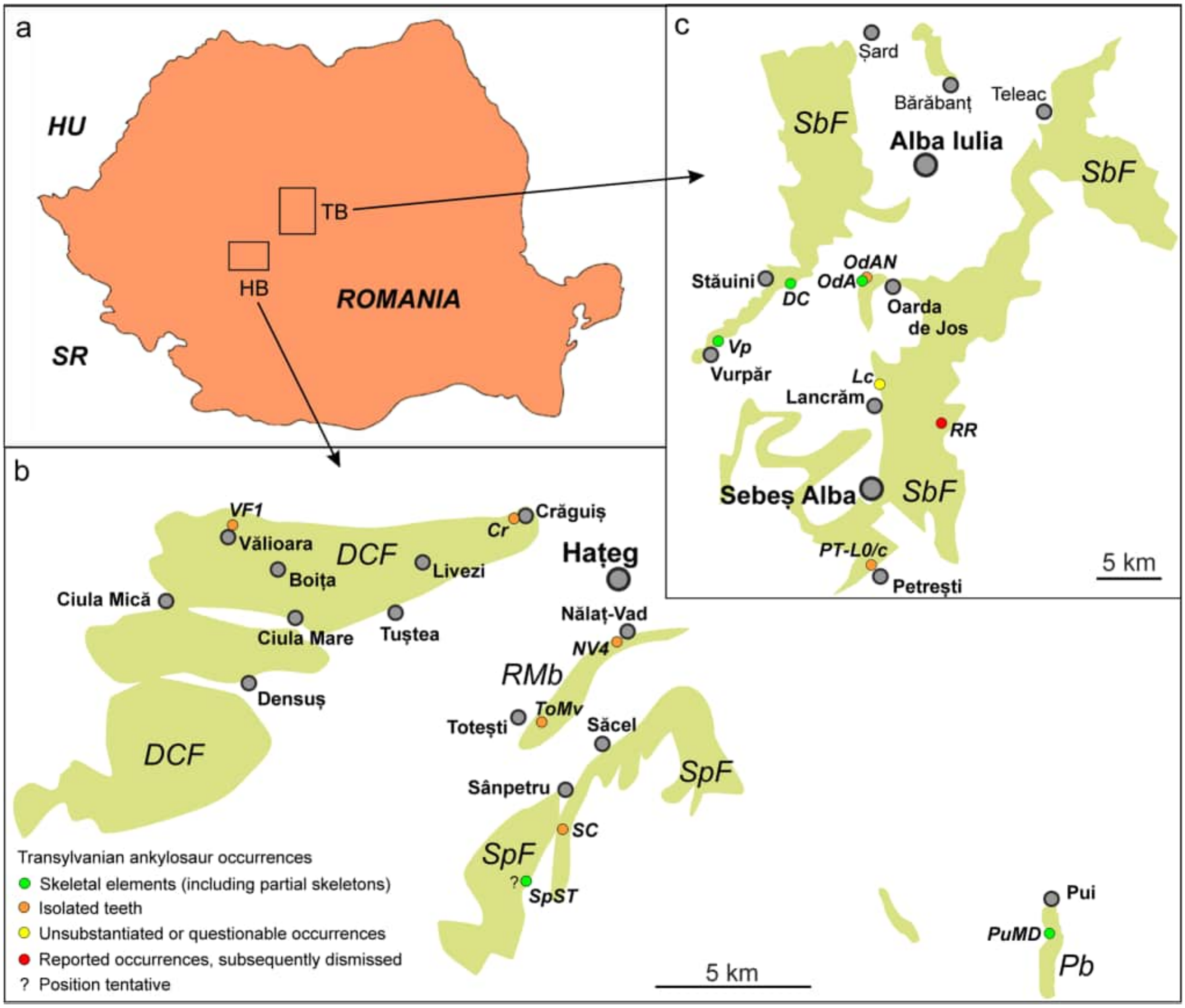


Fig. 2 Locality information for ankylosaur occurrences throughout the Haţeg and Transylvanian basins. **a** Geographical map showing the position (rectangles) of the Haţeg Basin (HB) and Transylvanian Basin (TB) within Romania. **b** Distribution of uppermost Cretaceous continental deposits in the Haţeg Basin, with ankylosaur occurrences indicated. **c** Distribution of uppermost Cretaceous continental deposits in the southwestern Transylvanian Basin, with ankylosaur occurrences indicated (**b** and **c** updated from Csiki-Sava et al. 2016). Abbreviations: *DCF* Densuş-Ciula Formation; *HU* Hungary; *Pb* 'Pui Beds'; *RMb* 'Râul Mare Beds'; *SbF* Sebeş Formation; *SpF* Sînpetru Formation; *SR* Serbia. For locality abbreviations, see Table 1

extensional basin formed during the Late Cretaceous and has since accumulated extensive sedimentary deposits (e.g. Willingshofer et al. 2001). The uppermost Cretaceous continental sedimentary rocks of the basin (together with those of the neighbouring Transylvanian Basin to the northeast and the Rusca Montană Basin to the west), mainly encompass alluvial mud-, silt- and sandstones as well as conglomerates, but also occasional layers with a high percentage of volcanoclastics (Therrien 2005; Csiki-Sava et al. 2016), deposited on a palaeo-island commonly referred to as "Haţeg Island" that was part of the larger Late Cretaceous European Archipelago fringing the northern margin of the Mediterranean Tethys area (Csiki-Sava et al. 2015, 2016). Within the Haţeg Basin, these continental deposits were historically grouped into two roughly synchronous lithostratigraphic units (e.g. Grigorescu 1992), the Densuş-Ciula Formation cropping out along the northwestern margin and characterised by the presence of locally high amounts of volcanoclastic material, and the Sînpetru Formation, which traditionally includes strata in the south-central, central and southeastern parts of the basin, although uppermost Cretaceous deposits from the last area have recently been referred to their own lithostratigraphic unit

Table 1 Uppermost Cretaceous (upper Campanian to upper Maastrichtian) occurrences of ankylosaurian remains in the Haţeg and Transylvanian basins. Occurrences are ordered by relative age (= biochronologic tier) for each basin separately, from oldest to youngest. Abbreviations for locality names (fourth column) are used in Figures 2 and 7

Taxon	Material	Tier/Lithostratigraphy/Palaeoenvironment	Locality/Lithology of the fossiliferous bed	References
Haţeg Basin				
Ankylosauria indet.	Two tooth fragments	T2/Densuş-Ciula Formation, "middle member"/distal alluvial fan with poorly to moderately drained floodplains, locally developed ponds and abandoned river channel fills	Vălioara – Fântânele microvertebrate site (VF1)/grey-greenish, massive pebble-bearing silty mudstones, locally slightly variegated	This paper
Struthiosaurus sp.	Partial right scapula	T2–T3/'Pui Beds'/meandering river system with well drained floodplains	Pui – MD site (PuMD)/greenish-grey pebbly sandstone	This paper
Struthiosaurus transylvanicus	Holotype: posterior part of a skull, vertebrae, ribs, right scapulocoracoid, osteoderms	T3/Sînpetru Formation/braided river system with poorly to moderately well drained floodplains	Sânpetru – type locality (SpST)/bluish mudstone	Described: (Nopcsa 1915, 1929)
"Nodosauridae indet."	Dentary fragment with implanted tooth	T3/Sînpetru Formation/braided river system with poorly to moderately well drained floodplains	Sânpetru – Cărare site (SC)/surface float, but likely from brownish siltstones	Described: (Ősi et al. 2014) Mentioned: (Ősi 2015; Csiki-Sava et al. 2016; Augustin et al. 2021)
Ankylosauria indet.	Tooth	T3/Sînpetru Formation/braided river system with poorly to moderately well drained floodplains	Sânpetru – Cărare site (SC)/greyish-greenish conglomeratic sandstone	This paper
"Nodosauridae indet."	Tooth	T3/'Râul Mare Beds'/meandering river system with poorly drained floodplains, water-logged wetlands and ponds	Nălaţ-Vad site 4 microvertebrate accumulation (NV4)/eggshell coquina limestone grading into black marls	Described: (Smith et al. 2002) Mentioned: (Csiki-Sava et al. 2016)
"Nodosauridae indet."	Tooth	T4/'Râul Mare Beds'/meandering river system with poorly drained floodplains, water-logged wetlands and ponds	Toteşti microvertebrate site (ToMv)/dark grey silty mudstone	Described: (Codrea et al. 2002) Mentioned: (Ősi et al. 2014; Csiki-Sava et al. 2016)
"Nodosauridae indet."	Tooth fragment	T4/Densuş-Ciula Formation, "upper member"/fluvial setting	Crăguiş micro site (Cr)/red mudstone	Described: (Csiki-Sava et al. 2016)
Transylvanian Basin				
"Nodosauridae indet."	Teeth	T1/basalmost Sebeş Formation/estuarine-deltaic changing into wetland-lacustrine and later into well-drained floodplains	Petreşti-Arini – PT-L0/c microvertebrate accumulation (PT-L0/c)/grey mudstone	Mentioned: (Vremir et al. 2015a; Vasile et al. 2021)
cf. *Struthiosaurus* sp.	F1 accumulation: fragmentary humerus and femora, ribs, right scapula, left scapulocoracoid, osteoderms	T1/2/lower Sebeş Formation/meandering river systems with well-drained floodplains	Vurpăr – F1 accumulation (Vp)/greyish to reddish mudstone	Described: (Ősi et al. 2014) Mentioned: (Therrien et al. 2002; Therrien 2005; Codrea et al. 2010a, b; Jipa-Murzea 2012; Brusatte et al. 2013; Ősi and Prondvai 2013; Ősi 2015)

Table 1 (continued)

Taxon	Material	Tier/Lithostratigraphy/Palaeoenvironment	Locality/Lithology of the fossiliferous bed	References
"Nodosauridae indet."	F1 accumulation: ulna	T1/2/lower Sebeş Formation/meandering river systems with well-drained floodplains	Vurpăr – F1 accumulation (Vp)/greyish to reddish mudstone	Described: (Ősi et al. 2014) Mentioned: (Therrien et al. 2002; Therrien 2005; Codrea et al. 2010a, b; Jipa-Murzea 2012; Brusatte et al. 2013; Ősi 2015; Ősi and Prondvai 2013)
"Nodosauridae indet."	F2 accumulation: ribs, osteoderms	T1/2/lower Sebeş Formation/meandering river systems with well-drained floodplains	Vurpăr – F2 accumulation (Vp)/red brownish calcareous mudstone	Described: (Ősi et al. 2014) Mentioned: (Therrien et al. 2002; Therrien 2005; Codrea et al. 2010a, b; Jipa-Murzea 2012; Brusatte et al. 2013; Ősi 2015; Ősi and Prondvai 2013)
"Nodosauridae indet."	Isolated, non-associated material: dorsal centrum, femur, osteoderms	T1/2/lower Sebeş Formation/meandering river systems with well-drained floodplains	Vurpăr area, isolated non-associated material (Vp)/not from the same horizon	Described: (Ősi et al. 2014) Mentioned: (Therrien et al. 2002; Therrien 2005; Codrea et al. 2010a, b; Jipa-Murzea 2012; Brusatte et al. 2013; Ősi 2015; Ősi and Prondvai 2013)
"Nodosauridae indet. (?*Struthiosaurus* sp.)"	Osteoderm	T2/lower Sebeş Formation/meandering river system with well-drained floodplains	Cuptorului Hill – DC-1 sub-site (DC)/dinoturbated pebbly sandstone	Mentioned: (Csiki-Sava et al. 2016; Codrea et al. 2010b; Brusatte et al. 2013; Vremir et al. 2015a)
"*Struthiosaurus transylvanicus*" (occurrence doubtful, see text)	No available information, ambiguous occurrence (see text)	T2/3/middle Sebeş Formation/meandering river systems with poorly drained floodplains, swampy streamside gallery-woodlands, forested inter-channel overbank environment	Lancrăm (Lc)/coarse to medium channel sandstones	Mentioned: (Codrea et al. 2010b; Csiki-Sava et al. 2016)
"Nodosauridae indet. (?*Struthiosaurus* sp.)" (here referred to Ankylosauria indet.)	Fragmentary tooth	T2/3/middle Sebeş Formation/meandering river systems with well or poorly drained floodplains as well as ponds and lakes	Oarda de Jos – Oarda de Jos lens (OdAN site) (OdAN)/grey greenish sandy-silty mudstones	Described: (Jipa-Murzea 2012) Mentioned: (Csiki-Sava et al. 2016; Ţabără and Csiki-Sava 2024)
"Nodosauridae indet. (?*Struthiosaurus* sp.)" (here referred to Ankylosauria indet.)	Rib fragment	T2/3/middle Sebeş Formation/meandering river systems with well or poorly drained floodplains as well as ponds and lakes	Oarda de Jos (OdA)/grey greenish sandy-silty mudstones	Described: (Jipa-Murzea 2012)

called the ‘Pui Beds’ (for an overview, see Csiki-Sava et al. 2016).

Uppermost Cretaceous continental deposits in the southeastern Haţeg Basin consist of fluvial red-beds that crop out along the Bărbat River south of the town of Pui and historically have been referred to the Sînpetru Formation (e.g. Nopcsa 1905; Mamulea 1953; Grigorescu 1992). In recent years, however, this referral has been questioned and those beds instead likely represent their own lithostratigraphic unit, informally known as the ‘Bărbat Formation’ (Therrien 2005) or the ‘Pui Beds’ (Csiki-Sava et al. 2016). The ‘Pui Beds’ consist of repeated fining-upwards sequences, deposited on a well-drained, high sinuosity, meandering floodplain (Therrien 2005; Csiki-Sava et al. 2016). The often-truncated sequences start with basal, greenish conglomeratic sandstones that formed the river bases, overlain by sandy channel fills that grade into brown to red silty mudstones deposited on the floodplains, with occasional intercalations of thin sandstone layers formed by crevasse splays (Van Itterbeeck et al. 2004; Bojar 2005; Therrien 2005). Within the red mudstones, calcareous nodules and calcrete layers record well developed palaeosols that formed under semi-arid climatic conditions with seasonal dry and monsoonal wet periods (Therrien 2005). Overall, the palaeosols of the ‘Pui Beds’ are much more mature compared to those of the other, roughly coeval units within the Haţeg Basin (cropping out in the northwestern and central parts), probably due to lower sediment accumulation rates and less frequent flooding events on a more stable floodplain (Van Itterbeeck et al. 2004; Bojar 2005; Therrien 2005). The channel deposits within the ‘Pui Beds’ are indicative of a northward palaeocurrent direction and of a source area in the nearby, mainly metamorphic Retezat Mountains to the south, as indicated by their compositional immaturity and angularity (Therrien 2005). Rare occurrences of locally restricted, dark greyish-blueish mudstones within the red beds along the Bărbat River section have been interpreted as pond or oxbow lake deposits (Codrea and Solomon 2012; Codrea et al. 2013; Csiki-Sava et al. 2016; Vasile et al. 2019).

Based on palynological data, the middle part of the ‘Pui Beds’ was dated to around the early to late Maastrichtian boundary (“mid”-Maastrichtian; Van Itterbeeck et al. 2005), although deposition might have started during the earliest Maastrichtian, based on the latest Campanian age of the underlying marine flysch and neritic deposits (Neagu 2006; Melinte-Dobrinescu 2010; Csiki-Sava et al. 2016). The ankylosaur scapula described herein was recovered from the lower part of the local succession and thus, given the local stratigraphical and depositional context, is likely early Maastrichtian in age.

Vertebrates within the ‘Pui Beds’ are mainly preserved as isolated remains or within microvertebrate bonebeds, alongside abundant gastropod operculae and shell fragments, eggshell fragments, and rare ostracods (Garcia et al. 2002; Pană et al. 2002; Folie and Codrea 2005; Csiki-Sava et al. 2016; Vasile et al. 2019). Although less common, associated elements of partial skeletons also are recovered (e.g. Van Itterbeeck et al. 2004; Csiki-Sava et al. 2018; Augustin et al. 2022). The local section hosts the type localities of several new taxa reported previously from the Haţeg Basin (highlighted below). Among the non-dinosaurian vertebrate remains, fishes, amphibians (anurans, albanerpetontids), kogaionid multituberculate mammals (*Barbatodon transylvanicus*, *Litovoi tholocephalos*), lizards (*Barbatteius vremiri*, *Becklesius nopcsai*, *Bicuspidon hatzegiensis*), snakes, turtles, crocodyliforms (*Aprosuchus ghirai*), and azhdarchid pterosaurs have been reported (Grigorescu et al. 1985, 1999; Rădulescu and Samson 1986; Grigorescu and Hahn 1987; Folie et al. 2002; Folie and Codrea 2003, 2005; Smith and Codrea 2003, 2015; Csiki et al. 2005; Vasile and Csiki 2010; Codrea and Solomon 2012; Venczel and Codrea 2016, 2019; Vremir et al. 2015b; Solomon et al. 2016; Codrea et al. 2017; Csiki-Sava et al. 2018, 2022; Vasile et al. 2019).

Dinosaur remains from the ‘Pui Beds’ have been assigned to rhabdodontids (including the holotype of *Transylvanosaurus platycephalus*), hadrosauroids, titanosaurian sauropods, and small sized maniraptoran theropods (Velociraptorinae indet.) (Grigorescu et al. 1985, 1999; Csiki and Grigorescu 1998; Van Itterbeeck et al. 2004; Vasile and Csiki 2010; Codrea and Solomon 2012; Csiki-Sava et al. 2016; Vasile et al. 2019; Augustin et al. 2022; Díez Díaz et al. 2025), with peculiar, thin eggshells further documenting the presence of indeterminate small-sized maniraptorans (Choi et al. 2020). Previously, fossil remains representing these different dinosaur clades were often referred to particular genera/species, such as *Zalmoxes robustus* and *Z. shqiperorum* among Rhabdodontidae (Grigorescu et al. 1999; Therrien 2005; Vasile and Csiki 2010; Codrea and Solomon 2012), *Telmatosaurus transsylvanicus* among Hadrosauroidea (Therrien 2005; Vasile and Csiki 2010; Codrea and Solomon 2012), and *Magyarosaurus dacus* among Titanosauria (Grigorescu et al. 1999; Therrien 2005). However, in most cases such referrals were not based on the presence of diagnostic features of the corresponding taxon, but on the assumption that these historically named taxa represent either the sole or the most common representative(s) of their respective clades within the uppermost Cretaceous of the Haţeg Basin, as discussed recently for rhabdodontids by Augustin et al. (2022; see also Augustin et al. 2023). Nevertheless, the presence of the lithostrotian titanosaur *M. dacus* in the ‘Pui Beds’ was substantiated recently by Díez-Díaz et al. (2025).

Material and methods

The ankylosaur scapula reported in this contribution was recovered during the 2019 field season by a crew from the University of Bucharest and is permanently housed in the palaeontological collection of the Faculty of Geology and Geophysics, University of Bucharest, Romania, under the inventory number LPB (FGGUB) R.2684. It was discovered in the lower part of the Bărbat River sedimentary succession, south of the town of Pui (Pui MD site, see Figs. 2, 7 and Table 1), in a greenish-grey conglomeratic sandstone interbedded between dm-to-1 m thick, dark red to brick red, sandy-muddy, pedogenetically modified siltstones and fine micaceous sandstones (i.e. the most common lithotype in the local succession). The outcrop yielding the specimen is located on the western (i.e. left) bank of the Bărbat riverbed, slightly upstream from the log deposit of the local saw mill and only a few meters downstream from the high-diversity Pui-Depozit vertebrate site reported by Codrea and Solomon (2012).

The scapula was found lying flat and more or less horizontally within the fossiliferous horizon, with its lateral side facing upwards. It was discovered alongside several other isolated and fragmentary vertebrate remains, including a partial rhabdodontid femur, turtle shell fragments, and an isolated crocodyliform tooth reminiscent of the anterior teeth of the basal eusuchian *Allodaposuchus precedens* (see Delfino et al. 2008). Additionally, the upper, mottled part of the sandstone transitional to the overlying red sandy siltstones have yielded an isolated titanosaur ischium and further associated titanosaur postcranial remains referable to *Magyarosaurus dacus* (Díez Díaz et al. 2025); they were excavated slightly upstream from LPB (FGGUB) R.2684 and within the same localised sedimentary sequence.

Institutional abbreviations

CEUM: Prehistoric Museum, College of Eastern Utah, Price, USA;
CJPM: Chaoyang Jizantang Paleontological Museum, Beipiao, China;
CMN: Canadian Museum of Nature, Ottawa, Canada;
FCPTD/MAP: Fundación Conjunto Paleontológico de Teruel-Dinópolis/Museo Aragonés de Palaeontología, Teruel, Spain;
IGM: Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia;
LPB (FGGUB): Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania;
MTM: Magyar Természettudományi Múzeum, Budapest, Hungary;
MC: Musée de Cruzy, Cruzy, France;
NHMUK: Natural History Museum, London, UK;
PIUW: Paläontologisches Institut der Universität Wien, Vienna, Austria;
UBB: Babeș-Bolyai University, Cluj-Napoca, Romania;
TMP: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada;
YPM: Yale Peabody Museum of Natural History, New Haven, USA.

Systematic palaeontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1888
Thyreophora Nopcsa, 1915
Ankylosauria Osborn, 1923
Struthiosauridae Nopcsa, 1923a (sensu Raven et al. 2023)
Struthiosaurus Bunzel, 1871

Struthiosaurus sp.
(Figs. 3, 4a, 5a, 6a)

Material: LPB (FGGUB) R.2684, an isolated right scapula missing small portions of the anterior and posterior ends.
Locality, horizon, and age: Pui MD fossil site (see Díez Díaz et al. 2025) in the lower part of the Bărbat River valley section, south of the town of Pui, southeastern Haţeg Basin. Previously assigned to the Sînpetru Formation (otherwise cropping out in the central Haţeg Basin), the local succession has more recently been suggested to represent a distinct lithostratigraphic unit, informally referred to as the 'Bărbat Formation' (Therrien 2005) or the 'Pui Beds' (Csiki-Sava et al. 2016). Probably early Maastrichtian.

Description

The specimen (Fig. 3) is a partial right scapula, missing both its posterior and anterior ends. Except for the missing parts, the bone is relatively well preserved. Its lateral surface has only a few cracks along the midline extending from the crushed anterior end, whereas its medial surface is more crushed, but displays the same fracture-pattern (likely the result of the way the specimen was preserved, see above). Overall, it is anteroposteriorly elongate and mediolaterally compressed, with a roughly blade-like shape. As preserved, the scapula has an anteroposterior length of 180 mm.

The posterior half of the scapula is plate-like and straight. It has an approximately constant dorsoventral height of about 65 mm, with the dorsal and ventral margins being straight and extending parallel to each other; only towards the preserved posterior end, is there a slight increase in dorsoventral height (to a maximum of 70 mm), where the ventral margin slopes gently posteroventrally. The posterior half of the scapula has a relatively consistent mediolateral width ranging between 10–13 mm, because the medial and lateral surfaces are parallel to each other and almost flat.

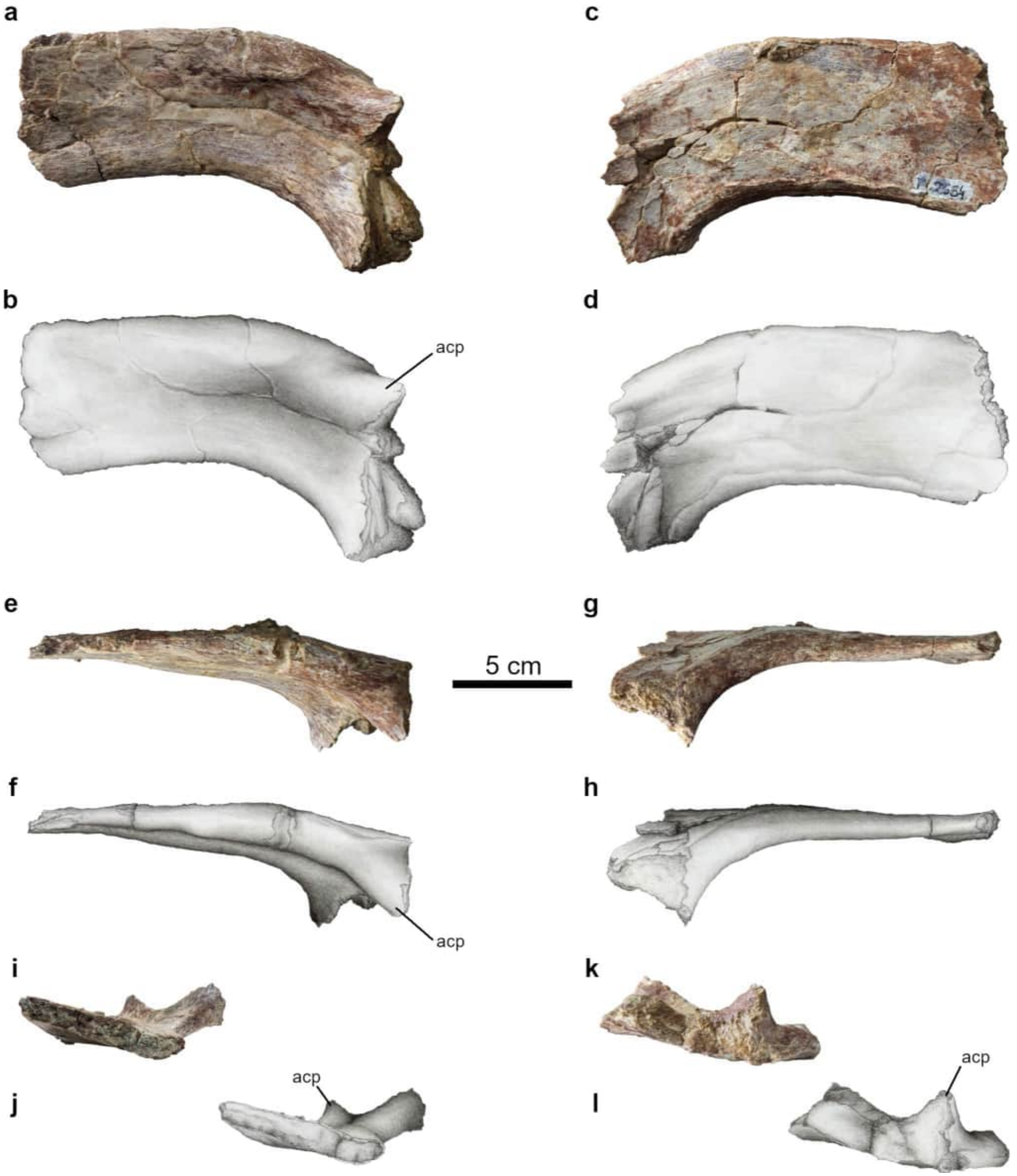


Fig. 3 Partial right scapula of *Struthiosaurus* sp., LPB (FGGUB) R.2684, from the lower Maastrichtian 'Pui Beds' of Pui, Haţeg Basin, Romania, in lateral (**a**, **b**), medial (**c**, **d**), dorsal (**e**, **f**), ventral (**g**, **h**), posterior (**i**, **j**) and anterior (**k**, **l**) views. Images in **a**, **c**, **e**, **g**, **i**, **k** are photographs, whereas **b**, **d**, **f**, **h**, **j**, **l** are interpretative drawings. Abbreviations: *acp* acromial process. All images at same scale; see 5 cm scale bar

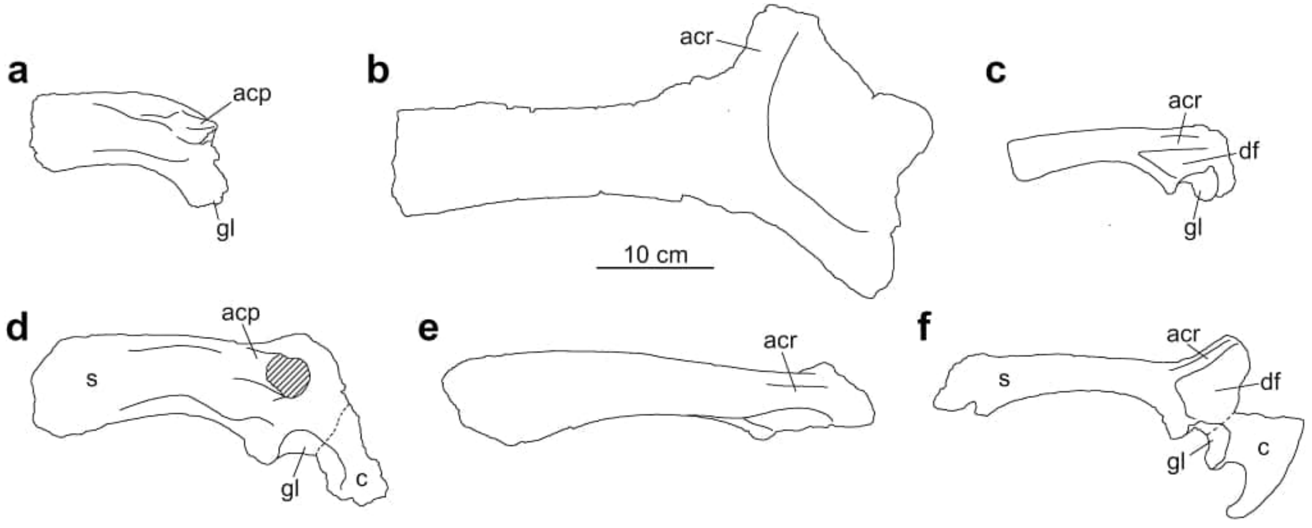


Fig. 4 Comparison of LPB (FGGUB) R.2684 with scapulae of major dinosaurian groups from the uppermost Cretaceous of Transylvania. All specimens in lateral view (left elements mirrored for easier comparison) and scaled to their relative sizes. **a** right scapula of *Struthiosaurus* sp. (LPB (FGGUB) R.2684), Pui, Haţeg Basin, Romania; 'Pui Beds', lower Maastrichtian. **b** left scapula of an indeterminate titanosaur (LPB (FGGUB) R.0003), Sânpetru, Haţeg Basin, Romania; Sînpetru Formation, Maastrichtian. **c** right scapula of *Zalmoxes robustus* (NHMUK R.3810), Sânpetru, Haţeg Basin, Romania; Sînpetru Formation, Maastrichtian (redrawn after Weishampel et al. 2003). **d** right scapulocoracoid of *Struthiosaurus transylvanicus* (NHMUK R.4966), Sânpetru, Haţeg Basin, Romania; Sînpetru Formation, Maastrichtian (redrawn after Nopcsa 1929). **e** left scapula of *Telmatosaurus transylvanicus* (LPB (FGGUB) R.0004), Sânpetru, Haţeg Basin, Romania; Sînpetru Formation, Maastrichtian. **f** left scapula of *Zalmoxes shqiperorum* (NHMUK R.4900), Sânpetru, Haţeg Basin, Romania; Sînpetru Formation (contra Weishampel et al. 2003; see Augustin et al. 2023: p. 176), Maastrichtian (redrawn after Weishampel et al. 2003). Abbreviations: *acp*, acromial process, with knob-like end indicated by cross-hatching; *acr* acromion; *c* coracoid; *df* deltoid fossa; *gl* glenoid; *s* scapula. Scale bar: 10 cm

At around the mid-length of the element, the dorsal and ventral margins begin to curve anteroventrally. This curvature is more pronounced along the ventral margin, and thus the dorsoventral height increases slightly anteriorly (to a maximum of 75 mm at the preserved anterior end). Additionally, the ventral portion of the scapula curves laterally in the anterior half, whereas the dorsal portion remains more or less straight, resulting in a slightly twisted appearance to the anterior half of the scapula. The dorsal margin thickens markedly in the anterior third of the scapula, mainly through the development of a lateral bulge that initially extends parallel to the dorsal margin (and is confluent with it), but anteriorly bends stronger ventrally and is separated from the dorsal margin by a narrow shelf. Close to the preserved anterior end, the lateral bulge rises markedly, forming a laterally projecting, well-developed and knob-like process, the acromion, which is only incompletely preserved and missing its anterior part.

Similar to the dorsal margin, the ventral margin of the scapula also becomes wider mediolaterally towards the anterior end and, at the level of the acromion, forms a massive laterally protruding process with a triangular cross-section, the glenoid process; farther anteriorly, the ventral margin is damaged and broken. Anterodorsal to the glenoid process, the lateral surface of the scapula seems to be anteromedially inclined, but that is not certain because the portion anterior to the acromion and glenoid process is only poorly preserved and broken. The lateral surface of the anterior half of the scapula (up to level of the acromion and glenoid process) is shallowly concave between the thickened dorsal and ventral margins, with a groove in the middle that runs approximately parallel to the long axis of the scapula (i.e. being straight posteriorly and bending ventrally towards the anterior end). Conversely, the medial surface of the anterior half is approximately flat and slanted dorsomedially.

Identification and comparison

Taxonomic identification of LPB (FGGUB) R.2684

The herein described scapula (Figs. 3, 4a, 5a, 6a) can be clearly identified as dinosaurian, based on its large size and robustness. Because the only medium-to large-sized dinosaurs known from the Transylvanian area are titanosaurs, rhabdodontids, hadrosauroids and struthiosaurids (Nopcsa 1923b; Grigorescu 1983; Weishampel et al. 1991; Csiki-Sava et al. 2015, 2016), comparisons can be limited to these groups. The scapulae of Transylvanian titanosaurian sauropods (e.g. LPB

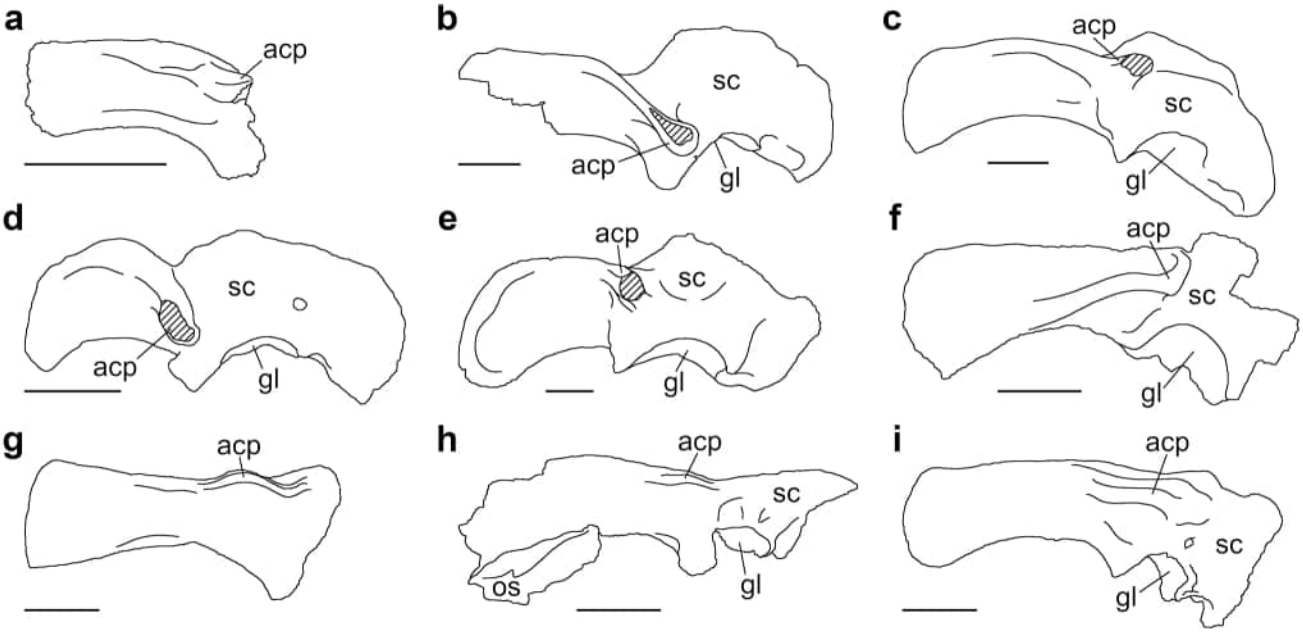


Fig. 5 Comparison of LPB (FGGUB) R.2684 with selected ankylosaur scapulae. All specimens in lateral view (left elements mirrored for easier comparison) and scaled to approximately the same size. **a** right scapula of the struthiosaurid *Struthiosaurus* sp. (LPB (FGGUB) R.2684), Romania; 'Pui Beds', lower Maastrichtian. **b** left scapulocoracoid of the ankylosaur of uncertain affinities *Sauropelta edwardsorum* (YPM 5179), USA; Cloverly Formation, middle Aptian–middle Albian (redrawn after Coombs 1978 and Ostrom 1970). **c** left scapulocoracoid of the panoplosaurid *Panoplosaurus mirus* (CMN 2759), Canada; Dinosaur Park Formation, Campanian (redrawn after Sternberg 1921). **d** left scapulocoracoid of the ? basal panoplosaurid *Animantarx ramaljonesi* (CEUM 6228), USA; Cedar Mountain Formation, Cenomanian (redrawn after Carpenter et al. 1999). **e** right scapulocoracoid of the polacanthid *Peloroplites cedrimontanus* (CEUM 11706), USA; Cedar Mountain Formation, Cenomanian (redrawn after Carpenter et al. 2008). **f** right scapulocoracoid of the polacanthid *Gastonia burgei* (CEUM 2356), USA; Cedar Mountain Formation, Barremian (redrawn after Kinneer et al. 2016). **g** right scapula of the ankylosaurid *Chuanqilong chaoyangensis* (CJPM V001), China; Jiufotang Formation, Aptian (redrawn after Han et al. 2014). **h** left scapulocoracoid of the ankylosaurid *Saichania chulsanensis* (IGM 100/1305), Mongolia; Barun Goyot Formation, upper Campanian (redrawn after Carpenter et al. 2011). **i** left scapulocoracoid of the ankylosaurid *Euoplocephalus tutus* (TMP 2001.42.19), USA; Two Medicine Formation, Campanian (redrawn after Arbour and Currie 2013). Abbreviations: *acp* acromial process, with knob-like end indicated by cross-hatching; *gl* glenoid; *os* osteoderm; *sc* scapulocoracoid. Scale bars: 10 cm

(FGGUB) R.0003, Fig. 4b) differ considerably from LPB (FGGUB) R.2684 in the following suite of characters: (i) along the dorsal margin of the scapula, the acromion protrudes dorsally, creating an almost 90° angle with the long axis of the scapular blade; (ii) the acromion, if laterally elevated at all, is restricted to a shallow acromial ridge, rather than a laterally protruding acromial process; (iii) the medial surface of the scapular blade is markedly concave dorsoventrally in its anterior part, bordered ventrally by a rounded longitudinal ridge and demarcated antero-dorsally by a prominent triangular tuberosity that is continued posteriorly by a short and acute ridge; and (iv) the anterior part of the lateral scapular blade is asymmetrically convex dorsoventrally, so that the cross-section of the scapular blade neck is crescentic and medially excavated (see Le Loeuff 1995, 2005: fig. 4.11; Díez Díaz et al. 2013: fig. 2, 2025: fig. 52 A–D; Vila et al. 2022: fig. 2f). Rhabdodontid scapulae (e.g. NHMUK R.3810 and NHMUK R.4900, Fig. 4c, f, respectively) show the following differences: (i) the scapular blade is considerably lower in dorsoventral height than seen in LPB (FGGUB) R.2684 and is proportionately wider mediolaterally, with a more ellipsoidal cross section along the scapular neck; (ii) the lateral surface of the anterior scapular blade is convex to flat, rather than showing a concave midline groove; and (iii) the scapula has a shallow and rounded acromial/deltoid ridge running right along the dorsal margin (see Weishampel et al. 2003: figs. 19, 28; Godefroit et al. 2009: fig. 15; Brusatte et al. 2017: figs. 11, 12; Magyar et al. 2024: fig. 7). Scapulae of basal hadrosauroids from Transylvania (e.g. LPB (FGGUB) R.0004, Fig. 4e) exhibit the following differences: (i) the scapular blade of hadrosauroids is much slenderer, with an ellipsoidal cross section at around mid-length; (ii) the lateral surface of the scapular blade (posterior to the glenoid process) is convex to flat and devoid of a concave midline groove; (iii) the anterior end curves only weakly anteroventrally; and (iv) the acromion forms a well-rounded acromial ridge along the dorsal margin and is oriented parallel to the long axis of the scapular blade

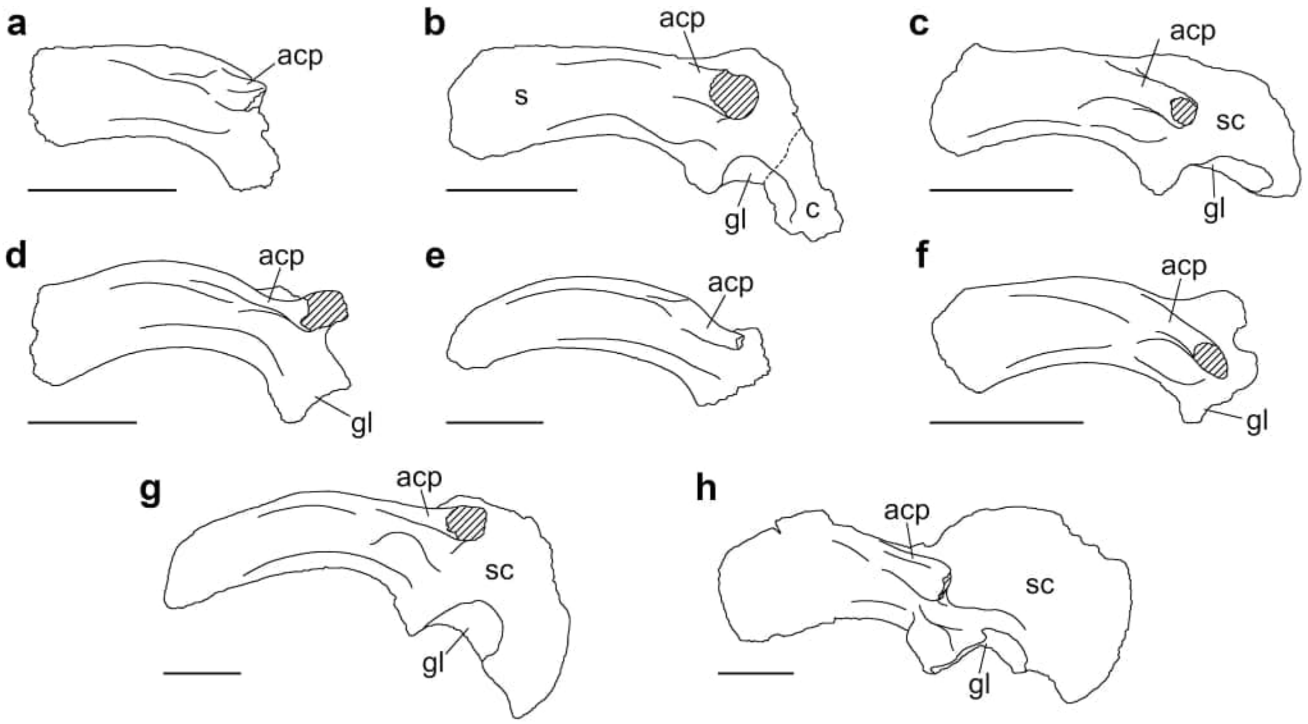


Fig. 6 Comparison of LPB (FGGUB) R.2684 with struthiosaurid scapulae from the uppermost Cretaceous of Europe. All specimens in lateral view (left elements mirrored for easier comparison) and scaled to approximately the same size. **a** right scapula of *Struthiosaurus* sp. (LPB (FGGUB) R.2684), Pui, Haţeg Basin, Romania; 'Pui Beds', lower Maastrichtian. **b** right scapulocoracoid of *Struthiosaurus transylvanicus* (NHMUK R.4966), Sânpetru, Haţeg Basin, Romania; Sînpetru Formation, Maastrichtian (redrawn after Nopcsa 1929). **c** right scapula of *Struthiosaurus* sp. (MC Mn 393), Montplo Nord, Hérault, southern France; Grès à Reptiles Formation, upper Campanian to lower Maastrichtian (redrawn after Csiki-Sava et al. 2015). **d** left scapula of *Struthiosaurus austriacus*, complete larger left specimen (PIUW 2349/uncatalogued [A2]), Muthmannsdorf, Austria; Grünbach Formation, lower Campanian (redrawn after Seeley 1888). **e** left scapula of *Struthiosaurus austriacus*, less complete larger left specimen (PIUW 2349/uncatalogued [B9]), Muthmannsdorf, Austria; Grünbach Formation, lower Campanian (redrawn after Bunzel 1871). **f** right scapula of *Struthiosaurus austriacus*, smaller right specimen (PIUW 2349/1 [C1]), Muthmannsdorf, Austria; Grünbach Formation, lower Campanian (redrawn after Seeley 1881). **g** left scapulocoracoid of the holotype of *Hungarosaurus tormai* (MTM V 2007.26.23.), Iharkút, Hungary; Csehbánya Formation, upper Santonian (redrawn after Ősi et al. 2019). **h** right scapulocoracoid of *Europelta carbonensis* (FCPTD/MAP AR – 1/116–6823), Ariño, Teruel Province, Spain; Escucha Formation, upper Aptian-lower Albian (J. Kirkland, pers. comm. 2025). Abbreviations: *acp* acromial process, with knob-like end indicated by cross-hatching; *c* coracoid; *gl* glenoid; *sc* scapulocoracoid. Scale bars: 10 cm

(see Weishampel et al. 1993: fig. 5A). Therefore, any close affinities of LPB (FGGUB) R.2684 to any of the above-mentioned groups can be reliably dismissed, leaving only struthiosaurid ankylosaurs among the mega- and meso-vertebrates known from the uppermost Cretaceous continental deposits of Transylvania as the group to which the individual represented by the Pui scapula may belong (Fig. 4).

Furthermore, the following features also strongly suggest ankylosaurian affinities for LPB (FGGUB) R.2684 (see also Fig. 5): (i) a scapular blade that is proportionately high dorsoventrally and thin mediolaterally, lacking a marked constriction posterior to the glenoid; and (ii) presence of a prominent, laterally projecting acromion process that extends onto the scapular blade (although the shape of the acromion is variable among ankylosaurs, ranging from knob-like to shelf-like; see below). Accordingly, we argue that all available evidence supports identification of this specimen as ankylosaurian.

It is worth emphasising that a new phylogeny of the Ankylosauria was proposed recently by Raven et al. (2023), who found Nodosauridae to be a polyphyletic clade, thus rejecting the long-established dichotomy of Ankylosauria into the families Nodosauridae and Ankylosauridae (e.g. Coombs 1978; Coombs and Maryanska 1990; Sereno 1999; Vickaryous et al. 2004; Thompson et al. 2012; Arbour and Currie 2016; Madzia et al. 2021). Instead, Raven et al. (2023) advocated splitting Ankylosauria into four families, listed here from basally branching to more derived: Struthiosauridae, Panoplosauridae, Polacanthidae and Ankylosauridae. We note here that the taxonomic composition of Struthiosauridae as recognised by Raven et al. (2023)—i.e. uniting the latest Cretaceous European *Hungarosaurus tormai* and *Struthiosaurus* spp. with the

Early Cretaceous *Europelta carbonensis* from Spain, as well as with the latest Early Cretaceous North American *Pawpawsaurus campbelli*—is largely similar to that of Struthiosaurinae, a clade originally proposed by Kirkland et al. (2013) to contain the Early Cretaceous *Anoplosaurus* from England alongside *Europelta*, *Hungarosaurus* and *Struthiosaurus*, and placed by those authors within the nodosaurid radiation, albeit without the support of a phylogenetic analysis. A clade with a roughly similar taxonomic composition to Struthiosaurinae sensu Kirkland et al. (2013) or to the newly recognised Struthiosauridae sensu Raven et al. (2023), and also placed within Nodosauridae, was recovered by Rivera-Sylva et al. (2018) to contain *Europelta*, *Hungarosaurus*, *Struthiosaurus* and *Pawpawsaurus*, together with the Late Cretaceous *Stegopelta* from the western USA. Although Rivera-Sylva et al. (2018) did not name this clade, Madzia et al. (2021) recently called it Struthiosaurini and formally defined it in compliance with the International Code of Phylogenetic Nomenclature (ICPN or PhyloCode), using the cladogram of Rivera-Sylva et al. (2018) as the reference cladogram. We herein follow the most recent systematic results of Raven et al. (2023), which are based on a broad-scale phylogenetic analysis of Thyreophora, and consequently use the term Struthiosauridae for the group containing, among others, *Struthiosaurus* spp. and *Hungarosaurus tormai* (i.e. the only valid ankylosaur taxa known from the Late Cretaceous of Europe). This group was placed at the base of the ankylosaurian radiation and defined "as all ankylosaurs more closely related to *Struthiosaurus austriacus* than to *Ankylosaurus*, *Panoplosaurus* or *Gastonia burgei*" (Raven et al. 2023: pp. 21–22).

Among ankylosaurs, LPB (FGGUB) R.2684 exhibits one ambiguous synapomorphy of Struthiosauridae, i.e. the absence of a medial buttress on the scapulocoracoid (Raven et al. 2023: online supplementary material, a reversal of character 195). The synapomorphic absence of a medial buttress definitively sets apart specimen LPB (FGGUB) R.2684, together with all struthiosaurids considered by Raven et al. (2023), with the exception of *Europelta carbonensis* (for which, however, the scapula has not been described yet, but this feature appears to be absent in this taxon as well; J. Kirkland, pers. comm. 2025), from the polacanthid and panoplosaurid clades within Ankylosauria. Nevertheless, it is worth noting that under the ACCTRAN optimisation option, this same character state was identified by Raven et al. (2023) as a synapomorphy of a somewhat more inclusive ankylosaur subclade, uniting Struthiosauridae with the small *Silvisaurus* + *Taohelong* grouping to the exclusion of all other ankylosaurs; thus the ambiguous nature of that feature at the root of Struthiosauridae is a consequence of missing data (i.e. the undescribed scapula of *Europelta*, which was not included by Raven et al. 2023) for the basal struthiosaurid *Europelta*.

Aside from struthiosaurids, the medial buttress is also apomorphically absent in a few ankylosaurid taxa (Raven et al. 2023: online supplementary material), but virtually all ankylosaurids can be differentiated from LPB (FGGUB) R.2684 by the presence of one unambiguous synapomorphy of the clade—i.e. a straight dorsal surface of the scapular blade—identified by Raven et al. (2023: online supplementary material, a reversal of character 198). Furthermore, ankylosaurids also clearly differ from the Pui scapula in the following two features (see also Fig. 5g–i): (i) the acromion is positioned more dorsally and is not ventrally displaced (interestingly, such a ventrally displaced acromion that is not confluent with the dorsal margin of the scapula was once listed as a synapomorphy of 'nodosaurids' by Coombs and Maryanska 1990); and (ii) possession of a ridge-like instead of a knob-like acromion process (e.g. see Carpenter 2004: fig. 15, for *Ankylosaurus magniventris*; Carpenter et al. 2011: pl. 6, for *Saichania chulsanensis*; Arbour and Currie 2013: fig. 10, for *Euoplocephalus tutus*; Han et al. 2014: fig. 5, for *Chuanqilong chaoyangensis*; Zheng et al. 2018: fig. 7, for *Jinyunpelta sinensis*).

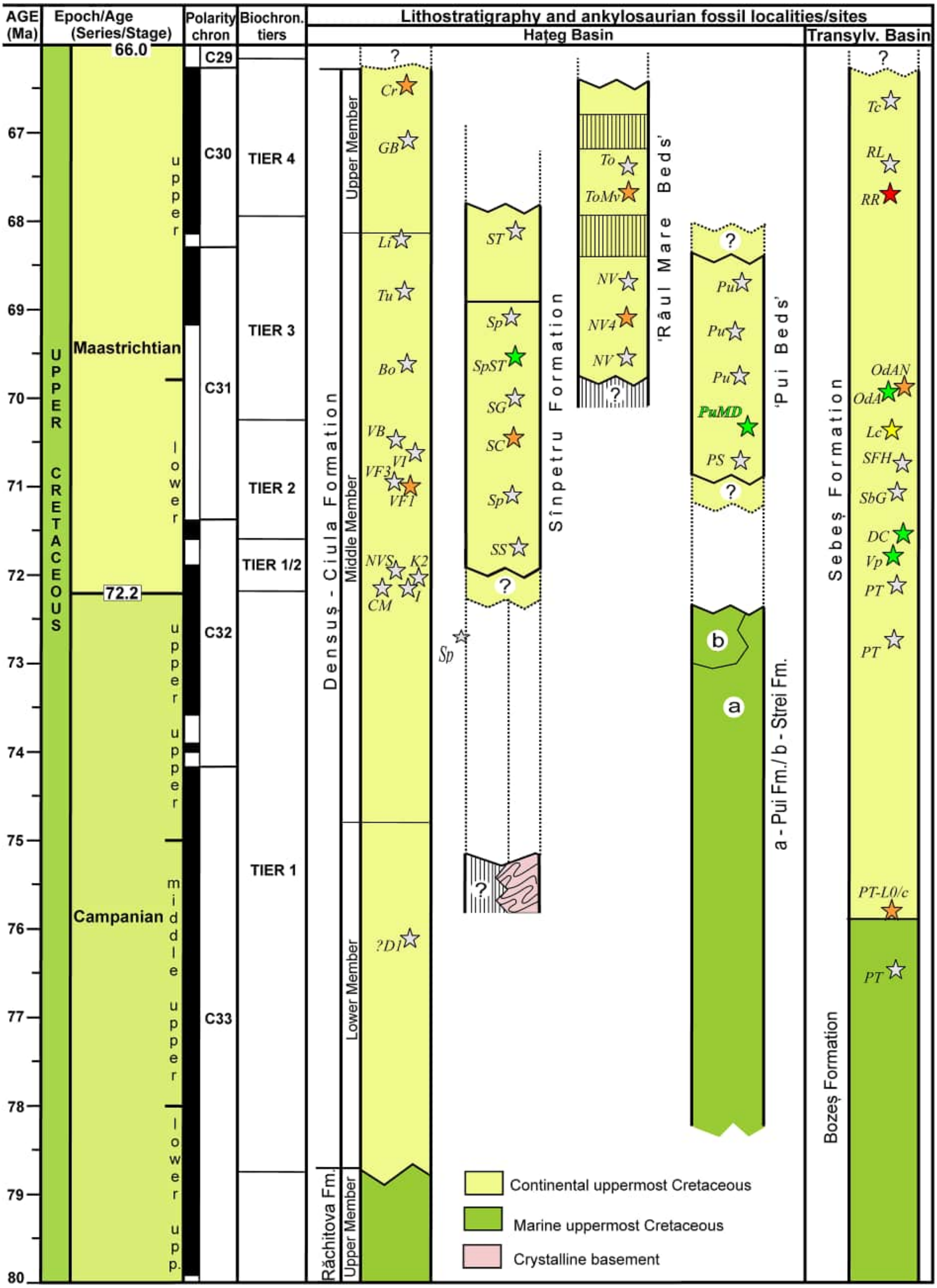
Although no scapular synapomorphies were identified by Raven et al. (2023) for Panoplosauridae, Polacanthidae can be diagnosed by two unambiguous scapular synapomorphies: (i) absence of a ventral process at the posteroventral margin of the glenoid (reversal of character 192), and (ii) acromion process shelf-like, laterally extending (reversal of character 193, from state 3 – acromion process ridge-like, terminating in a knob-like prominence). The former synapomorphy cannot be properly assessed in LPB (FGGUB) R.2684 due to its incomplete preservation. However, the Pui scapula clearly displays the more derived, knob-like acromial morphology (Figs. 3a, b, e, f, 4a, 5a), further differentiating it from polacanthids.

An additional scapular synapomorphy of Struthiosauridae (as Struthiosaurinae) proposed by Kirkland et al. (2013)—the position of the acromial process dorsal to the midpoint of the scapula-coracoid suture—was questioned subsequently (Ősi 2015; Madzia et al. 2021). The diagnostic utility of this feature is irrelevant in the present discussion, however, because the corresponding part is missing in LPB (FGGUB) R.2684.

Therefore, using a combination of recently identified synapomorphies and other detailed morphological differences mapped across Ankylosauria, we confidently assign LPB (FGGUB) R.2684 to Struthiosauridae—a clade containing the sole representatives of Ankylosauria in the latest Cretaceous of Europe.

Comparison with other members of Struthiosauridae

Given the established struthiosaurid affinities of the Pui scapula, we provide here detailed comparisons with the other Late Cretaceous European struthiosaurids—i.e. *Struthiosaurus transylvanicus* from the Maastrichtian


AGE (Ma)
Epoch/Age (Series/Stage)
Polarity chron
Biochron. tiers
Lithostratigraphy and ankylosaurian fossil localities/sites
Haţeg Basin
Transylv. Basin
66.0
67
68
69
70
71
72
73
74
75
76
77
78
79
80
UPPER CRETACEOUS
Maastrichtian
upper
lower
72.2
Campanian
upper
upper
middle
upper
lower
upp.
C29
C30
C31
C32
C33
TIER 4
TIER 3
TIER 2
TIER 1/2
TIER 1
Densuș - Ciula Formation
Upper Member
Middle Member
Lower Member
Răchitova Fm.
Upper Member
?
Cr
GB
Li
Tu
Bo
VB
VI
VF3
VF1
NVS
K2
CM
I
?DI
Sp
ST
Sp
SpST
SG
SC
Sp
SS
?
?
Sînpetru Formation
To
ToMv
NV
NV4
NV
?
'Râul Mare Beds'
?
Pu
Pu
Pu
PuMD
PS
?
'Pui Beds'
b
a
a - Pui Fm./ b - Strei Fm.
?
Tc
RL
RR
OdAN
OdA
Lc
SFH
SbG
DC
Vp
PT
PT
PT-L0/c
PT
Sebeș Formation
Bozeș Formation
Continental uppermost Cretaceous
Marine uppermost Cretaceous
Crystalline basement

◀**Fig. 7** Synthetic stratigraphical and tier distribution of ankylosaur occurrences throughout the Haţeg and Transylvanian basins. For colour coding of occurrences, see Figure 2; grey stars indicate other important sites lacking ankylosaur material. Modified and updated from Csiki-Sava et al. (2016: fig. 14). Absolute ages for stage boundaries follow Cohen et al. 2013, updated v2024/12. Abbreviations: *Bo* Boiţa; *CM* Ciula Mică; *Cr* Crăguiş; *DC* Cuptorului Hill; *D1* Densuş; *GB*, Berthelot; *I* site I of Kadić, Vălioara; *K2* site K2, Vălioara; *Lc* Lancrăm; *Li* Livezi; *NV* Nălaţ-Vad (*); *NVS* New Vertebrate Site, Vălioara; *NV4* Nălaţ-Vad, site 4, microvertebrate accumulation; *OdA* Oarda de Jos locality A; *OdAN* Oarda de Jos locality A, lens; *Pu* Pui (*); *PuMD*, Pui – MD (this paper, highlighted in green); *PS* Pui Swamp; *PT* Petreşti-Arini (*); *PT-L0/c* Petreşti-Arini, site L0/c, microvertebrate accumulation; *RL* Râpa Lancrămului; *RR* Râpa Roşie; *SbG*, Sebeş-Glod; *SC* Sânpetru Cărare; *SFH* Secaş, Fetilor Hill; *SG* Sânpetru Groapă; *Sp* Sânpetru (*); *SpST* Sânpetru *Struthiosaurus transylvanicus* type locality; *SS* Sânpetru Scoabă; *ST* Sânpetru Terminus; *Tc* Teleac; *To* Toteşti (*); *ToMv* Toteşti, microvertebrate site; *Tu* Tuştea; *VB* Vălioara-Budurone; *VF1* Vălioara – Fântânele, microvertebrate site; *VF3* Vălioara – Fântânele 3; *VI* site VI of Kadić, Vălioara; *Vp* Vurpăr. (*) indicates several different sites known for the respective localities and stratigraphic position illustrative only

of Transylvania (Fig. 6b), *Struthiosaurus* sp. from the Campanian–Maastrichtian of southern France (Fig. 6c), *S. austriacus* from the early Campanian of eastern Austria (Figs. 6d–f), and *Hungarosaurus tormai* from the Santonian of western Hungary (Fig. 6g)—as well as the Early Cretaceous struthiosaurid *Europelta carbonensis* from Spain (Fig. 6h). No scapulae are known for the other currently recognised struthiosaurids (the Early Cretaceous *Pawpawsaurus campbelli* and the latest Cretaceous *S. languedocensis*) and, thus, these species cannot be compared to LPB (FGGUB) R.2684.

Europelta carbonensis. The remains of *Europelta carbonensis* from the upper Aptian-lower Albian Escucha Formation of Ariño, Teruel Province, Spain, did not include a scapula when it was originally described by Kirkland et al. (2013). However, a complete right (FCPTD/MAP AR – 1/116–6823, Fig. 6h) and heavily distorted left scapulocoracoid (FCPTD/MAP AR – 1/116–6892) have since been recovered, but are yet to be properly described (J. Kirkland, pers. comm. 2025). The scapula of *Europelta* shows certain similarities to LPB (FGGUB) R.2684, yet it differs in the following characters: (i) the scapular blade is dorsoventrally constricted in its anterior part (in this feature, *Europelta* also differs from *Hungarosaurus tormai*, *Struthiosaurus austriacus*, *Struthiosaurus transylvanicus* and *Struthiosaurus* sp. from southern France); (ii) the dorsal margin of the scapular blade is more curved in its posterior half in *Europelta*, whereas it is completely straight in LPB (FGGUB) R.2684; and (iii) the acromion process in the anterior portion of the scapular blade begins to rise in elevation more posteriorly than seen in LPB (FGGUB) R.2684.

Hungarosaurus tormai. Four scapulae have been described and figured for *Hungarosaurus tormai* from the Santonian Csehbánya Formation of Iharkút, western Hungary; these belong to the holotype specimen (MTM V 2007.26.23., Fig. 6g), as well as to the fifth and ninth ankylosaur skeletons from that locality (Ősi 2005; Ősi and Makádi 2009; Ősi et al. 2019). The overall scapular morphology of this species is quite similar to LPB (FGGUB) R.2684, reinforcing referral of the latter to Struthiosauridae. LPB (FGGUB) R.2684 differs from scapulae of *H. tormai* as follows: (i) the dorsal margin in the anterior part of the scapular blade and around the acromion is straighter, leading to a greater increase in dorsoventral height of the scapula in this area (in this feature, *H. tormai* also differs from *Struthiosaurus austriacus* and *S. transylvanicus*); (ii) the acromial process appears to be positioned slightly farther dorsally, though this part is only incompletely preserved in LPB (FGGUB) R.2684; (iii) the concave midline groove on the lateral surface of the scapular blade is restricted to the anteriormost part in *H. tormai*, whereas it extends farther posteriorly in LPB (FGGUB) R.2684; and (iv) the acromial process is located farther posteriorly in *H. tormai*.

Struthiosaurus austriacus. Three scapulae (Fig. 6d–f) belonging to three different individuals are known from the lower Campanian Grünbach Formation of Muthmannsdorf, Austria. These individuals were each regarded as separate species in the past (Bunzel 1871; Seeley 1881; see below), but are currently all referred to *Struthiosaurus austriacus* (Pereda-Suberbiola 1992; Pereda-Suberbiola and Galton 2001; Csiki-Sava et al. 2015;). The two larger, left scapulae (PIUW 2349/uncatalogued [A2] and PIUW 2349/uncatalogued[B9]; Fig. 6d, e, respectively) were originally described as ribs under the name "*Danubiosaurus anceps*" and figured as such by Bunzel (1871: pl. 5, figs. 7–9 and pl. 6, figs. 1–3, respectively). A third, smaller, right scapula (PIUW 2349/1 [C1]; Fig. 6f) was subsequently described by Seeley (1881: 661–663, fig. 1B) as "*Crataeomus lepidophorus*" and in the same paper the previously misidentified larger scapulae were correctly identified as such and re-described as "*Crataeomus pawlowitschi*", with the more complete of the two specimens being figured again (Seeley 1881: p. 654–657, fig. 1A). These three scapulae all differ from LPB (FGGUB) R.2684 as follows: (i) the dorsal margin of the posterior portion of the scapular blade is curved (instead of straight as in LPB [FGGUB] R.2684 and in the scapula of *S. transylvanicus*, see below); and (ii) the acromial process is much longer anteroposteriorly and extends farther posteriorly onto the scapular blade. Moreover, the smaller right scapula differs from both LPB (FGGUB) R.2684 and the other two scapulae from Muthmannsdorf in that the acromial process is located more ventrally and curves ventrally towards the glenoid.

Struthiosaurus transylvanicus. The holotype skeleton of *S. transylvanicus* from the Maastrichtian Sînpetru Formation (Haţeg Basin) includes a complete right scapulocoracoid, NHMUK R.4966 (Fig. 4d, 6b) (Nopcsa 1915, 1929). The scapula is overall similar to LPB (FGGUB) R.2684, only showing four minor differences: (i) the anteroventral curvature of the dorsal margin of the anterior scapular blade is less pronounced; (ii) anteriorly, the scapula curves weakly medially instead of laterally; (iii) the acromion is located slightly farther posteriorly (though considerably less so than in *Struthiosaurus* sp. from southern France, *S. austriacus, Hungarosaurus tormai* and *Europelta carbonensis,* making it most similar to LPB (FGGUB) R.2684 in this respect); and (iv) no bulge is present posterior to the acromion. Nonetheless, specimen LPB (FGGUB) R.2684 most closely resembles the scapula of *S. transylvanicus* than those of *S. austriacus*, *H. tormai* and *E. carbonensis* in that the posterior portion of the scapular blade has a relatively straight dorsal margin.

Ősi et al. (2014) described a partial ankylosaur skeleton referred to *cf. Struthiosaurus sp.* from the Maastrichtian Sebeş Formation in the Transylvanian Basin, Romania. Although that specimen includes parts of the left and right scapulocoracoid, due to the fragmentary nature of those bones no meaningful comparisons can be made.

Struthiosaurus sp. from southern France. A complete scapula referred to *Struthiosaurus* sp. (Fig. 6c) from the upper Campanian to lower Maastrichtian Grès à Reptiles Formation, Montplo Nord, Hérault, France was figured in Csiki-Sava et al. (2015: fig. 7F). The specimen (MC Mn 393) is overall similar in morphology to LPB (FGGUB) R.2684, although it shows the following differences: (i) the dorsal margin does not curve anteroventrally towards its anterior end; (ii) the acromion starts to rise farther posteriorly on the scapular blade; and (iii) the acromion curves strongly anteroventrally towards the glenoid. Nevertheless, the scapula from southern France resembles both LPB (FGGUB) R.2684 and the scapula of *S. transylvanicus* (see above) in that the dorsal margin of the posterior portion of the scapular blade is relatively straight (as opposed to a more curved dorsal margin in this region in *Europelta carbonensis*, *Hungarosaurus tormai* and *S. austriacus*). Interestingly, the ventrally deflected acromion process of the Montplo Nord scapula is similar to that seen in the small right scapula of *S. austriacus* (see above).

Overall, the above comparisons reveal a high degree of morphological similarity between LPB (FGGUB) R.2684 and the scapulae referred to *Europelta carbonensis*, *Hungarosaurus tormai* and, especially, to *Struthiosaurus* spp. Among the scapulae assigned to *Struthiosaurus*, LPB (FGGUB) R.2684 resembles most closely the scapula of the holotype of *Struthiosaurus transylvanicus* with which it shares a relatively straight posterior part of the scapular blade. Nevertheless, it differs from all known scapulae referred to *Struthiosaurus* spp. in the following characters: (i) the acromial process has a more anterior position, starting to project laterally only just before the preserved anterior end of the scapula, as opposed to extending considerably farther posteriorly onto the scapular blade, which is particularly evident in *S. austriacus* and *Struthiosaurus* sp. from southern France, although this extension is less marked in *S. transylvanicus*; and (ii) the scapula bends laterally in its anterior part. Due to the overall similarity of LPB (FGGUB) R.2684 to the scapulae of *S. transylvanicus* and (to a lesser degree) *S. austriacus*, we assign this specimen to *Struthiosaurus* sp., albeit distinct from *Struthiosaurus* sp. from France, but refrain from an identification to a lower taxonomic level because of its isolated nature and incomplete preservation. Other, *Struthiosaurus*-like occurrences reported from the Transylvanian Basin (Table 1) cannot meaningfully be compared to LPB (FGGUB) R.2684 because these remains either include scapulae that are too fragmentary (i.e. cf. *Struthiosaurus* sp.) or lack scapulae (i.e. "Nodosauridae indet, (?*Struthiosaurus* sp.)"). Finally, we note that the minor differences seen between LPB (FGGUB) R.2684 and the scapula of *S. transylvanicus*, albeit possibly attributable to intraspecific variation, could also indicate that the Pui specimen belongs to a different, closely related taxon. More complete and associated ankylosaur material from Transylvania is needed to resolve the identity of LPB (FGGUB) R.2684.

The Transylvanian latest Cretaceous ankylosaur record and its implications for faunal evolution

Struthiosaurid ankylosaurs were an important, albeit minor, component of the latest Cretaceous dinosaur fauna(s) of "Haţeg Island" (Weishampel et al. 2010; Csiki-Sava et al. 2015, 2016). The first diagnostic remains were discovered as early as 1912 and described as the new species *Struthiosaurus transylvanicus* in 1915 (Nopcsa 1915, 1929). Despite their early recognition, their fossil remains have remained comparatively rare, amounting to only around a dozen documented occurrences throughout the entire Transylvanian region (Figs. 2, 7, Table 1). The newly identified specimen from Pui is thus an important addition to the Transylvanian ankylosaur record.

Reviews of the European (including here the Transylvanian) ankylosaur record previously were provided by Ősi (2015) and Ősi et al. (2014). All currently known ankylosaur remains from Transylvania originate from the continental, upper Campanian to upper Maastrichtian deposits of the Haţeg and Transylvanian basins (Fig. 7). Occurrences in the two basins, discussed according to their stratigraphic placement and ordered from oldest to youngest, are reviewed here separately (Table 1), because precise stratigraphic correlation is difficult between the basins. We group these occurrences into the stratigraphic/

biochronologic tiers defined previously by Csiki-Sava et al. (2016), as follows: tier 1 – upper Campanian–lowermost Maastrichtian; tier 2 – lower Maastrichtian; tier 3 – upper part of lower to lower part of upper Maastrichtian; and tier 4 – upper Maastrichtian, with a transitional tier 1/2 used to denote lower Maastrichtian localities within tier 2 that are assumed to plot close to the Campanian-Maastrichtian boundary.

Finally, it is important to note that until recently, the term Struthiosaurinae (considered to be sub-clade of Nodosauridae) was usually used to refer to the group comprising the European Late Cretaceous ankylosaurs, i.e. *Struthiosaurus* spp. and *Hungarosaurus tormai* (see above). Accordingly, in the past, indeterminate ankylosaur remains from Transylvania were often referred to as Nodosauridae indet. or Struthiosaurinae indet. (see below), although, using the recent nomenclature proposed by Raven et al. (2023) and followed here, these remains should instead be assigned to Struthiosauridae or Ankylosauria indet.; thus, we use quotation marks where mentioning the original taxonomic assignment of those specimens.

Ankylosaur record of the Haţeg Basin

The Haţeg Basin ankylosaur record currently consists of eight occurrences (Figs. 2, 7, Table 1). The possibly oldest occurrence, belonging to tier 2, is represented by two ankylosaur tooth fragments, LPB (FGGUB) R.2118, that are as yet undescribed, coming from the greyish green silty, pebbly mudstones of the Vălioara – Fântânele microvertebrate site (VF1) (Csiki-Sava et al. 2016; Grigorescu et al. 1999; Vasile and Csiki 2010). These fragmentary teeth are here tentatively referred to as Ankylosauria indet. pending a more detailed description and taxonomic assessment.

Most previously described ankylosaur remains can be placed within tier 3. Among these, the Sibişel River Valley section south of Sânpetru hosts two occurrences. The stratigraphically younger of the two is the holotype of *Struthiosaurus transylvanicus* (SpST), consisting of a partial skeleton including elements of the skull, axial skeleton and pectoral girdle (Nopcsa 1929). The remains were discovered in 1912 in a blue mudstone layer in close proximity to one another, over a surface of around one square meter. Unfortunately, the precise locality from which the specimen was recovered is currently unknown, but is possibly located in the southern part of the outcropping succession and, thus, in the middle part of the local section (Ősi et al. 2014).

The second Sibişel River valley ankylosaur occurrence comes from the Cărare macrovertebrate bonebed (SC), on the eastern side of the valley and, thus, probably lower in the local stratigraphic section than the holotype of *Struthiosaurus transylvanicus* (Ősi et al. 2014). The Cărare macrovertebrate bonebed is a multitaxic, attritional, parautochthonous to allochthonous accumulation of fossils that have undergone various amounts of fluvial transport. It is preserved within a greyish-green conglomeratic sandstone channel deposit that grades upwards into sandy channel and brownish silty-sandy channel fill deposits (for more details, see Augustin et al. 2021). The ankylosaur material at this site includes a dentary fragment containing a single well-preserved tooth, LPB (FGGUB) R.2182, described by Ősi et al. (2014) and referred to as "Nodosauridae indet.". The specimen was discovered as surface float in 2008, well after excavations at the site had stopped. A second, as-yet undescribed ankylosaur tooth, LPB (FGGUB) R. 2075, has also been recovered from the site (SC) and is here tentatively assigned to Ankylosauria indet., pending a detailed taxonomic assessment.

From another tier 3 site, Nălaţ-Vad, Smith et al. (2002) briefly noted the presence of a possibly juvenile ankylosaur tooth assigned to "Nodosauridae indet." that was recovered from the streambed of the Râul Mare River. That locality mostly exposes greyish to yellowish conglomeratic sandstones interbedded with reddish to dark greyish silt- and mudstones, the latter with thin, light greyish sandstone intercalations (Smith et al. 2002). The tooth comes from the high-diversity microvertebrate bonebed (NV4) identified as 'locality 4' by Smith et al. (2002: fig. 1), and discovered in an eggshell coquina limestone lens grading into blackish marls. Csiki-Sava et al. (2016) mentioned the specimen again as a "peculiar nodosaurid", though erroneously cited Ősi et al. (2014) instead of Smith et al. (2002) as the original report. According to Smith et al. (2002) the tooth exhibits a peculiar crown morphology comparable to that of another ankylosaur tooth reported from farther upstream along the Râul Mare River at Toteşti (see below). At present, the stratigraphic placement of the Nălaţ-Vad and Toteşti localities, as well as that of the entire Râul Mare River section is still under debate, being considered either as part of the Sînpetru or of Densuş-Ciula formations, or as a distinct lithostratigraphic unit (see Csiki-Sava et al. 2016).

The two stratigraphically youngest ankylosaur occurrences from the Haţeg Basin are placed in tier 4. The first of these is a complete tooth that was assigned to "Nodosauridae indet." and recovered from a microvertebrate accumulation discovered within the streambed of the Râul Mare River, near the barrage of Toteşti village (ToMv) (Codrea et al. 2002; Ősi et al. 2014).

The second tier 4 ankylosaur occurrence also is a single tooth fragment, LPB (FGGUB) R.2288, from Crăguiş (Cr) in the northern part of the Haţeg Basin, and was assigned to "Nodosauridae indet." by Csiki-Sava et al. (2016). The specimen comes from the "upper member" of the Densuş-Ciula Formation, which makes it possibly the youngest occurrence of an ankylosaur from the Haţeg Basin, documenting the presence of this group well into the late Maastrichtian (Csiki-Sava et al. 2016). The uppermost Cretaceous continental deposits near Crăguiş consist of red mudstones and greyish sandstones, as well as red conglomerates. The tooth was found by screen washing a 1.5 m-thick red mudstone layer overlain by grey conglomerates (Vasile et al. 2011; Csiki-Sava et al. 2016).

The Cărare tooth LPB (FGGUB) R.2182, as well as the teeth from Toteşti and Crăguiş (and possibly also that from Nălaţ-Vad), are notable in that they resemble one another in their general morphology and represent a morphotype that is remarkably distinct from other ankylosaur teeth, including those reported from the uppermost Cretaceous of Europe (i.e. *Hungarosaurus tormai*, *Struthiosaurus austriacus*, *S. languedocensis*). Whether or not this tooth morphotype is attributable to *S. transylvanicus* is unclear, because no teeth have been unquestionably identified for that species. Due to their peculiar and conservative morphology, these isolated teeth have been suggested to represent a new taxon of nodosaurid (possibly struthiosaurid) ankylosaur, distinct from other latest Cretaceous ankylosaurs from Europe (Codrea et al. 2002; Csiki-Sava et al. 2016; Ősi 2015; Ősi et al. 2014).

The herein described ankylosaur scapula LPB (FGGUB) R.2684 is assessed to originate from around the tier 2 to tier 3 transition. This new occurrence from Pui (PuMd) expands the Haţeg ankylosaur record to the eastern part of the basin. It is the first ankylosaur material recovered from the 'Pui Beds', despite the abundant and diverse vertebrate record known previously from this lithostratigraphic unit (see Introduction). Thus, the characteristic latest Cretaceous rhabdodontid-titanosaur-hadrosauroid-struthiosaurid dinosaur faunal assemblage of the Transylvanian area (e.g. Nopcsa 1923b; Grigorescu 1983; Weishampel et al. 2010; Csiki-Sava et al. 2015, 2016) was also present in the 'Pui Beds'. Moreover, the new specimen represents one of the oldest ankylosaur occurrences from the Haţeg Basin.

Ankylosaur record of the Transylvanian Basin

Whereas ankylosaurs are rare within the Haţeg Basin (in terms of numbers of specimens), their remains appear to be somewhat more common in the Transylvanian Basin, particularly due to the higher abundance of ankylosaurian remains in the Vurpăr area (Codrea et al. 2010b; Ősi et al. 2014; Vremir 2010). In the Haţeg Basin, up to three separate lithostratigraphic units (the Şard, Sebeş, and Vurpăr formations) have been recognised for roughly coeval continental deposits ranging in age from the late Campanian to the late Maastrichtian, and possibly up to the Paleocene. Herein, we follow the suggestion of Vremir et al. (2015a), who referred all uppermost Campanian to upper Maastrichtian deposits in the southwestern Transylvanian Basin to the Sebeş Formation (in the following accounts, but not in Table 1, previous lithostratigraphic identifications are listed in brackets).

The ankylosaur record of the Transylvanian Basin (Figs. 2, 7, Table 1) starts in tier 1, with the stratigraphically oldest ankylosaur occurrence located in the Petreşti-Arini section along the Sebeş River; it includes as-yet undescribed ankylosaur teeth assigned to "Nodosauridae indet." (Vremir et al. 2015a; Vasile et al. 2021). The remains were recovered through screenwashing from the upper Campanian PT-L0/c microvertebrate accumulation (PT-L0/c) within a grey mudstone horizon at the base of the Sebeş Formation (Vasile et al. 2021). The Petreşti section is important because it documents the transition from deep to shallow marine as well as transitional, coastal-brackish environments of the upper portion of the underlying Bozeş Formation into paludal-fluvial environments at the base of the Sebeş Formation (Vremir et al. 2014; Bălc et al. 2024). Thus, it both records an unusual palaeoenvironment among Upper Cretaceous localities in the Transylvanian area, and hosts one of the oldest, temporally well-constrained vertebrate assemblages to contain ankylosaurs (Vremir et al. 2014, 2015a; Vasile et al. 2021).

The second oldest Transylvanian Basin occurrence at Vurpăr (Vp) is unique among uppermost Cretaceous localities of the Transylvanian area in that ankylosaur fossils are fairly common there (Codrea et al. 2010b; Ősi et al. 2014; Vremir et al. 2015a). The locality is placed in tier 1/2 and thus of an earliest Maastrichtian age, close to the Campanian/Maastrichtian boundary (Vremir et al. 2015a; Csiki-Sava et al. 2016), and is within the lower part of the Sebeş Formation (= Şard Formation in Ősi et al. 2014). The local section is dominated by reddish silt- and mudstones with pedogenic calcareous paleosol horizons representing floodplain deposits and conglomerates grading into sandstones that document channel lags deposited by meandering or braided rivers (Ősi et al. 2014; Vremir et al. 2015a). Throughout the Vurpăr outcropping area, isolated, non-associated postcranial remains referred to "Nodosauridae indet."—including eight osteoderms, a partial femur, and a single centrum of a dorsal vertebra—have been found in various locations (= "Vurpăr area" in Table 1) indicating an unusual abundance of ankylosaur material in this area (Ősi et al. 2014). Most notable at this locality, however, is the presence of two accumulations of associated ankylosaur material discovered in different locations (F1 and F2) that have yielded most of the ankylosaur specimens from Vurpăr. At site F1, the ankylosaur remains were found within a lens-like bone accumulation in a greyish to reddish mudstone alongside fossils of rhabdodontids (originally identified as *Zalmoxes* sp. by Ősi et al. 2014). The ankylosaur material from that site consists of four incomplete dorsal ribs and one sacrodorsal or sacrocaudal rib, a fragment of a right scapula and the left scapulocoracoid, the proximal portion of a right humerus, the distal portion of a left femur, an almost complete right femur, and five osteoderms, all of which are considered to represent a single (but disarticulated) individual assignable to cf. *Struthiosaurus* sp. based on their comparable size, similar preservation, and their spatial distribution within the lens (Ősi et al. 2014). A single, fragmentary right ulna referred to as "Nodosauridae indet." from the same association (i.e. site F1) belongs to a second individual, based on its larger size (Ősi et al. 2014). Site F2 yielded, besides a few turtle remains, ankylosaurian material consisting of eight incomplete dorsal ribs and two osteoderms. This accumulation is also attributed to a single disarticulated individual, referred to as "Nodosauridae indet." (Ősi et al. 2014).

From the tier 2 Cuptorului Hill locality (DC), a single ankylosaur osteoderm (Codrea et al. 2010b; Vremir et al. 2015a; Csiki-Sava et al. 2016) was referred to "Nodosauridae indet. (?*Struthiosaurus* sp.)" by Brusatte et al. (2013), although the specimen has not been described or figured. The deposits at Cuptorului Hill comprise reddish mud- and siltstones as well as intercalations of sandstones and conglomerates, assigned to the lower part of the Sebeş Formation (Codrea et al. 2010b; Vremir et al. 2015a). Here, the ankylosaur osteoderm was recovered from sandstones of the DC-1 sub-site, which represents a dinoturbated bedding plane, preserving various dinosaurian footprints (Vremir et al. 2015a).

Two occurrences from the Transylvanian Basin are referrable to tier 2/3, close to the tier 2/tier 3 boundary; they come from the Sebeş Formation at Oarda de Jos (Jipa-Murzea 2012; Ţabără and Csiki-Sava 2024). Here, fluvial channel fill sandstones, silty crevasse splay deposits and brownish-red, silty overbank mudstones document a poorly drained floodplain within a meandering fluvial system, with interspersed small ponds or abandoned channels indicated by restricted, lens-shaped, grey-greenish silts and mudstones (Vremir 2010; Codrea et al. 2013, 2017; Solomon et al. 2022; Ţabără and Csiki-Sava 2024). One such richly fossiliferous abandoned channel pond within otherwise reddish mudstone deposits in the upper part of the Oarda de Jos (OdA) section is known as the Oarda de Jos lens (OdAN) and represents a multi-taxic microvertebrate bonebed. A single, fragmentary tooth from this lens (UBB ODAN-42) was mentioned and briefly described, but not figured, by Jipa-Murzea (2012), who assigned it to "*Struthiosaurus transylvanicus*". By contrast, Ţabără and Csiki-Sava (2024) listed this specimen as "Nodosauridae indet. (?*Struthiosaurus* sp.)" and emphasised that due to its fragmentary nature, it probably cannot be identified with any certainty to the species level, especially considering that no teeth are reliably known for *S. transylvanicus*. Curiously, although Jipa-Murzea (2012: fig. 6.10) implies the discovery of two ankylosaur teeth from the Oarda de Jos lens, such a count is not supported by data in any other part of his thesis and, thus, it should be considered erroneous. Given its incomplete preservation, the general descriptions provided by Jipa-Murzea (2012), and the absence of proper characterisation and illustration of the tooth, that specimen is best identified only as Ankylosauria indet. Besides the tooth, Jipa-Murzea (2012: p.122, 126, fig. 4.26) also described and figured a partial ankylosaur rib (UBB ODA-15) that he similarly referred to "*S. transylvanicus*", although it is probably more properly identified only as Ankylosauria indet. (Table 1) due to its non-diagnostic morphology. Unlike the isolated tooth, this rib was found as a dispersed element within the deposits of Oarda de Jos A outcrop (OdA). Although it was once considered to belong to the lower part of the upper Maastrichtian (e.g. Vremir 2010), the deposits of the OdA outcrop were constrained more recently by Ţabără and Csiki-Sava (2024) to the upper part of the lower Maastrichtian; this reassessment suggests that the OdA locality (including the OdAN lens) may fall in the basalmost part of tier 3, close to the tier 2/tier 3 boundary (Fig. 7; T2/3 in Table 1).

Another occurrence reported previously and then regarded as representing tier 3 is even more questionable. Codrea et al. (2010b) noted the presence of ankylosaur material at Lancrăm (Lc) and assigned it to "*Struthiosaurus transylvanicus*", but without providing any further information on the nature of this material. This identification was also followed by Csiki-Sava et al. (2016). However, no other reviews of the Transylvanian fossil record (e.g. Vremir 2010; Jipa-Murzea 2012; Vremir et al. 2015a) have listed the Lancrăm ankylosaur occurrence. Because the Lancrăm material was never described, figured, and has not been mentioned subsequently, this particular occurrence and, especially, its referral to *Struthiosaurus transylvanicus* must be deemed doubtful for the moment, pending the outcome of ongoing efforts to relocate the material. Finally, it should be noted that the Lancrăm locality, once considered to represent tier 3 (e.g. Csiki-Sava et al. 2016), is stratigraphically lower than Oarda de Jos. Because the latter locality has been reassigned recently to the basal part of tier 3 (tier 2/3) by Ţabără and Csiki-Sava (2024), the position of the Lancrăm locality should be shifted accordingly; it most probably belongs to the upper part of tier 2, close to the tier 2/tier 3 boundary (Fig. 7; T2/3 in Table 1).

Although not listed in Table 1, another purported ankylosaur occurrence that has been repeatedly mentioned is a fragmentary humerus, preserving a large part of the diaphysis and part of the proximal end, from Râpa Roşie (RR) (a tier 4 locality; Csiki-Sava et al. 2016; Figs. 2, 7). The specimen was first reported, described and figured as “Ankylosauria indet.” by Grigorescu (1987), and was subsequently listed as such by various authors (Codrea et al. 2010b, 2023; Jipa-Murzea 2012). Other mentions of this occurrence—as “Nodosauridae indet. (?*Struthiosaurus* sp.)”—are found in Brusatte et al. (2013) and Vremir (2010). The ankylosaurian affinity of these limb fragments, however, can be definitively dismissed (see also Vremir et al. 2015a: p. 710, footnote), because the proximal portion of the humerus reported by Grigorescu (1987; LPB [FGGUB] R.1141) belongs instead to an indeterminate titanosaurian sauropod, whereas the partial diaphysis is too non-diagnostic to allow any taxonomic identification, although based on its size and non-distinct overall flattened cylindrical shape it may represent the mid-shaft section of either a humerus or, more likely, a femur of a titanosaur.

Implications for Transylvanian and European faunal evolution during the latest Cretaceous

As reviewed above, ankylosaurs were present in different faunal assemblages of the Transylvanian Landmass from the latest Campanian to the late Maastrichtian (see also Csiki-Sava et al. 2016; Bălc et al. 2024; Albert et al. 2025; Fig. 7). Based on the relative rarity of their remains, ankylosaurs likely represented a minor component of these assemblages, being far less common than contemporary large dinosaurian herbivores, the hadrosauroids and, especially, the even more abundant rhabdodontids and titanosaurs, as was already noted by some previous studies (e.g. Grigorescu 1983; Csiki et al. 2010; Csiki-Sava et al. 2015). Our updated version of previous reviews of the regional fossil record for ankylosaurs (e.g. Ősi et al. 2014; Csiki-Sava et al. 2016) sheds new light on latest Cretaceous faunal composition, distribution and evolution, both on Haţeg Island and within the wider Late Cretaceous European Archipelago.

One commonly held opinion concerning the latest Cretaceous Transylvanian ankylosaurs (often lumped together as *Struthiosaurus transylvanicus*) is that they were part of a distinct palaeo-community and one that was environmentally segregated from the common rhabdodontid-titanosaur-hadrosauroid assemblages of Haţeg Island (e.g. Nopcsa 1923b; Grigorescu 1983). According to this view, rhabdodontids, hadrosauroids and possibly titanosaurs preferred moist, poorly drained environments such as marshes, swamps and lakes, whereas ankylosaurs lived in more distal, drier floodplain areas, and their largely allochthonous remains became entombed accidentally together with those of the former three groups—hence the relative rarity of ankylosaur fossils. Based on the few occurrences then known, Csiki et al. (2010) found no support for any marked sedimentary facies- or taphonomic mode-dependant distribution of ankylosaur remains within Haţeg Basin. That finding weakened support for the idea that ankylosaurs were environmentally segregated and, instead, indicated that they were present at low abundance in the local ecosystems. Nevertheless, the perceived higher abundance of their remains in the southwestern Transylvanian Basin areas compared to the Haţeg Basin (a perception based mostly on the then-newly identified Vurpăr vertebrate assemblages, reported by Codrea et al. 2010b and Vremir 2010) was interpreted as potentially supporting geographical segregation, and their preference for more lowland-type environments, compared to the intermontane setting in the Haţeg Basin. Accordingly, their occurrences in the Haţeg Basin were interpreted as documenting occasional geographical range expansions (Csiki et al. 2010).

In containing an expanded number of fossil occurrences and more precisely identified sedimentological-palaeoenvironmental context data (Table 1), our review allows a fresh look and reassessment of these previous hypotheses. Based on occurrences, ankylosaurs appear equally well represented in the Haţeg and the southwestern Transylvanian areas by the number of fossil sites throughout the basins. By contrast, their absence from other areas of the Haţeg Island with uppermost Cretaceous fossiliferous deposits (i.e. the northwestern Transylvanian and Rusca Montană basins; see Codrea et al. 2010a, b; Csiki-Sava et al. 2016) can be probably explained, at least in part, by preservational bias, due to the scarcity of sites in these areas. Nonetheless, the limited number of ankylosaur occurrences from the Haţeg and southwestern Transylvanian basins appears to lend support to the idea of their low original abundance in the local assemblages.

Most importantly, however, the facies-independent distribution of ankylosaur fossils (Table 1) argues against any palaeoenvironmental segregation between them and other dinosaurian meso-and megaherbivores. Ankylosaurs appear to be equally rare, regardless of the sedimentary facies type (poorly drained versus well drained) or the taphonomic context of their fossil occurrences (isolated elements versus associated material). Although the relatively abundant occurrences at Vurpăr, which preserve even partial skeletons, originate from well-drained, pedogenetically altered floodplain environments—as would be predicted by Nopcsa’s (1923b) and Grigorescu’s (1983) original habitat preference suggestion—the holotype partial skeleton at Sânpetru was discovered in fine-grained greyish sediments indicating a more poorly drained palaeoenvironment.

Furthermore, the Sînpetru Formation deposits from the Sibişel Valley at Sânpetru, and the ‘Râul Mare Beds’ at Nălaţ-Vad and Toteşti are interpreted as being deposited in more poorly to only moderately well-drained floodplain settings (Van Itterbeeck et al. 2004; Therrien 2006), as are those of the lower part of the ‘middle member’ of the Densuş-Ciula Formation at Vălioara (Vasile and Csiki 2010;

Albert et al., 2025; see Table 1)—yet these successions yielded the bulk of the Haţeg Basin ankylosaur record (albeit in the form of mostly isolated remains). The same pattern is also present in southwestern Transylvania, where both the Oarda de Jos and the Petreşti occurrences originate from (micro)vertebrate bonebeds in deposits indicating poorly drained palaeoenvironments (Jipa-Murzea 2012; Vasile et al. 2021; Ţabără and Csiki-Sava 2024), and such wetter deposits also dominate the local succession at Lancrăm (e.g. Vremir et al. 2015a), the location of a further, albeit largely unsubstantiated ankylosaur occurrence (see above and Table 1). To conclude, there is little to no evidence for palaeoenvironmental segregation of ankylosaurs relative to the other sympatric herbivorous dinosaur clades or for ankylosaurs preferring drier floodplain settings, as proposed previously. Instead, all available data suggest that ankylosaurs were widely distributed, but numerically subordinate members of the Haţeg Island palaeofauna(s).

Another insight gleaned from our review of the Transylvanian ankylosaur fossil record concerns the spatio-temporal distribution patterns of these animals on Haţeg Island. Csiki-Sava et al. (2016) noted that the earliest occurrence in the southwestern Transylvanian Basin (then assessed to fall into tier 1/2) predates the earliest occurrence in the Haţeg Basin (placed as late as tier 3). Data in our updated and expanded database continues to support such a diachronism between the two basins (Fig. 7). First occurrences in both basins are now shifted earlier, with their earliest occurrences dating to the latest Campanian at Petreşti (tier 1) in the southwestern Transylvanian Basin and possibly as early as the earliest Maastrichtian at Vălioara (tier 2) in the Haţeg Basin. These revised first occurrences significantly expand the documented temporal range for ankylosaurs in both areas.

Given that across the former Haţeg Island biochronologic tier 1 fossil localities are currently known with certainty only from the southwestern Transylvanian Basin, it is tempting to explain the above noted diachronism in the appearance of ankylosaurs between it and other regions as an artifact of unequal spatio-temporal sampling of vertebrate assemblages. However, it is worth noting that the (albeit rare) presence of ankylosaurs in the Haţeg area can be tracked continuously throughout tiers 2 to 4 (Fig. 7, Table 1), starting from the basalmost Maastrichtian Vălioara – Fântânele site (lower part of tier 2), through the lower Maastrichtian site at Pui yielding the scapula LPB (FGGUB) R.2684 reported here (PuMD, probably around the tier 2 to tier 3 transition), the upper part of lower to lower part of upper Maastrichtian (tier 3) of Sânpetru (Cărare site and type locality of *Struthiosaurus transylvanicus*) and Nălaţ-Vad, and finally to the uppermost Maastrichtian (tier 4) of Toteşti and Crăguiş (see also Csiki-Sava et al. 2016). Conversely, ankylosaurs appear to be absent from recently identified and fossil-rich, diverse vertebrate assemblages excavated from several sites located in the western Vălioara area (e.g. Botfalvai et al. 2021) and that most probably belong to the basalmost Maastrichtian, close to the Campanian-Maastrichtian boundary (thus, tier 1/2; Albert et al. 2025). Ankylosaur fossils also are unknown from other previously identified tier 1/2 sites in the Haţeg area (Csiki-Sava et al. 2016). Such differences provide further support for the diachronic first occurrences of ankylosaurs between the southwestern Transylvanian and Haţeg basins, respectively.

Although not specifically acknowledged in the past, a similar diachronism also appears to characterise the last known ankylosaur occurrences between the two basins (see Csiki-Sava et al. 2016). Based on our review of ankylosaur distribution across the Transylvanian area (Fig. 7, Table 1), combined with new biostratigraphic constraints, it appears that the youngest occurrence of the clade in the southwestern Transylvanian Basin (at Oarda de Jos) is late early Maastrichtian in age (Ţabără and Csiki-Sava 2024), which places it in the early part of tier 3 (tier 2/3), roughly contemporaneously with the Pui scapula. This occurrence datum is clearly older than those of most ankylosaur occurrences known from Haţeg Basin (tiers 3 to 4), indicating that ankylosaurs may have had a shorter temporal range in the Transylvanian Basin. Although it is possible that this last occurrence datum diachronism is biased by the small number of diversified vertebrate assemblages from younger localities in the Transylvanian Basin (e.g. Vremir et al. 2015a), it is worth noting that such younger occurrences are also relatively uncommon in the Haţeg Basin (Csiki-Sava et al. 2016), and yet nevertheless they yielded (rare) ankylosaur remains. Further discoveries of uppermost lower to upper Maastrichtian vertebrate localities from both basins are needed to reliably establish whether this distribution pattern is artificial or reflects a genuine diachronism in the presence of ankylosaurs between the different regional assemblages.

Our updated overview of latest Cretaceous ankylosaur occurrences from the Transylvanian area has some wider-ranging implications as well. For four decades it has been proposed that the Ibero-Armorican Landmass on the western edge of the Late Cretaceous European Archipelago underwent a profound faunal turnover around and across the early/late Maastrichtian boundary (e.g. Le Loeuff et al. 1994; Vila et al. 2016). This turnover (= Maastrichtian Dinosaur Turnover, MDT) was assumed to primarily consist of the replacement of titanosaurs as main mega-herbivores by diverse derived hadrosauroids that immigrated into the region. Nonetheless, other important MDT-related changes had been also noted within the meso- and mega-herbivore communities (e.g. Fondevilla et al. 2019; Pérez-Pueyo et al. 2021), such as the replacement of smaller-sized, presumably dwarfed and endemic titanosaurs with larger immigrant taxa (e.g. Vila et al. 2022), as well as the disappearance of rhabdodontid ornithopods (see also Augustin et al. 2023) and struthiosaurid ankylosaurs. Recently, it has been proposed that some of the faunal changes involving titanosaurs that characterise the MDT may also be recognised on the Haţeg Island (Vila et al. 2022), and this suggestion begs the question whether such synchronous faunal changes might have affected other vertebrate clades as well, including ankylosaurs. Inspection of our updated ankylosaur distribution overview (Fig. 7, Table 1) shows, however, that this is not the case. Ankylosaurs continue to be present, albeit with uniformly low abundances, throughout the Maastrichtian in this area, unlike on the Ibero-Armorican Landmass. Incidentally, such widely different faunal evolution patterns between the eastern and western landmasses of the Late Cretaceous European Archipelago have also been pointed out recently for rhabdodontids (Augustin et al. 2023) and titanosaurs (Díez Díaz et al. 2025), suggesting that different areas of the archipelago experienced different, and not tightly correlated, faunal evolutionary histories towards the end of the Cretaceous.

Conclusions

In this paper, we describe an isolated right scapula, LPB (FGGUB) R.2684, from the continental uppermost Cretaceous ('mid'-Maastrichtian) 'Pui Beds' that crop out along the Bărbat River south of Pui, southeastern Haţeg Basin. The specimen can be confidently assigned to an ankylosaur, and most probably to a struthiosaurid based on its morphological similarity to the scapulae of other struthiosaurids from the Upper Cretaceous of Europe. Moreover, a detailed comparison between the scapula from Pui and those of other Cretaceous European struthiosaurids (i.e. the Early Cretaceous *Europelta carbonensis* from Spain, and the Late Cretaceous *Hungarosaurus tormai* from Hungary, *Struthiosaurus* sp. from southern France, *S. austriacus* from eastern Austria and *S. transylvanicus* from western Romania) demonstrates that, not unexpectedly, LPB (FGGUB) R.2684 shows the closest resemblance to *S. transylvanicus*. This, in turn, may indicate a particularly close relationship with *S. transylvanicus*, which is likewise known from the Haţeg Basin, albeit from a different lithostratigraphic unit (the roughly coeval Sînpetru Formation in the south-central part of the basin). Despite these overall similarities, the presence of minor morphological differences between the Pui scapula and that of *S. transylvanicus* led us to refrain from formally referring the former specimen to the latter taxon, and to identify it for the moment being as *Struthiosaurus* sp.

Identification of the Pui ankylosaurian scapula is important because it represents the first record of this group from the southeastern Haţeg Basin. The distribution of the rhabdodontid-titanosaur-hadrosauroid-struthiosaurid communities that characterise many of the better-studied vertebrate assemblages during the latest Cretaceous on Haţeg Island can thus be extended into the 'Pui Beds' and demonstrates that the dinosaur fauna of the latter unit had a broadly similar taxonomic composition (at least at a higher taxonomic level) to that of several other well-known vertebrate-bearing localities from the continental uppermost Cretaceous of Transylvania.

In addition, we provide an overview of the ankylosaur fossil record from the uppermost Cretaceous of Transylvania. Whereas ankylosaur remains are generally rare throughout the upper Campanian to upper Maastrichtian deposits of Transylvania, they nonetheless had a widespread distribution, having been reported from several of the important (and well sampled) fossil localities in the Haţeg and Transylvanian basins. Nevertheless, most ankylosaur occurrences are limited to isolated bones and teeth, which cannot be reliably identified at an alpha-taxonomic level. The only exceptions being the associated bones belonging to the holotype of *Struthiosaurus transylvanicus* recovered from Sânpetru (south-central part of the Haţeg Basin) and a lens-like accumulation (F1) with cf. *Struthiosaurus* sp. from Vurpăr (southwestern Transylvanian Basin).

Ankylosaur remains in the Haţeg and Transylvanian basins originate from a wide variety of depositional settings, including poorly drained and well-drained floodplains, channel deposits, and small ponds of abandoned channels, thus ranging from paludal to fluvial environments. Such a wide distribution undermines previous assertions that ankylosaurs had selective habitat preferences, favouring more distal and better-drained, dry floodplain settings compared to the other, more common large herbivorous dinosaurs of the local faunas. As a further consequence, the relative rarity of ankylosaur remains in both basins within Transylvania likely reflects their original low abundance in these ecosystems, instead of an allochthonous origin of their remains in the fossiliferous localities.

Notably, the current Transylvanian ankylosaur record reinforces previous observations that ankylosaurs first appeared in the Transylvanian Basin, and only later show up in Haţeg Basin, while their earliest appearances are pushed further back in time for each basin, to the latest Campanian in the Transylvanian Basin and to the earliest Maastrichtian in the Haţeg Basin. Furthermore, the record shows that their disappearance from the fossil record is also diachronous, taking place around the end of the early Maastrichtian in southwestern Transylvania, while they persisted into the late Maastrichtian in the Haţeg area. Whether these occurrence patterns mirror their true distributional pattern through time and space, or they are biased by other factors (i.e. the general rarity of ankylosaur remains, habitat preferences, palaeogeographic segregation in the Haţeg and Transylvanian basins, and/or sampling bias) is currently difficult to assess.

Finally, our updated fossil record overview continues to document the survival of ankylosaurs into the late Maastrichtian on Haţeg Island, unlike the situation in the more westerly Ibero-Armorican Landmass, where ankylosaurs disappeared by the early/late Maastrichtian boundary. These differences indicate a clear disconnection between faunal evolutions that characterised different regions of the Late Cretaceous European Archipelago towards the end of the Cretaceous.

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Declarations

Conflict of interest The authors declare no coct of interests.

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