New ankylosaurian material from the Upper Cretaceous of Transylvania

Nouveau matériel d'ankylosaure du Crétacé supérieur de Transylvanie

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ABSTRACT

Ankylosaurian remains from the Transylvanian Basin, Romania, are extremely rare. More than 100 years after the discovery of the first and only better-known assemblage, namely the type material of *Struthiosaurus transylvanicus*, new ankylosaurian material has been discovered in the Maastrichtian of the Haţeg Basin, as well as at another locality (Vurpăr), in the Transylvanian Basin, that is described here. The material consists of one tooth in a small jaw fragment (from the Haţeg Basin) and at least two accummulations of associated, as well as several isolated, postcranial elements (from Vurpăr). No diagnostic elements are preserved that would overlap with the type of *S. transylvanicus*, so we cannot assign any of the new specimens to this species. The tooth shows marked differences compared to those of other anklyosaurs including *Struthiosaurus austriacus* and *Hungarosaurus* in having only six, more or less equally sized, apically pointed cusps separated by deep grooves. The postcranial material from Vurpăr represents at least three different individuals. The humerus is the most diagnostic element among the postcranial remains being most similar both in size and morphology to humeri referred to as *Struthiosaurus* from different European localities, thus here we refer the humerus and probably associated elements preserved in one assemblage to as cf. *Struthiosaurus* sp; the remaining specimens from Vurpăr are retained as Nodosauridae indet. Histological studies have confirmed the adult nature of all sampled bones in the Vurpăr ankylosaur material suggesting that these fully grown animals were of similar size to *Struthiosaurus*, a small-bodied nodosaurid the ontogenetic status of which, however, has never been investigated histologically. The obviously diminished body size of the Transylvanian ankylosaurs compared to other members of the clade could be explained by insular dwarfism using the same histology-based argument as presented for *Magyarosaurus.*

Keywords: ankylosaurs, *Struthiosaurus*, Late Cretaceous, Transylvania

Résumé – Les restes fossiles d'ankylosaure provenant du Bassin de Transylvanie, en Roumanie, sont extrêmement rares. Plus d'un siècle après la première découverte, qui est également l'association la mieux préservée, à savoir le matériel-type de *Struthiosaurus transylvanicus,* le nouveau matériel içi décrit provient du Maastrichtien du Bassin de Haţeg et aussi d'une autre localité (Vurpăr) du Bassin de Transylvanie. Le matériel comprend un petit fragment de mâchoire avec une dent (du Bassin de Haţeg) et au moins deux accumulations d'éléments postcrâniens associés, mais aussi isolés (à Vurpar). Aucun élément diagnostique en concordance avec le type de *S. transylvanicus* n'étant conservé, il n'est pas possible de rapporter ces nouveaux spécimens à cette espèce. La dent présente des différences par rapport aux autres ankylosaures, y compris *Struthiosaurus austriacus* et *Hungarosaurus*, dans la mesure où elle présente seulement six denticules, de tailles plus ou moins égales, pointus apicalement et séparés par des sillons profonds. Le matériel postcrânien de Vurpăr appartient à au moins à trois individus différents. L'humérus étant l'élément le plus diagnostique parmi les restes postcrâniens ayant plus de similitudes dimensionnelles et morphologiques aves les humérus attribués à *Struthiosaurus* provenant de différentes localités européennes, il est par conséquent attribué, ainsi que probablement les autres éléments préservés dans l'une des associations, à cf. *Struthiosaurus* sp; les autres spécimens de Vurpăr sont rapportés à un Nodosauridae indet. Les études histologiques ont confirmé l'état adulte de tous les os d'ankylosaure échantillonnés de Vurpăr, suggérant que ces animaux matures étaient de taille comparable à *Struthiosaurus*, un nodosauridé de petite taille dont l'état ontogénétique n'a jamais été étudié d'un point de vue histologique. La taille manifestement réduite des ankylosaures de Transylvanie comparée à celle d'autres membres du clade pourrait être expliquée du fait d'un nanisme insulaire, si l'on prend en compte le même argument histologique que celui présenté pour *Magyarosaurus.*

Mots-clés : ankylosaures, *Struthiosaurus*, Crétacé supérieur, Transylvanie.

INTRODUCTION

For a long time, Late Cretaceous ankylosaurs of Europe were known only on the basis of very fragmentary material. In chronological order, the earliest discoveries were the remains of *Struthiosaurus austriacus* from the Lower Campanian of Muthmannsdorf, eastern Austria, containing both cranial and postcranial elements of more than one individual (Bunzel, 1870, 1871; Seeley, 1881; Nopcsa, 1929; Pereda Suberbiola and Galton, 1992, 1994, 2001). Depéret (1900) noted bones of a *Struthiosaurus*-like dinosaur from the Upper Cretaceous of southern France that were later described in detail by Nopcsa (1929). Based on a poorly preserved vertebral centrum, some rib fragments with T-shaped cross section, and osteoderms identified by Nopcsa in the collections of the Museum of Marseille, he referred this material to a new taxon, as *Rhodanosaurus lugdunensis* (later it was used as *Struthiosaurus lugdunensis*, Lapparent, 1947, 1954); due to the lack of diagnostic elements, however, this taxon is regarded as nomen dubium (Pereda Suberbiola, 1993b; Vickaryous et al., 2004). The first discovery of ankylosaurian remains in Transylvania was made by Nopcsa's secretary, Bajazid Elmas Doda in 1912, in Maastrichtian deposits close to Sânpetru (Szentpéterfalva), in the Haţeg Basin. The material, published briefly by Nopcsa in 1915, was described later in more detail and named as *Struthiosaurus transylvanicus* (Nopcsa, 1915, 1929).

During the following 60 years no significant ankylosaurian material has been unearthed from the Upper Cretaceous of Europe (for an overview of this period see Pereda Suberbiola, 1992, 1993a), preventing the recognition of the true diversity and distribution of this group. Recent discoveries of new ankylosaurian material in northern Spain (Astibia et al., 1990; Pereda Suberbiola et al., 1995; Pereda Suberbiola, 1999) and southern France (Buffetaut and Le

Loeuff, 1991; Le Loeuff, 1991; Pereda Suberbiola, 1993a; Garcia and Pereda Suberbiola, 2003) supported the presence of *Struthiosaurus* in western Europe; a third species of the genus, *Struthiosaurus languedocensis*, has been also described (Garcia and Pereda Suberbiola, 2003) from the Campanian of Villeveyrac (southern France). Furthermore, associated and isolated postcranial elements referred to as *Struthiosaurus* sp. have been recently reported from eastern Spain (Chera) by Company (2004).

The next chapter in the discovery of European Late Cretaceous ankylosaurs is related to the Santonian aged Iharkút vertebrate site in western Hungary. Discovered in 2000, this locality provided the richest and best preserved ankylosaur material from Europe: on the basis of five partial skeletons and several isolated elements a new ankylosaur, *Hungarosaurus tormai*, was described (Ősi, 2005; Ősi and Makádi, 2009). During the fieldwork of 2012 two additional associated specimens composed of postcranial elements were found which, based on their size, are most probably referable to *Hungarosaurus*. Besides *Hungarosaurus* the occurrence of another, small-bodied ankylosaur referred to as cf. *Struthiosaurus* sp. was also pointed out recently on the basis of a complete humerus, demonstrating the existence of two sympatric ankylosaur species in Iharkút (Ősi and Prondvai, 2013).

Although the Transylvanian Basin is one of the richest regions with Late Cretaceous vertebrates in Europe (e.g., Benton et al., 2010 ; Codrea et al., 2010a), ankylosaurian remains continue to be extremely rare. For a long time following Bajazid's discovery in 1912, only an isolated tooth (Codrea et al., 2002a) has been reported from this region. Recently, however, additional ankylosaur postcranial material has been unearthed at Vurpăr in the Sebeş-Alba area (see Codrea et al., 2010a, 2010b; Vremir, 2010) which, though fragmentary and composed of only a few elements, plays a significant role in the understanding of the Transylvanian ankylosaurs.

In this paper, we describe these new ankylosaur remains from Vurpăr, besides a minute jaw fragment preserving a single tooth, discovered in the Haţeg Basin, and discuss the taxonomic position and significance of this material in the light of the significantly improved European ankylosaurian record.

Institutional abbreviations: **DMNH**, Denver Museum of Natural History, Denver, USA; **LPB (FGGUB)**, Facultatea de Geologie şi Geofizică, Universitatea din Bucureşti, Bucharest, Romania; **MC**, Mechin Collection (private collection), Vitrolles, France; **MCNA**, Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz, Basque Country, Spain; **MTM**, Hungarian Natural History Museum, Budapest, Hungary; **PIN**, Palaeontologicheskii Institut (Paleontological Institute), Russian Academy of Sciences, Moscow, Russia; **PIUW**, Paläontologisches Institut, University of Vienna, Vienna, Austria; **UBB**, Paleontological Collection, Catedra de Geologie, Facultatea de Biologie şi Geologie, Universitatea Babeş-Bolyai, Cluj-Napoca, Romania; **ZPAL**, Institute of Palaeobiology (Zaklad Palaeobiologii) of the Polish Academy of Sciences, Warsaw, Poland.

LOCALITY AND GEOLOGICAL SETTING

The Maastrichtian Transylvanian landmass, also known as "Haţeg Island" (Csiki and Benton, 2010) is actually documented by several exposures of continental deposits located mainly along the northwestern, western and southwestern borders of the Transylvanian Basin (Nopcsa, 1905; Codrea and Godefroit, 2008; Codrea et al., 2001, 2010a), as well as in the neighbouring Haţeg (Nopcsa, 1905; Grigorescu, 2010) and Rusca Montană (Codrea et al., 2009, 2012; Vasile and Csiki, 2011) basins. Although spread over a large surface, all these deposits sharing common lithological and paleontologial features, as well as tectonic setting. They represent areas spared by erosion of several former sedimentary basins developed after the latest Cretaceous ("Laramian") tectogenesis affecting the Apuseni Mountains and the

Southern Carpathians, and which represent the post-tectonic sedimentary cover of the Inner and Median Dacides, as well as the Western Transylvanides (see Săndulescu, 1984). All these deposits are dominated by fluvial sediments (Van Itterbeeck et al., 2004; Therrien, 2005; Therrien et al., 2002, 2009; Codrea et al., 2010a) reflecting similar depositional environments (Therrien et al., 2002; Therrien, 2005; Csiki et al., 2010); and, finally, their fossil assemblages, mainly vertebrates, are largely similar in composition (e.g., Therrien, 2005; Grigorescu, 2010; Benton et al., 2010; Codrea et al., 2010a, 2012). Nevertheless, there are also local differences between the different areas, such as frequency of the different lithotypes (e.g., Therrien, 2005; Mariş, 2012), degree of participation of volcanogenic input to the sediments (Bărzoi and Şeclăman, 2010; Grellet-Tinner et al., 2012), or the presence of plants, known mainly in the Rusca Montană Basin (Petrescu and Duşa, 1980, 1985).

In the Haţeg Basin, the uppermost Cretaceous continental deposits cover discontinuous areas over the north-western and central parts of the basin; these were grouped into the roughly synchronous northwestern Densuş-Ciula and the south-central Sânpetru formations (e.g., Grigorescu, 1992), of Maastrichtian age (Panaiotu and Panaiotu, 2010; Bojar et al., 2011). Both units are dominated by medium-to-fine grained clastics (sandstones, siltstones, and mudstones), representing mainly floodplain depositional environments (Therrien, 2005; Therrien et al., 2009), with interbedded coarse sandstone to conglomeratic channel deposits; the deposits of the Densuş-Ciula Formation also include variable amounts of volcanoclastic material, while those of the Sânpetru Formation are almost completely devoid of such component.

The stratotype of the latter unit, cropping out along the Sibişel River valley mainly south of the localities of Sânpetru and Săcel yielded in 1912 the holotype material of *Struthiosaurus transylvanicus*. Unfortunately, the exact location of the type locality is unknown ; nonetheless, based on the brief account available in the monographic description of the taxon

(Nopcsa, 1929), it can be placed with approximation in the southern part of the outcropping area, i.e., in the upper part of the local stratigraphic succession. Besides *Struthiosaurus*, several other Maastrichtian vertebrate taxa were recovered from the Sibişel Valley succession starting with the last years of the 19th century (see reviews in Grigorescu, 2005, 2010; Therrien, 2005; Benton et al., 2010); their remains are usually found as isolated elements or partial skeletons, as well as mixed within stratiform or lenticular bonebeds (Csiki et al., 2010). One of the most important vertebrate fossil localities from the Sibişel succession is represented by the Cărare macrovertebrate bonebed (see Csiki et al., 2010:fig. 1C, for the location of the site), a stratiform accumulation of high-diversity assemblage preserved in a greyish-green sandstone-conglomeratic channel-lag body grading into sandy channel and brownish silty-sandy channel-fill deposits (C21 type accumulation of Csiki et al., 2010). The Cărare site appers to be placed lower in the local stratigraphic succession than the type locality of *Struthiosaurus transyvanicus*. Excavated mainly between 1992 and 1996, it yielded a large number of mostly isolated vertebrate remains, including turtles, crocodilians, dinosaurs (the euornithopod *Zalmoxes* being especially common) and pterosaurs. The poor dimensional, morphological and hydraulical sorting, the wide range of observed weathering and abrasion stages, as well as the multitaxic composition of the assemblage suggest attritional, parautochthonous to allochtonous within-channel accumulation of the vertebrate remains, most of these being buried following variable amounts of fluvial transport and maybe even short-term intraformational reworking. The small ankylosaurian jaw fragment with implanted teeth was collected as surface float when the site was revisited in 2008. The pristine preservation state shown by the tooth is not uncommon within the material from Cărare, as it is also documented in several fragile *Zalmoxes* cranial bones or isolated teeth, as well as in a referred maxilla of the atoposaurid *Theriosuchus sympiestodon* (Martin et al., in press).

Besides the already classical Haţeg Basin region, from where Baron Nopcsa first reported his presumably insular latest Cretaceous fauna with peculiar dwarf dinosaurs and other reptiles, the other Transylvanian areas listed above also yielded illustrative taxonomic assemblages. In the last decades, researches focused on the southwestern corner of the Transylvanian Basin, named the Metaliferi sedimentary area, where uppermost Cretaceous and Paleogene continental formations are exposed (e.g., Codrea and Dica, 2005). Several lithostratigraphic units were defined in this area, reflecting a transition from marine to continental settings during the latest Cretaceous. The Maastrichtian continental deposits are documented by the Vurpăr (early Maastrichtian) and Şard (Maastrichtian–?Early Cenozoic) formations, both of them lying over the folded nappes of the Western Transylvanides (Codrea et al., 2010b). The Vurpăr Formation is made up of deltaic deposits, interbedded with repetitive short-term marine ingressive sequences, while the Şard Formation is dominanted by continental redbeds reflecting typical fluvial environments.

The Şard Formation is the unit richest in fossil vertebrates, including dinosaurs and other associated reptiles, but also fish, amphibians, birds, and mammals (e.g., Codrea et al., 2010a, 2010b). The base of this formation can be observed in several outcrops at Vurpăr, on the right bank of the Mureş River, just upstream from the confluence with Vinţului Valley, on the road 105A between Vurpăr and Pârău lui Mihai, mainly in the place named “Râpele din susul Dumbrăvii” (Fig. 1). In this place, the basalmost section of the unit is lying over the Vurpăr Formation.

At Vurpăr, the lithology of the Şard Formation is dominanted by red silty mudstones, often rich in white mica, documenting floodplain deposits, interbedded by sandy-microconglomeratic channel fills, and, sometimes, conglomerates mainly as basal lags (Fig. 2; Codrea et al., 2001, 2002b; Therrien et al., 2002; Therrien, 2005). These deposits were interpreted as resulting from mixed solid load flows involving sand and subordinately pebbles. The channel fills show typical braided and meandering internal architecture, with numerous internal bars. The discharge of the streams was highly variable; the instability of the channels generated several meters thick fining-upward infilling sequences. The energy of fluvial streams increased towards the top of the formation, where the channels are becoming very frequent, as it can be observed at Şard (Codrea et al., 2010a).

Paleosoils with rhizoliths occur in carbonate-rich horizons, clearly indicative for a seasonably variable climate (Codrea et al., 2001, 2002b). Fluvial oncoids are also reported, but these are restricted to a single level (Săsăran and Codrea, 2012).

The Şard Formation deposits at Vurpăr yielded several vertebrate fossils, while invertebrates are extremely scarce (represented by rare snails). The recovered bones and teeth belong mainly to dinosaurs; the euornithopod *Zalmoxes* is very frequent, its remains documenting the presence of both *Z. robustus* and *Z. shqiperorum*; it is associated with the basal hadrosaur *Telmatosaurus transylvanicus* and with ankylosaurians. Besides dinosaurs, the presence of the crocodilian *Allodaposuchus* and of two turtle taxa, *Kallokibotion* and a dortokid, was also reported (e.g., Codrea et al., 2010a). The vertebrate remains often occur as lens-like accumulations of disarticulated bones (corresponding to the C12 type lenticular bonebeds of Csiki et al., 2010), all bones being white with weathering-induced fissure cracks on their surfaces. More rarely, incomplete fragmentary skeletons can be unearthed too, sometimes even with articulated bones. Occasionally in such lens-like occurrences bone distribution suggests the probability that the skeletal elements belonged to the same individual, even in absence of anatomical connections, pointing to the presence of taphonomic mode B22 of Csiki et al. (2010).

Several ankylosaurian bones were collected at Vurpăr in the last decade; these are rather frequent, differentiating the locality from other Maastrichtian sites in the Transylvanian area, where remains of such dinosaurs are extremely rare. Apart from a few osteoderms and postcranial elements found isolated in different places of the Vurpăr outcrops, the majority of bones are originating from two locations (marked as F1 and F2 on Fig. 1). F1 was a lens-like bone accumulation in grey-reddish mudstone where all bones were found isolated, but suggesting some degree of skeletal association (Fig. 3). Here, the ankylosaurian bones occurred in association with those of the euornithopod *Zalmoxes*. Site F2 yielded almost exclusively ankylosaurian rib fragments and osteoderms, probably originating from the same individual. Apart from these, only some turtle remains were recovered in F2.

MATERIAL AND METHODS

Material and preparation

The ankylosaurian material described here includes both isolated and associated elements. The jaw fragment with a single tooth has been found in the Haţeg Basin; in the Transylvanian Basin, the Vurpăr material, mainly composed by postcranial elements, are coming chiefly from two small bone accumulations (F1 and F2; see above and Fig. 1). Although the material from these sites was found in two associated assemblages, the bones clearly represent at least three individuals of different sizes. The isolated jaw fragment with a single tooth belongs to the collections of the Facultatea de Geologie şi Geofizică, Universitatea din Bucureşti in Bucharest (LPB (FGGUB)), and all the other material is housed in the Departementul de Geologie, Facultatea de Biologie şi Geologie, Universitatea Babeş-Bolyai, in Cluj-Napoca (UBB).

Most of the material was discovered while hand quarrying the bone-bearing levels (see Locality and geological setting above). The material was prepared in the technical labs of the institutes listed above, using needles and vibro-tools. After removing matrix from the bones, superglue (cyano-acrylate) was used to repair breaks.

Bone histology

Six specimens, UBB VP 12 (right humerus), UBB VP 14 (rib), UBB VP 16 (right ulna), UBB VP 26 (right femur), UBB VP 27 (left femur), and UBB VP 32 (left femur), were sampled for histological investigation in order to assess their developmental stages. Whereas entire cross section was taken of the rib, only slices about one-third of the entire cortical area were sawed off transversely from the anteromedial cortex of both left femora and the right humerus; the samples were taken from the distal-diaphyseal region of the femora, and from the mid-diaphysis of the humerus, respectively. Core drilling method (Stein and Sander, 2009) was used for the sampling of the right femur and ulna, at the posterior and lateral part of their mid-diaphysis, respectively. Transverse thin sections were prepared of all bone samples following standard methods (Wells, 1989). Histology of the acquired thin sections was examined under Nicon LV 100 polarized light microscope. Pictures of the slides were taken with QImaging MP5.0 digital microscope camera and processed with Image Pro Insight software. Interpretative figures were obtained using CorelDRAW X5 software. Histological nomenclature applied in microstructural descriptions follows Francillon-Vieillot et al. (1990), Marotti (2010), and Stein and Prondvai (2013).

RESULTS

Description and comparisons

Tooth. Among the new ankylosaurian material, the cranium is represented only by a single tooth-bearing jaw fragment (LPB (FGGUB) R.2182; Fig. 4). The tooth (mesiodistal length: 7.58 mm, apicobasal height: 3.88 mm, labiolingual width: 3.45 mm) is preserved in a small piece of jaw fragment (length: 14.5 mm, height: 11.5 mm, width: 12.5 mm). We suggest that it was part of the dentary because in ankylosaurs the maxilla is usually a relatively thin bony walled element, and only slightly thicker than the tooth crown itself. The bone surfaces bordering the tooth are slightly convex lateromedially ; the dentary fragment is crushed and incomplete both mesiodistally and dorsoventrally, thus preventing the determination of its rough position in the lower jaw. In parasagittal view, it is obvious that the tooth is still deeply nested within the alveolus suggesting its incompletely erupted status.

The crown is virtually complete, well preserved, and no wear pattern can be observed on its surface further suggesting that the tooth was never in use. In occlusal view (Fig. 4C), it has a mesiodistally elongated, labiolingually strongly flattened shape. In contrast to the teeth of most ankylosaurians with a thicker central body/main cusp, this tooth is mesiodistally longer than its apicobasal height and has a flat or slightly concave, labiolingually narrow crown. It bears well developed blade-like cingula both labially and lingually, and these cingula are connected mesially and distally to form a continuous basal shelf all around the crown. One side of the surrounding cingulum is still partly buried in matrix, but the other can be well observed. The cingulum is not as crenelated as seen, for example, in the teeth of *Hungarosaurus* (Ősi, 2005), but is rather blade-like with fine serrated apical edge. The exposed cingulum shows some weak waving mesiodistally, a feature that can be also seen on the cingulum of other ankylosaurians (Coombs, 1990).

The crown appears to have a unique morphology among ankylosaurs: instead of having a central cusp and five to seven secondary cusps arranged mesiodistally, LPB (FGGUB) R.2182 has six (one is broken), more or less similarly sized, apically oriented, large pointed cusps which are markedly separated by five deep quasi-vertical grooves (Fig. 4A). Three of these grooves reach the base of the crown. The first cusp (C1), being almost completely separated from the rest of the crown, is low, triangular, and mesiodistally relatively wide with straight, blade-like edges. No accessory cusps can be observed on these blades. The second cusp (C2) is more pointed with two small accessory cusps on its side facing C1. The third, and highest, cusp (C3) appears to be split into two cusps apically, both of them having a small bump on their side facing C4. The fourth cusp is the most complex, with the main cusp lying towards C3 and a row of three small, accessory cusps on the side facing C5. The fifth and last preserved cusp (C5) is also very complex, with at least two small accessory cusps on each of the mesial and distal blades (Fig. 4A). Small, bump-like accessory cusps on the secondary cusps are also present in the teeth of *Hungarosaurus* (Ősi, 2005), but those teeth show the typical ankylosaurian pattern of ‘central cusp with 7–7 secondary cusps arranged mesiodistally’, and they are relatively wider and more massive labiolingually. The first, and only other known ankylosaurian tooth from the Romanian Upper Cretaceous was published by Codrea et al. (2002a). This very small tooth (mesiodistal length 2.5 mm) has an even more reduced cuspidate crown with only four quasi-equal cusps. It is similar to the new specimen is having deep grooves separating the carinate cusps and in the presence of a massive cingulum. The cingulum is, however, not as completely set apart around the cuspidate crown (e.g., it merges with the first and fourth cusps; see Codrea et al. 2002a:fig. 4g) as seen on the new specimen, and no accessory cusps are present.

Dorsal vertebra. A fragmentary dorsal centrum (UBB VP 121, Fig. 5I-L) is one of the few axial ankylosaurian elements dicovered after those of *Struthiosaurus transylvanicus* published by Nopcsa (1929). It is not part of the two skeletal associations listed above but was found as an isolated element. It is anteroposteriorly longer than high, lateromedially narrow, and platycoel with subcircular articulation surfaces. The originally fused (no sutures can be recognized on its dorsal surface) neural arch is missing. Both the ventral and the lateral sides are concave, and no crests or grooves are present on these surfaces. This specimen is quite similar in proportions and morphology to a *Struthiosaurus* dorsal vertebra illustrated by Nopcsa (1929:plate 2, fig.11–13).

Ribs. At least four fragmentary dorsal ribs (UBB VP 14, 21, 23, 25) and one possible sacrodorsal or sacrocaudal rib (UBB VP 22) have been found with the first, more complete associated skeleton (F1), and eight fragmentary dorsal ribs (UBB VP 84–91; Fig. 5G, H) were part of the second skeleton (F2). As typically seen in ankylosaurs, the proximal third of the dorsal ribs has a T-shaped cross section that tends to become more flattened distally. In addition, the distal part of the most complete rib (UBB VP 85) is anteromedially rotated relative to its proximal part. UBB VP 22 has a typical oval-shaped cross section distally, but proximally is strongly widened, ending in a massive part that might had been attached to a sacrocaudal or sacrodorsal vertebra.

Scapulocoracoid. The more complete association (F1) includes two fragments of the scapulacoracoid (UBB VP 28, Fig. 5A-F). As represented on the bone map (Fig. 3), the two pieces were found close to each other and their original position might suggest they were fragmentary pieces of a single scapulocoracoid. The two pieces, however, clearly represent fragments of the left and right scapulacoracoid, respectively, of perhaps the same individual. The larger, more informative specimen is part of the left scapulocoracoid (Fig. 5A-C) and preserves the scapular half of the glenoid and proximal parts both from the scapula and the coracoid which are otherwise completely fused. The glenoid is massive and lateromedially more expanded than the rest of the bone. The glenoid surface is rugose for the attachment of the cartillageous articular surface. The circular coracoid foramen (diameter ca. 5 mm) is slightly closer to the glenoid than to the dorsal edge of the coracoid. Dorsal to the coracoid foramen a relatively large, dorsoventrally oriented protuberance is present. A small part of the dorsal edge of the coracoid is preserved, that is slightly convex anteroposteriorly and rounded. This edge is relatively thick in UBB VP 28, in contrast to the thin edge seen in *Sauropelta* (Coombs, 1978) and *Hungarosaurus* (Ősi, 2005), and, at least on the preserved portion of the element, no grooves for muscle attachments can be observed, while these are also present in the latter two genera.

The acromion process is completely missing in UBB VP 28. Based on the curvature of the scapular blade, as typical in ankylosaurs, and the position of the thickened edge dorsal to the acromion process, the scapular blade fragment is from a right scapulocoracoid (Fig. 5D-F). It is more flattended distally with roughly parallel, slightly concave ventral and slightly convex dorsal edges.

Except for the dorsal centrum described above, these pectoral girdle elements are the only overlapping bones with the type material of *Struthiosaurus transylvanicus* (Nopcsa, 1929). From the pectoral girdle of *S. transylvanicus* the right scapula with only a small piece of the glenoidal part of the fused coracoid is preserved (Nopcsa, 1929:plate 3, figs. 5, 6), thus the more dorsal and anterior regions, including the coracoid foramen or the dorsal edge of the coracoid, cannot be directly compared. Nevertheless, the comparable parts are quite similar in both Transylvanian specimens.

Humerus. The proximal two thirds of a well preserved right humerus (VP 12, Fig. 6A-E) is one of the most important elements of the new assemblages for comparative purposes. In general, it is quite similar to the humeri of most ankylosaurs, especially to the humerus (MTM PAL 2012.30.1) referred to cf. *Struthiosaurus* sp. from the Santonian of Hungary (Ősi and Prondvai, 2013) in having an expanded proximal epiphysis and a relatively narrow and short diaphysis. The caput humeri faces anterodorsally and it is latero-medially wider than antero-posteriorly high. The surface of the humeral head is ornamented by wide and deep, approximately radially oriented grooves and larger pits for attaching the cartilagous articular surface. A rim around the caput humeri separating it from the neck region is well preserved. The humeral head is not in the longitudinal axis of the bone. The good preservation state of the specimen allows to demonstrate that the well developed deltopectoral crest curves almost anteriorly with an angle of ca. 80° relative to the lateromedial axis of the bone. Although a small piece is missing from the diaphyseal region, the deltopectoral crest most probably extended approximately to the mid-length of the bone.

Various muscle attachment regions have been preserved on the humerus. One of them is on the posterior surface of the shaft. It is oval shaped and positioned distally, being slightly laterodistal to the humeral head. The scar is rather large, 13 mm wide and 15 mm long proximodistally; it has approximately 3 mm high margins while its central part is slightly concave. The same muscle scar is present on the humerus of various other ankylosaurs (Coombs, 1978) including an almost complete humerus (MC 512) from the upper Campanian–lower Maastrichtian of Fox-Amphoux Syncline in the Aix Basin, southern France, the right humerus fragment (PIUW 2349/18) of *Struthiosaurus austriacus* from the lower Campanian of Austria and the humerus of cf. *Struthiosaurus* sp. from the Santonian of Hungary (MTM PAL 2012.30.1 ; Ősi and Prondvai, 2013), but not in *Hungarosaurus*. In the latter two *Struthiosaurus* specimens this scar is in a more medial position relative to the humeral head. This muscle scar corresponds to the insertion area of *Musculus teres major* and *M. latissimus dorsi* (Coombs, 1978). In the Hungarian specimen referred to cf. *Struthiosaurus* sp. the insertion area of the latter muscle corresponds to a separated, laterally positioned, proximodistally extended ridge (Ősi and Prondvai, 2013).

A large (diameter 18 mm), 9 mm high protuberance is preserved on the ventral-ventrolateral side of the deltopectoral crest, just lateral-proximolateral to the former muscle scar (Fig. 6B). The same scar is also present on the Hungarian specimen (MTM PAL 2012.30.1), though there it is not as high as in UBB VP 12. This scar, also described in *Euoplocephalus* and present in *Ankylosaurus* and *Sauropelta* (Coombs, 1978), corresponds to the insertion surface of *M. scapulohumeralis anterior*. A third, prominent scar is crest-like, 3-4 mm high and 4 cm long, and extends from the former protuberance proximomedially towards the humeral head (Fig. 6B). This crest takes a rectangular curvature and ends 2.6 cm distal to the humeral head.

Although not as well developed, a similar crest (actually a group of smaller crests) also occurs on the Hungarian cf. *Struthiosaurus* sp. humerus (MTM PAL 2012.30.1). In the case of *Euoplocephalus*, Coombs (1978) identified this region as the origin surface of *M. triceps caput humerale laterale*.

The bicipital crest is well developed with a straight medial margin that has a pointed proximal end, similar to the humerus of cf. *Struthiosaurus* sp. from the Santonian of Hungary (Ősi and Prondvai, 2013). Similarly to the Hungarian specimen, a clear demarcation separates the humeral head from the pointed end of the bicipital crest. A demarcation is also present laterally beween the humeral head and the deltopectoral crest; this is, however, not as deep as that seen in the Hungarian specimen. The diaphyseal part of the humerus is short, relatively narrow, and oval to subcircular in cross-section. At its distalmost, broken end the shaft becomes wider suggesting the proximity of the distal epiphysis.

Ulna. A right fragmentary ulna (UBB VP 16, Fig. 6F-I) has been found within the first, more diverse association (F1) that also includes the humerus and the scapulocoracoid fragments already described. The massive and relatively large size of the ulna clearly suggests, however, that it comes from a different, larger individual than that represented by the humerus. The specimen preserves the main body of the ulna, but most of the olecranon process, the anteriormost part of the humeral articular facet, and the distal epiphysis are missing. Only a 2.5 cm long part from the articular surface of the proximal epiphysis is preserved. Among European ankylosaurs, the type material of *Struthiosaurus austriacus* (PIUW 2349/uncatalogued; Pereda Suberbiola and Galton, 2001), respectively the holotype specimen (Ősi, 2005) and the fifth skeleton (Ősi and Makádi, 2009) of *Hungarosaurus* possess an ulna. In addition, an isolated ulna is known from the Upper Cretaceous of Laño, northern Spain (Pereda Suberbiola, 1993a). The new specimen from Vurpăr is intermediate in morphology between the unusally elongated ulna of *Hungarosaurus* and the short, isolated ulna from

Laño. It is approximately one third times longer than the ulna from Laño. The Austrian specimen preserves only the distal half of the bone, but the angle between the anterior and posterior edges is similar to that seen in the Vurpăr ulna, suggesting a somewhat similar, moderately elongated element.

Femur. Three fragmentary femora are known in the new Transylvanian ankylosaurian material. Two of them, a more complete right one (UBB VP 26, Fig. 6N-R) and the distal end of a left one (UBB VP 27, Fig. 6J-M), are from the more diverse, first assemblage (F1). The third specimen (UBB VP 32), the distal end of a left femur, was found isolated. Whereas VP 26 and VP 27 are of the same size and most probably represent a single individual, the third specimen is slightly smaller. The most complete femur only lacks the proximal epiphysis. It is straight in anterior view, with straight lateral and slightly concave medial margins of the diaphysis. The shape of the proximal diaphyseal end shows that the proximal epiphyis became slightly widened mediolaterally. The fourth trochanter is a proximodistally extended, 3-4 cm long, shallow crest being quite similar to that seen on the femur of *Struthiosaurus austriacus* (PIUW 2349/32), but more developed than that of *Hungarosaurus* (MTM 2007.26.30). Both the Romanian and the Austrian specimens preserve the original cross section of the bone; these show that the distal part of the diaphysis is thicker in the Vurpăr femur (UBB VP 26) than in *S. austriacus*. The distal epiphysis strongly widens relative to the shaft and it is formed by the anteroposteriorly expanded lateral and medial condyles. The medial condyle is slightly larger, being more extended both anteroposteriorly and proximodistally. A deep and wide intercondylar notch is present posteriorly, but this is more shallow anteriorly. The femur of *S. austriacus* has a laterally expanded ectepicondyle; this condition is less well developed on the Vurpăr femora, where this ectepicondyle is slightly larger in UBB VP 27.

Osteoderms. Altogether 15 osteoderms from Vurpăr (five from the first partial skeleton [UBB VP 13, 15, 17, 18, 20], two in the second one [UBB VP 82, 83], and 8 additional isolated specimens [UBB VP 4, 33, 39, 52, 65, 66, 113, 114]) can be referred to ankylosaurs. Most of them are low, oval or rectangular scutes possessing a longitudinal crest with variable height (Fig. 7). Some scutes (e.g., UBB VP 15, 17, 52, 65) are quite similar to the osteoderms of *Hungarosaurus* in having an oval-shaped base and a central dorsal crest that increases posteriorly. Specimens UBB VP 82 and 83 have oval shaped bases, and high and strongly posterodorsally projecting crests. UBB VP 4 is an unusual osteoderm in having a single, high posterodorsally pointed crest and a rounded base (Fig. 7F-H). This specimen is apparently not broken from another, larger osteoderm, neither from a skull element, but was an isolated element of the armor. UBB VP 18 has a rectangular base that is slightly convex ventrally, and bears a high, scalloped crest dorsally.

Bone histology

Unfortunately, the microstructural preservation is very poor in all sampled specimens, with extensive areas of diagenetic staining. The cortical wall is moderately thick and merges into the medullar cavity first through larger erosion rooms that finally turn into trabecular structures of cancellous bone. Although the surface of the outermost cortex is apparently eroded in UBB VP 12, 14, 26, and 27, based on the morphological preservation state of the bones and on the histological characteristics observable towards the cortical periphery, the missing layer does not seem to have been as thick as to prevent or considerably modify our ontogenetic inferences.

The most obvious and uniformly present histological feature of all investigated specimens is the extensive secondary remodelling throughout the cortex with only little or no primary bone preserved (Fig. 8). The cortex of the right humerus UBB VP 12, the rib UBB VP 14, and the right femur UBB VP 26 is completely remodelled with two or more generations of secondary osteons in some areas. In the right ulna (UBB VP 16) and the left femur (UBB VP 27), restricted areas of primary bone are still detectable between secondary osteons in the outermost cortical region. Here, mostly longitudinal primary vascular canals are present embedded in highly organized primary bone (HOPB). Based on the lacunocanalicular appearance and optical behaviour of the primary bone matrix under cross polarized light, HOPB has mainly longitudinal to slightly oblique (probably helical) structural organization, but around the vascular channels this becomes circularly oriented with lamellar appearance. Nevertheless, in spite of occurring in the peripheralmost cortex, primary bone also seems to contain patches of woven bone with lacunar features, typical of those derived from static osteogenesis (SO). Closely spaced lines of arrested growth (LAGs) can be observed in the left femur UBB VP 27, whereas no LAGs are evident in the primary bone of the right ulna UBB VP 16. Locally, the most extensive primary areas are found in the left femur UBB VP 32 where secondary osteons in the outermost cortical layer are more scattered, and hence the structure of primary bone between them becomes visible. The primary bone of this specimen has very few primary vascular canals all running longitudinally and having very narrow lumen. Several densely packed LAGs cross this area sometimes running right through the primary vascular channel. The orientation of HOPB is longitudinal. Although there are still some very sparsely distributed longitudinal canals, the overall appearance of the primary cortical area with closely spaced LAGs implies that the outermost cortex had developed an external fundamental system (EFS; Cormack, 1987). Densely packed LAGs found in the restricted primary area of UBB VP 27 suggest that this specimen also exhibited EFS in the outermost cortex before the remodelling front reached the periosteal surface; however, in contrast to UBB VP 16 and 27, no woven bone could be observed in the primary bone of UBB VP 32 (Fig. 8H).

DISCUSSION

The ankylosaurian remains described here are of great importance because they augment the otherwise extremely poorly known Late Cretaceous ankylosaur record of the Transylvanian area. Nevertheless, the taxonomic assignment of this material is problematic for at least two reasons: 1) except from the single tooth preserved in a small jaw fragment, there are no other cranial remains to provide precise taxonomic identification; and, 2) apart from the non-diagnostic dorsal vertebral centrum and the ribs, as well as the proximal end of the fragmentary scapulacoracoid, no elements from the new material overlap with the type material of *Struthiosaurus transylvanicus*, the only known ankylosaur from the Haţeg Basin (Nopcsa, 1915, 1929), part of the former Transylvanian landmass (Benton et al., 2010; Codrea et al., 2010a). In addition, the tooth and the postcranial remains were found in stratigraphically and geographically different units (the tooth in the Haţeg Basin, the postcranial remains in Vurpăr locality, within the Transylvanian Basin, about 75 km away from the Haţeg Basin), so it cannot be ruled out that they may represent two different taxa.

Taxonomic assignment of the tooth

The tooth (LPB (FGGUB) R.2182) markedly differs from those of other ankylosaurs (e.g., *Struthiosaurus austriacus* [PIUW 2349/105b, Pereda Suberbiola and Galton, 2001:fig. 10.2N], *Struthiosaurus languedocensis* [Garcia and Pereda Suberbiola, 2003], *Edmontonia* spp, *Sauropelta edwardsorum* and *Euoplocephalus tutus* [Coombs, 1990; Ő.A. personal observation], *Ankylosaurus magniventris* [Carpenter, 2004], *Gargoyleosaurus parkpini* [DMNH 27726], *Hungarosaurus tormai* [MTM 2007.25.2], *Peloroplites* [Carpenter et al., 2008], *Pinacosaurus grangeri* [ZPAL MGD-II/1], *Tarchia gigantea* [PIN N3142 250], or *Saichania chulsanensis* [Carpenter et al., 2011]) in the lack of a central cusp surrounded mesiodistally by several minor cusps, and in having only six, more or less equally sized, apically pointed cusps separated by deeply incised grooves. The number and development of the mesial and distal secondary cusplets on the main cusps are also more pronounced than in other ankylosaurs (e.g., *Hungarosaurus*; Ősi, 2005). The isolated tooth from Toteşti-baraj (Maastrichtian of Haţeg Basin, Romania; Codrea et al., 2002a:fig. 4g) shares many similarities with LPB (FGGUB) R.2182 in having a low number (only four) of well separated cusps; the cingulum region is, however, slightly different between the two specimens. Both of these teeth came from the Maastrichtian deposits of the Haţeg Basin (although from different localities spaced about 3.5 km apart), so they conceivably might belong to the same taxon. The only ankylosaur taxon possessing relatively similar tooth morphology, characterized by the reduced number of cusps (4 in the premaxillary teeth and 7 in the maxillary teeth), presence of deep grooves between the cusps, and lack of a central cusp, is *Liaoningosaurus paradoxus* from the Lower Cretaceous of China (Xu et al., 2001). Most importantly, however, these teeth are markedly different from those of *Struthiosaurus austriacus* (although most teeth of the latter taxon are strongly worn or broken) and *S. languedocensis* (Garcia and Pereda Suberbiola, 2003). Unfortunately, the type material of *S. transylvanicus* does not contain teeth so it is unclear whether the tooth LPB (FGGUB) R.2182 represents the same taxon or not; it is noteworthy, nonetheless, that these remains are coming from the same general area, although from somewhat different stratigraphic levels. Here we tentatively refer this isolated tooth specimen to Nodosauridae indet., while noting that its quite unusual shape, compared to the ankylosaurian teeth characterized by generally conservative morphology, might suggest that this Haţeg nodosaurid was different from the other Late Cretaceous European ankylosaurs (i.e. *Struthiosaurus*, *Hungarosaurus*) not only at species but also at generic level.

Taxonomic assignment of the postcranial material

In comparison with other ankylosaurs the glenoid is the only taxonomically edifying region on the small scapular fragment, preserved in fused contact with the proximal end of the coracoid, as the scapular blade or the acromion process are missing.. This feature, a mediolaterally widened, rugose articular surface with massive, rounded lateral margin, can be found however in other ankylosaurs, e.g., in two of the scapulae referred to *Struthiosaurus austriacus* (PIUW 2349/uncatalogued and PIUW2349/C[1]), or in that of *Hungarosaurus tormai* (MTM 2007.26.23), and is thus of limited diagnostic value. Accordingly, the humerus (UBB VP 12) is the most informative specimen among the postcranial material discovered at Vurpăr. In addition, it is also the most useful element for comparisons, since ankylosaurian humeri are known from various European Late Cretaceous continental vertebrate assemblages; these were referred to: *Struthiosaurus austriacus* [PIUW 2349/18] from Muthmannsdorf, Austria (Pereda Suberbiola and Galton, 2001); *Struthiosaurus* sp. [MCNA 6528] from Laño, Spain (Pereda Suberbiola, 1999); *Hungarosaurus tormai* [MTM 2007.25.3] (Ősi and Makádi, 2009) and cf. *Struthiosaurus* sp. [MTM PAL 2012.30.1] (Ősi and Prondvai, 2013) from Iharkút, Hungary; as well as an unpublished ankylosaurian humerus (MC 512) from the Fox-Amphoux Syncline of the Aix Basin, France (Ősi and Prondvai, 2013).

The Vurpăr humerus has a strongly expanded proximal epiphysis with well developed deltopectoral crest and dorsomedially pointed bicipital crest, as in the humerus MC 512 from Provence. The size and general morphology of this ontogenetically adult specimen from Vurpăr also clearly resemble those of the humerus MTM PAL 2012.30.1 from the Santonian of Iharkút, Hungary, referred to cf. *Struthiosaurus* (Ősi and Prondvai, 2013), while definitively distinguishing it from the humerus of *Hungarosaurus* (MTM 2007.25.3), described from the same locality. Especially the muscle attachment areas are remarkably similar between the Romanian and Hungarian specimens: similar morphology and position of the insertion surface (protuberance) of *M. scapulohumeralis anterior*, as well as of the origin surface (crest) of *M. triceps caput humerale laterale*, are observed on both. The only difference is that in the Vurpăr specimen the insertion surfaces of *M. teres major* and *M. latissimus dorsi* appear to be united into a single oval-shaped muscle scar as seen in certain other ankylosaurs (e.g., *Sauropelta* and *Panoplosaurus*; Coombs, 1978), including *S. austriacus*, whereas on the Iharkút specimen the latter muscle attached nearby the oval-shapes scar, on an elongated crest (Ősi and Prondvai, 2013). These shared morphological features of UBB VP 12 and MTM PAL 2012.30.1 also suggest similar proportions and relative masses of the respective forelimb muscles.

Although the Vurpăr postcranial material in overall is too fragmentary to detect any of the synapomorphic characters listed by Thompson et al. (2012) for different ankylosaurian clades, observed size differences and taphonomical aspects clearly demonstrate that it represents at least three different individuals of nodosaurid ankylosaurs. Based on their similar preservational characteristics, comparable size, pattern of distribution within the site, and non-overlapping nature, we consider that the bones from the F1 assemblage (Fig. 3) might represent associated remains of a single individual, except for the ulna (UBB VP 16) with significantly larger size. Part of this assemblage, the right humerus (UBB VP 12, Fig. 6A-E) bears several important features that clearly distinguish it from *Hungarosaurus* and suggest closest affinities with *Struthiosaurus* (see also Ősi and Prondvai, 2013). In this regard, here we tentatively refer the Vurpăr F1 assemblage (except for the ulna) to as cf. *Struthiosaurus* sp. The remaining ankylosaurian postcranial material from Vurpăr is not diagnostic at lower taxonomic levels. Accordingly, we choose to refer these specimens simply to as Nodosauridae indet., while noting that there are no features that would neither contradict, nor definitively support their referral to the same taxon as that represented by F1.

Bone histology

The most characteristic histological feature of all sampled Vurpăr specimens is the extreme cortical remodelling, reminiscent of that revealed in the humerus of cf. *Struthiosaurus* sp. described from Iharkút, the Santonian vertebrate locality of Hungary (Ősi and Prondvai, 2013). Since secondary remodelling is considered to be a time-consuming process, completely remodelled cortex is assumed to characterize skeletally mature individuals (Kerley, 1965; Kerley and Ubelakker, 1978; Castanet et al., 1993; Thomas et al., 2000; Klein and Sander, 2008; Stein et al., 2010). The extensive remodelling, sometimes with more generations of secondary osteons, makes the bone histology of these ankylosaurs evocative of another inhabitant of the Late Cretaceous Haţeg Island, the titanosaur *Magyarosaurus dacus*. The extensively remodelled cortical bone microstructure of this sauropod dinosaur combined with its diminutive size was used as evidence that it represents a real island dwarf (Stein et al., 2010). By direct comparison, it follows that all investigated Romanian ankylosaurian specimens from our sample must be considered as fully grown adults. Because the growth record reflected in their primary cortex has been almost entirely obliterated by the extensive Haversian remodelling, little can be said about their possible metabolic rates or growth rates as younger individuals. However, unless it is only a diagenetic alteration of the lacunae, the presence of woven bone in the outermost primary cortex of the right ulna UBB VP 16 and left femur UBB VP 27 suggests high diametrical bone growth rate until quite late phases of their ontogeny. This means that the sampled specimens could have grown to their adult sizes rapidly; the onset of secondary remodelling took place after or possibly even already during the time the animal was nearing adulthood, and soon reached the outer surface of the bone.

If relative ages are to be assigned to the sampled specimens based on their histological features, the right ulna UBB VP 16 shows the most immature microstructural characters, with the largest and most frequent patches of woven bone and no detectable LAGs in its primary cortex. Strangely enough, UBB VP 16 seems to have belonged to a larger specimen than the humerus and femora from the F1 assemblage. Although the isolated left femur UBB VP 32 preserves the most extensive areas of primary bone in the peripheral cortex, it clearly shows EFS which verifies its skeletal maturity. The rest of the specimens may be considered 'older' or being in a more advanced absolute age, because secondary remodelling have reached the outer surface of the cortex destroying all remnants of primary bone.

However, before jumping into any conclusions in this regard, it also must be taken into consideration that 1) one element is not necessarily representative of the ontogenetic stage of an animal due to allometric development of different parts of the skeleton; and 2) reasonable comparisons can only be made, and relative developmental sequence can only be reconstructed, if the investigated specimens represent the same skeletal element and have been sampled from the same standardized location. Since these requirements are not completely met in our study, in which we sampled different elements at different locations from at least three different individuals, the only reasonable conclusion that can be drawn is that each specimen, be it larger or smaller in size, belonged to a skeletally mature individual. The inferred adult ontogenetic stage at small body size, as seen in the Transylvanian ankylosaurs described in this study, is also concordant with the idea that these bones might well represent the genus *Struthiosaurus,* widely acknowledged as a small-sized nodosaurid. The type material of *Struthiosaurus*, however, has never been investigated histologically to confirm its skeletally mature status. In case the holotype of *Struthiosaurus transylvanicus* also represents an adult individual, then adult body size of all ankylosaurs recovered so far from the Transylvanian area is visibly smaller than that of their relatives known from other localities, especially from outside Europe. Although this size difference is not as striking as it is between *Magyarosaurus dacus* and other titanosaurian sauropods, the histological argument for insular dwarfism presented in the case of *Magyarosaurus* (Stein et al., 2010) can also be applied to the Transylvanian nodosaurids (but see Pereda Suberbiola and Galton, 2009, for an alternative view), for which however this presumably autapomorphic size decrease (Gould and MacFadden, 2004) was not as dramatic as in the case of *Magyarosaurus*. More specimens with precise details on their taxonomic status along with systematic histological sampling and numerical analysis would be necessary to support (or discard) such a hypothesis of autapomorphic dwarfing.

CONCLUSIONS

The ankylosaurian remains described here are of great importance because since the 1912 discovery of the first and single known ankylosaurian record from the Transylvanian area (i.e., the very fragmentary type material of *Struthiosaurus transylvanicus*), no other armoured dinosaur material has been documented, despite passing mention of a single tooth (Codrea et al., 2002a) and a few of the here described postcranial elements (Codrea et al., 2010a). Consequently, this material really enriches the otherwise extremely poorly known local (and European) Late Cretaceous ankylosaur record. The new material, consisting of one tooth from the Maastrichtian of Sînpetru (Haţeg Basin) and two disarticulated partial skeletons (as well as isolated remains) from the Maastrichtian of Vurpăr (Transylvanian Basin), does not share unambiguously diagnostic anatomical features with previously described taxa. Only a few non-diagnostic elements (glenoidal region of the scapula, dorsal vertebral centrum, dorsal ribs) from Vurpăr overlap with the type material of *S. transylvanicus*, impeding assignment of any of the specimens to this taxon.

The tooth from Haţeg (LPB (FGGUB) R.2182) strongly differs from those of other ankylosaurs in the absence of a central cusp with mesiodistally cuspidate carina and having only six, apically pointed cusps separated by deep grooves. This tooth is most similar to one isolated tooth published previously by Codrea et al. (2002a) suggesting that, based on their dentition, at least some of the Haţeg nodosaurids were different from other European members of the clade (i.e., *Hungarosaurus tormai*, *Struthiosaurus austriacus*; the teeth of *S. transylvanicus* are unknown) not only at species but perhaps also at generic level.

Of the postcranial material, the humerus of the F1 assemblage (UBB VP 12) is the most informative specimen showing great similarity with the humeri referred to as *Struthiosaurus* from other Late Cretaceous European localites. Hence we tentatively refer this material, along with other, comensurate postcranial elements of the F1 assemblage (interpreted as representing the scattered remains of one individual) to as cf. *Struthiosaurus* sp.

Histological studies revealed the adult nature of all sampled bones in the Vurpăr material. This indicates that these fully grown Vurpăr ankylosaurs were rather small, of similar size as the known three species of *Struthiosaurus*, the ontogenetic status of which, however, is still not confirmed by bone histological investigation. Pending the documentation of the adult nature of *S. transylvanicus*, the evidently smaller body size of the Transylvanian ankylosaurs compared to their relatives could be explained by insular dwarfism using the same histology-based argument as presented previously for the titanosaur *Magyarosaurus.* Nevertheless, more specimens of clear taxonomic identity as well as extensive histological and numerical phylogenetic analysis are needed to draw firm conclusions on this matter.

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Figure captions:

Figure 1. Location map of the Haţeg and Sebeş-Alba areas within Romania, with details on the location of Vurpăr locality. A, Position of Romania in Europe. B, Position of the Haţeg and Sebeş-Alba areas within Romania. C, The two sites (F1, F2) providing ankylosaurian remains at Vurpăr.

Figure 1. Localisation des régions de Haţeg et Sebeş-Alba sur la carte de la Roumanie, avec des détails sur la position de la localité de Vurpăr. A, Localisation de la Roumanie sur la carte de l'Europe. B, Localisation des aires Haţeg et Sebeş-Alba en Roumanie. C, Les deux sites fossilifères (F1, F2) avec des restes d'ankylosaure à Vurpăr.

Figure 2. Geological log profile of the Vurpăr locality, Transylvanian Basin, Romania. CH, channel deposit, F, floodplain deposit, P, paleosol deposit.

Figure 2. Colonne géologique à Vurpăr, Bassin de Transylvanie, Roumanie. CH, dépôts de canal, F, plaine fluviale, P, paléosol.

Figure 3. Bone map of the partial ankylosaurian skeleton F1 (cf. *Struthiosaurus* sp.) from the Maastrichtian of Vurpăr, Transylvanian Basin, Romania. Abbreviation: **Os**, osteoderm.

Figure 3. Distribution en surface des os du squelette de l'ankylosaure F1 (cf. *Struthiosaurus* sp.) du Maastrichtien de Vurpăr, Bassin de Transylvanie, Roumanie. Abréviation : **Os**, ostéoderme.

Figure 4. Nodosauridae indet. tooth (LPB (FGGUB) R.2182) from the Maastrichtian of Sânpetru, Haţeg Basin, Romania, in labial? (A) distal? (B), and occlusal (C) views.

Abbreviations: ci, cingulum; gr, groove, j, jaw; sc, secondary cusp, se, serration; C1–C6, individual cusps. Scale bar equals 2 mm.

Figure 4. Dent de Nodosauridae indet. (LPB (FGGUB) R.2182) du Maastrichtien de Sânpetru, Bassin de Haţeg, Roumanie, en vues labiale ? (A) distale ? (B) et occlusale (C). Abréviations: ci, cingulum; gr, sillon, j, mâchoire; sc, cuspide secondaire, se, serration; C1–C6, cuspides principales. Echelle : 2 mm.

Figure 5. Nodosaurid axial and appendicular skeletal elements from the Maastrichtian of Vurpăr, Transylvanian Basin, Romania. A-C, cf. *Struthiosaurus* sp., fragment of the left scapulocoracoid (UBB VP 28) in lateral (A), ventral (B), and medial (C) views. D-F, cf. *Struthiosaurus* sp., fragment of the right scapula (UBB VP 28) in medial (D), lateral (E), and dorsal (F) views. G-H, Nodosauridae indet., dorsal rib (UBB VP 85) in posterior (G) and anterior (H) views. I-L, Nodosauridae indet., dorsal vertebral centrum (UBB VP 121) in ventral (I), lateral (J), dorsal (K), and anterior (L) views. Abbreviations: cf, coracoid foramen; co, coracoid; gl, glenoid; nc, neural canal; sc, scapula. Scale bars equal 2 cm.

Figure 5. Eléments du squelette axiale et appendiculaire du nodosauridé du Maastrichtien de Vurpăr, Bassin de Transylvanie, Roumanie. A-C, cf. *Struthiosaurus* sp., scapulocoracoïde gauche (UBB VP 28), en vues latérale (A), ventrale (B) et médiale (C). D-F, cf. *Struthiosaurus* sp., fragment de scapula droite (UBB VP 28) en vues médiale (D), latérale (E) et dorsale (F). G-H, Nodosauridae indet., côte dorsale (UBB VP 85) en vues postérieure (G) et antérieure (H). I-L, Nodosauridae indet., centrum de vertèbre dorsale (UBB VP 121) en vues ventrale (I), latérale (J), dorsale (K) et antérieure (L). Abréviations: cf, foramen du coracoïde; co, coracoïde; gl, glénoïde; nc, canal neural; sc, scapula. Échelle: 2 cm.

Figure 6. Nodosaurid limb bones from the Maastrichtian of Vurpăr, Transylvanian Basin, Romania. A-E, cf. *Struthiosaurus* sp., fragmentary right humerus (UBB VP 12) in posterior (A), lateral (B), medial (C), proximal (D) and anterior (E) views. F-I, Nodosauridae indet., fragmentary right ulna (UBB VP 16) in medial (F), lateral (G), anterior (H), posterior (I) views. J-M, cf. *Struthiosaurus* sp., distal end of a left femur (UBB VP 27) in posterior (J), anterior (K), medial (L), proximal (M) views. N-R, cf. *Struthiosaurus* sp., fragmentary right femur (UBB VP 26) in posterior (N), anterior (O), lateral (P), medial (Q), distal (R) views. Abbreviations: bc, bicipital crest; dpc, deltopectoral crest; haf, humeral articular facet; hc, humeral condyle; isca, insertion area of *Musculus scapulohumeralis anterior*; itmld, common insertion area of *Musculus teres major* and *Musculus latissimus dorsi*; lc, lateral condyle; mc, medial condyle; otrl, origin surface of *Musculus triceps caput humerale laterale*. 4tr, fourth trochanter; Scale bars equal 2 cm.

Figure 6. Os appendiculaires de nodosauridé du Maastrichtien de Vurpar, Bassin de Transylvanie, Roumanie. A-E, cf. *Struthiosaurus* sp. humérus droit fragmentaire (UBB VP 12) en vues postérieure (A), latérale (B), médiale (C), proximale (D) et antérieure (E). F-I, Nodosauridae indet., ulna droite fragmentaire (UBB VP 16) en vues médiale (F), latérale (G), antérieure (H) et postérieure (I). J-M, cf. *Struthiosaurus* sp., fémur gauche fragmentaire (UBB VP 27) en vues postérieure (J), antérieure (K), médiale (L) et proximale (M). N-R, cf. *Struthiosaurus* sp., fémur droit fragmentaire (UBB VP 26) en vues postérieure (N), antérieure (O), latérale (P), médiale (Q), distale (R). Abréviations: crête bicipitale; dpc, crête deltopectorale; haf, facette articulaire de l'humérus; hc, tête humérale; isca, zone d'insertion du *Musculus scapulohumeralis anterior*; itmld, zone d'insertion commune des *Musculus teres major* et *Musculus latissimus dorsi*; lc, condyle

latérale; mc, condyle médiale; otrl, surface originaire du *Musculus triceps caput humerale laterale* ; 4tr, quatrième trochanter. Échelle: 2 cm.

Figure 7. Nodosaurid dermal osteoderms from the Maastrichtian of Vurpăr, Transylvanian Basin, Romania. A-C, cf. *Struthiosaurus* sp., dermal osteoderm (UBB VP 18) from the ?dorsal region in dorsal (A), ?anterior (B) and ventral (C) views. D-E, Nodosauridae indet., crest-like, marginal osteoderm (UBB VP 83) in posterior (E) and lateral (F) views. F-H, Nodosauridae indet., osteoderm (UBB VP 4) from the ?cervical region in ?lateral (F), anterior (G) and medial (H) views. I-J, Nodosauridae indet., crested osteoderm (UBB VP 65) from the ?dorsal region in posterior (I) and dorsal (J) views. K-L, cf. *Struthiosaurus* sp., crested osteoderm (VP 17) from the ?dorsal region in lateral (K) and dorsal (L) views. Scale bars equal 2 cm.

Figure 7. Ostéodermes dermiques de nodosauridé du Maastrichtien de Vurpăr, Bassin de Transylvanie, Roumanie. A-C, cf. *Struthiosaurus* sp., ostéoderme dermique (UBB VP 18) de la région ?dorsale en vues dorsale (A), ?antérieure (B) et ventrale (C). D-E, Nodosauridae indet., ostéoderme à quille, marginale (UBB VP 83) en vues postérieure (E) et latérale (F). F-H, Nodosauridae indet., ostéoderme (UBB VP 4) de la région ?cervicale en vues ?latérale (F), antérieure (G) et médiale (H). I-J, Nodosauridae indet., ostéoderme à quille (UBB VP 65) de la région ?dorsale en vues postérieure (I) et dorsale (J). K-L, cf. *Struthiosaurus* sp., ostéoderme à quille (VP 17) de la région ?dorsale en vues latérale (K) et dorsale (L). Échelle: 2 cm.

Figure 8. Details of the bone histology of the rib UBB VP 14 (A, B), right ulna UBB VP 16 (C, D, E), and two left femora, UBB VP 27 (F, G) and UBB VP 32 (H). VP 14 exhibits (A) the eroded periosteal surface (eps), the effect of strong diagenetic staining (ds), and

(B) the complete secondary remodelling (csr) of the cortex up to the outermost cortical region. These features characterize most of the sectioned specimens. C, Transition of the cortex into the medullar cavity (mc) with large erosion rooms in the middle in the core sample of UBB VP 16. Although secondary remodelling reaches the periosteal surface, primary bone (pb) appears between some less densely arranged secondary osteons (so). D, E, Magnification of the area marked by the white square in C revealing the restricted area of primary bone under crossed polarized light (D) and single plane polarizers (E). Primary bone contains longitudinal vascular canals (pvc) and comparatively extensive patches of woven bone (wb). F, Close-up of the outer cortical area of UBB VP 27 showing primary bone with longitudinal canals and densely packed lines of arrested growth (LAGs). Some woven bone can still be observed in the vicinity of the primary canals as shown by the osteocyte lacuna features (olw) in G which represents the magnified area indicated by the white square in F. H, The locally most extensive primary cortex is exhibited by UBB VP 32 which also shows closely packed LAGs and very poor vascularization referring to the presence of an external fundamental system (EFS).

Figure 8. Détails sur la histologie de la côte UBB VP 14 (A, B), ulna droite UBB VP 16 (C, D, E), et deux fémurs gauches, UBB VP 27 (F, G) et UBB VP 32 (H). VP 14 expose (A) la surface periostéale érodée (eps), l'effet du puissant tache diagénétique (ds), et (B) la complète réorganisation (csr) du cortex jusqu'à la région corticale la plus externe. Ce sont des caractères communs pour la plupart des spécimens sectionnés. C, Transition du cortex dans la cavité médullaire (mc) avec des chambres d'érosion au milieu de la carotte échantillonnée dans UBB VP 16. Bien que la réorganisation secondaire touche la surface periostéale, l'os primaire (pb) est observable entre quelques ostéons secondaires moins compactes (so). D, E Grandissement de la zone marquée par un rectangle blanc en C décelant la zone de l'os primaire en lumière polarisée croisée (D) et en plan unique des

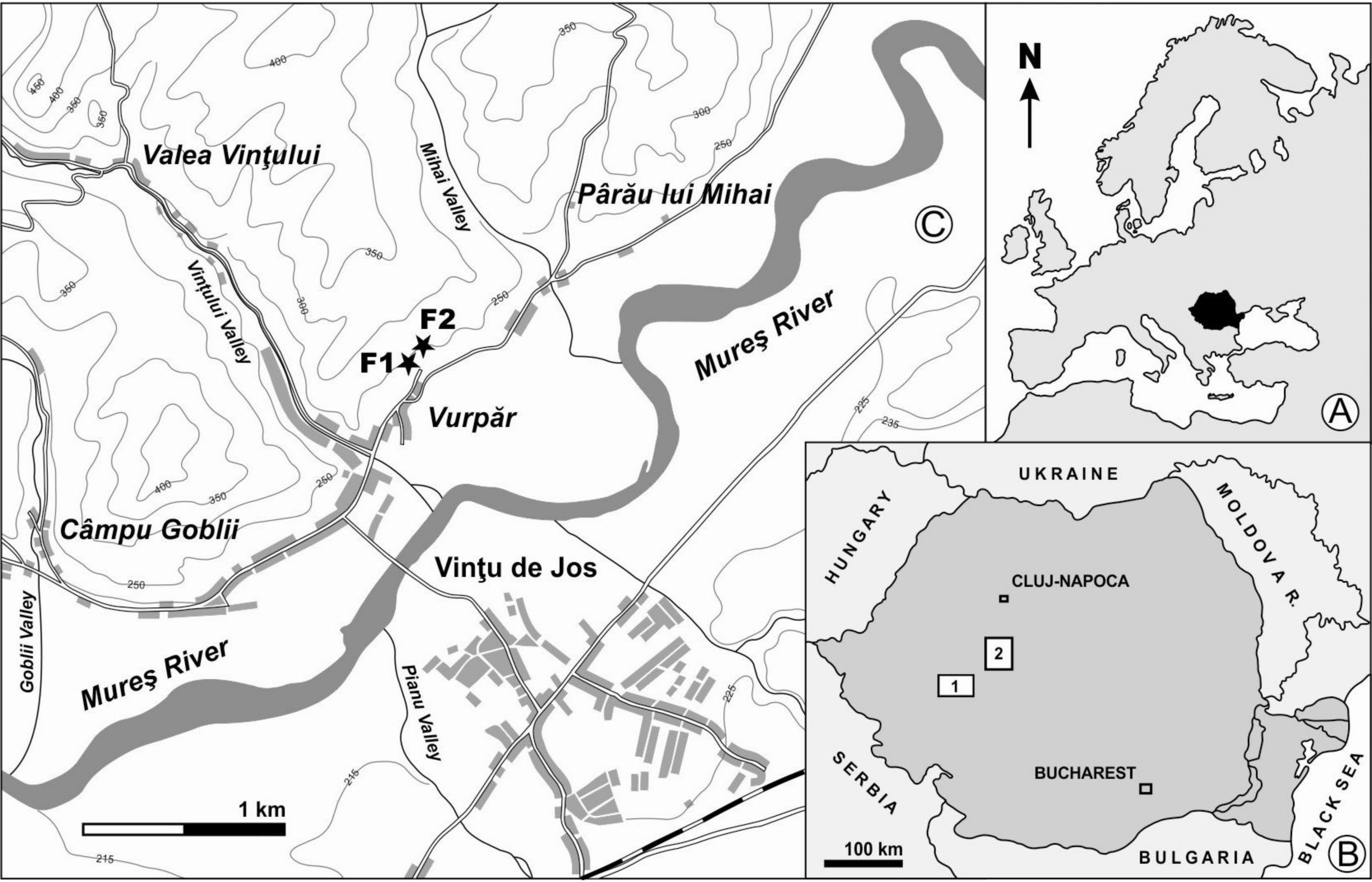
polariseurs (E). L’os primaire contient des chenaux longitudinaux vascularisés (pvc) et des parties relativement larges d’os tissé (wb). F, Détail sur la zone corticale externe de UBB VP 27 montrant l’os primaire avec des chenaux longitudinaux et des paquets denses d’arrêt de croissance (LAGs). Une partie de l’os tissé peut être encore observée dans le voisinage des chenaux primaires montrés par les caractères des lacunes d’ostéocytes (olw) en G qui représente la zone agrandie marquée par le rectangle blanc F. H, l’extension la plus grande du cortex primaire est observée sur UBB VP 32 qui montre aussi des paquets compacts de LAGs et une très pauvre vascularisation liée à la présence d’un système fondamental externe (EFS).

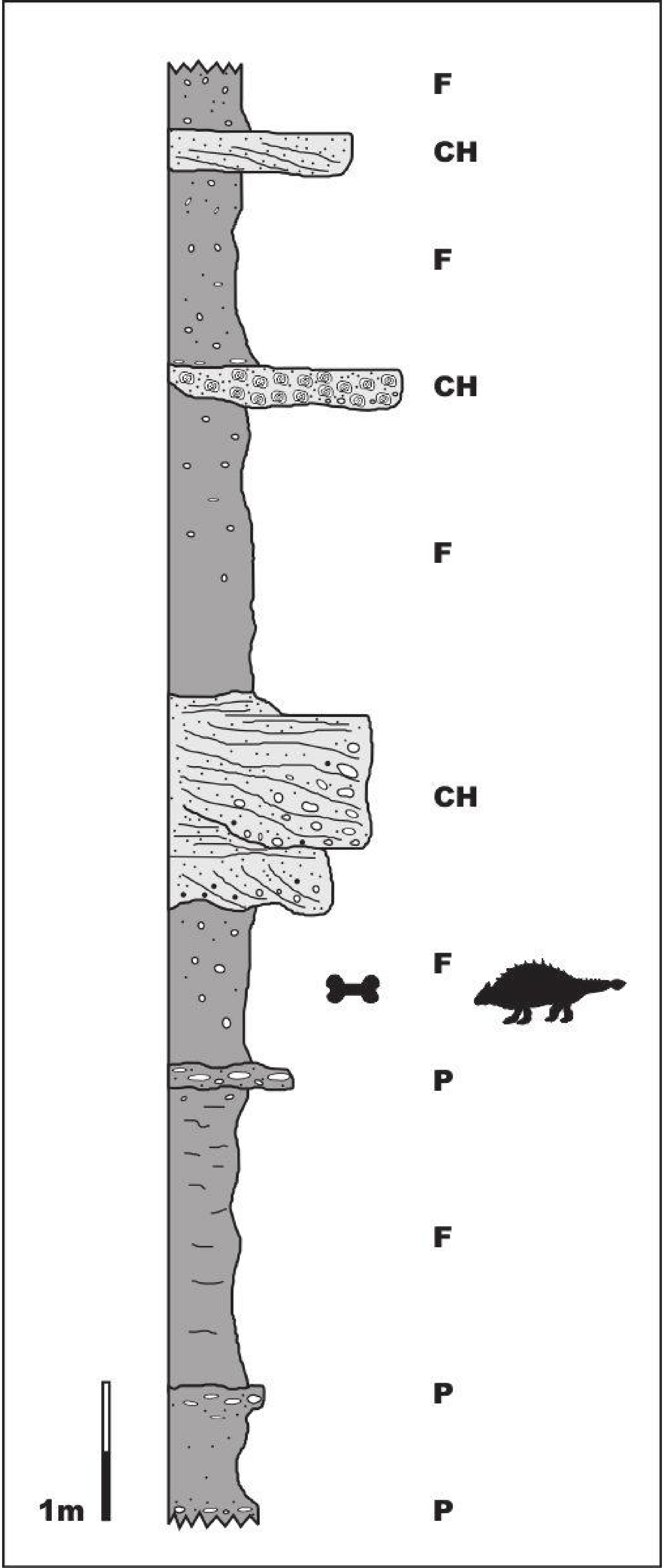
Table 1. Latest Cretaceous ankylosaurian remains from Europe listed in chronostratigraphical order.

Table 1. Restes d'ankylosaures du Crétacé final d'Europe, désignés en ordre chronostratigraphique.

Name	**Material**	**Age**	**Locality**	**Reference(s)**
Hungarosaurus tormai	Seven partial skeletons and hundreds of isolated elements including both cranial and postcranial material	Santonian	Iharkút, western Hungary	Ősi, 2005; Ősi and Makádi, 2009; Ősi et al., 2014
cf. *Struthiosaurus* sp.	humerus	Santonian	Iharkút, western Hungary	Ősi and Prondvai, 2013
Struthiosaurus austriacus	Fragmentary basicranium and other cranial elements, dentary teeth, postcranial material of more than one individual	Early Campanian	Muthmannsdorf, eastern Austria	Bunzel, 1870, 1871; Seeley, 1881; Pereda-Suberbiola and Galton, 1992, 1994, 2001
Struthiosaurus languedocensis	Articulated sacral region including synsacrum and hip elements	?Early Campanian	Villeveyrac, southern France	Garcia and Pereda Suberbiola, 2003
Nodosauridae indet.	Osteoderms	Campanian	Hérault, southern France	Le Loeuff, 1992; Pereda Suberbiola, 1993b
Nodosauridae indet.	Osteoderm Cranial and postcranial remains (most of them still unpublished)	Campanian	Chera, Spain	Sanz, 1986; Company, 2004
cf. *Struthiosaurus* sp.	Cervical neural arch, two osteoderms	Late Campanian	Hérault, southern France	Pereda Suberbiola, 1993b
Nodosauridae indet. (*Rhodanosaurus* [*Struthiosaurus*] *ludgunensis*)	Caudal centra, rib fragments, osteoderms	Campanian-Maastrichtian	Quarante and Montouliers, southern France	Depéret, 1900; Nopcsa, 1929; de Lapparent, 1947, 1954; Pereda Suberbiola, 1993b
Nodosauridae indet.	Teeth, rib fragment, humerus, osteoderms	Campanian-Maastrichtian	Var, Ariége, southern France	Pereda Suberbiola, 1993b
Nodosauridae indet.	Osteoderms	Early Maastrichtian	Le Mas d'Azil, southern France	Le Loeuff, 1991; Pereda Suberbiola, 1993b
Struthiosaurus transylvanicus	Posterior part of a skull, some vertebrae, ribs, scapula, osteoderms	Maastrichtian	Haţeg Basin, western Romania	Nopcsa, 1915, 1929; Pereda-Suberbiola and Galton, 1994
Struthiosaurus sp.	Sacral region including synsacrum and hip elements	Maastrichtian	Laño, Spain	Garcia and Pereda Suberbiola, 2003
Struthiosaurus sp.	Dentary, maxilla fragment, teeth, rib fragments, ulna, osteoderms	Maastrichtian	Laño, Spain	Astibia et al., 1990; Pereda Suberbiola, 1999 ; Pereda Suberbiola et al., 1993a, 1995
cf. *Struthiosaurus* sp.	Fragmentary humerus and femora, ribs, right scapula, left scapulocoracoid, osteoderms	Maastrichtian	Vurpăr, Romania	This paper
Nodosauridae indet.	Isolated tooth	Maastrichtian	Toteşti, Romania	Codrea et al., 2002

Nodosauridae indet.	Tooth in jaw fragment	Maastrichtian	Sânpetru, Romania	This paper
Nodosauridae indet.	Fragmentary limb elements, dorsal centrum, osteoderms	Maastrichtian	Vurpăr, Romania	This paper
Nodosauridae indet.	Osteoderms	Maastrichtian	Aude, southern France	Clottes & Raynaud, 1983; Pereda Suberbiola, 1993b
Nodosauridae indet.	Teeth	?Maastrichtian	Quintanilla del Coco, Spain	Pol et al., 1992
Nodosauridae indet.	Teeth	Late Cretaceous	Taveiro, Portugal	Antunes and Sigogneau-Russell, 1996
Nodosauridae indet.	Tooth	Maastrichtian	Fontllonga 6, Spain	Alvarez Sierra et al., 1994 ; Escaso et al., 2010


A
N
B
UKRAINE
HUNGARY
MOLDOVA R.
CLUJ-NAPOCA
2
1
SERBIA
BUCHAREST
BLACK SEA
BULGARIA
100 km
C
Valea Vinţului
Mihai Valley
Pârău lui Mihai
Vinţului Valley
F2
F1
Vurpăr
Mureş River
Câmpu Goblii
Vinţu de Jos
Goblii Valley
Mureş River
Pianu Valley
1 km
450
400
350
300
250
225
235
215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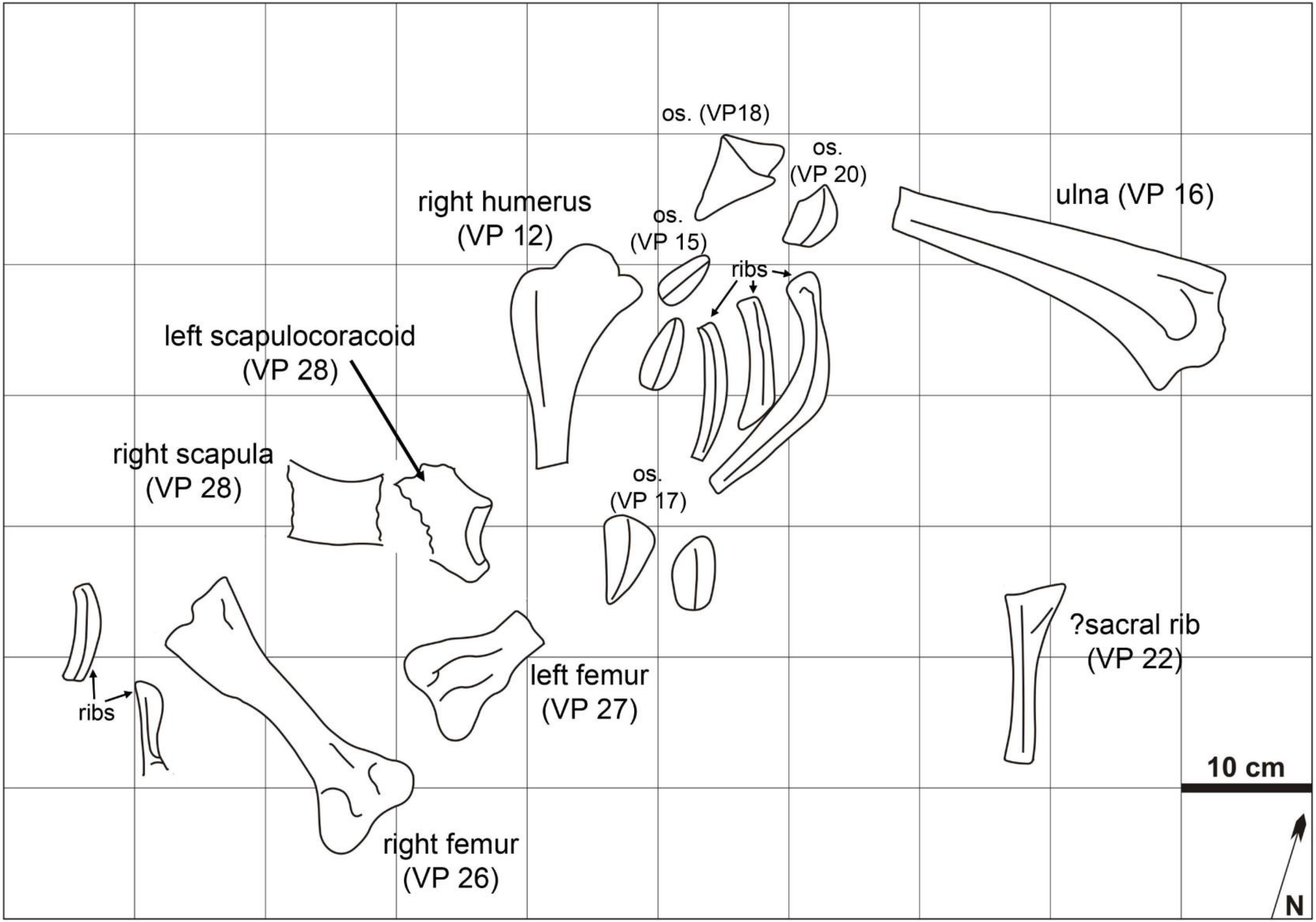
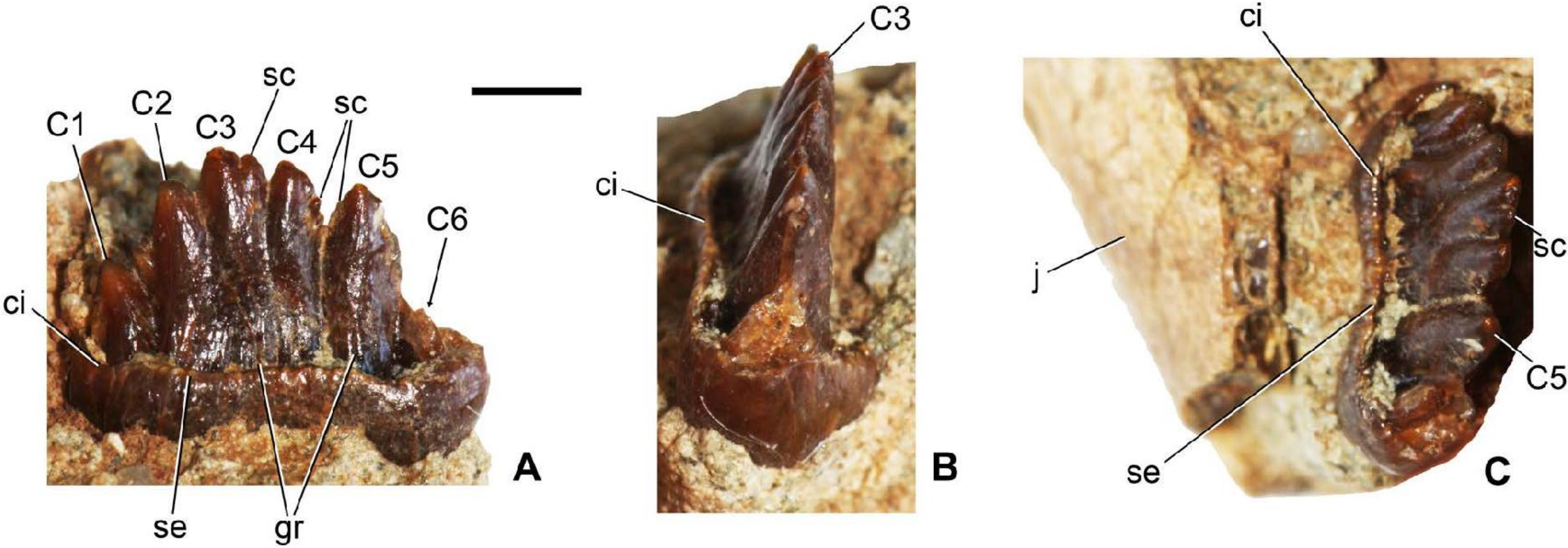
1m


os. (VP18)
os. (VP 20)
ulna (VP 16)
right humerus (VP 12)
os. (VP 15)
ribs
left scapulocoracoid (VP 28)
right scapula (VP 28)
os. (VP 17)
?sacral rib (VP 22)
left femur (VP 27)
ribs
right femur (VP 26)
10 cm
N


C1
C2
C3
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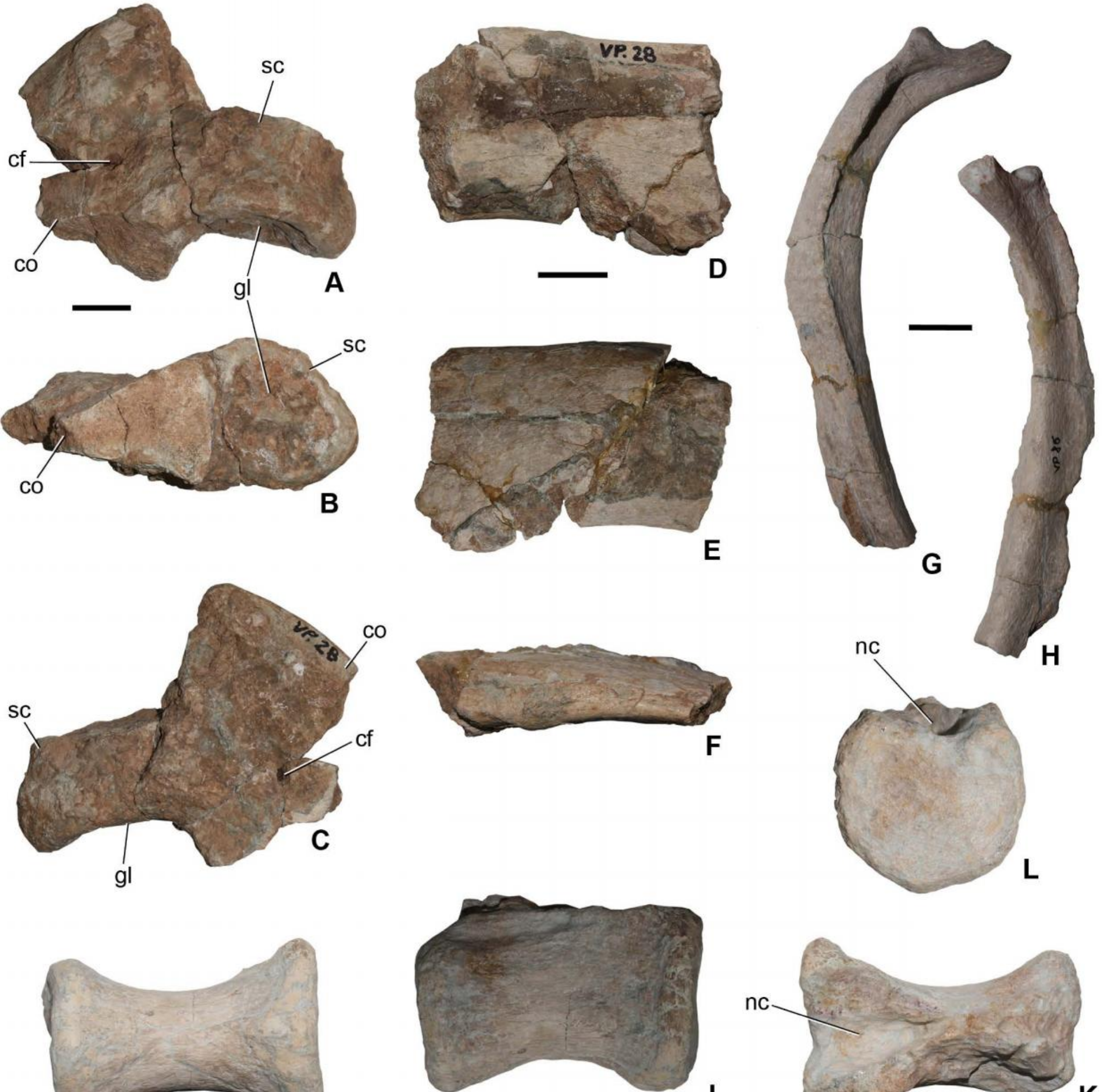
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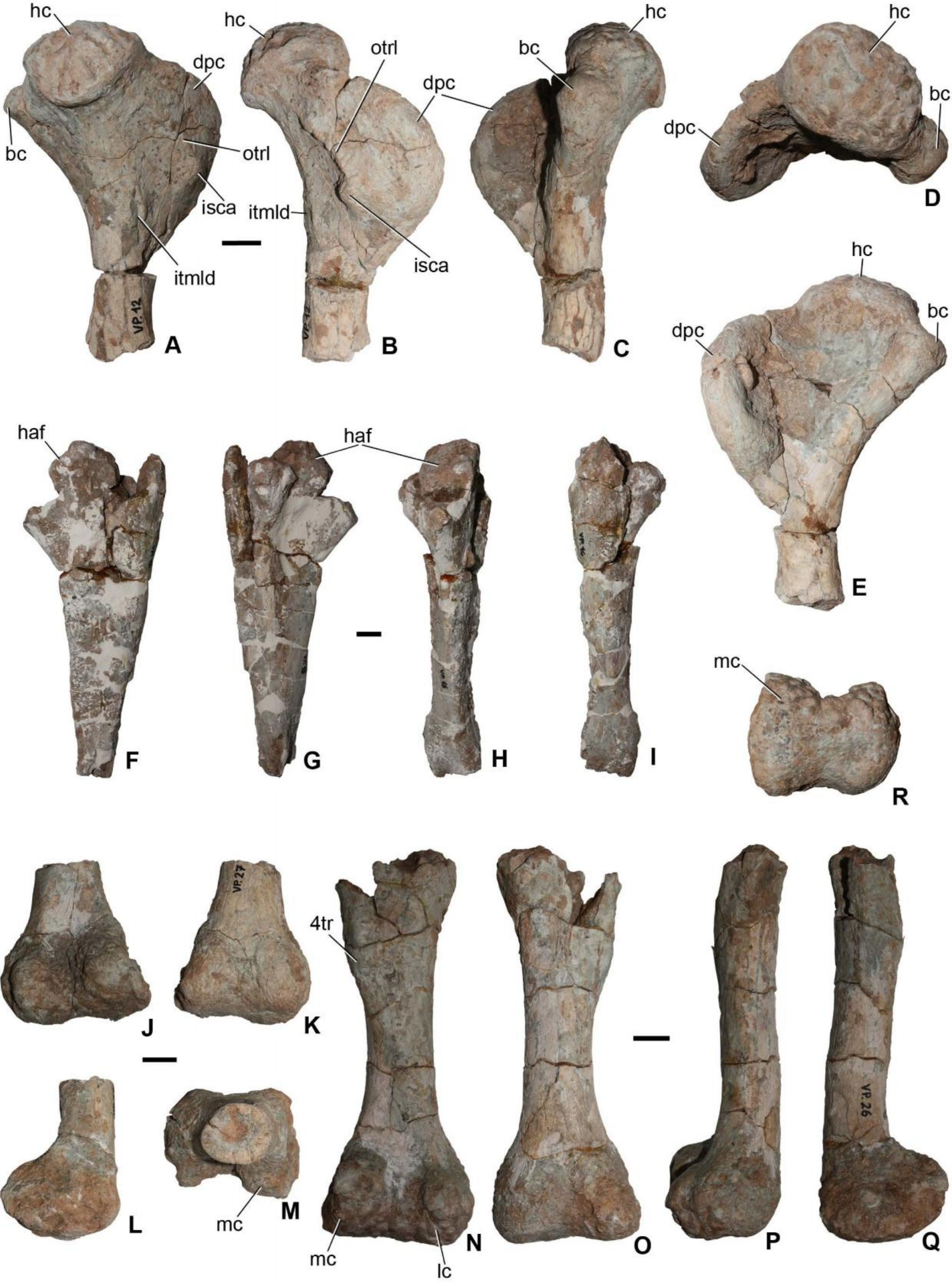
hc
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dpc
otrl
isca
itmld
VP.12
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hc
otrl
dpc
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isca
VP.12
B
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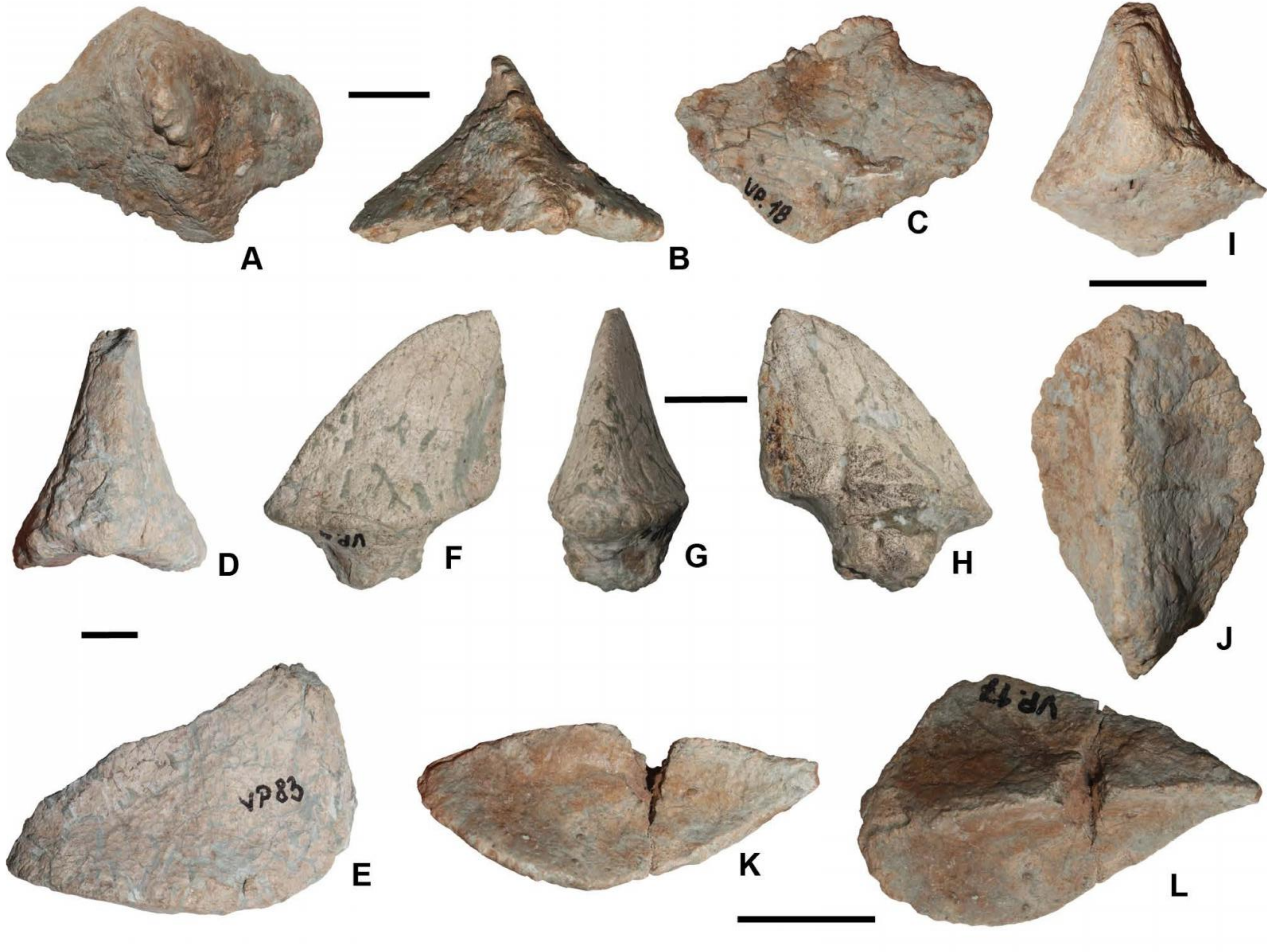
bc
dpc
C
hc
dpc
bc
D
hc
bc
dpc
E
haf
haf
F
G
VP.16
H
VP.16
I
mc
R
J
VP.27
K
L
mc
M
4tr
mc
lc
N
O
P
VP.26
Q


A
B
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D
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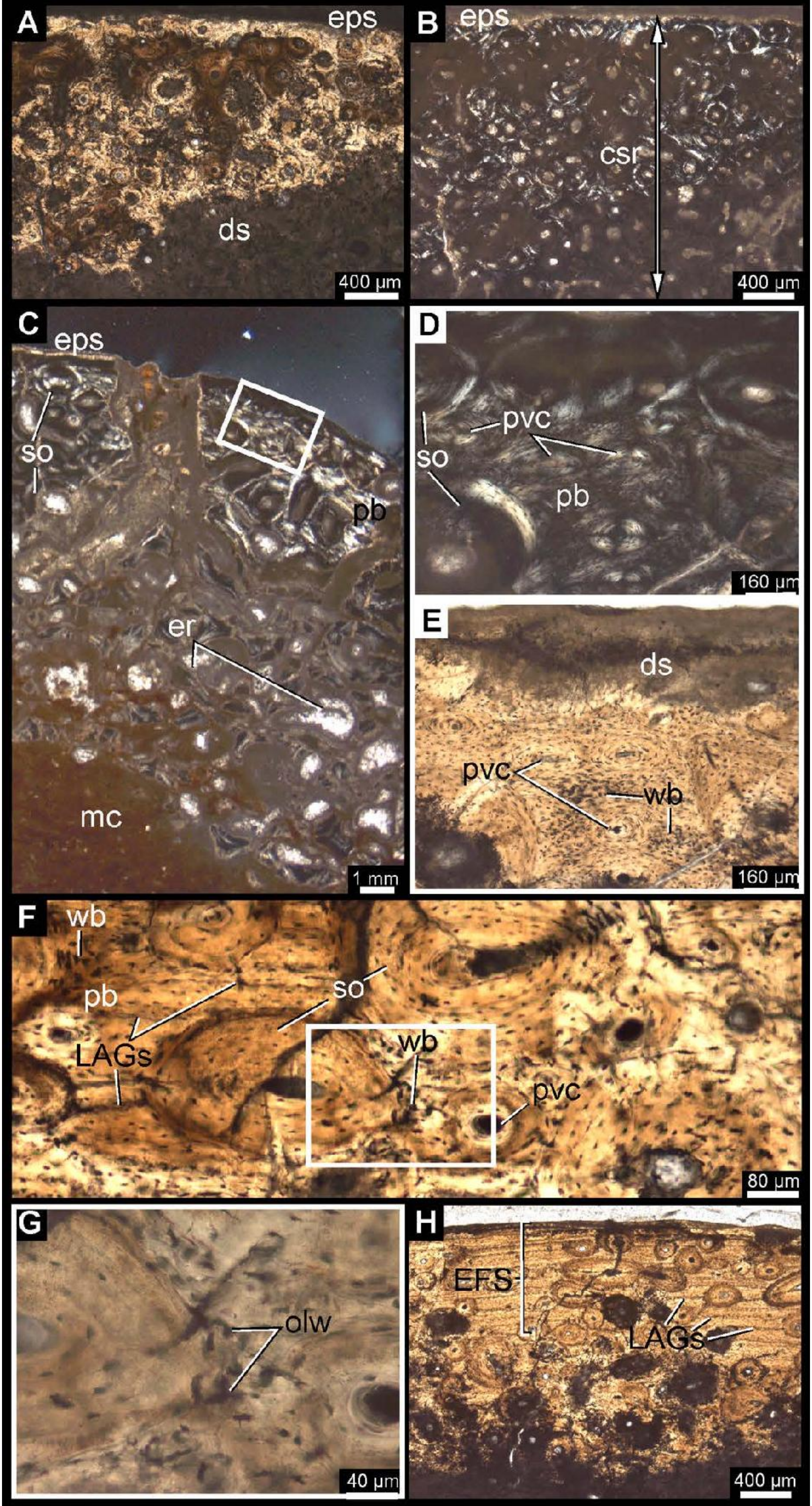
VP83
E
K
VP.17
L


A
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400 µm
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D
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160 µm
E
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pvc
wb
160 µm
F
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so
LAGs
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pvc
80 µm
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olw
40 µm
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EFS
LAGs
400 µm