

1 **Sympatry of two ankylosaurs (*Hungarosaurus* and cf. *Struthiosaurus*) in the Santonian**
2 **of Hungary**

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14 **Keywords:** *Hungarosaurus*, cf. *Struthiosaurus*, co-existence, Late Cretaceous, Hungary

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16 **Highlights:** We describe a complete ankylosaur humerus from the Santonian of Hungary. The

17 specimen is here referred to as cf. *Struthiosaurus*. It dates back the first occurrence of this

18 genus to the Santonian. It documents the sympatry of two ankylosaurs in Iharkút.

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24 **Abstract**

1 A complete and well preserved right ankylosaurian humerus from the Upper Cretaceous
2 (Santonian) Csehbánya Formation of Iharkút, western Hungary is described here. Based on its
3 osteological features and 21.5 cm adult length, the new specimen is markedly different from
4 the slender humerus of *Hungarosaurus*, the previously known ankylosaur from the locality,
5 and more similar to that of *Struthiosaurus*. Thus, the new Hungarian specimen is tentatively
6 assigned here to cf. *Struthiosaurus* thereby dating back the first occurrence of this genus to
7 the Santonian. The new fossil demonstrates the sympatric co-existence of two different
8 nodosaurid ankylosaurs (a smaller, robust form with 2–2.5 m total body length and a larger,
9 cursorial form with 4–4.5 m body length) in the Iharkút fauna. This also suggests that the
10 pattern of the European ankylosaur diversity was more complex than previously thought.

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12 **1. Introduction**

13 Ankylosaur remains from the Upper Cretaceous of Europe are relatively poorly known and up
14 to now only two valid genera have been identified. *Struthiosaurus* Bunzel, 1871 is widespread
15 in Europe, having been reported from several important continental vertebrate localities of
16 early Campanian–Maastrichtian age (e.g., Seeley, 1881; Nopcsa, 1929; Pereda-Suberbiola,
17 1992, 1999; Buffetaut et al., 1996; Garcia and Pereda-Suberbiola, 2003, Codrea et al., 2010).
18 Three currently valid species of this genus are known. In stratigraphical order, *S. austriacus*
19 Bunzel, 1871 was described from the lower Campanian Gosau beds of Austria based on some
20 cranial and mainly postcranial material of at least three individuals of different ontogenetic
21 stages (Pereda Suberbiola and Galton, 2001). Similarly aged, early Campanian *Struthiosaurus*
22 *languedocensis* Garcia and Pereda-Suberbiola, 2003 from Villeveyrac, southern France was
23 described on the basis of an articulated skeleton consisting of the pelvic girdle, synsacrum and
24 posterior dorsal vertebrae. The youngest species is *S. transylvanicus* Nopcsa, 1915 from the
25 Maastrichtian deposits of the Hațeg Basin, Romania that is known on the basis of most

1 probably associated cranial and postcranial material (Nopcsa, 1929). Additional ankylosaur
2 material referred to as *Struthiosaurus* sp. was described from the upper Campanian to lower
3 Maastrichtian of Laño (Pereda Suberbiola, 1999) and some unpublished ankylosaur material
4 is also known from the Campano-Maastrichtian of Chera in the Iberian Peninsula (J.
5 Company pers. comm.), and from the upper Campanian – lower Maastrichtian of Cruzy,
6 southern France (E. Buffetaut, 2005).

7 The other Late Cretaceous European ankylosaur genus, being almost double the size of
8 *Struthiosaurus* (total body length ca. 4.5 m), is *Hungarosaurus tormai* from the Santonian of
9 Iharkút, western Hungary (Ősi 2005; Ősi and Makádi, 2009). This taxon is known on the
10 basis of five published and one unpublished skeleton (a hip region, discovered in the summer
11 of 2012), the latter of which is the first articulated vertebrate specimen discovered in Iharkút.

12 *Acanthopholis horridus* Huxley, 1867 from the Cenomanian of England is regarded as a
13 nomen dubium (Pereda-Suberbiola and Barrett, 1999; Vickaryous et al., 2004).

14 New excavations at the Iharkút continental vertebrate site resulted in a complete and well-
15 preserved right humerus of an ankylosaur that is markedly different from that of

16 *Hungarosaurus* suggesting the co-occurrence of another ankylosaur taxon in the region. The
17 results of the comparative anatomical and histological investigation presented here clearly
18 support this hypothesis.

19 Institutional abbreviations: **AMNH**, American Museum of Natural History, New York, USA;

20 **MC**, Mechin Collection (private collection), Vitrolles, France; **MCNA**, Museo de Ciencias

21 Naturales de Alava; **MHN**, Muséum d'Histoire Naturelle d'Aix-en-Provence, Aix-en-

22 Provence, France; **MTM**, Magyar Természettudományi Múzeum, Budapest, Hungary;

23 **PIUW**, Paläontologisches Institut, University of Vienna, Vienna, Austria.

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25 **2. Materials and methods**

1 The specimen MTM PAL 2012.30.1, as all other fossils collected from the Iharkút vertebrate
2 site, is housed in the Hungarian Natural History Museum. Preparation of the specimen was
3 made mechanically by vibro-tool in the laboratory of the Hungarian Natural History Museum.
4 Histological investigation was carried out to determine the ontogenetic stage of the new
5 specimen in order to exclude the possibility that potential morphological differences reflect
6 ontogenetic allometries of *Hungarosaurus*. The humeral shaft was sampled on its anterior
7 surface, at the mid-diaphysis following the core drilling method described by Stein and
8 Sander (2009). The core sample has been embedded in epoxy resin and processed into
9 transverse thin section with standard methods (Wells, 1989). The obtained slide was studied
10 under a Leica DMLP polarized light microscope, photographed with Leica DFC420 digital
11 camera, and processed with Imagic ImageAccess software. Interpretative figures were
12 compiled using CorelDRAW X5, Corel PHOTO-PAINT and Photoshop 7.0 softwares.

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14 **3. Locality and geology**

15 Similarly to the remains of *Hungarosaurus*, MTM PAL 2012.30.1 was also collected from the
16 Santonian Csehbánya Formation exposed in the Iharkút open-pit mine close to the villages
17 Németsbánya and Bakonyjákó. The specimen was found approximately 200 m eastwards from
18 the classical outcrop of the Szál-6 vertebrate-bearing beds (for geological details see Ősi et
19 al., 2012a) that provided most of the *Hungarosaurus* bones, besides other remains. The
20 sediment containing this specimen (and other elements such as ankylosaur dermal scutes, ribs,
21 *Iharkutosuchus* mandible and tooth, and hundreds of turtle shell fragments) is a greyish, fine
22 sandstone–siltstone enclosing some carbonized plant fossils. Although the succession in this
23 new outcrop is quite similar to that seen in the Szál-6 outcrop, there is no direct evidence that
24 the fossiliferous bed of this new fossil site is stratigraphically equivalent (within the ca. 50 m
25 thick Csehbánya Formation) with those of the Szál-6 locality. Based on their stratigraphical

1 positions relative to the underlying Upper Triassic Main Dolomite, the fossiliferous bed of the
2 new outcrop is perhaps a few meters lower in position, thus probably slightly older than that
3 of the Szál-6 locality, but their age difference, if any, cannot be resolved.

4 5 **4. Description and comparisons**

6 The right humerus (MTM PAL 2012.30.1, Fig. 1A–E) is complete, only slightly compressed
7 anteroposteriorly and has a total length of 21.5 cm which is less than half the length of the
8 humerus of *Hungarosaurus* (45.5 cm, Fig. 1G). In general, the new specimen is much more
9 robust than the elongate and slender humerus of *Hungarosaurus* thereby being more
10 reminiscent of the humeri of other ankylosaurs (see e.g. that of *Sauropelta edwardsi* in
11 Carpenter et al., 1995 or that *Gastonia burgei* in Kirkland, 1998). Whereas the greatest width
12 to length ratio (width measured from the medialmost point of the bicipital crest to the
13 lateralmost point of the deltopectoral crest) of the new humerus is 0.55, this ratio is 0.4 in
14 *Hungarosaurus*, 0.52 in *Niobrarasaurus*, and 0.57 in *Sauropelta*. The shaft of the new
15 specimen shows great similarities with that of the right fragmentary humeri of *Struthiosaurus*
16 *austriacus* (PIUW 2349/18) and *Struthiosaurus* sp. (MCNA 6528) in having diverging
17 contours of the medial and lateral margins (Fig. 1H). Nevertheless, the lateral and especially
18 medial margins are more widely divergent in the new Iharkút specimen than those in *S.*
19 *austriacus*. The fragmentary specimen from Laño (MCNA 6528) appears to have a slightly
20 shorter, and lateromedially wider diaphysis (Pereda Suberbiola, 1999:fig. 5A) compared to
21 new Hungarian specimen.

22 Both the Hungarian and Austrian bones possess a prominent, approximately 2 cm long, oval-
23 shaped muscle scar on the posterior side of the proximal half of the shaft. A similar
24 pronounced muscle scar is also present on an unpublished, almost complete humerus (private
25 collection, MC 512) from the upper Campanian–lower Maastrichtian of Fox-Amphoux

1 Syncline of the Aix Basin, southern France (Fig. 1F). In MTM PAL 2012.30.1, this scar has
2 two distinct parts: the medial part is subcircular (proximodistal length ca. 16 mm), while the
3 lateral part is proximodistally elongated, ridge-like ending distally in a small but prominent
4 protuberance. Based on the reconstruction of Coombs (1978), this muscle scar or at least its
5 lateral part corresponds to the insertion area of *Musculus latissimus dorsi*. The medial part
6 may correspond to the insertion area of *Musculus teres major* (Fig. 1A). A similar, divided
7 muscle scar is present in *Ankylosaurus* (AMNH 5895). Coombs (1978) noted that in
8 *Sauropelta* and *Panoplosaurus*, this muscle scar is present but not divided suggesting a
9 common tendinous origin for *latissimus dorsi* and *teres major*. However, on the humerus of
10 AMNH 3035 of *Sauropelta*, the distally, laterodistally extended ridge of this muscle scar is
11 also present suggesting a divided attachment of *M. latissimus dorsi* and *M. teres major*. In *S.*
12 *austriacus*, though the bone is not complete, this muscle scar does not have the lateral ridge
13 (Fig. 1H) observed in the Hungarian specimen. This scar is oval-shaped on the unpublished
14 French specimen (MC512) and the lateral ridge, i.e. the possible separated insertion surface
15 for *latissimus dorsi*, cannot be seen. The muscle scar is entirely missing in *Hungarosaurus*
16 (Fig. 1G) and *Polacanthus* (NHM R1106).

17 The deltopectoral crest is relatively more developed than in *Hungarosaurus*, its dorsoventral
18 extent makes up half of the total bone length, and it projects strongly laterally and slightly
19 anteriorly. Its posterior surface is ornamented by several crests and ridges indicative of well-
20 developed muscles attaching here. Especially the insertion surface for *M. scapulothoracalis*
21 *anterior* could have been highly developed, which is indicated by the protuberance-like
22 muscle scar. In contrast to *Hungarosaurus* (Ősi and Makádi, 2009), the step-like demarcation
23 between the humeral head and the deltopectoral crest is as well developed as in
24 *Panoplosaurus* (Sternberg, 1921). The humeral head is displaced medial to the longitudinal
25 axis of the bone. It has a transversely wider, oval shape just as in *Hungarosaurus* but

1 narrower transversely than in *Sauropelta* (Ostrom, 1970) and *Niobrariasaurus* (Carpenter et
2 al., 1995). The bicipital crest is well developed with straight and posteriorly rugose medial
3 margin that has a pointed proximal end. Similarly to the condition present on the lateral side,
4 a marked but narrower demarcation separates the humeral head from the pointed
5 proximomedial end of the bicipital crest. As in most ankylosaurs (Vickaryous et al., 2004),
6 the distal epiphysis is strongly divergent and not as narrow as in *Hungarosaurus*. The lateral
7 and medial condyles are similar in size and a well-developed, rugose, crest-like ectepicondyle
8 is present lateral to the lateral condyle. The medial condyle is also bordered medially by a less
9 developed medial entepicondyle. Distally and anteriorly, the two condyles are separated by a
10 shallow groove.

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12 **5. Histology-based ontogenetic status**

13 The transverse thin section acquired from the mid-diaphyseal region of the humerus MTM
14 PAL 2012.30.1 shows strong pyritization due to which the microstructural preservation of this
15 element is very poor. Details of the structural organization, such as the original long-range
16 fiber orientation, cannot be inferred, nor are the osteocyte lacunae preserved. However, some
17 histological characters that are indispensable for assigning ontogenetic stage to the specimen
18 can still be observed. One of them is the extensive remodeling of the entire cortex by
19 numerous secondary osteons except for a thin layer of primary bone adjacent to the periosteal
20 surface (Fig. 2A, B). In this primary layer, the vascular canals are all longitudinal and of
21 narrow lumen, the latter of which refers to their well-compacted, mature state. The largest part
22 of this layer is devoid of secondary osteons and exhibits a feature of crucial importance: the
23 onset of an external fundamental system (EFS). In the incipient EFS, primary vascular canals
24 still occur but they are very sparse, and there is a number of closely packed lines of arrested
25 growth (LAGs) the spacing of which gets denser towards the periosteal surface (Fig. 2C). The

1 presence of an EFS is generally considered as the most reliable signal of the cessation of
2 diametrical bone growth. The onset of an EFS means that only negligible degree of bone
3 deposition, the so called residual bone growth could have happened even if the animal had
4 lived any longer. Hence, the onset of an EFS along with the extensive secondary remodeling
5 and the advanced state of infilling of the longitudinal primary vascular spaces all imply
6 skeletal maturity of this specimen. Thus, despite the bad preservation obscuring finer
7 microstructural details, it can be concluded with high confidence that the skeletal growth of
8 this individual had nearly ceased by the time of its death, i.e. this specimen can be considered
9 as a fully grown adult. The histological results unequivocally prove that this specimen is not
10 the juvenile form of *Hungarosaurus*, hence excluding the possibility that the prominent
11 morphological differences are the result of ontogenetic allometry.

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13 **6. Discussion**

14 Assessing the information on the new humerus (MTM PAL 2012.30.1) from Iharkút, it can be
15 concluded that it markedly differs from that of *Hungarosaurus*. In addition to its smaller size,
16 the shape and morphological details clearly indicate its different taxonomic status. The new
17 specimen is similar to the fragmentary humerus of *Struthiosaurus austriacus* (PIUW
18 2349/18), that of *Struthiosaurus* sp. from Laño (MCNA 6528), and the unpublished French
19 specimen (MC 512), though the latter is more robust and it possesses more divergent distal
20 epiphysis. Unfortunately, no published humerus is known in *S. languedocensis*, and only a
21 silhouette drawing of the humerus is available yet for a new, associated specimen of *S.*
22 *transylvanicus* (Codrea et al., 2010). The spherical radial condyle, present distally in MTM
23 PAL 2012.30.1, is typically seen in most nodosaurids (Pereda Suberbiola 1999, Vickaryous et
24 al. 2004) thus strengthening its supposed nodosaurid status. Due to their fragmentary nature,
25 neither diagnostic features nor a unique combination of characters have been described on any

1 humeri published and referred to as *Struthiosaurus* which are part of a fossil assemblage
2 including other skeletal elements (i.e. the type material of *S. austriacus* and the Laño
3 material). Thus, the Hungarian specimen cannot be assigned to *Struthiosaurus* with high
4 confidence. On the other hand, following parsimony, the only known Late Cretaceous
5 ankylosaur from Europe besides *Hungarosaurus* is *Struthiosaurus* the humerus of which,
6 although fragmentary, shows great similarities with the new Hungarian specimen, hence we
7 tentatively refer to this specimen as cf. *Struthiosaurus* sp.

8 Accepting the former hypothesis, the new humerus from the Santonian of Iharkút represents
9 the earliest occurrence of the genus thus extending its temporal range to encompass more than
10 17 million years (Santonian to Maastrichtian), (Fig. 3). Since the shaft of the Hungarian
11 specimen is similar to that of *S. austriacus* in being more gracile and elongate and not as
12 robust and divergent distally as that of the French specimen (MC 512), MTM PAL 2012.30.1
13 from Iharkút is likely to be more closely related to *S. austriacus* than to the western European
14 form. This close relationship of the Austrian and Hungarian faunas has already been
15 supported by other faunal elements such as the congeneric rhabdodontid taxa (*Mochlodon*
16 *suessi* in Austria and *M. vorosi* in Hungary, Ósi et al., 2012b) and the identical basal
17 Tetanurae teeth known from both sites (Ósi et al., 2010). Nevertheless, it has to be noted that
18 among the three species of *Struthiosaurus*, only the material referred to as *S. austriacus*
19 includes fragmentary humeri, thus comparison with that of *S. languedocensis* and *S.*
20 *transylvanicus* is not yet possible. Perhaps the new, still undescribed material from Romania
21 (Codrea et al., 2010) will help solve this problem, at least in the case of the latter species.
22 The new humerus from Iharkút unambiguously reveals the co-existence of two different
23 ankylosaurs in the Santonian of Iharkút (Fig. 3). The 21.5 cm long, fully grown adult humerus
24 (MTM PAL 2012.30.1) referred to as cf. *Struthiosaurus* sp. represents a typical, relatively
25 massive element as seen in most ankylosaurs. It also shows that similarly to the other species

1 of *Struthiosaurus*, the Hungarian taxon could also have been a small-bodied but robust form
2 with a body length of no more than 2–2.5 m. In contrast, *Hungarosaurus* with a gracile and
3 elongate humerus (45.5 cm) and a forelimb–hindlimb length ratio of 1.0 could have been
4 more cursorial with a total body length of 4–4.5 m (Ősi and Makádi, 2009). The different size,
5 body proportions and the supposed difference in locomotory abilities suggest different
6 lifestyles for the two, probably sympatric Iuharkút ankylosaurs.

7 The occurrence of two different ankylosaurs in the Santonian Hungarian fauna revives an
8 earlier hypothesis (e.g. Seeley 1881), namely that the ankylosaurs of European Late
9 Cretaceous faunas were more diverse than previously thought. One classic example of this
10 presumed diversity is the number of ankylosaur taxa represented in the early Campanian
11 Austrian fauna. Several authors tried to approach this question but were always confronted by
12 the lack of enough diagnostic skeletal elements. Seeley (1881) and later on Molnar (1980)
13 distinguished two different taxa on the basis of postcranial material, while Nopcsa (1929) and
14 more recently Pereda Suberbiola and Galton (2001) considered the ankylosaur material of the
15 Gosau beds as representing several (at least three) individuals of a single ankylosaurian
16 species. However, it has to be noted that, for example the scapulae used by Seeley (1881) to
17 distinguish the two different Austrian taxa are extremely similar to those of *Hungarosaurus*
18 (Ősi, 2005: fig. 11). This indicates that certain postcranial elements (e.g. scapula, dorsal and
19 caudal vertebrae, femur) might not be useful for making taxonomic inferences. Other
20 elements, such as the humerus, on the other hand are certainly useful to define taxonomic
21 differences. The Hungarian remains, representing two different, probably sympatric taxa,
22 may refresh the previous „high diversity”-hypotheses; nonetheless, discovery of more
23 material is instrumental in offering a better view on the ankylosaurian diversity of Europe.
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1 **Figure captions**

2 Figure 1. Ankylosaur humeri from the upper Cretaceous of Europe. A, *Struthiosaurus* sp.
 3 right humerus (MTM PAL 2012.30.1) from the Santonian Csehbánya Formation of Iharkút,
 4 western Hungary in posterior, B, anterior, C, lateral, D, medial, E, proximal views. F,
 5 Unpublished humerus (MC 512) from the upper Campanian–lower Maastrichtian of Fox-
 6 Amphoux Syncline of the Aix Basin, southern France in posterior view. G, Right humerus of
 7 *Hungarosaurus tormai* (MTM 2007.25.3) in posterior view. H, Right humerus of
 8 *Struthiosaurus austriacus* (PIUW 2349/18) in posterior view. Abbreviations: **bc**, bicipital
 9 crest; **dpc**, deltopectoral crest; **hc**, humeral condyle; **his**, place of histological sampling; **imld**,
 10 insertion area of *Musculus latissimus dorsi*; **imtm**, insertion area of *Musculus teres major*;
 11 **lec**, lateral ectepicondyle; **mec**, medial ectepicondyle; **pr**, protuberance in the insertion
 12 surface for *M. scapulohumeralis anterior*; **rac**, radial condyle; **ulc**, ulnar condyle.

13

14 Figure 2. Histology of the mid-diaphyseal cortex of the humerus (MTM PAL 2012.30.1) in
 15 transverse section. The most intact region of the slide (A) demonstrates the extensive
 16 remodeling throughout the cortex. The white and grey squares indicate the magnified areas
 17 (B) and (C), respectively. Histological abbreviations: **LAG**, lines of arrested growth; **oEFS**,
 18 onset of an external fundamental system; **pb**, primary bone; **pvc**, primary vascular canal; **so**,
 19 secondary osteon; **src**, secondary remodeled cortex.

20

21 Figure 3. Geographical distribution and temporal range of *Struthiosaurus* and *Hungarosaurus*
 22 in the Late Cretaceous of Europe. **AA**, Austroalpine block, **HI**, Hațeg Island. Basic map of R.
 23 Blakey (<http://www2.nau.edu>) modified.