The European ankylosaur record: a review

Attila Ősi¹,²

¹Eötvös University, Department of Palaeontology, Budapest, Hungary
²MTA–ELTE Lendület Dinosaur Research Group, Budapest, Hungary, Pázmány Péter sétány 1/c, 1117; hungaros@gmail.com

Keywords: Ankylosauria, late Middle Jurassic to Late Cretaceous, Struthiosaurinae, Europe

Abstract
Ankylosaur skeletal remains and tracks from the European Middle Jurassic to Upper Cretaceous are reviewed here. Whereas the Jurassic material assigned to four species are known mostly by isolated elements, the Early Cretaceous record is more complete, including better cranial material and some partial skeletons. Jurassic to Early Cretaceous material is known almost exclusively from western Europe. The first half of the Late Cretaceous begins with a 12 My long gap without any ankylosaur material from the continent (not counting the earliest Cenomanian, dubious ‘Acanthopholis’ material). The first systematically valuable Late Cretaceous assemblages are from the Santonian of Hungary. The Campano-Maastrichtian record is only represented by different species of Struthiosaurus both in the western and eastern parts of the European archipelago. Characters used to define the recently resurrected European clade Struthiosaurinae by Kirkland and colleagues are also reviewed.

Introduction
Although the earliest evidence of ankylosaurs in Europe goes back into the late Middle Jurassic (GALTON 1980a, 1983a) and their record extends up to the Maastrichtian (e.g. NOPCSA 1929, PEREDA-SUBERBIOLA 1993a, 1999, PEREDA-SUBERBIOLA et al. 1995, CODREA et al. 2002, GARCIA & PEREDA-SUBERBIOLA 2003, ŐSI et al. 2014a), remains of these quadruped, low-level browsers are sporadical and relatively poorly known from the continent. Most of the remains are associated, or in a few cases, articulated elements of the postcranium generally with the lack of associated cranial elements. Skull or mandibular bones, being the most important elements to clarify taxonomic assignment and systematic relationships, are in many cases either isolated specimens or non-overlapping, fragmentary remains making comparison highly questionable. Whereas the western European record is characterized by a wide temporal range (ca. 90 My, though not always continuously, Fig. 1), ankylosaur remains east from the River Rhein are known almost exclusively from Santonian to Maastrichtian deposits (ca. 20 My, but see JURCSÁK & KESSLER 1991). In addition, at least in the later part of record diversity is further biased by the endemic nature of continental vertebrate faunas, especially in eastern Europe, a phenomenon supported by dwarf, relict and sometimes quite unusual forms (BENTON et al. 2010, STEIN et al. 2010, ŐSI et al. 2012, 2014b, CSIKI-SAVA et al. 2015).

The aim of the present study is to give a brief overview of the European ankylosaur record, and, in the light of new discoveries and recent phylogenetic works, to present the affinities and some further anatomical comments on some taxa. Characters used to resurrect the European clade Struthiosaurinae (KIRKLAND et al. 2013) are also reviewed. Catalogue numbers of the different specimens are not listed in this paper, but can be found in the related papers cited either in the summary of an individual species or in Table 1.

The Jurassic record
Ankylosaur remains from Jurassic sediments of Europe are extremely rare and most of them are isolated bones (for a detailed overview see GALTON 1983a). Four different species have been identified, but a big problem is the almost complete lack of overlapping elements between these species, since only some osteoderms can be compared between Dracopelta zbyszewskii and Sarcolestes leedsi. Whereas CARPENTER (2001) regarded all of them as nomina dubia, VICKARYOUS et al. (2004) listed Sarcolestes and Dracopelta as Ankylosauria incertae sedis and Cryptodraco and Priodontognathus as nomina dubia.

**Sarcolestes leedsi**
The oldest representative of European ankylosaurs based on skeletal remains is Sarcolestes leedsi known by a fragmentary but well preserved left mandible from the Middle Callovian Lower Oxford Clay, England (LYDEKKER 1893, GALTON 1980a, 1983a, b, Fig. 2A).

According to THOMPSON et al. (2012) S. leedsi is certainly ankylosaurian in having a glenoid posteromedial to the mandibular adductor fossa (ch. 67), a closed mandibular fenestra (ch. 68), a sinuous ventral margin of dentary in lateral view (ch. 71), and an osteoderm on the lateral side of the postdental part of the mandible (ch. 91). Mandibular remains among the few Jurassic ankylosaurids are known in Gargoylesaurus parkinorum from the Kimmeridgian of Wyoming, USA (KILBOURNE & CARPENTER 2005) and Tianchiasaurus (DONG 1993) from the Middle Jurassic of China. Sarcolestes differs from Gargoylesaurus in having a ventrally more bent anterior part of the dentary and a medially more convex tooth row bordered labially by a wide shelf. On the other hand, the latter form has a relatively higher coronoid process indicating a relatively greater mass of external adductor muscles in this species.

Besides the holotype mandible, three osteoderms from the Middle Jurassic of England have been referred to Sarcolestes (GALTON 1983b, 1994). One of them, certainly a median element, was first interpreted as covering the frontoparietal region of the skull (GALTON 1983b:fig. 1I-N), that was later reinterpreted as a median osteoderm sitted somewhere along the vertebral column (GALTON 1994). The second osteoderm, being similar to the previous element, is also a median scute. Both of these scutes have at least one side with complex, concave margins (GALTON 1994:fig. 1B, D). Among ankylosaurs, median osteoderms (as a single unit without the median suture between two obviously fused elements as seen in some ankylosaurs or Edmontonia) are quite rare (for armour compositions see YOUNG 1935, COOMBS & MARYNSKA 1990, BLOWS 2001, FORD 2000, FORD & KIRKLAND 2001). Regarding nodosaurids, the Santonian Hungarosaurus from Hungary possesses a large and massive, boomerang-shaped osteoderm with concave posterior margin and two conical spikes (Fig. 3J) laterally on its dorsal surface (ŐSI 2005). This element should have been in a median position, perhaps in the sacral or anterior caudal region of the body (ŐSI & MAKÁDI 2009), since it was found together with the pelvic elements of the fourth skeleton of this species. A common feature of these median elements is that their lateral side ends in a narrow, slightly pointed, supposedly posterolaterally oriented part bordering the concave, posterior margin.

**Cryptodraco eumerus and Dracopelta zbyszewskii**

*Cryptodraco eumerus* (SEELEY 1869, LYDEKKER 1889) from the Middle Upper Oxfordian of England is known on the basis of a single right femur (GALTON 1980a, 1983a). Following THOMPSON et al. (2012) this femur is most similar to that of nodosaurid ankylosaurs in having a femoral head well separated from greater trochanter by a distinct notch (ch. 150). *Dracopelta zbyszewskii* from the Kimmeridgian of Portugal has been described on the basis of a partial rib cage with armour (GALTON 1980b, Fig. 2D). GALTON (1980b) pointed out that the wide variety in the form of individual osteoderms along the lateral side of the rib cage and the connecting or sometimes overlapping position of the osteoderms occur only in
ankylosaurs. In addition to this material, an articulated partial autopodium, probably a right manus with three digits have been assigned to the holotype and referred to D. zbyszewskii. The specimen is one of the few articulated autopodias of an ankylosaur, and indicates an autopodium morphology quite similar to those of later, more derived species (Pereda-Suberbiola et al. 2005).

Besides these Late Jurassic ankylosaurian remains, some osteoderms from the Kimmeridgian (DeLair 1973) and a caudal vertebra from the Tithonian of England (Casey 1963) have been referred to Ankylosauria indet (Galton 1983a).

**Priodontognathusphillipsii**

*Priodontognathus phillipsii* is known based on a left maxilla from the Upper Jurassic or Lower Cretaceous of England (Seeley 1875, Galton 1980c, 1983a, Fig. 2B, C). Its systematic position is highly controversial. Seeley (1869) described it originally as *Iguanodon phillipsii*, and later, under the name *P. phillipsii*, he referred it to stegosaurs (Seeley 1893). Ostrom (1970) concluded that it might be stegosaurian or ankylosaurian and Galton (1980c) referred it to ankylosaurs. More recent workers (e.g. Carpenter 2001a, Vickaryous et al. 2004) regarded it as nomen dubium. The features against its ankylosaurian affinity are as follows: 1) it lacks a rugose ornamentation on the lateral surface (ch. 77 of Thompson et al. 2012, Fig. 2B). [Attila! Eddig már több ch. xx sorszám szerepelt, de nem tudni, hogy honnét valók ezek a soszámok. Kirklandéi? Vagy ezek mind Thompson munkájára vonatkoznak, amelyre itt először történik említés?] although Galton (1980c) noted that most of the lateral surface had been eroded; 2) the buccal shelf is weakly developed only slightly overhanging the maxillary tooth row. In all ankylosaurs, including the Kimmeridgian *Gargoyleosaurus*, this shelf is well developed laterally, widely overhanging the relatively thin base of the maxillary tooth row. Whereas Galton (1980c) noted that the replacement teeth of *Priodontognathus* are similar to ankylosaurs in various aspects, Barrett (2001) concluded that they are rather unusual among ankylosaurs showing some similarities with those of *Scelidosaurus harrisonii*. Unfortunately, it is not clear, if the antorbital fenestra, clearly lacking in all ankylosaurs, is present on the specimen or the whole posterodorsal segment of the maxilla is for the articulation of the jugal and lacrimal. At present, it is ambiguous if *Priodontognathus* is an ankylosaurian or a basal thyreophoran, but the latter option is at least supported by the inset of the maxillary tooth row as synapomorphy of the group (ch. 25 of Thompson et al. 2012), even if it is not so pronounced.

**Ankylosaur tracks**

Accepting the Berriasian age of the ankylosaur track from the Purbeck beds in England (Ensom 1987, Lockley 1991, Lockley & Meyer 2000, McCrea et al. 2001), one possible occurrence of Jurassic ankylosaurs (or stegosaurs) tracks has to be mentioned from Aalenian-Bajocian of Yorkshire, England (McCrea et al. 2001). Named as *Deltapodus brodericki*, they have been originally described as sauropod tracks (Whyte & Romano 1994), but later on Lockley et al. (1994) referred them to as possible ankylosaurian. If this latter interpretation is correct than these prints record the earliest indication of ankylosaurs in Europe.

**Early Cretaceous record**

Compared to the Jurassic and Late Cretaceous assemblages, the Early Cretaceous record of ankylosaurs is more abundant and diverse including at least five valid species of four genera (according to Vickaryous et al. 2004). On the other hand, cranial elements definitely belonging to these species are poorly known. Whereas Carpenter (2001) referred *Hylaeosaurus* and the two species of *Polacanthus* (*P. foxii* and *P. rudgwickensis*) to Polacanthidae, later authors (Vickaryous et al. 2004) did not find support for this clade in
their phylogenetic analysis, and THOMPSON et al. (2012) referred these species, together with Anoplosaurus curtonotus, among nodosaurids. VICKARYOUS et al. (2004) regarded Hylaeosaurus and the two species of Polacanthus as Ankylosauria incertae sedis, and Anoplosaurus curtonotus as provisional Ankylosauria incertae sedis. The fifth Early Cretaceous species Europelta carbonensis, together with A. curtonotus and the Late Cretaceous forms (see below) has been assigned to Struthiosaurinae, a monophyletic clade of European nodosaurids (KIRKLAND et al. 2013). Besides the skeletal remains of ankylosaurs, trackways assigned to this group has to be also mentioned.

Hylaeosaurus armatus
The stratigraphically oldest species is Hylaeosaurus armatus from the Valanginian of England known by two partial skeletons including a great part of the postcranium and some poorly known skull elements (MANTELL 1833, 1841, OWEN 1858, PEREDA-SUBERBIOLA 1993b, CARPENTER 2001b), in addition to some referred isolated elements from western Europe (e.g. BARRETT 1996 and see PEREDA-SUBERBIOLA 1993b for an overview). Based on its holotype (Fig. 2E) and a referred specimen (BMNH 3789, MANTELL 1849) this species is the only European form with a partly articulated armour preserved in the presacral and caudal regions (articulated sacral armour is only known in Polacanthus foxii, see Fig. 2F). Isolated bones tentatively referred to Hylaeosaurus outside from England have been described from other western European localities as well. A distal humerus and a fragmentary elongated bone, being possibly a cervical spike, has been documented from the Valanginian of western Germany (SACHS & HORNUNG 2013). Some metapodia and a possible spike-like osteoderm from the Berriasian of Cornet, Romania (JURCSÁK & KESSLER 1991, POSMOSANU 2003) have been referred to Hylaeosaurus, but the remains are too fragmentary for a more precise taxonomic assignment and regarded here as cf. Ankylosauria indet. Nevertheless, if this material is truly ankylosaurian, then the are the only ankylosaurian bone elements prior to the Santonian in Central and East Europe.

Polacanthus foxii
Polacanthus foxii was a medium- to large-sized ankylosaur known from Barremian to Aptian deposits of England (mostly from the Wealden of the Isle of Wight, but other localities on the mainland as well) and Spain (OWEN 1865, HULKE 1882, 1888, BLOWS 1982, 1987, PEREDA-SUBERBIOLA 1994, NAISH & MARTILL 2001). The holotype specimen consists of a partial postcranium with dorsal vertebrae and ribs, synsacrum with pelvic region, numerous caudal vertebrae, hindlimb elements, ossified tendons, and dermal armour including the ossified sacral shield and various osteoderms with different morphology. Among the referred specimens a partial skeleton including some cranial elements, different parts of the vertebral column with a partial synsacrum, pelvic girdle remains and numerous elements of the dermal armour is the most complete one (BLOWS 1987). Besides these articulated/associated specimens, a fragmentary ilium with armour (type of Polacanthus becklesi HENNIG, 1924) and numerous isolated elements have been referred to this species (e.g. LEE 1843, DELAIR 1982, NOPCSA 1929, GASULLA et al. 2003, see PEREDA-SUBERBIOLA 1994 for an overview). Among the latter ones, a fragmentary basicranium from the Barremian of the Isle of Wight, described by NORMAN & FAIERS (1996), has to be mentioned (but see CARPENTER & KIRKLAND 1998). The only overlapping element between this specimen and the cranial remains described by BLOWS (1987) would be the supraoccipital. NORMAN & FAIERS (1996), however, could not identify this bone in the BLOWS collection and questioned the affinity of that specimen. Isolated teeth referred to Polacanthus are also known from Barremian deposits of the Isle of Wight (NAISH & MARTILL 2001: text-fig. 7.7). Since the type specimens does
not have teeth, the identity of these isolated teeth are only based on their similar stratigraphic occurrences.

Ankylosaurian remains referred to Polacanthus outside from England are known from different localities of Spain. SANZ (1983) reported a hollow-based, spike-like osteoderm from the Barremian to Aptian of Burgos, Spain. Two caudal spike-like osteoderms (PEREDA-SUBERBIOLA et al. 1999) and a more diverse material including dorsal vertebrae and ribs, a fragmentary sacrum and different types of osteoderms have been assigned to this genus (PEREDA-SUBERBIOLA et al. 2007). Specimens reported from France cannot be assigned to Polacanthus (PEREDA-SUBERBIOLA 1993b). The only cranial material referred to Polacanthus outside of England is two teeth described by CANUDO et al. (2004). The more complete specimen, however, clearly differs from the one illustrated by NAISH & MARTILL (2001) in the absence of a cingulum and the distal curvature of the crown, that might be related to taxonomic difference.


**Polacanthus rudgwickensis**

This recently erected species of Polacanthus is based on a fragmentary skeleton comprising two anterior dorsal vertebrae, several caudal fragments, a proximal end of the left scapula with a fragment of fused coracoid, distal end of a humerus, a nearly complete right tibia, rib fragments, and two osteoderms (BLOWS 1996). This species is only known from the Barremian of Sussex (unknown on the Isle of Wight, where *P. foxii* occurs) and is 30% larger than *P. foxii*. Additional, minor differences between the two species are in the morphology of the dorsal and caudal vertebrae, tibia, and presacral dermal spines (BLOWS 1996). Whereas the validity of this species has been accepted by most of the recent systematic workers (see e.g. CARPENTER 2001, VICKARYOUS et al. 2004, THOMPSON et al. 2012), its phylogenetic relationships remain controversial. CARPENTER (2001) listed it among polacanthids, VICKARYOUS et al. (2004) referred it with uncertain placement to Ankylosauria, and a more conventional analysis of THOMPSON et al. (2012) recovered it among nodosaurids, but not as the sister species *P. foxii*.

**Europelta carbonensis**

This recently described species is one of the most completely known ankylosaurs of Europe comprising two published (KIRKLAND et al. 2013) and three, additional, unpublished skeletons (LUIS ALCALÁ, pers. comm, 2014). The type specimen is composed of a partial skull (Fig. 21, L) and mandible, teeth, and most of the postcranium including a quite diverse collection of osteoderms. The paratype has no cranial but mandibular material, teeth and many elements from the postcranium. The forelimb is a poorly known region in both specimens preserving only the partial humeri (KIRKLAND et al. 2013: fig. 21). The early Albian Europelta carbonensis is of great importance, since it fills an almost unknown horizon in the late Early Cretaceous ankylosaur record. The only considerable ankylosaur material close to this period is Anoplosaurus curtonotus from the British late Albian (see below), and the possibly reworked and non-diagnostic ‘Acanthopolis material’ from the lowermost Cenomanian of Folkstone, England (PEREDA-SUBERBIOLA & BARRETT 1999).

**Anoplosaurus curtonotus**
This late Albian species from the ?Upper Gault Clay or ?Cambridge Greensand (RAWSON et al. 1978) of Cambridge, England is based on a partial skeleton including the anterior half of the left dentary with 13 alveoli (Fig. 2G, H), numerous centra from all regions of the vertebral column, dorsal ribs, a partial right scapula and both fragmentary coracoids, and various limb elements (SEELEY 1879, but see also NOPCSA 1923a, PEREDA-SUBERBIOLA & BARRETT 1999). A thyreophoran synapomorphy (SERENO 1986) recognized in the Anoplosaurus curtonotus material is the tooth row being sinuous in dorsal and lateral views. The shallow symphyseal ramus (less than half the maximum depth of the mandibular ramus in lateral view, THOMPSON et al. 2012, ch. 69) indicates an eurypod (stegosaurs and ankylosaurs) affinity. Although the phylogenetic analysis of THOMPSON et al. (2012) recovered A. curtonotus among nodosaurid ankylosaurs, none of their listed ankylosaurian or nodosaurid synapomorphic characters can be identified on the material. Nevertheless, the ventrally bending anterior end of the dentary with the first preserved alveolus very close to the symphysis, the ridge-like acromial process of scapula terminating in a knob-like eminence, and the shape and robustness of the humerus are all features suggesting its ankylosaurian affinity.

Ankylosaur tracks
Early Cretaceous footprints inferred to have been produced by ankylosaurs are known from several localities in Europe. ENSOM (1987) described ankylosaurian tracks from the Berriasian Purbeck beds of Yorkshire, England. The ankylosaurian affinity of these footprints have been supported by later authors (LOCKLEY 1991, LOCKLEY & MEYER 2000, MCCREA et al. 2001). One trackway from the Berriasian Wealden Beds of Germany, named as Metatetrapous valdensis, has been referred to ankylosaurs (NOPCSA 1923b, HAUBOLD 1971, McCREA et al. 2001, HORNUNG & REICH 2014). Various ankylosaur tracks have been reported from Lower Cretaceous carbonate deposits of Italy. Hauterivian–Barremian footprints are known from the Gargano Promontory in southern Italy (PETTI et al. 2008, SACCHI et al. 2009), and most recently a nice trackway, interpreted as ankylosaurian, has been documented from the lower Aptian shallow-marine carbonate deposits of Puglia, southern Italy (PETTI et al. 2010). Although ankylosaur skeletal remains are unknown from the central and southern parts of Europe, these footprints strongly indicate their presence in the Early Cretaceous western Tethyan archipelago.

The Late Cretaceous record
The Late Cretaceous ankylosaur record starts with a huge gap until the Santonian. The only ankylosaur material from the first half of the Late Cretaceous has been assigned to different species of Acanthopholis (for a review see PEREDA-SUBERBIOLA & BARRETT 1999). The type material of Acanthopholis horridus (Huxley 1867) was collected from the Albian-Cenomanian Cambridge Greensand of England (most probably lowermost Cenomanian, RAWSON et al. 1978) and composed of a fragmentary basicranium, three isolated teeth, a dorsal vertebra, and some osteoderms revised by PEREDA-SUBERBIOLA & BARRETT (1999). (HUXLEY listed some other elements as well, but the latter authors could not identify them). Later on, additional remains have been found and described (SEELEY 1869, 1879, LYDEKKER 1888), but their localities and their relationships to the type material and to each other are dubious. PEREDA-SUBERBIOLA & BARRETT (1999) concluded that all the five erected species of Acanthopolis are nomina dubia, since the material is fragmentary, non-diagnostic, and in some cases a composite of different species/individuals.
The Santonian to Maastrichtian ankylosaurian record is more complete including four different species referred to two genera. Material is not restricted to western Europe but relatively abundant in Central and East Europe as well.
Hungarosaurus tormai

Hungarosaurus tormai is the best known Late Cretaceous ankylosaur described on basis of numerous partial skeletons from the Santonian of western Hungary (Ősi 2005). For today, altogether nine partial skeletons (Fig. 3K) and hundreds of isolated cranial and postcranial elements can be referred to this medium-sized (estimated body length 4-4.5 m) ankylosaur species. Phylogenetic analysis recovered it as a basal nodosaurid closely related to the other European form Struthiosaurus (Ősi & Makádi 2009, Thompson et al. 2012). Hungarosaurus was quite unique among ankylosaurs in having gracile and elongate limb elements, a forelimb-hindlimb proportion of 1:1, a hypertrophied cerebellum, and paravertebral elements. These features let us to conclude that this Santonian form have had a sophisticated cerebral coordination of posture and movement and a more cursorial locomotory habit than predicted for other ankylosaurs (Ősi et al. 2014b). Furthermore, analysis of the wear pattern of the in situ mandibular teeth revealed a sophisticated tooth-tooth contact and a palinal jaw movement demonstrating a complex feeding mechanism of this nodosaurid (Ősi et al. 2014c).

Struthiosaurus austriacus

Struthiosaurus is the most wide-spread taxon of European ankylosaurs ranging from westernmost locality of Laño, Spain to the east of Haţeg Basin, Romania. Remains of this small- to medium-sized genus are known from Santonian to Maastrichtian deposits having one of the longest temporal distribution (ca. 17 My) of an ankylosaur genus (Ősi & Protiva 2013).

The earliest discoveries of Struthiosaurus were the remains of S. austriacus from the Lower Campanian of Muthmannsdorf, eastern Austria (Bunzel 1870, 1871, Seeley 1881, NOPCSA 1929, Pereda-Suberbiola & Galton 1992, 1994, 2001). Based on multiple scapulae, the Austrian material belongs to at least three different individuals representing at least two size categories (NOPCSA 1929, for a historical and taxonomic overview of this material see Pereda-Suberbiola & Galton 2001). Cranial elements are a small (probably subadult, Pereda-Suberbiola & Galton 1994) basicranium with partial skull roof (Fig. 3A) (plus an endocranial cast), the anterior half of a right dentary (Fig. 3B), a symphyseal end of a larger dentary, and a few teeth. The postcranial record is more abundant comprising cervical and dorsal vertebrae and ribs, pectoral (Fig. 3C) and pelvic elements, numerous elements of the fore- and hindlimbs, and various osteoderms including ossified cervical half rings (Fig. 3D) and conical spikes (Fig. 3E) with uncertain position. Vickaryous et al. (2004) tentatively assigned S. austriacus to the Nodosauridae based on the presence of a knob-like acromion. According to Thompson et al. (2012) the following unambiguous ankylosaurian synapomorphies can be found in this species: supratemporal fenestrae (most probably) closed (ch. 3), cranial sutures in adult specimens obliterated (ch. 17), cranial ornamentation from the elaboration of skull bones is present (ch. 77). The nodosaurid affinity is supported by the distinct notch between the femoral head and the greater trochanter (ch. 150) and by the domed parietal surface (ch. 31).

Struthiosaurus transylvanicus

Struthiosaurus transylvanicus is based on a fragmentary cranium (skull roof, occipital region, posterior and ventral parts of the orbital region, quadrates, plus an endocranial cast, Fig. 3G-I) and some additional postcranial bones (cervical dorsal and caudal vertebrae, ribs, fragmentary right scapulocoracoid, Fig. 3F) from the Maastrichtian of Haţeg Basin, Transylvania, Romania (NOPCSA 1915, 1929). Concerning the phylogenetic affinities of S. transylvanicus the same ankylosaurian and nodosaurid synapomorphies (except for ch. 150, see above) listed by Thompson et al. (2012) can be observed. On the other hand, two unambiguous
synapomorphies of Ankylosauria (presence of postorbital/squamosal and quadratojugal horns [ch. 84, 86, respectively]) are not present on the skull of *S. transylvanicus* suggesting the quite basal position of this species among nodosaurids. While some authors (PEREDA-SUBERBIOLA & GALTON 1994, PARISH 2005, THOMPSON et al. 2012) regarded *S. transylvanicus* potentially synonymous with *S. austriacus*, CARPENTER (2001) and VICKARYOUS et al. (2004) distinguished the two different species. The latter opinion might be supported by the highly anysochrone stratigraphic position of the two species. *S. austriacus* is ca. 13-15 My older (early Campanian) than *S. transylvanicus* and the two species existed on two different landmasses in the western Tethyan archipelago (see CSIKA-SAVA et al. 2015). Nevertheless, the most comprehensive study on the basis of osteological traits made by PEREDA-SUBERBIOLA & GALTON (1994) could not distinguish the two species from each other. Recently, some additional remains referred to *Struthiosaurus* has been published from the Upper Cretaceous of Transylvania including a tooth in a small jaw fragment (from the Haţeg Basin) and numerous postcranial elements (from the Transylvanian Basin) belonging to at least two individuals (ŐSI et al. 2014a). The affinity of the postcranial remains with *Struthiosaurus* was based on the morphology of the proximal half of a humerus being strongly similar to those described from various European localities (ŐSI & PRONDVAI 2013). A dorsal centrum and a fragmentary scapulocoracoid are the only overlapping elements with those of the type of *S. transylvanicus*, but the lack of diagnostic characters on these elements prevent their assignment to this species. The tooth was described as Nodosauridae indet. and shows significant differences compared to those of other ankylosaurs (including *S. austriacus*, *S. languedocensis* and *Hungarosaurus*) in having only six, more or less equally sized, apically pointed cusps separated by deep grooves and surrounded by a marked cingulum. The cusps frequently bear further secondary cusps or small cusplets mesiodistally. This tooth is most similar to one isolated tooth published by CODREA et al. (2002) These two teeth suggest, that in the aspect of tooth morphology, at least some of the Haţeg nodosaurids were different from other European members of the clade not only at species but perhaps also at generic level. Besides these assemblages of *Struthiosaurus*, a complete, well-preserved humerus referred to cf. *Struthiosaurus* sp. has been described from the Santonian of Iharkút, western Hungary providing the first evidence for two sympatric ankylosaurs (*Hungarosaurus*, *Struthiosaurus*) in a European continental fauna (ŐSI & PRONDVAI 2013). In addition various other bones from Iharkút, including a partial hip region, might be referable to *Struthiosaurus*. Work on this material is in progress that hopefully will help in clarifying the specific diversity of *Struthiosaurus* in Central Europe.

*Struthiosaurus* languedocensis

The most recently described species of *Struthiosaurus* is *S. languedocensis* from the lower Campanian of southern France (GARCIA & PEREDA-SUBERBIOLA 2003). It is based on an articulated hip region including the sacrum and most of the pelvic elements, three teeth, four posterior dorsal and one caudal vertebrae and three osteoderms. The main problem in distinguishing this species from the other *Struthiosaurus* species is that the overlapping parts are only the dorsal vertebrae and ribs, the ilium and ischium. In their differential diagnosis GARCIA & PEREDA-SUBERBIOLA (2003) concluded that *S. languedocensis* differs from *S. austriacus* by its robust, parallel-sized ischium that ends distally in a blunt knob. However, the ischium described from the Austrian material was only tentatively identified as this element, and its proximal and distal ends are missing (PEREDA-SUBERBIOLA & GALTON 2001). So, at present, I see that the *S. languedocensis* cannot be unambiguously distinguished from *S. austriacus* or from *S. transylvanicus*. Hopefully, new material helps to clarify this problem.
Besides the discovery of the third *Struthiosaurus* species, various other ankylosaurian material from Campano-Maastrichtian sediments in northern Spain (ASTIBIA et al., 1990; PEREDA-SUBERBIOLA 1993a, 1999, PEREDA-SUBERBIOLA et al. 1995, GARCIA & PEREDA-SUBERBIOLA 2003) and southern France (BUFFETAUT & LE LOEUFF 1991, LE LOEUFF 1991, PEREDA-SUBERBIOLA 1993c) supported the presence of *Struthiosaurus* in western Europe (see Table 1).

Ankylosaur tracks
Isolated Upper Cretaceous ankylosaur tracks have been reported from the Turonian-Coniacian of Altamura, Italy (DAL SASSO 2003, PETTI 2006) suggesting the presence of ankylosaurs in the pre-Santonian Late Cretaceous European archipelago.

The European clade Struthiosaurinae
NOPCSA (1923a) discussed the affinities of *Acanthopolis*, and in an other paper (NOPCSA 1923b:126) he proposed the subfamilies Struthiosaurinae and Ankylosaurinae under the family of Acanthopolidae without any comment. COOMBS (1978) rejected the previously proposed subfamilies and accepted two clades within Ankylosauria: Ankylosauridae and Nodosauridae. KIRKLAND et al. (2013) recognized many similarities among some of the Cretaceous European ankylosaurs and united *Europelta, Anoplosaurus, Hungarosaurus* and all species assigned to *Struthiosaurus* into the clade Struthiosaurinae. They defined the clade by the following characters to which my comments are as follows:
1) Narrow predentary. Although the predentary is unknown in all of these forms, the symphyseal end of the dentary is preserved in all of these genera with a quite short, edentulous part accepting the concave articular surface of the predentary. In *Anoplosaurus* the very end of the dentary is missing, but the position of the first alveolus suggests a short (if any) edentulous part. On the other hand, a relatively short edentulous part (the length of 4-5 alveoli as in *Hungarosaurus* and *Europelta*) anterior to the first alveolus can be observed in other basal ankylosaurs (e.g. *Sauropelta, Gargoylesaurus, Sarcolestes*) as well.
2) A nearly horizontal, unfused quadrate that is oriented less than 30° from the skull roof. This is not clear. The quadrate of *Europelta* is not nearly horizontal but according to the skull reconstruction of KIRKLAND et al. (2013) it is obliquely positioned (ca. 30-40° relative to the vertical plane) as in many ankylosaurs (e.g. *Pawpawsaurus, Edmontonia*). The quadrate-paraoccipital-squamosal contact can be observed only in *Europelta* (unfused) and in *Struthiosaurus transylvanicus* (the right one preserved, appears to be fused to me, Fig. 3G). 3) Mandibular condyles that are 3 times transversely wider than long. While this is true in *Europelta*, in *Struthiosaurus austriacus* and *S. transylvanicus* the distal quadrate condyles are only two times wider mediolaterally than long anteroposteriorly, in *Hungarosaurus* this ratio is 1.3 (ŐSI 2005, fig:5C, D). Similar ratio (ca. 1.5-2.0) can be observed in various other nodosaurid ankylosaurs (e.g. *Pawpawsaurus, Edmontonia, Panoplosaurus*).
4) Premaxillary teeth and dentary teeth that are near the predentary symphysis. Direct evidence for premaxillay teeth are known only in *Hungarosaurus*. Caution is needed when concluding premaxillary teeth simply on the basis of the presence of dentary teeth close to the symphysis, since, for example, in the right dentary of *Edmontonia* (TMP 98.98.01 housed in the Royal Tyrell Museum, Alberta, Canada) there are no upper teeth opposite to the anteriormost dentary teeth (even if they are worn).
5) Dorsally arched sacrum. The synsacrum is known only in *Europelta, S. languedocensis* (plus one specimen referred to *Struthiosaurus* sp. by GARCIA & PEREDA-SUBERBIOLA 2003) and in *Hungarosaurus*. In *Anoplosaurus* the sacrum is composed of unfused vertebrae suggesting its subadult ontogenetic status. A slightly dorsally arched synsacrum indeed
present in *Struthiosaurus* and *Hungarosaurus* (as probably in most ankylosaurs) but this is similar to that of the type of *Polacanthus foxii* (Pereda-Suberbiola 1994). The strongly arched posterior segment of the sacrum of *Europelta* appears to be rather an autapomorphy of this genus.

6) An acromion process dorsal to midpoint of the scapula-coracoid suture. This feature cannot be seen in *Europelta* and *S. languedocensis*. In *Anoplosaurus* the acromion process is rather posterodorsal to midpoint of the scapula-coracoid suture. Similar dorsal or slightly posterodorsal position of this process can be seen in *Panoplosaurus* (Russell 1940) as well.

7) Straight ischium, with a straight dorsal margin. The ischium is unknown in *Anoplosaurus* and *S. transylvanicus*. It seems to me that the dorsal side of the ischium of *Europelta* (Kirkland et al. 2013, fig. 23D, H) is not straight but convex and the distal end of the bone is curved ventrally and seems to be not complete, so this character appears to be ambiguous.

8) Relatively long slender limbs. Limb elements of the species referred to Struthiosaurinae are poorly known. The only form with complete fore- and hindlimbs is *Hungarosaurus* where the elongate and gracile limb bones are clearly present. Among the *Struthiosaurus* species, only *S. austriacus* has comparable limb elements. Whereas the femur is relatively slender, compared to *Polacanthus* or *Sauroptela* (Pereda-Suberbiola & Barrett 1999), the humerus is quite short and massive (Ósi & Pronvai 2013) as seen also in *Europelta* (Kirkland et al. 2013:fig. 21E-H) suggesting that at least the forelimb of *S. austriacus* was not really long and slender but rather short, though the lower arm bones are not preserved.

9) A sacral shield of armor. Except for *Europelta* and probably *Struthiosaurus* sp. from Lano, Spain (Pereda-Suberbiola 1999), there is no evidence for this type of armor among the type material of struthiosaurine forms. Actually this armour type is not the typical sacral shield as seen in some basal nodosaurids (polacanthids of Ford 2000), but a complex of coossified polygons (category 3 of Arbour et al. 2011) with large, subequal-sized osteoderms that are tightly sutured together. Similar blocks of coossified, subequal-sized osteoderms are known in an unpublished specimen of a nodosaurid ankylosaur from the Santonian of Iharkút, but still it is not clear if it belongs to *Hungarosaurus* or *Struthiosaurus*. This kind of sacral armour is present in many other forms including *Aletopelta* (Ford & Kirkland 2001), *Stegopelta* (Burns 2008), or *Glyptodontopelta* (Ford 2000).

10) Erect pelvic osteoderms with flat bases. Since there is no articulated pelvic armor in any of the taxa referred to this clade, it is quite questionable to use this feature as a diagnostic character. A flat-based, massive, and bomerang-shaped osteoderm with the bases of two conical spikes have been found associated with one of the referred skeletons of *Hungarosaurus*. Ósi & Makádi (2009) suggested this element to be dorsal to the posterior part of the sacrum but its exact position is still unknown.

Assuming the review of the struthiosaurine characters listed by Kirkland et al. (2013), in my opinion, it is problematic to unite these European species based on these osteological features. At present I cannot accept any of these characters with high confidence to define this clade. Using these characters as a combination of traits might be useful, but the problem is that in case of many characters they are either not preserved or ambiguous due to preservational biases.

**Conclusions**

Review of the European ankylosaur record indicates that remains until the Valanginian are quite sporadical and some of these fossils are hard to be referred to Ankylosauria. *Hylaeosaurus* is the earliest ankylosaur with enough diagnostic material to conclude phylogenetic relationships. *Europelta carbonensis* from the Spanish late Albian appears to be a key species of nodosaurid ankylosaurs that can be a kind of missing link between the older and more basal ”polacanthine” and the later more derived ”struthiosaurine” forms. It seems
very probable that European ankylosaurs, at least the Late Cretaceous forms, were members of a monophyletic clade (namely the Struthiosaurinae) originating from a common ancestor existed already in the early Cretaceous. This is supported by the close relationship of *Struthiosaurus* and *Hungarosaurus* (OSI & MAKÁDI 2009, THOMPSON et al. 2012), the only two genera from the second half of the European Late Cretaceous. However, chronostratigraphically the closest taxon with enough good material is *Europelta* being at least 25 My older than *Hungarosaurus* and *Struthiosaurus*

Acknowledgements
This work is dedicated to Prof. Dr. BARNABÁS GÉCZY for his 90th birthday, as a full member of the Hungarian Academy of Sciences, former Head of the Department of Palaeontology of the Eötvös University. Among others, his grandiose work and support helped the author in many cases to reveal the secrets of Hungarian dinosaurs.

The author wishes to thank ZSÓFIA HAJDU (MTA–ELTE Lendület Dinosaur Research Group, Budapest) for her generous help in making the basic figures and the reference list. PETER M. GALTON (University of Bridgeport, Bridgeport, USA), XABIER PEREDA-SUVERBIOLA (Universidad del País Vasco, Bilbao, Spain), and MÁRTON SZABÓ (Hungarian Natural History Museum, Budapest) are thanked for sending pictures on different ankylosaur taxa used in this paper.

This research was supported by the MTA–ELTE Lendület Dinosaur Research Group (Grant no. 95102), Hungarian Scientific Research Fund (OTKA T–38045, PD 73021, NF 84193), Hungarian Natural History Museum and the Eötvös Loránd University.

References


COOMBS, W. P. 1978: The families of the ornithischian dinosaur, Order Ankylosauria. – Palaeontology 21/1, 143-170.


DAL SASSO, C. 2003: Dinosaurs of Italy. – Comptes Rendus Palevol 2/1, 45-66.


DONG, Z. 1993: An ankylosaur (ornithischian dinosaur) from the Middle Jurassic of the Junggar Basin, China. – Vertebrata Palasiatica 10/31/4, 257-266.


GALTON, P. M. 1980c: Priodontognathus philipsii (Seeley), an ankylosaurian dinosaur from the Upper Jurassic (or possibly Lower Cretaceous) of England. – Neues Jahrbuch für Geologie und Paläontologie Monatshefte 8, 477-489.

GALTON, P. M. 1983a: Armored dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of Europe. – Palaeontographica Abteilung A 182/1-3, 1-25.


GALTON, P. M. 1994: Dermal scutes of Sarcolestes, an ankylosaurian dinosaur from the Middle Jurassic of England. – Neues Jahrbuch Für Geologie und Palaontologie Monatshefte 12, 726-732.


Nopcsa, F. 1929: Dinosaurierreste aus Siebenbürgen. – V. Geologica Hungarica (Paleontologia) 4, 1–76.


Ösi, A., Pereda-Suberbiola, X. & Földes, T. 2014b: Partial skull and endocranial cast of the ankylosaurian dinosaur Hungarosaurus from the Late Cretaceous of Hungary: implications for locomotion. – Palaeontologia Electronica 17/1, 1A, 18p.


and mammals from the Late Cretaceous new locality Quintanilla del Coco (Burgos Province, Spain). – Neues Jahrbuch für Geologie und Paläontologie Abhandlung 184, 279–314.


RUSSELL, L. S. 1940: Edmontonia rugosidens (Gilmore), an armored dinosaur from the Belly River Series of Alberta. – University of Toronto Studies, Geology Series 43, 3-27.


**Figure captions**

Figure 1. Chronostratigraphic distribution of the European ankylosaur taxa in western and eastern Europe.


Table 1. Ankylosaur remains from Europe listed in chronostratigraphical order.

<table>
<thead>
<tr>
<th>Name</th>
<th>Material</th>
<th>Age</th>
<th>Locality</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sarcolestes leedsi</em></td>
<td>fragmentary left mandible</td>
<td>Middle Callovian</td>
<td>Fletton, England</td>
<td>LYDEKKER 1893, GALTON 1980a, 1983a, b, 1994</td>
</tr>
<tr>
<td><em>Cryptodraco eumerus</em></td>
<td>right femur</td>
<td>Middle-Upper Oxfordian</td>
<td>Great Gransden, England</td>
<td>(SEELEY 1869, LYDEKKER 1889, GALTON 1980a, 1983a</td>
</tr>
<tr>
<td><em>Dracopelta zbyszewskii</em></td>
<td>partial rib cage with armour, an articulated partial autopodium</td>
<td>Kimmeridgian</td>
<td>Ribomar, Portugal</td>
<td>GALTON 1980b, 1983a, PEREDA-SUBERBIOLA et al. 2005</td>
</tr>
<tr>
<td>Ankylosauria indet.</td>
<td>caudal vertebra</td>
<td>Tithonian</td>
<td>Weymouth, Dorset, England</td>
<td>CASEY 1963, GALTON 1983a</td>
</tr>
<tr>
<td><em>Priodontognathus phillipsii</em></td>
<td>left maxilla</td>
<td>Upper Jurassic or Lower Cretaceous</td>
<td>Yorkshire or Sussex, England</td>
<td>SEELEY 1875, GALTON 1980c, 1983a</td>
</tr>
<tr>
<td>?Ankylosauria indet.</td>
<td>tooth</td>
<td>Upper Jurassic or Lower Cretaceous</td>
<td>Lulworth, Dorsetshire, England</td>
<td>GALTON 1980a, 1983a</td>
</tr>
<tr>
<td>Ankylosauria indet.</td>
<td>metapodia and a possible spike-like osteoderm</td>
<td>Berriasian</td>
<td>Cornet, Romania</td>
<td>JURCSÁK and KESSLER 1991, POSMOSANU 2003</td>
</tr>
<tr>
<td><em>Metatetrapous valdensis</em></td>
<td>trackway</td>
<td>Berriasian</td>
<td>Bückeburg, northwestern Germany</td>
<td>NOPCSA 1923b, HAUBOLD 1971, MCCREA et al. 2001, HORNUNG and REICH 2014</td>
</tr>
<tr>
<td><em>Hylaeosaurus armatus</em></td>
<td>two partial skeletons with postcranium and some poorly known skull elements, additional isolated elements</td>
<td>Valanginian</td>
<td>England</td>
<td>MANTELL 1833, 1841, 1849, OWEN 1858, PEREDA-SUBERBIOLA 1993b, BARRETT 1996, CARPENTER 2001b</td>
</tr>
<tr>
<td><em>Hylaeosaurus</em> sp.</td>
<td>isolated postcranial elements</td>
<td>Valanginian</td>
<td>Western Germany</td>
<td>SACHS and HORNUNG 2013</td>
</tr>
<tr>
<td><em>Polacanthus rudgwickensis</em></td>
<td>partial skeleton with postcranium</td>
<td>Barremian</td>
<td>Sussex, England</td>
<td>BLOWS 1996</td>
</tr>
<tr>
<td>Genus</td>
<td>Group</td>
<td>Age</td>
<td>Locality</td>
<td>Reference</td>
</tr>
<tr>
<td>--------------------------</td>
<td>------------------------</td>
<td>--------------</td>
<td>-------------------------------</td>
<td>----------------------------</td>
</tr>
<tr>
<td>cf. <em>Polacanthus</em> sp.</td>
<td>fragmentary basicranium</td>
<td>Barremian</td>
<td>Isle of Wight, England</td>
<td>NORMAN and FAIERS 1996</td>
</tr>
<tr>
<td>Ankylosauria indet.</td>
<td>trackway</td>
<td>early Aptian</td>
<td>Puglia, Italy</td>
<td>PETTI et al. 2010</td>
</tr>
<tr>
<td><em>Europelta carbonensis</em></td>
<td>two partial skeletons</td>
<td>early Albian</td>
<td>Ariño, Teruel Province, Spain</td>
<td>KIRKLAND et al. 2013</td>
</tr>
<tr>
<td></td>
<td>with partial skull</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>and postcranium</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Anoplosaurus curtonotus</em></td>
<td>partial skeleton with</td>
<td>late Albian</td>
<td>Cambridge, England</td>
<td>SEELEY 1879, NOPCSA 1923a,</td>
</tr>
<tr>
<td></td>
<td>fragmentary dentary</td>
<td></td>
<td></td>
<td>PEREDA-SUBERBIOLA and</td>
</tr>
<tr>
<td></td>
<td>and postcranium</td>
<td></td>
<td></td>
<td>BARRETT 1999</td>
</tr>
<tr>
<td>Ankylosauria indet.</td>
<td>fragmentary basicranium, three teeth, fragmentary postcranial elements</td>
<td>lowermost Cenomanian</td>
<td>Folkestone, Kent, England</td>
<td>HUXLEY 1867, SEELEY 1869, 1879, LYDEKKER 1888, PEREDA-SUBERBIOLA and BARRETT 1999</td>
</tr>
<tr>
<td>the ’Acanthopilis material’</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hungarosaurus tormai</td>
<td>Nine partial skeletons and hundreds of isolated elements including both cranial and postcranial material</td>
<td>Santonian</td>
<td>Iharkút, western Hungary</td>
<td>ÖSI 2005, ÖSI and MAKADI 2009, ÖSI et al. 2014b, c</td>
</tr>
<tr>
<td>cf. <em>Struthiosaurus</em> sp.</td>
<td>humerus</td>
<td>Santonian</td>
<td>Iharkút, western Hungary</td>
<td>ÖSI and PRONDVAI 2013</td>
</tr>
<tr>
<td><em>Struthiosaurus australicus</em></td>
<td>Fragmentary basicranium and other cranial elements, dentary teeth, postcranial material of more than one individual</td>
<td>Early Campanian</td>
<td>Muthmannsdorf, eastern Austria</td>
<td>BUNZEL 1870, 1871, SEELEY 1881, PEREDA-SUBERBIOLA and GALTON 1992, 1994, 2001</td>
</tr>
<tr>
<td><em>Struthiosaurus languedocensis</em></td>
<td>Articulated sacral region including synsacrum and hip elements</td>
<td>?Early Campanian</td>
<td>Villeveyrac, southern France</td>
<td>GARCIA and PEREDA-SUBERBIOLA 20031</td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>Osteoderms</td>
<td>Campanian</td>
<td>Hérault, southern France</td>
<td>LE LEOUFF 1992, PEREDA-SUBERBIOLA 1993c</td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>Osteoderm Cranial and postcranial remains (most of them still unpublished)</td>
<td>Campanian</td>
<td>Chera, Spain</td>
<td>SANZ 1986, COMPANY 2004</td>
</tr>
<tr>
<td>cf. <em>Struthiosaurus</em> sp.</td>
<td>Cervical neural arch, two osteoderms</td>
<td>Late Campanian</td>
<td>Hérault, southern France</td>
<td>PEREDA-SUBERBIOLA 1993c</td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>teeth, rib fragment,</td>
<td>Campanian-</td>
<td>Var, Ariège, southern France</td>
<td>PEREDA-SUBERBIOLA 1993c</td>
</tr>
<tr>
<td>(Rhodanosaurus [Struthiosaurus] ludginensis)</td>
<td>humerus, osteoderms</td>
<td>Maastrichtian</td>
<td>France</td>
<td></td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>caudal centra, rib</td>
<td>Campanian-</td>
<td>Quarante and Montouliers, southern France</td>
<td>DEPERET 1900, NOPCSA 1929; DE LAPPARENT 1947, 1954 PEREDA-SUBERBIOLA 1993c</td>
</tr>
<tr>
<td></td>
<td>fragments, osteoderms</td>
<td>Maastrichtian</td>
<td>Le Mas d'Azil, southern France</td>
<td></td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>Teeth in jaw fragment</td>
<td>Maastrichtian</td>
<td>Sânpetru, Romania</td>
<td>ÖSI et al. 2014a</td>
</tr>
<tr>
<td>cf. <em>Struthiosaurus</em> sp.</td>
<td>Fragmentary limb</td>
<td>Maastrichtian</td>
<td>Vurpár, Romania</td>
<td>ÖSI et al. 2014a</td>
</tr>
<tr>
<td></td>
<td>elements, dorsal centrum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nodosauridae</em> indet.</td>
<td>Osteoderms</td>
<td>Early</td>
<td>Le Mas d'Azil, southern France</td>
<td>LE LEOUFF 1991, PEREDA-SUBERBIOLA 1993c</td>
</tr>
<tr>
<td><em>Struthiosaurus transylvanicus</em></td>
<td>Posterior part of a skull, some vertebrae, ribs, scapula, osteoderms</td>
<td>Maastrichtian</td>
<td>Hăteş Basin, western Romania</td>
<td>NOPCSA 1915, 1929, PEREDA-SUBERBIOLA and GALTON 1994</td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>Tooth in jaw fragment</td>
<td>Maastrichtian</td>
<td>Sânpetru, Romania</td>
<td>ÖSI et al. 2014a</td>
</tr>
<tr>
<td>cf. <em>Struthiosaurus</em> sp.</td>
<td>Fragmentary limb</td>
<td>Maastrichtian</td>
<td>Vurpár, Romania</td>
<td>ÖSI et al. 2014a</td>
</tr>
<tr>
<td></td>
<td>elements, dorsal centrum</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Note: *Osteoderms refer to bony armor plates commonly found in armored dinosaurs.*
<table>
<thead>
<tr>
<th><strong>Species</strong></th>
<th><strong>Fossil Descriptions</strong></th>
<th><strong>Geological Period</strong></th>
<th><strong>Location</strong></th>
<th><strong>References</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Struthiosaurus</em> sp.</td>
<td>Sacral region including synsacrum and hip elements</td>
<td>Maastrichtian</td>
<td>Laño, Spain</td>
<td>GARCIA and PEREDA SUBERBIOLA 2003</td>
</tr>
<tr>
<td><em>Struthiosaurus</em> sp.</td>
<td>Dentary, maxilla fragment, teeth, rib fragments, ulna, osteoderms</td>
<td>Maastrichtian</td>
<td>Laño, Spain</td>
<td>ASTIBIA et al. 1990, PEREDA SUBERBIOLA 1999, PEREDA SUBERBIOLA et al. 1993a, 1995</td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>osteoderms</td>
<td>Maastrichtian</td>
<td>Aude, southern France</td>
<td>CLOTTES and RAYNAUD 1983, PEREDA SUBERBIOLA 1993c</td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>Teeth</td>
<td>?Maastrichtian</td>
<td>Quintanilla del Coco, Spain</td>
<td>POL et al. 1992</td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>Teeth</td>
<td>Late Cretaceous</td>
<td>Taveiro, Portugal</td>
<td>ANTUNES and SIGOGNEAU-RUSSELL 1996</td>
</tr>
<tr>
<td>Nodosauridae indet.</td>
<td>Tooth</td>
<td>Maastrichtian</td>
<td>Fontllonga 6, Spain</td>
<td>ALVAREZ SIERRA et al. 1994, ESCASO et al. 2010</td>
</tr>
</tbody>
</table>