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„Long bone histology of the European Late Cretaceous nodosaurid dinosaur *Struthiosaurus austriacus* “

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1. Abstract

The nodosaurid dinosaur *Struthiosaurus austriacus* (Bunzel, 1871) from the Late Cretaceous of Austria encompasses cranial and numerous postcranial elements. Some of these bones can be attributed to different individuals, due to obvious size differences. In the past, *Struthiosaurus austriacus* was considered an unusually small species in comparison to its closest relatives. There are different theories attempting to explain this feature, like island dwarfism or the retention of small body size as a plesiomorphic trait within the Thyreophora. Through morphological and histological examination of the fossil material of *Struthiosaurus austriacus*, this study aims to gain insight into the ontogenetic status of the specimens from Muthmannsdorf and clarify their size- and age relations. To this end, five long bones (four femora and one undefined long bone) were measured and digitised with photogrammetry. Furthermore, thin sections were made of one femur and the undefined long bone, which were examined through a microscope under polarised and unpolarised light. The examined femur comes from a larger specimen and although it only comprises a fragment of the shaft, the size difference to two of the other femora can be inferred from the diameter. Three sections were made along the shaft, all of which paint a similar histological picture. The cortex shows comprehensive remodelling of the bone material in the shape of secondary osteons. These osteons overlap in some areas and are present in multiple generations. The outermost layer of the shaft is especially dense and has practically no vascularization, suggesting that the bone has ceased growth within the animal's lifetime. Based on these observations, it can be said with some certainty, that the examined femur belongs to an adult animal which has reached its maximum body size. The four femora from Muthmannsdorf can be grouped into a smaller and a larger pair, based on the minimal diameter of their shafts. Assuming that the larger individual, which was histologically examined, is an adult, the smaller individual is likely subadult. External features of the femora, especially the morphology of the *linea intermuscularis cranialis* and *linea intermuscularis caudalis*, confirm that they belong to the same species. Unfortunately, neither of the larger femora is complete, complicating a direct size comparison with the smaller pair. However, it is possible to approximately calculate the size relation through the diameter of the shaft and the position of the fourth trochanter. When assuming similar body proportions of adult and subadult animals within the species, this results in a maximum body size for *Struthiosaurus austriacus* of over 4 metres and therefore significantly above the previous estimates of 2,5 to 3 metres. These insights also question the portrayal of *Struthiosaurus austriacus* as a pedomorphic member of the Nodosauridae, as well as its relationship to the other species referred to *Struthiosaurus*. The fossil material of *S. transylvanicus* (Nopsca, 1915) and *S. languedocensis* (Garcia & Pereda-Suberbiola, 2003) show no diagnostic morphological traits that would clearly affiliate them with the genus *Struthiosaurus*, aside from their similar size. If it turns out that *Struthiosaurus austriacus* is farther apart in body size from the other species than previously thought, that would give reason to assume that the different species of *Struthiosaurus* are in fact members of different genera.

2. Zusammenfassung

Der Nodosaurier *Struthiosaurus austriacus* (Bunzel, 1871) aus der späten Kreidezeit Österreichs umfasst craniale und zahlreiche postcraniale Elemente. Die Knochen sind mehreren Individuen zuzuordnen und weisen teilweise deutliche Größenunterschiede auf. Bislang wurde *Struthiosaurus austriacus* als ungewöhnlich kleine Art im Verhältnis zu den nächsten Verwandten angesehen. Dazu gibt es unterschiedliche Erklärungsversuche wie Inselverzwergung oder das Beibehalten von geringer Körpergröße als plesiomorphes Merkmal innerhalb der Gruppe der Thyreophora. Diese Arbeit versucht mithilfe morphologischer und histologischer Untersuchungen des Skelettmaterials von *Struthiosaurus austriacus* Informationen über den ontogenetischen Status der Exemplare aus Muthmannsdorf zu gewinnen und die Größen- und Altersverhältnisse der verschiedenen Individuen aufzuklären. Dazu wurden fünf Langknochen (vier Femora und ein unbestimmter Langknochen) vermessen und durch Photogrammetrie digitalisiert. Weiterhin wurden von einem der Femora und von dem unbestimmten Langknochen Dünnschliffe angefertigt. Diese wurden unter einem Mikroskop bei normalem sowie polarisiertem Licht untersucht. Bei dem untersuchten Femur handelt es sich um eines der größeren Exemplare und obwohl es sich nur um ein Fragment der Diaphyse handelt, ist am Durchmesser deutlich der Größenunterschied zu zwei der anderen Femora erkennbar. Es wurden drei Querschnitte entlang der Diaphyse vorgenommen, die alle ein ähnliches histologisches Bild ergeben. Der Kortex weist flächendeckende Remodellierung des Knochenmaterials in Form von sekundären Osteonen auf. Diese überlappen sich an manchen Stellen und sind in mehreren Generationen vorhanden. Die äußerste Schicht der Diaphyse ist besonders dicht und weist nahezu keine Vaskularisation mehr auf, was darauf hinweist, dass das Knochenwachstum noch zur Lebenszeit des Tieres praktisch vollständig eingestellt wurde. Anhand all dieser Merkmale lässt sich mit einiger Sicherheit sagen, dass es sich bei dem untersuchten Femur um ein adultes Tier handelt, das bereits die volle Körpergröße erreicht hat. Die vier Femora aus Muthmannsdorf lassen sich anhand des minimalen Durchmessers der Diaphysen in ein größeres und ein kleineres Paar unterteilen. Unter der Annahme, dass das größere Individuum, an dem die histologischen Untersuchungen durchgeführt wurden, adult ist, kann man davon ausgehen, dass es sich bei dem kleineren Individuum um ein subadultes Tier handeln muss. Äußere Merkmale an den Femora, insbesondere die Ausprägung von *linea intermuscularis cranialis* und *linea intermuscularis caudalis,* bestätigen die Zugehörigkeit zur gleichen Art. Unglücklicherweise ist keiner der beiden größeren Femora vollständig erhalten, was einen direkten Größenvergleich mit dem kleineren Paar

erschwert. Jedoch kann anhand des Durchmessers der Diaphyse und der Position des vierten Trochanters eine ungefähre Berechnung der Größenverhältnisse durchgeführt werden. Wenn man von ähnlichen Körperproportionen adulter und subadulter Tiere innerhalb der Art ausgeht, ergibt sich daraus eine maximale Körpergröße von *Struthiosaurus austriacus* von mehr als 4 Metern, die damit deutlich über den bisher angenommenen 2,5 bis 3 Metern liegt. Durch diese Erkenntnisse ist auch die Darstellung von *Struthiosaurus austriacus* als zwergenwüchsigen Vertreter der Nodosauridae in Frage zu stellen. Weiterhin werden dadurch die verwandtschaftlichen Beziehungen zu den anderen Arten innerhalb der Gattung *Struthiosaurus* in Zweifel gestellt. Sowohl das Fossilmaterial von *S. transylvanicus* (Nopsca, 1915), als auch das von *S. languedocensis* (Garcia & Pereda-Suberbiola, 2003) weist, abgesehen von einem ähnlichen Größenspektrum, keine diagnostischen morphologischen Merkmale auf, die eine klare Zuordnung zur Gattung *Struthiosaurus* erlauben. Wenn sich nun *Struthiosaurus austriacus* in seiner Körpergröße mehr von den anderen Arten unterscheidet als bisher angenommen, gäbe das Grund zur Annahme, dass es sich bei den verschiedenen *Struthiosaurus-Arten* in Wirklichkeit um Vertreter verschiedener Gattungen handelt.

3. Introduction

3.1 Dinosauria

The taxon Dinosauria encompasses a diverse group of archosaurian reptiles that originated in the early Mesozoic era, with Triassic species like *Herrerasaurus* and *Plateosaurus* that can unambiguously be attributed to the taxon Dinosauria (Brusatte, 2012a). The very earliest members of this group date back to the Carnian of South America. The Santa Maria and Caturrita Formations in Brazil, as well as the Ischigualasto Formation in Argentina yielded the richest fossil records of that age anywhere in

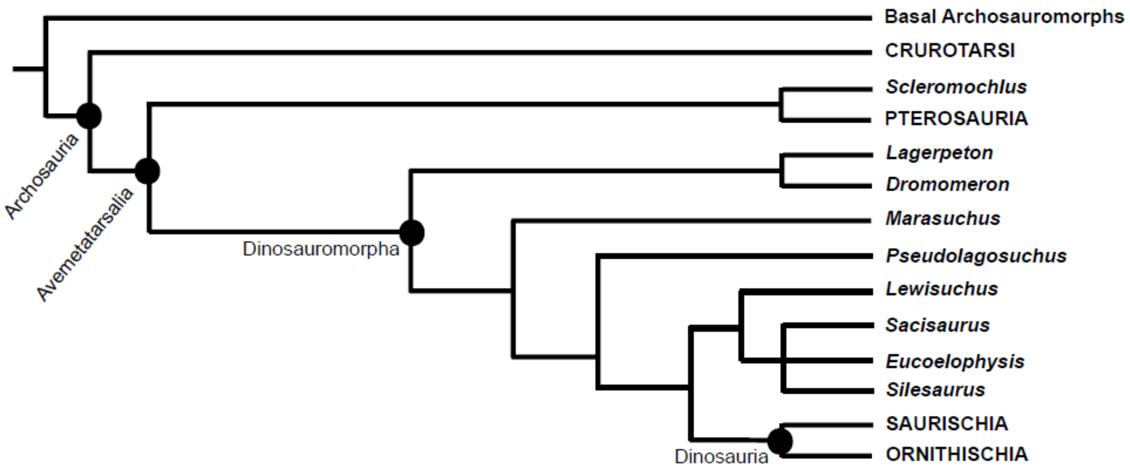

FIGURE 1: This simplified cladogram shows the phylogenetic placement of the group Dinosauria (referred to as "true dinosaurs") and other members of the Dinosauromorpha (referred to as "stem dinosaurs"), as well as the split between Avemetatarsalia and Crurotarsi. (from Brusatte, 2012a.)

the world. The fact that fossils of some of the closest relatives to dinosaurs, *Marasuchus* and *Legerpeton*, were also discovered there, points towards the origin of dinosaurs in South America (Langer et al., 2010). While there are several Carnian fossils from other continents that vaguely resemble early dinosaurs, like *Saltopus* from Scotland (Benton & Walker, 2010) or the jaws of a presumed prosauropod from Madagascar (Flynn et al., 1999), all of them have been written off as either non-diagnostic or members of close outgroups (Benton, 2012). Together with the pterosaurs, a group that evolved and went extinct alongside non-avian dinosaurs, they constitute the clade of Avemetatarsalia, which form the sister group to the "crocodilian" archosaur lineage Crurotarsi (Fig. 1). The latter makes up all extinct, as well as extant crocodylomorphs and their closest relatives (Sereno, 1991; Juul, 1994; Benton, 1999a, 2004; Irmis et al., 2007; Nesbitt, 2007; 2009; Brusatte et al., 2010; Nesbitt et al., 2010a, 2010b). For that reason, Dinosauria itself is defined as "members of the least inclusive clade containing *Triceratops horridus* and *Passer domesticus* (the living house sparrow)'' (Padian and May, 1993; Sereno, 1998; Sereno et al., 2005). Brusatte (2012a) listed seven characteristic features that are exclusive to dinosaurs (which he therefore referred to as "true dinosaurs") and are absent even in their closest dinosauromorph relatives (or "stem dinosaurs") like *Silesaurus* and *Marasuchus*. Some of these features are the presence of epipophyses (protrusions on the vertebrae that serve as muscle attachments) (Sereno & Arcucci, 1994; Dzik, 2003; Piechowski & Dzik, 2010) and the arrangement of the temporal musculature (Holliday, 2009).

3.2 Ornithischia and Saurischia

The most basic subdivision of dinosaurs is by the structure of their pelvis. In the Saurischia, the pubis is projecting in the anterior direction, like in most extant reptiles (Seeley, 1888). This group includes the Sauropodomorpha, medium-sized to very large herbivores characterized by long necks and tails, as well as the Theropoda, bipedal, predominantly carnivorous dinosaurs of various sizes. In the ornithischian condition, the pubic shaft is positioned posteriorly and parallel to the ischium, with a prepubic process on the anterior side (Seeley, 1888). Ornithischians are exclusively herbivorous, and as a result of that, have developed further adaptations to set them apart from saurischians (Norman, 1984; Weishampel, 1984; Weishampel & Norman, 1989; Sereno, 1997, 1999; Weishampel et al., 2004; Butler et al., 2007b; Irmis et al., 2007; Butler et al., 2008; Butler, 2010), including an increased number of sacral vertebrae and a more massive dentary. The saurischian group also possesses several unique features (Sereno, 1997, 1999; Langer & Benton, 2006; Nesbitt et al., 2009; Martinez et al., 2011), such as elongated vertebrae with epipophyses along the entire neck. Notably, the lineage of avian dinosaurs, i.e. birds, is in fact part of the Saurischia, and possesses a secondarily altered condition in the morphology of the pelvis, which evolved convergently to that of the ornithischians (Brusatte, 2012b).

3.3 Thyreophora

The genus *Struthiosaurus* is part of the ornithischian suborder of Ankylosauria. All members are exclusively quadrupedal herbivores, with keratinous beaks similar to those of turtles. Premaxillary teeth are still present in basal taxa of all three families, but were lost in the course of evolution (Carpenter, 2012). The most conspicuous trait shared by the Ankylosauria, as well as their sister group, the Stegosauria, is the presence of ossified body armour in some shape or form. In Stegosauria, this usually takes the shape of plates or spikes along the backbone and tail (Brusatte, 2012c). *Scutellosaurus*, *Scelidosaurus* and *Emausaurus* are regarded as either the closest relatives of the Thyreophora, or the most basal members of that very group (Lucas, 2016). They all possess osteoderms, albeit to a lesser degree than Stegosauria or Ankylosauria, as well as comparatively small body sizes that may have even allowed for facultative bipedalism in some cases and was more representative of basal ornithischians (Lucas, 2016). Ankylosauria, especially more derived members of the Ankylosauridae family, have most of their dorsal side, including head and tail, covered in numerous plate- or spike shaped osteoderms of varying sizes. Additionally, the larger elements are surrounded by marble- to pea- sized osteoderms that can also cover parts of the limbs and ventral regions of the body (Carpenter, 2012). The arrangement and shape of these elements can vary greatly across species of ankylosaurs, but they all share a robust microstructure of compact bone on the outside and porous bone, supported by collagen fibres, on the inside (Scheyer & Sander, 2004; Main et al., 2005; Cerda & Powell, 2010; Hayashi et al., 2010). At first glance, the most obvious distinction between ankylosaurids and other ankylosaurians might be the presence/absence of a tail club, which can vary in its morphology (Coombs, 1995). But the fact that even within the ankylosaurids, members of the Shamosaurinae, sister group to the Ankylosaurinae (Arbour & Currie, 2015), do not seem to possess this feature, somewhat invalidates the presence/absence of a tail club as a diagnostic feature for the families (Carpenter, 2012). All members of the ankylosaur suborder possess broad ribcages that are fused with the pelvic girdle at multiple points. Their flat and wide skulls are dorsally covered in osteoderms. In ankylosaurids, even the temporal fenestrae are covered and the posterior corners of their heads had horn-like osteoderms. Their heavy bodies are carried by strong, hoofed limbs, of which the forelimbs are slightly shorter than the hindlimbs. Another characteristic feature of ankylosaurids is the folded structure of their nasal passages, compared to their more conventional and straight structure in nodosaurids (Carpenter, 2012). This may suggest an increase in surface of the olfactory epithelium to improve the sense of smell, but endocasts of the ankylosaurid braincase reveal that the forebrain region, which includes the olfactory lobes, was not particularly well developed (Coombs, 1978b). Overall, ankylosaurs had relatively small brains for their body sizes when compared to modern reptiles (Carpenter, 2012). Other suggestions for the

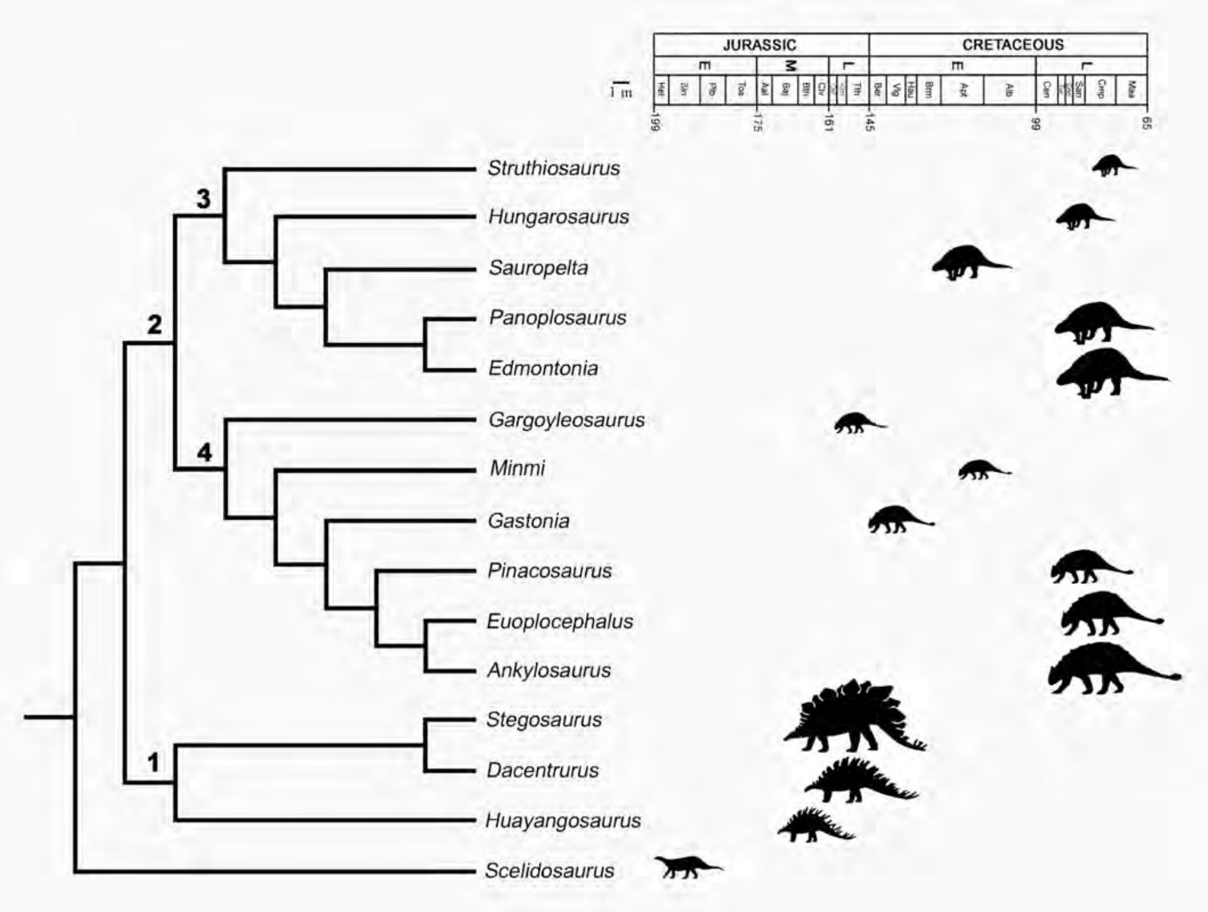

FIGURE 2: Simplified phylogeny of Thyreophora. Outlines on the right indicate approximate body size and temporal distribution. (from Pereda Suberbiola & Galton, 2008) (10); Data from Galton and Upchurch, 2004, Norman et al., 2004, Vickaryous et al., 2004, and Ösi, 2005)

conspicuous structure of the nasal passages include the use as a resonating chamber for sound amplification, or to regulate the temperature and humidity of the respiratory air (Carpenter, 2012).

The second family of the ankylosaur suborder are the Nodosauridae, which also includes *Struthiosaurus* (Coombs, 1978a). They differ from the Ankylosauridae in that they neither possess tail clubs, nor the ossified tendons necessary to stabilize the tail, as well as through their comparatively narrower skulls (Lucas, 2016). Compared to ankylosaurids, whose body armour mostly consisted of flat plate- like osteoderms, nodosaurids also developed large protruding spikes for defensive purposes, as seen in the large nodosaurid *Edmontonia* from North America, as well as three rows of large plate-like osteoderms covering the neck (Carpenter, 2012). Besides the two commonly accepted groups of Ankylosauridae and Nodosauridae, some scientists acknowledge a third, more primitive group of ankylosaurians, the Polacanthidae (Kirkland, 1998). Members of this group can be described as intermediate forms between Ankylosauridae and Nodosauridae, although their phylogenetic placement is still controversial. While some hypothesized them to be more closely related to ankylosaurids (Fig. 3), in the phylogenetic analysis made by Thompson et al. (2012), the group is incorporated at the base of the Nodosauridae. One potential feature to distinguish the three groups is the shape of the coracoid and scapula. In ankylosaurids and nodosaurids, the coracoid is rectangular in shape (shorter and sometimes more square-shaped in ankylosaurids), while having a disk shape in polacanthids that is pierced by the coracoid foramen. The scapula possesses a knob above the shoulder socket that attaches to the scapulohumeralis anterior muscle, the so-called acromion process. In polacanthids, this structure is broader than in the other two groups and projects downward and outward. The exact position of this structure is also diagnostic for different nodosaurid taxa, as is the case with *Struthiosaurus* (see below). Unlike in ankylosaurids and nodosaurids, the actetabulum of the pelvic joint was still partially open in polacanthids (Carpenter, 2012). The three groups also differ from each other in the histological structure of their osteoderms, with the version seen in polacanthids most closely resembling that of *Scelidosaurus* (Scheyer and Sander, 2004). Due to many similarities of the ankylosaurs from the Cretaceous of Europe, who were all members of the nodosaurid family, Kirkland et al. (2013) assigned the genera *Europelta*, *Anoplosaurus*, *Hungarosaurus* and *Struthiosaurus* to the monophyletic clade of Struthiosaurinae. However, Ösi (2015) raised several concerns over the plausibility of this group, since not every trait can be determined in every species due to the incomplete fossil record.

Since large body sizes of over five metres and several tons in weight have evolved independently in Stegosauria (e.g. *Stegosaurus*), Ankylosauridae (e.g. *Ankylosaurus*) and Nodosauridae (e.g. *Edmontonia*), small body size is considered a plesiomorphic condition for Thyreophora (Pereda Suberbiola & Galton, 2008) (Fig. 2). The earliest reliable records of ankylosaurs come from the Late Jurassic and consist exclusively of polacanthids like *Gargoyleosaurus* from the Morrison Formation or *Dracopelta* from Portugal. There are fragmentary remains of even earlier supposed ankylosaurs like *Cryptodraco*, but they do not provide sufficient information to attribute them to this group unequivocally. The other two families, nodosaurids and ankylosaurids, appeared in the Early Cretaceous. It is likely at this time, more precisely during the late Barremian, that the last polacanthids like *Polacanthus* and *Gastonia* disappeared, which also coincides with the appearance of the first flowering plants, although there is no clear causality between these events (Carpenter, 2012). The evolution of nodosaurids is poorly understood since most species are only known from very fragmented remains, with the exception of *Edmontonia*. The oldest known nodosaurid is *Sauropelta* from North America. But since this species already possesses all the typical nodosaurid features, it is unlikely to be an early member of the group (Carpenter, 2012).

Therefore, it remains unknown whether nodosaurids originated in North America or Europe, before spreading to Asia (Tumanova et al., 2003), South America (Coria & Salgado, 2001) and Antarctica (Salgado & Gasparini, 2006). The ankylosaurids most likely first appeared in North America and later spread to Asia, but unlike the other two groups, they are not known from Europe or the Southern Hemisphere. By the end of the Cretaceous, both nodosaurids and ankylosaurids were also in decline (Carpenter & Breithaupt, 1986).

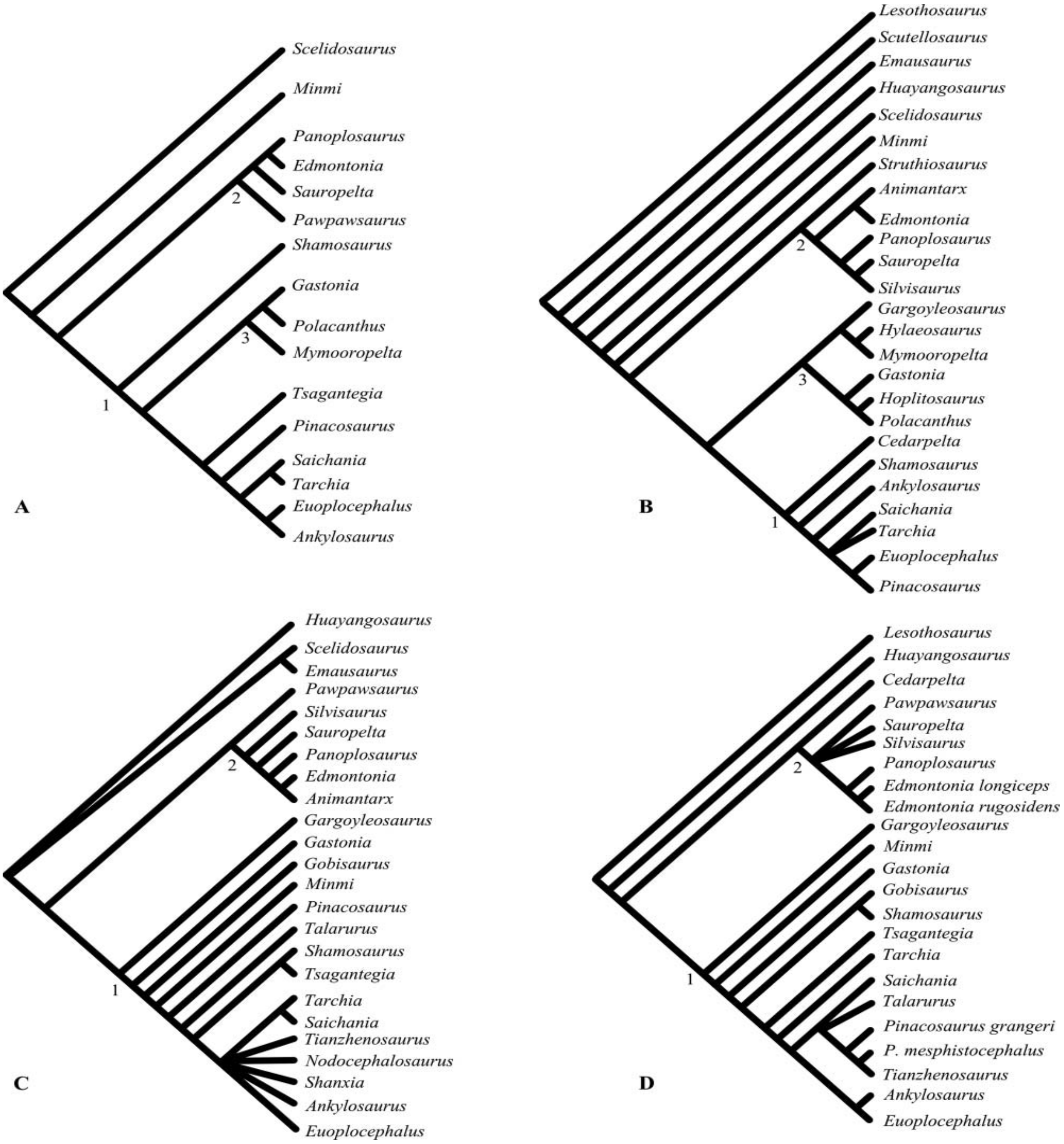

FIGURE 3: Different hypothesis of the ankylosaurian phylogeny and the placement of polacanthid taxa. Abbreviations: 1- Ankylosauridae, 2- Nodosauridae, 3- Polacanthidae (Carpenter 2001) or Polacanthinae (Kirkland 1998). (from Thompson et al., 2012(A - recovered by Kirkland (1998), B- presented by Carpenter (2001), C- recovered by Hill et al., (2003), D- recovered by Vickaryous et al., (2004))

3.4 Late Cretaceous ankylosaurs of Europe

The exact phylogenetic interrelationships of the genus *Struthiosaurus* remain uncertain. Cladistic analyses perfomed by Ösi (2005) resulted in the genus being placed at the base of the nodosaurian family tree, while according to Arbour et al. (2016) and Rivera-Sylva et al. (2018), it assumes a more derived position.

The distribution of the genus *Struthiosaurus* ranged from Laño in Spain to Haţeg basin in Romania and from the Santonian to the Maastrichtian (Ösi & Prondvai, 2013). According to Pereda Suberbiola and Galton (2001), it is defined by the combination of the following characters:

1. A basisphenoid that projects ventrally below the general level of the basioccipital in posterior view.
2. A nearly oval, symmetrical, distal articular condyle of the quadrate.
3. Cervical centra that are longer than wide.
4. A hooklike acromion process, centrally on the scapula.
5. Postcranial armour with distinctive elements.

Struthiosaurus, as currently understood, includes three species:

1. *S. austriacus*- The type species of *Struthiosaurus* comes from the lower Campanian and was discovered in eastern Austria in the 1860s, before the fossil material was described by several authors (Bunzel 1870, 1871, Seeley 1881, Nopsca 1929, Pereda Suberbiola & Galton 1992, 1994, 2001). It includes cranial and postcranial remains of several individuals of different ontogentic stages.
2. *S. transylvanicus*- This species was described based on fossil remains from the Maastrichtian of the Haţeg basin in Romania (Nopsca 1915, 1929). While the most convincing reason to separate this species from *S. austriacus* is the gap in temporal distribution (the fossils of *S. transylvanicus* are approximately 13- 15 My younger, Fig. 4), there are no significant morphological differences to justify this distinction (Ösi, 2015).
3. *S. languedocensis* (formerly *Rhodanosaurus languedocensis*)- Known from the lower Campanian of southern France (Garcia & Pereda Suberbiola, 2003). The reason for Garcia & Pereda Suberbiola (2003) to identify *S. languedocensis* as its own species was the different structure of the ischium. But due to the incomplete and damaged condition of the ischium of the bones of *S. austriacus* from Austria, Ösi (2015) did not consider this sufficient evidence for the definition of a new species.

Hungarosaurus from the Santonian of Hungary is considered the most closely related genus to *Struthiosaurus* (Csiki-Sava et al., 2015). The species *H. tormai* is known from the Santonian of Iharkút, Hungary and is estimated to be approximately four metres long (Ösi, 2005; Ősi & Makádi, 2009). The estimates for body mass of *H. tormai* vary between 650 and 700 kg (Ösi & Makádi, 2009), but it's build was comparably lighter and more cursorial than that of other nodosaurids, including *Struthiosaurus*, indicated by the larger but more slender humerus (Ösi & Prondvai, 2013). The reconstruction of postcranial body armour is mostly hypothetical, but it clearly differs from that of *Struthiosaurus.* It lacks the two large spikes, whose positions on the body are still unclear, but includes a boomerang shaped plate with two smaller spikes attached to it (Ösi & Makádi, 2009).

Furthermore, a humerus of another ankylosaur from the Late Cretaceous was discovered in Iharkút, Hungary and osteohistologically investigated by Ösi and Prondvai (2013). The humerus of this new ankylosaur shows some similarities to those of the *Struthiosaurus* specimens from France and Spain and especially to *S. austriacus. B*ut since the humeri of those species are incomplete themselves and lack any diagnostic feautures for the genus, the new species cannot be reliably assigned to the genus *Struthiosaurus* (Ösi & Prondvai, 2013). Because of that and the fact that *Struthiosaurus* and *Hungarosaurus* are currently the only known ankylosaur taxa from the Late Cretaceous of Europe, the new specimen was tentatively described as cf. *Struthiosaurus* sp.. According to this hypothesis,

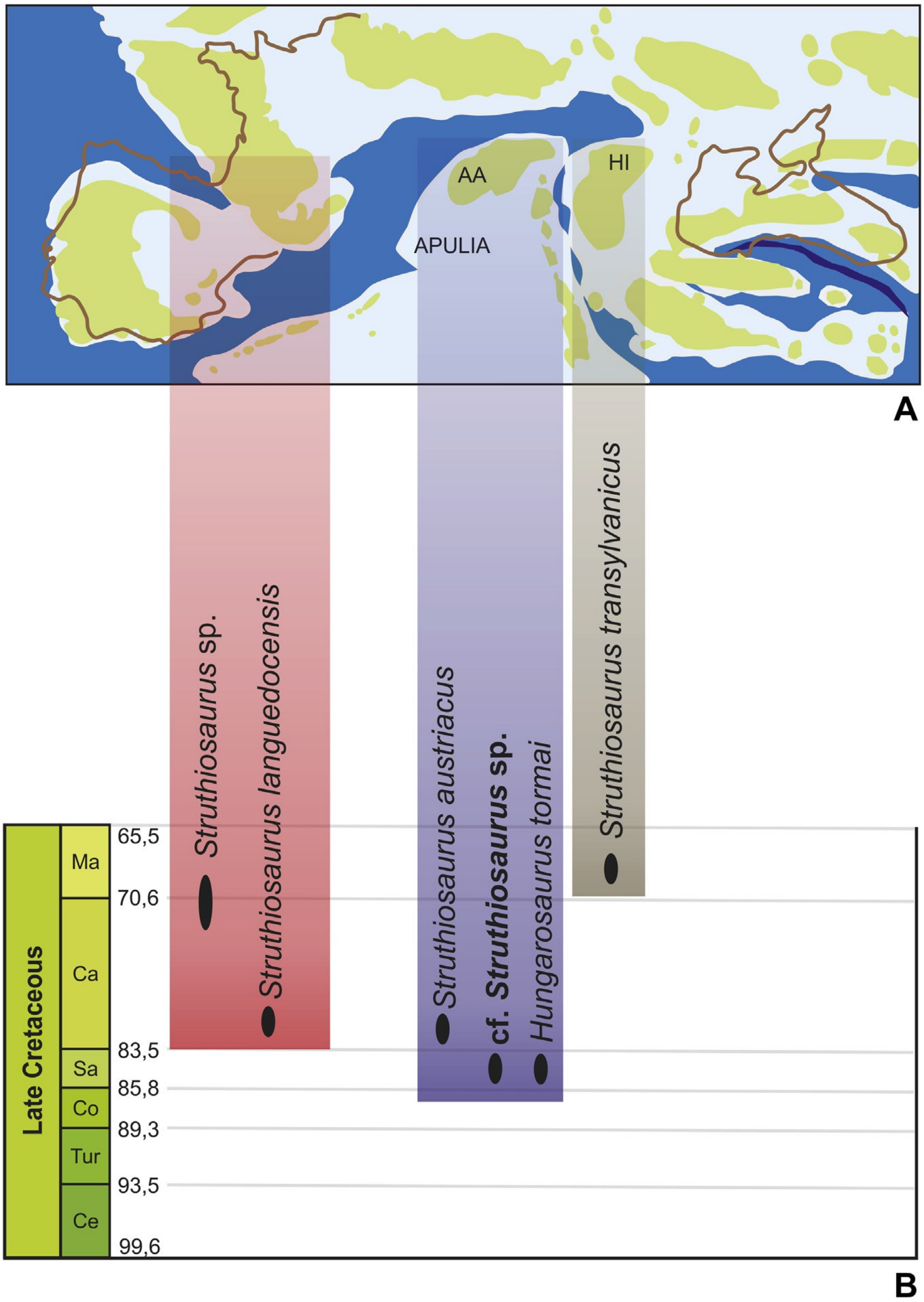

FIGURE 4: Differences in geographical and temporal distribution of *Hungarosaurus* and different *Struthiosaurus* species. Abbreviations: AA= Austroalpine block, HI= Hateg Island. Basic map of R. (from Ösi & Prondvai (2013).

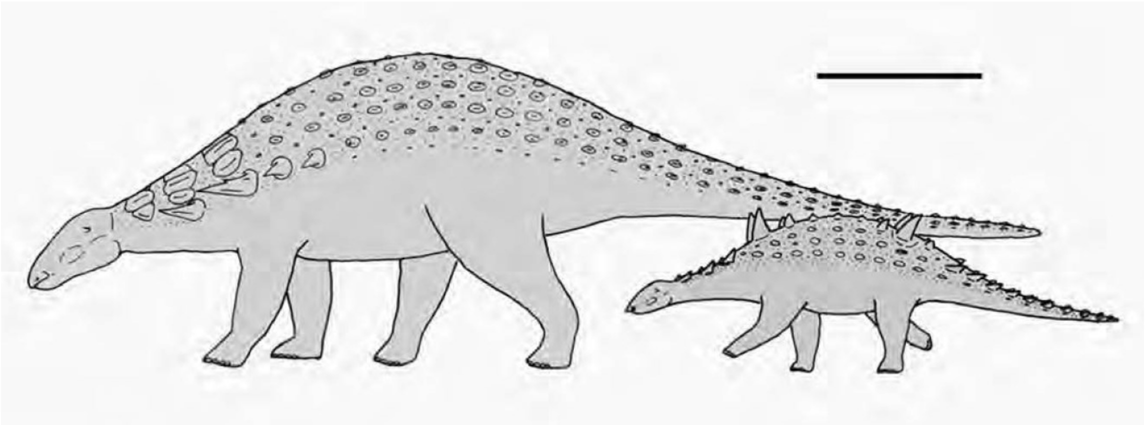

FIGURE 5: Reconstroction of the small nodosaurid *Struthiosaurus* from the Late Cretaceous of Europe, with an estimated body length of three metres and estimated body mass of less than 300 kg, compared to its larger relative *Edmontonia* from North America, who reached up to seven metres in length and weighed more than 2 tonnes. scale bar: 1m (from Suberbiola & Galton, 2008)

the genus *Struthiosaurus* was already present in the Santonian and it also suggests a close relationship between the faunas of Austria and Hungary in the Late Cretaceous (Ösi & Prondvai, 2013). The latter is already supported by the rhabdodontid *Mochlodon suessi*, which was discovered in the same location as *S. austriacus*, and its Hungarian relative *M. vorosi* (Ösi et al., 2012).

3.5 Struthiosaurus austriacus

The holotype of *Struthiosaurus austriacus*, a partial braincase, was discovered in a coal mine in Muthmannsdorf, west of Wiener Neustadt during the 1860s by Eduard Suess. This fossil site belongs to the Grünbach Formation of the early Campanian, which itself is part of the Lower Gosau Subgroup. The first examination of these bones was conducted by Bunzel (1870). Due to the morphology of the skull, that reminded Bunzel more of a bird's than that of a dinosaur, the animal received the name "ostrich-lizard", and he suggested it's placement in a novel order of extinct reptiles- "Ornithocephala". In the following decade, additional fossils were recovered from a different locality in the immediate vicinity. These bones were described by Seeley (1881), who also re- examined the previous material described by Bunzel. After that, the vertebrate fauna from Muthmannsdorf was once again reviewed by Nopsca (1902, 1926, 1929). Besides *Struthiosaurus*, the site also contained remains of an ornithopod, an azhdarchid pterosaur, an unidentified theropod, a turtle, several different crocodylomorphs and a choristoderan (Csiki-Sava et al., 2015). In those descriptions of the fossil material from Muthmannsdorf, the new species *Crataeomus pawlowitschii* (Seeley 1881), *C. lepidophorus* (Seeley 1881), *Danubiosaurus anceps* (Bunzel 1871), *Pleuropeltus suessii* (Seeley 1881) and *Rhadinosaurus alcimus* (Seeley 1881) were identified, all of which are now considered synonymous with *Struthiosaurus austriacus* (Pereda Suberbiola & Galton, 2001). The mine is inoperative since the end of the nineteenth century, so there have been no further findings since then (Csiki-Sava et al., 2015). The most recent examination of the *Struthiosaurus* material from Muthmannsdorf was conducted by Schade et al. (2022), regarding its neuroanatomy and ecology.

3.6 Geological setting

The Gosau Group of Grünbach lies in the north-eastern calcareous Alps and can be split up into two groups (Summesberger et al., 2007) (Fig. 6):

- The Lower Gosau Subgroup includes the late Santonian, with the Kreuzgraben and Maiersdorf Formations, and the Grünbach Formation (former "Coalbearing Series") of the early Campanian, which yielded the vertebrate fauna of Muthmannsdorf, including *Struthiosaurus austriacus,* which was found in a coal mine. The Grünbach Formation is composed of alternating carbonaceous shales and coals with conglomerates and sandstones of freshwater or shallow-water marine origin (Csiki-Sava et al., 2015; Summesberger et al., 2007).
- The Upper Gosau Subgroup begins with the late Campanian and ends with the Paleocene and includes the Piesting (former "Inoceramus Beds") and Zweiersdorf Formations. The dating of this formation is based on foraminifers, spores and pollen, as well as the stratigraphically important marine fossils of the adjacent Maiersdorf and Piesting Formations (Herman & Kvaček, 2006).

3.7 Paleobiogeography

The ankylosaur suborder likely originated in the Middle or Upper Jurassic and continued to exist throughout the entire Cretaceous period. Most taxa are known from North America, Asia and Europe, with only a few exceptions like the Australian taxon *Minmi,* or *Antarctopelta* from Antarctica (Arbour & Currie, 2016).

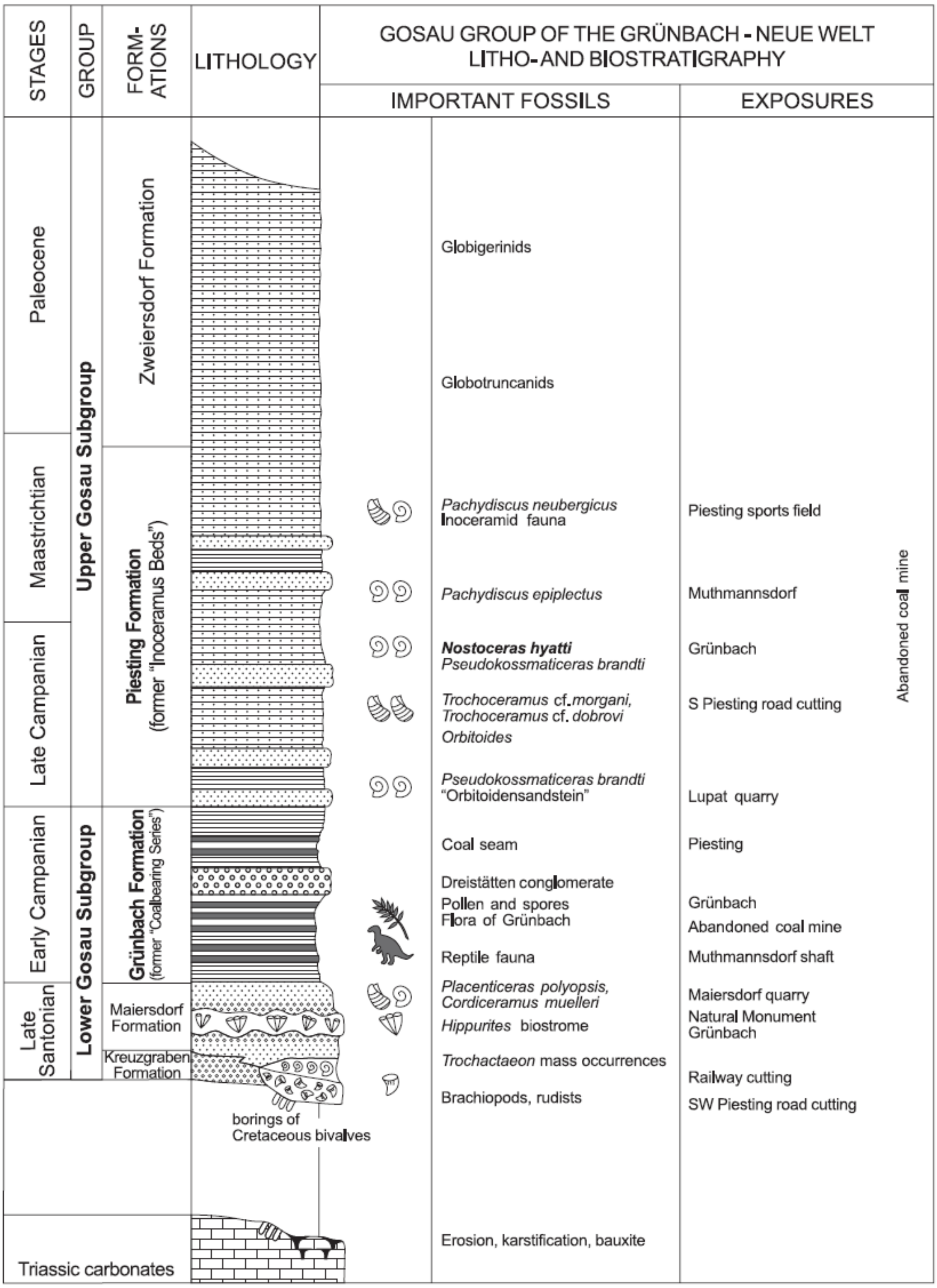

FIGURE 6: Overview of the geological setting and important fossils of the Gosau group, Austria. (from Summesberger et al., (2007).

In the Late Cretaceous, Europe consisted of several larger and smaller islands, separated from each other by shallow, continental seas. This geography was a result of the break-up of Pangea and the subsequent rise of sea levels (Csiki-Sava et al., 2015). By the time of the Campanian, the south-eastern regions of Europe started to converge, resulting in a continental uplift and orogenesis of the Carparthian, Balkan and Dinarian Mountains (Dabovski et al., 2002; Schuller, 2004; Otoničar, 2007; Schmid et al., 2008; Venturini et al., 2008). Due to the increase in exposed land area, the fossil record of the Campanian is more comprehensive than that of the earlier Late Cretaceous. However, the majority of Austria was still submerged under water at that time (Csiki-Sava et al., 2015). A small island in the eastern region of the country overlaps with the fossil site of Muthmannsdorf. Therefore, *Struthiosaurus austriacus* and the other species from the same fossil assemblage can be considered island species.

Compared to ankylosaurids, nodosaurid fossils are significantly more common in coastal and fluvial environments. This likely indicates a habitat preference of the latter, which may also have had an influence on the likelihood of post-mortem transportation and deposition in marine sediments (Butler et al., 2007a).

The floral and faunal species composition of the Grünbach Formation, including large foraminifers, rudists and corals, as well as the accumulation of coal suggest a subtropical climate with high humidity and no frost (Herman & Kvaček, 2006).

3.7.1 Island rule

According to the so called "island rule", postulated by Van Valen (1973) and based on the earlier work of Foster (1964), there are certain evolutionary patterns that can be observed in island habitats. Most notably that large animals develop smaller forms, while the opposite is true for small species. There have been many attempts to explain these changes in morphology, several of which have been neglected by the scientific community. According to Benton et al. (2010), the most commonly accepted hypotheses are ecological release (Foster, 1964; Carlquist, 1965; Van Valen, 1973; Azzarolli, 1982; Lomolino, 1985; Lomolino, 2005; Raia & Meiri, 2006), niche expansion (Grant, 1965; Van Valen, 1973; Heaney, 1978), resource limitation (Foster, 1964; Case, 1978; Lomolino, 1985; Burness et al., 2001; Lomolino, 2005; Raia & Meiri, 2006) and optimization of life-history traits (Foster, 1964; Case, 1978; Lomolino, 1985; Burness et al., 2001; Lomolino, 2005; Raia & Meiri, 2006).

Other characteristics of island ecosystems are a low alpha-diversity of species, a high degree of endemism and many relictual taxa that are extinct in most other parts of the world (Csiki-Sava et al., 2015). While the general validity of this rule is questionable (Meiri et al., 2007; Itescu et al., 2014) and certain taxa seem to be stronger affected than others, there are still several contemporary examples of insular dwarfing or gigantism that give credibility to the island rule in some respects (Bromham & Cardillo, 2007; Meiri et al., 2007).

An osteohistological study conducted by Ösi and Prondvai (2013) on a nodosaurid they tentatively assigned to the genus *Struthiosaurus* (see above) came to the result that the specimen was a fully grown adult with an estimated body length of no more than 3 metres, similar to the current size estimate of *Struthiosaurus austriacus* (Nopsca, 1929; Pereda-Suberbiola, 1992) (Fig. 5). Research by

Benton et al. (2010) on other presumed dwarf species that shared the same habitat, like the sauropod *Magyarosaurus* and the ornithopod *Telmatosaurus*, who were both considerably smaller than other members of their respective groups at the time, suggested that these animals had comparably slower growth rates, while at the same time, maturity and the subsequent cessation of growth were reached earlier in life.

The islands of the Late Cretaceous European archipelago served as refugia for many relictual taxa, not only of dinosaurs (Weishampel et al., 2003; Ösi, 2005; Sues and Averianov, 2009; Prieto-Márquez, 2010; McDonald 2012; Ősi et al., 2012; Kirkland et al., 2013) but also several other vertebrate groups (Csiki and Grigorescu, 2006; Martin et al., 2010; Archibald and Averianov, 2012; Nydam, 2013; Rabi et al., 2013; Martin et al., 2014; Sterli et al., 2015). The species represent evolutionary lines that had long since gone extinct in other parts of the world or had undergone significant evolutionary changes (Csiki-Sava et al., 2015).

4. Dinosaur bone histology

In order to assess the ontogenetic stage of an individual, we look at the microstructure within the bone. Assuming that most bones in the bodies of dinosaurs were formed endochondrally (from

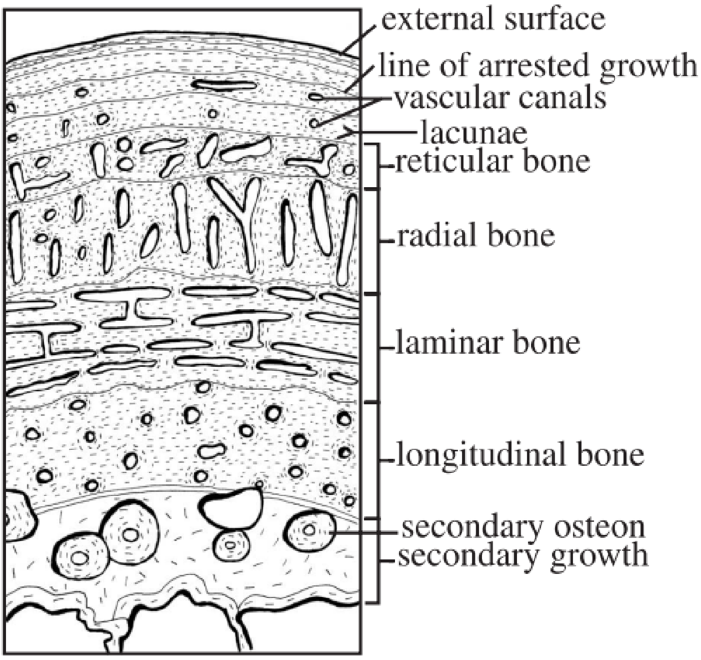

FIGURE 7: Schematic depiction of histological structures that can be found within cortical bone. The different types of fibrolamellar bone are separated by lines of arrested growth. (from de Boef, Larsson 2007)

ossified cartilage), two growth processes can be distinguished. Growth in thickness happens by accumulating periosteal bone in the outermost layer (periosteum) by osteoblast. The bone grows in length through the continuous formation of cartilage at both ends, which is then partly resorbed by the chondroclasts, creating the so-called endosteum, and subsequently replaced with endochondral bone. Part of both processes is the resorption of bone, conducted by osteoclasts, and the subsequent remodelling. The periosteal bone of dinosaurs differs from the endochondral bone in that it is denser, while the latter has a cancellous structure with many cavities that are filled with marrow during life (Reid, 2012).

The thermal physiology of dinosaurs is of central importance when it comes to their growth and life-history and remains a hotly debated topic. In endothermal animals like mammals and birds, periosteal growth happens continuously, as opposed to reptiles, where periodic growth can be observed. Dinosaurs seem to apply a combination of both within different parts of their skeleton (Reid, 2012). Continuous growth paired with a fast growth rate is possibly linked to the formation of fibrolamellar bone (de Ricqlès, 1974), that is built of cancellous bone which subsequently gets compacted into primary osteons. In comparison, periodic periosteal growth can be observed as an alternation of dense nuli, that represent the phases of growth, and LAGs (lines of arrested growth) that were formed during growth pauses, both of which appearing as circular layers around the bone (Fig. 7). By the number of these growth rings, it is theoretically possible to estimate the age of the individuum, if it can be assumed that they are formed annually, as it is known from crocodilians. However, since older growth rings will be resorbed and replaced by secondary tissue during the animal's life cycle, only the outermost layers are still present. Because of this, the total number of rings can only be inferred by the thickness of each ring and the remaining space (Ferguson et al., 1982). An additional indicator of adulthood is the formation of an external fundamental system (EFS), a dense layer of avascular, lamellar bone in the outer cortex of the bone (Benton et al., 2010).

Apart from the histology, the outer surface can also yield some information about the ontogenetic status of the animal. The points for muscle attachments in form of processes or ridges are more strongly developed in adults (Coombs, 1986) and the articular ends of the bones show a higher level of ossification (Benton et al., 2010).

4.1 Growth and physiology

Heterochronies can be described as changes in the timing or rate of development relative to the same events in the ancestor (McNamara, 1990; Pereda Suberbiola & Galton, 2008). This results in either less or more growth, either of the individual as a whole, or just certain body parts (McNamara & Long, 2012). Two different forms of heterochrony can be distinguished:

- Paedomorphosis: During ontogeny, the individual shows less growth than its ancestor (either a geologically younger species, or a direct ancestor within the same population). As a result, a paedomorphic animal tends to resemble the juvenile form of the ancestor, hence the name "child-shape" (McNamara & Long, 2012).
- Peramorphosis: The individuum undergoes more development than the ancestor, resulting in modification of ancestral features or the formation of entirely new ones (Pereda Suberbiola & Galton, 2008; McNamara & Long, 2012).

These terms are merely used to describe morphology, rather than the underlying evolutionary processes. In general, heterochrony also affects body size, with paedomorphic animals being smaller and peramorphic animals larger than their respective ancestral state, although this is not always the case and dwarfism or gigantism cannot always be attributed to heterochrony either (Pereda Suberbiola & Galton, 2008; McNamara & Long, 2012). The most iconic feature of dinosaurs is their massive size. In many dinosaur lineages (i.e. Sauropoda, Theropoda, Thyreophora) a gradual increase in size over the course of their evolution can be observed, so it's likely that peramorphosis played a part in that development (Pereda Suberbiola & Galton, 2008). Paedomorphosis is less well known from dinosaurs, with the famous exception of birds descending from larger theropods (McNamara, 1998; Pereda Suberbiola & Galton, 2008).

5. Materials and methods

5.1 Material

The dinosaur material described herein is housed in the Department of Palaeontology, University of Vienna, and includes four isolated femora (PIUW 2349/29, PIUW 2349/31, PIUW 2349/32, PIUW 2349/uncatalogued), which are here tentatively interpreted as belonging to two individuals of different ontogenetic stages, and one indeterminate long bone (PIUW 2349/20). Dimensional measurements of the bones were taken with Vernier calliper.

5.2 Photogrammetry

The femora were digitized using photogrammetry following the methodology outlined by Mallison and Wings (2014). The 3D models were generated using Agisoft Metashape Professional v1.7.4 by processing a total number of 113 (PIUW 2349/29), 125 (PIUW 2349/31), 125 (PIUW 2349/32) and 135 (PIUW 2349/uncatalogued) photographs that were acquired using a Fujifilm X-T3 digital camera equipped with a 16-50 mm f/3.5 lens. The 3D models were further processed utilizing Blender v.3.0.0

(Figs. 8, 9, 12) to obtain ambient occlusion shading, which was combined with global illumination for soft lighting. Photographs shown in Figs. 8-12 in the text were obtained using a Nikon D5300 DSLR camera equipped with an AF-S DX Micro NIKKOR 40 mm f/2.8G lens and Adobe Photoshop CC 2021 was used for colour balance and contrast optimization. The accompanying figures were finalized utilizing Adobe Illustrator CC 2021.

5.3 Specimen preparation

Two specimens (PIUW 2349/20 and PIUW 2349/uncatalogued) were sampled for histological investigation in order to evaluate their ontogenetic stages. Following the methodology outlined by Cerda et al. (2020), transverse thin sections were prepared and ground to a thickness of about 120 to 80 µm. The histology of the acquired thin sections was studied using a Leica DM4500 P LED petrographic microscope (housed in the Department of Geology, University of Vienna). The accompanying figures were compiled using Adobe Illustrator CC 2021. The histological terminology used in this study follows that of Francillon-Vieillot et al. (1990).

6. Results

6.1 Systematic paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Thyreophora Nopsca, 1915

Ankylosauria Osborn, 1923

Nodosauridae Marsh, 1890

Struthiosaurus Bunzel, 1871

Type species: *Struthiosaurus austriacus* Bunzel, 1871

Diagnosis (emended from Ősi et al., 2019): armoured dinosaur, estimated body length ca. 3,4m to 4,3 m; differs from all other known ankylosaurs in having relatively narrow, high occipital region, ventrally projected basisphenoid; small, oval, almost symmetrical distal quadrate condyle; longer than wide cervical vertebrae; ridge-like lesser trochanter, *linea intermuscularis cranialis* and *linea intermuscularis caudalis* of the femur; three cervical bands (sagitally unfused half-rings) with two, fused, complex elements in each band; cervical armour elements built up by the fusion of a high, triangular, posteriorly not bending lateral plate with straight or slightly convex anteroposterior edge; a central base formed by two to 16, circular to polygonal, sometimes pointed or crested osteoderms; and a medial, dorsally or slightly postero-dorsally oriented, short triangular plate or spike; pelvic armour is composed of oval-shaped, crested osteoderms that are surrounded by a fused matrix of small polygonal osteoderms, and these oval, crested osteoderms are present centrally just above the fused neural arch of the synsacral vertebral series as well.

Included species:

Struthiosaurus austriacus Bunzel, 1871

Struthiosaurus transylvanicus Nopsca, 1915

Struthiosaurus languedocensis Garcia and Pereda-Suberbiola, 2003

Known distribution: Campanian to Maastrichtian of Europe.

Struthiosaurus austriacus

(Figs. 8- 14)

Holotype: PIUW 2349/6, a partial braincase (see Schade et al., 2022 and references therein).

Material in this study: PIUW 2349/31, right femur; PIUW 2349/32, left femur; PIUW 2349/29, incomplete right femur; PIUW 2349 uncatalogued, incomplete left femur; PIUW 2349/20, indeterminate long bone fragment.

6.2 Morphological description

Left femur (Figs. 8, 10, 13, PIUW 2349/32):

The shaft is sigmoideally deformed (Fig. 8- B, G, I, M). It broadens medio-laterally (Fig. 8- A, H, E, F, L) and flattens anterio-posteriorly in the proximal half, where parts have broken off both on the anterior and posterior side. The distal half of the shaft is round and posteriorly flat and the *linea intermuscularis cranialis*, as well as the *linea intermuscularis caudalis* are visible as small ridges along the proximo-distal axis in the center of the anterior and posterior side respectively (Figs. 8- H, L, 13). The entire proximal surface is rugose and the head is anterio-medially round (Figs. 8- C, J, 10- A, B). The anterior edge formed by the head and the greater trochanter is concave, within this groove is a ridge along the proximo-distal axis (Figs. 8- C, J, 10- A). The proximo-posterior edge forms an almost straight line (Fig. 10- A, B). Proximally, the lateral side forms a very slim edge that ends in a roughly 90° corner with the greater trochanter (Fig. 10- A, B). The greater trochanter is oriented medially on the anterior side (Fig. 8- C, J). The fourth trochanter is oriented posterio-medially and is located roughly in the middle of the shaft, it gradually flattens proximally and distally (Fig. 8- B, E, F, I, L). Anterio-distally, there is a proximo-distal ridge on the shaft, the distal part of this ridge (just proximal if the condyles) is broken off (Fig. 8- A, H). Both condyles are largely intact, with a rugose surface mostly on the posterior side (Fig. 10- C, D). Both form a large hump on the posterior side (the medial one is broader than the lateral one) (Fig. 8- D, K). The distal surface of the distal condyle is flat while the medial surface of the medial condyle is concave (Fig. 8- D, K). The shaft has mostly horizontal fractures and a few vertical ones on the proximal end.

Right femur (Figs. 9 & 11, PIUW 2349/31):

The distal half of the shaft is straight, anteriorly round and posteriorly concave (Fig. 9- C, G, I, M). Proximally, the medial edge has an inverted sigmoideal shape and the proximal half of the shaft is overall flatter and broader (on the anterio-posterior axis) (Fig. 9- A- C, F- I, L, M). A large part of the shaft is missing posterio-proximally, the fracture reaches from the head to the middle of the shaft (Figs. 9- F, L, 11- A). The head has a rugose surface, is posteriorly flattened and round anteriorly and medially (Figs. 9- D, J, 11- A, B). The anterior edge formed by the head and the greater trochanter is concave, within this groove is a ridge along the proximo-distal axis (Figs. 9- D, J, 11- B). The greater trochanter has a flat surface on the lateral side and forms a slim hump anteriorly, which is almost parallel to the lateral edge (Figs. 9- D, J, 11- A, B). The fourth trochanter is roughly in the middle of the shaft and oriented posterio-medially (Figs. 9- A, C, F, H, I, L, 11- A). There are several bulbous structures visible on the surface of the fourth trochanter that are notably brighter than the rest of the bone (Fig. 11- A). Both anteriorly and posteriorly, there is a deep groove between the two condyles (Fig. 11- C, D). The anterior part of the medial condyle is broken off (Figs. 9- E, K, 11- C). Posteriorly, both condyles form a hump with rugose surface (the medial one is broader than the lateral one) (Figs. 9- E, K, 11- D). The medial side of the medial condyle is concave (Figs. 9- A, B, F, H, L, 11- C). Proximally, a subtle proximo-distal ridge with a slight sigmoideal shape is visible just beside the lateral edge (Fig. 9- G, M). The shaft has many horizontal and vertical fractures.

Right femur (Figs. 12, 13 PIUW 2349/29 (A5a)):

Both ends are missing. The remaining shaft is almost straight and significantly more massive than that of PIUW 2349/31 and PIUW 2349/32 (Fig. 12- C, E, I, K). The *linea intermuscularis cranialis* is prominently developed in the center of the anterior side and goes from the proximal end across more than half of the shaft (Fig. 12- A, B, H). Medially of the *linea intermuscularis cranialis*, the surface of the bone is concave and forms another ridge on the proximal end parallel to the first one (Fig. 12- A, B, H). The distal half of the shaft is round and on the posterior side, part of the groove between the (missing) condyles is still visible (Fig. 12- D, J). Within this groove is a small proximo-distal ridge. Starting from the middle, the shaft gradually broadens medio-laterally in proximal direction (Fig. 12- A, B, D, H, J). The posterior side of the shaft's proximal half is deformed and flattened (Fig. 12- D, E, J, K). The fourth trochanter is located medially and not very prominent (Fig. 12- A, H). It stretches from the middle of the shaft to the proximal end of the bone (where it broke off).

Left femur fragment (Fig. 12 PIUW 2349/uncatalogued):

Both ends are missing. The shaft has a larger diameter than PIUW 2349/31 and PIUW 2349/32, similar to PIUW 2349/29. Both the *linea intermuscularis cranialis* as well as the *linea intermuscularis caudalis* are faintly visible (Fig. 12- L, M). The anterior side of the shaft has a round profile, compared to the flatter posterior side. Remains of the fourth trochanter are visible anteriorly on the proximal end (Fig. 12- M).

FIGURE 8: Left femur (PIUW 2349/32) in posterior (E, F, L), anterior (A, H), distal (D, K), proximal (C, J), medial (G, M) and lateral (B, I) view. Images "A-E" and "G" are photographs, "F" is a drawing by Seeley (1881) and "H-M" show a 3-D-model created with photogrammetry. Abbreviations: ft= fourth trochanter, gt= greater trochanter, h= head, lc= lateral condyle, lic= *linea intermuscularis cranialis*, lica= *linea intermuscularis caudalis*, mc= medial condyle.

FIGURE 9: Right femur (PIUW 2349/31) in anterior (A, B, H), posterior (F, L), distal (E, K), proximal (D, J), medial (C, I) and lateral (G, M) view. Images "A" and "C-G" are photographs, "B" is a drawing by Seeley (1881) and "H-M" show a 3-D-model created with photogrammetry. Abbreviations: ft= fourth trochanter, gt= greater trochanter, h= head, lc= lateral condyle, mc= medial condyle. Abbreviations: ft= fourth trochanter, gt= greater trochanter, h= head, lc= lateral condyle, lic= *linea intermuscularis cranialis*, mc= medial condyle.

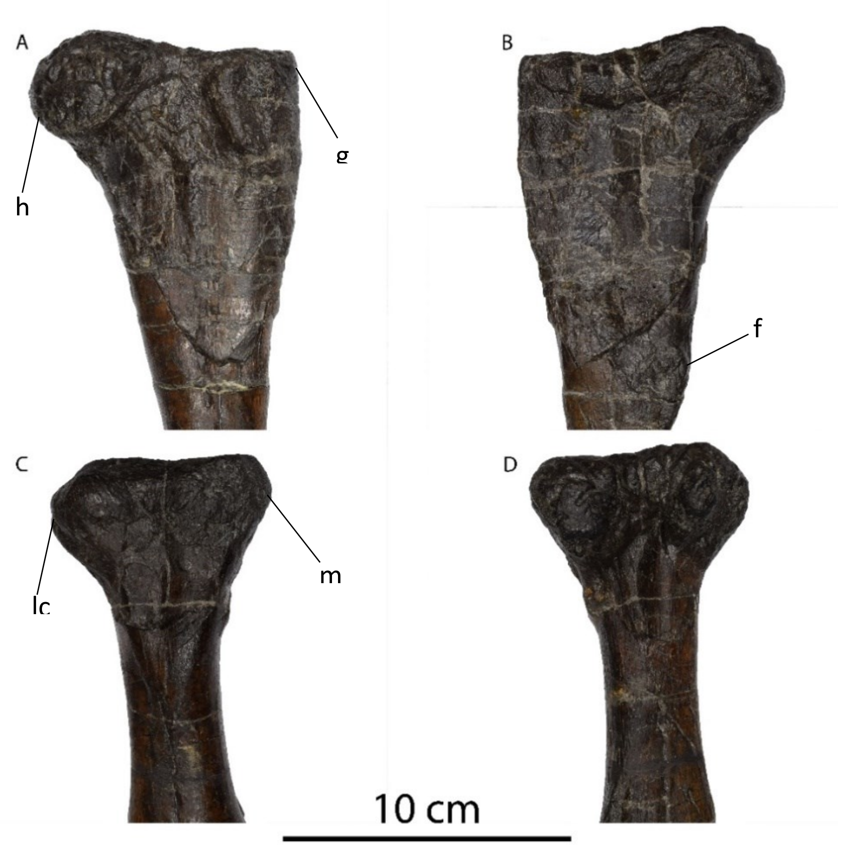

Figure 10: Left femur (PIUW 2349/32). Proximal end in anterior (A) and posterior (B) view. Distal end in anterior (C) and posterior (D) view. Abbreviations: ft= fourth trochanter, gt= greater trochanter, h= head, lc= lateral condyle, mc= medial condyle.

Figure 11: Right femur (PIUW 2349/31). Proximal end in posterior (A) and anterior (B) view. Distal end in anterior (C) and posterior (D) view. Abbreviations: ft= fourth trochanter, gt= greater trochanter, h= head, lc= lateral condyle, mc= medial condyle.

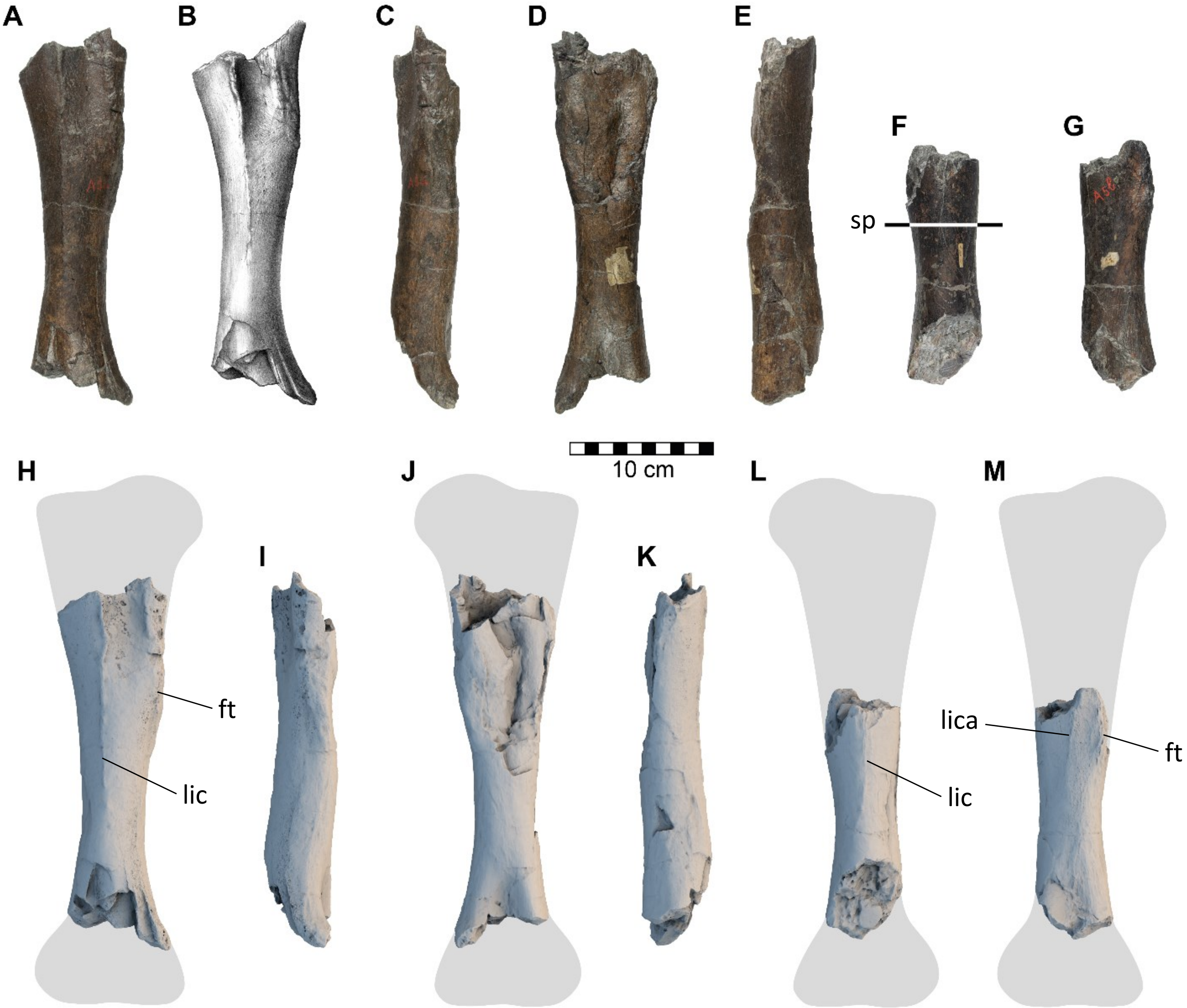

Figure 12: Right femur (PIUW 2349/29) in anterior (A, B, H), medial (C, I), posterior (D, J) and lateral (E, K) view. Left femur fragment (PIUW 2349/uncatalogued) in posterior (F, L) and anterior (G, M) view. Images "A" and "C-G" are photographs, "B" is a drawing by Seeley (1881) and "H-M" show a 3-D-model created with photogrammetry. Total size of the bones was calculated from diameter and position of the fourth trochanter in relation to the smaller, more complete femora (H, J, L, M). This results in an approximate length of 365 mm for both PIUW 2349/29 and PIUW 2349/uncatalogued. Abbreviations: lic= linea intermuscularis cranialis, lica= *linea intermuscularis caudalis*, ft= fourth trochanter, sp= section plane.

FIGURE 13: digital 3D-models of the right femur (PIUW 2349/29) (bottom) and the left femur (PIUW 2349/32) (top) created with photogrammetry, both showing the *linea intermuscularis cranialis*. With (left) and without (right) texture. Abbreviations: lic= *linea intermuscularis cranialis*.

TABLE 1: Measurements of the examined long bones. * In the cases of PIUW 2349/29, -20 and -uncatalogued, where the articular ends of the bone are missing, the measured values represent the width at the most proximal/distal part of the remaining bone.

In mm	*Left femur (2, PIUW 2349/32)*	*Right femur (4, PIUW 2349/31)*	*Right femur (5, PIUW 2349/29 (A5a))*	*Humerus fragment (distal end) (PIUW 2349/20 (A4))*	*Left femur fragment (PIUW 2349/uncatalogued)*
maximum length	255	265	265	108	175
*maximum distal width of articular end **	78	73	66	74	56
minimum distal width of articular end	43	34	N/A	N/A	N/A
*maximum proximal width of articular end **	95	80	75	46	50
minimum proximal width of articular end	81	65	N/A	N/A	N/A
head depth	42	41	N/A	N/A	N/A
medial condyle maximum depth	54	54	N/A	N/A	N/A
lateral condyle maximum depth	51	48	N/A	N/A	N/A
minimum shaft diameter	25	25	42	37	43

6.2.1 Comparison with other Ankylosauria

The *linea intermuscularis cranialis* is a proximo-distal ridge on the anterior or anterolateral side of the femur and separates the *musculus femorotibialis externus* and the *m. femorotibialis internus* (Hutchinson, 2001). In similar fashion, the *linea intermuscularis caudalis separates* the *m. femorotibialis externus* and the *m. adductor femoris* (Hutchinson, 2001). Both traits are seen as synapomorphies for archosaurs (Hutchinson, 2001) and are also known, albeit in a more primitive form, from early ornithischians such as *Lesothosaurus* and *Scutellosaurus (*Maidment & Barrett, 2011). Otero (2010) also recognized the *linea intermuscularis cranialis* in the Late Cretaceous sauropod *Neuquensaurus*, while some earlier sauropods like *Vulcanodon* or *Brachiosaurus* lack this trait and proposed it as a derived character that was lost and re-gained in saltasaurine sauropods. The morphology of these lines can vary considerably between taxa. In the femora of *Hoplitosaurus marshi* and another unnamed Argentinian ankylosaur, both the *linea intermuscularis cranialis* and the *linea intermuscularis caudalis* can be seen running parallel to each other from the anterior to the anterolateral side (Arbour & Currie, 2016), unlike in *Struthiosaurus austriacus*, where the *linea intermuscularis cranialis* is located medially on the anterior side of the shaft.

When comparing the femur of *Struthiosaurus* with that of the closely related species *Europelta carbonensis,* the latter is not only larger with an approximate length of 500 mm, but also significantly more robust than that of *Struthiosaurus* (Kirkland et al., 2013). They share similarities in the position of the fourth trochanter proximal of the shaft's midpoint, as well as the mostly dorsal orientation of the femoral head (Kirkland et al., 2013). The femora of several different individuals of *Hungarosaurus* presented by Ősi et al. (2019) differ from those of *Struthiosaurus* through the relatively uniform diameter of the shaft, while in *Struthiosaurus,* the shaft diameter clearly decreases from proximal to distal.

6.3 Long bone histology

The fragmented left femur (PIUW 2349/uncatalogued, sections A1 – A3) was sectioned at three different points on the shaft. The medullar cavity is filled out with minerals and shows several small cavities and crystals, while the medullar cavity of the undefined long bone is almost entirely crystallized.

The perimedullary region consists of many large erosion cavities, the insides of which are crystallized, surrounded by woven-fibered bone that appears in a dark red colour (Fig. 14- C). Primary bone of this structure is deposited rapidly in the immature individuum (Padian & Lamm, 2013). The cavities gradually get smaller with increasing distance from the center. Some isolated small cavities are even present in the outermost layers of the cortex, but none of them connect to the surface of the bone (Fig. 14- B). The entirety of the mid and outer cortex was heavily remodelled and is made up of large quantities of secondary osteons in highly irregular arrangement (=haversian bone), which is a strong sign for a mature individuum (Ösi et al., 2014). This degree of secondary remodelling is characteristic for all ankylosaurs (Stein et al., 2013). There is no clear boundary between the primary bone of the perimedullary region, and the secondary bone of the outer cortex. Instead, the number of secondary osteons gradually increases going outwards. In some areas, multiple generations of secondary osteons overlap, but not as frequently as seen the ischium of *Hungarosaurus* (Company & Ösi, 2012). The colour of the mid cortex appears brighter than in the perimedullary region, and gradually darkens again in the outer cortex. The outermost layer of the cortex is dense and darker than the rest of the bone, making it difficult to examine the histological structure (Fig. 14- A, B). The density and the lack of vascularization in this layer suggest that growth has practically ceased at that point in ontogeny. In certain areas, osteons are also visible within this layer (Fig. 14- B), however this only seems to be the case where the actual surface part of the layer appears damaged. The layer directly

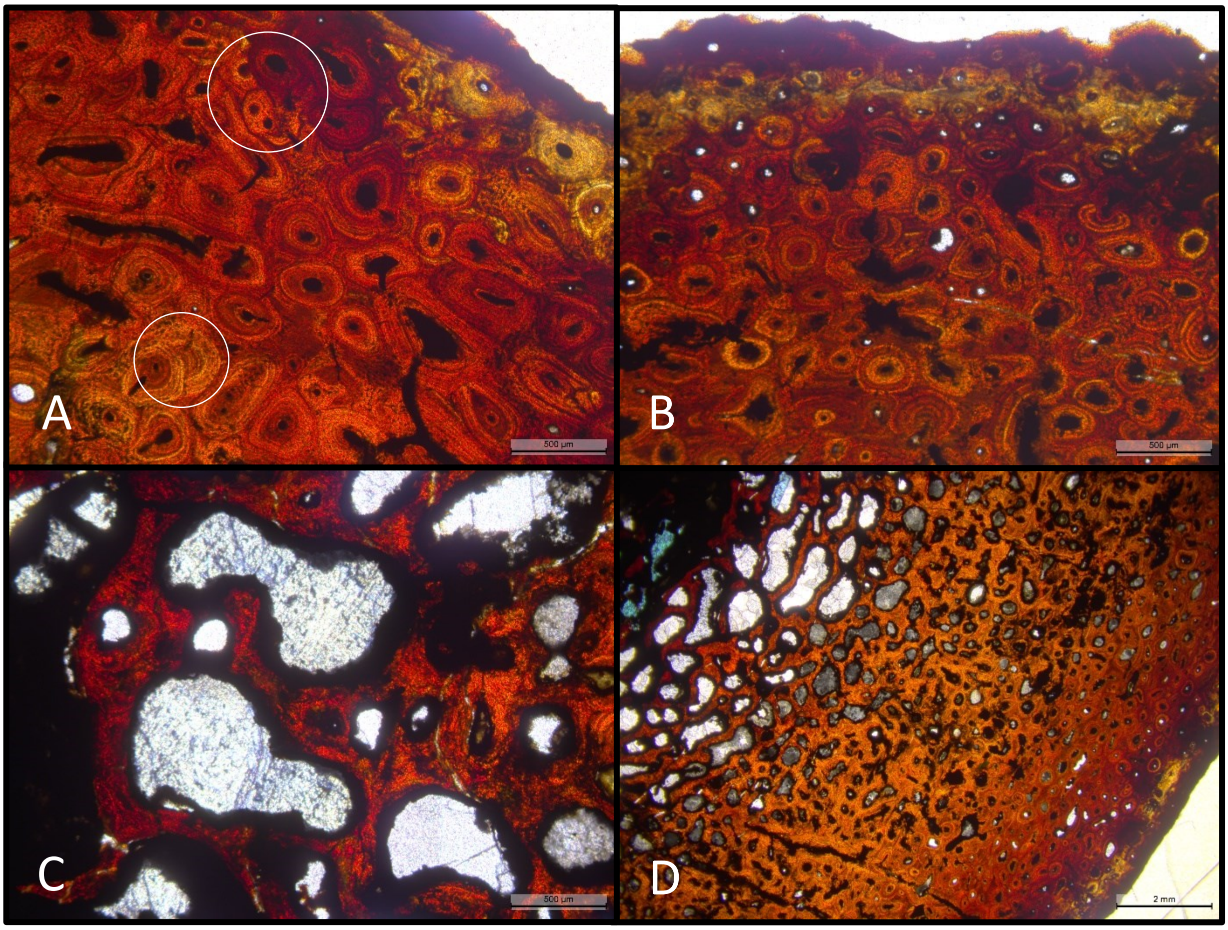

FIGURE 14: Histological samples of the left femur (PIUW 2349/uncatalogued). The outer cortical regions show extensive remodelling and a dense, dark surface layer (A, B). White circles indicate osteons of multiple generations overlapping each other. The inner cortical region is dominated by large erosion cavities and woven-fibered primary bone (C). The number of secondary osteons increases in the outer regions of the cortex, while the size and abundance of haversian canals decreases (D).

beneath appears in a bright yellow and also shows secondary osteons. This layer forms a clear boundary to the outermost layer, but a much more gradual transition towards the inner, orange layer of the cortex. Within many of the secondary osteons, concentric layers of different colours are visible. The vascular canals inside these secondary osteons (=haversian canals) are visible as black spots of varying sizes, giving information about the age of each individual osteon (Francillon-Vieillot et al, 1990). Surprisingly, haversian canals appear to be larger and more abundant in the inner regions of the cortex (Fig. 14- D). Additionally, secondary osteons appear to be more densely packed in the outer regions of the cortex. These observations suggest that secondary remodelling started earlier in the outer cortex and then continued inwards, unlike seen in the dwarf-sauropod *Europasaurus*, where histological samples show secondary remodelling only in the inner cortex regions (Sander et al., 2006).

There are no visible growth marks, likely due to the high degree of secondary remodelling in the cortex replacing most of the primary bone tissue.

7. Discussion

Initially, we intended to use CT-scans as a less destructive method of examining the long bone histology, but due to the high degree of mineralization of the bones, this method would not have yielded useful results. The similar position and morphology of the *linea intermuscularis cranialis* and -caudalis in both the small and large femora (Fig. 13) support the assumption that the two individuals indeed belong to the same species. These features have been acknowledged by other authors (Seeley, 1881; Pereda Suberbiola & Galton, 2001) (as seen in the illustrations made by Seeley (1881) (Figs. 8, 9, 12)), but not identified as *linea intermuscularis cranialis* and -*caudalis* respectively. The histological examination of one of the larger femora showed extensive secondary remodelling, multiple generations of overlapping osteons and a dense, avascular outer cortex layer, not unlike the external fundamental system described by Benton et al. (2010). All of these features clearly point towards a mature individuum that has reached its full size. The additional thin section made from the undefined long bone labelled "PIUW 2349/20" had a very similar appearance and while the bone itself is too incomplete to identify it, this at least suggests it belongs to the larger, more mature *Struthiosaurus* specimen. Previous estimates of the total body length of *Struthiosaurus austriacus by* Nopsca, (1929) and Pereda-Suberbiola (1992) did not exceed three metres (Fig. 5). Nopsca in particular did acknowledge the fact that the collected fossils from Muthmannsdorf contained multiple *Struthiosaurus* specimens of different sizes. He subsequently attempted to calculate a mean size for the bones where duplicates were present and for the missing bones, he looked at better known nodosaurids like *Polacanthus* and *Nodosaurus* for reference. After confirming the adult status of the larger pair of femora, the minimum shaft diameter and the position of the fourth trochanter were used to get the size relation of the differently sized specimens (Fig. 12). Although according to the new estimate, *Struthiosaurus austriacus* still lies on the smaller end of the ankylosaurian size spectrum, it is similar in size to other Late Cretaceous nodosaurids like *Stegopelta landerensis* (Paul, 2016)*, Silvisaurus condrayi* (Paul, 2016) and *Hungarosaurus tormai* (Ösi, 2005; Ősi & Makádi, 2009). Therefore, referring to *Struthiosaurus austriacus* as a dwarf species within the Nodosauridae seems inappropriate. This subsequently raises the question of the relationship between the different species of *Struthiosaurus*. Both *S. languedocensis* and *S. transylvanicus* show no significant skeletal similarities to *S. austriacus* (Ösi, 2015). Furthermore, in case of *S. transylvanicus*, the temporal distribution is over 10 My apart from the other species (Ösi, 2015) (Fig. 4). As for the phylogenetic position of *Struthiosaurus austriacus,* Pereda Suberbiola & Galton (1995) identified several skeletal traits in members of the genus *Struthiosaurus,* which they defined as symplesiomorphies of the Nodosauridae. Additionally, there is an abundance of other relictual taxa known from the Late Cretaceous islands of Europe (Weishampel et al., 2003; Ösi, 2005; Csiki and Grigorescu, 2006; Sues and Averianov, 2009; Martin et al., 2010; Prieto-Márquez, 2010; Archibald and Averianov, 2012;

McDonald 2012; Ősi et al., 2012; Kirkland et al., 2013; Nydam, 2013; Rabi et al., 2013; Martin et al., 2014; Csiki-Sava et al., 2015; Sterli et al, 2015). But since newer phylogenetic analyses by Arbour et al. (2016) and Rivera-Sylva et al. (2018) have each placed the genus *Struthiosaurus* at a highly derived position, the validity of those symplesiomorphies should be questioned.

8. Conclusions

Up until this study, no histological examination of the species *Struthiosaurus austriacus* has been performed. For that reason, the insights gained from this study contradict some previous theories and greatly change our image of this animal. The fossil deposit from Muthmannsdorf most likely contains a larger, mature specimen of *Struthiosaurus austriacus* and a smaller, immature one. When inferring the missing parts of the larger pair of femora through their smaller counterparts (Fig. 12), the new size estimate for the fully grown individuum could increase to over four metres, which, in our opinion, is enough to refute its status as a paedomorphic dwarf. The new results of this study also indicate that the genus *Struthiosaurus* may in fact contain species of multiple genera, since their most unifying trait used to be their similar size. Although *Struthiosaurus austriacus* may not be a case of island dwarfism, the possibility of it being a basal member of the Nodosauridae, while highly questionable, cannot be entirely ruled out. But when considering its temporal distribution, paired with recent phylogenetic analyses, it seems much more reasonable to assume the genus *Struthiosaurus* to be a derived taxon within the Ankylosauria.

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