The first skeletal evidence of an Upper Triassic (Rhaetian) diapsid reptile from the Western Carpathians (Strážov Highlands, Slovakia)

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Abstract: Here we describe the first skeletal evidence of a tetrapod from Rhaetian (Upper Triassic) marine deposits of the Western Carpathians. The material consists of an isolated left femur and comes from the Úbočka locality near Čičmany in the Strážov Highlands. Based on morphological, histological, and stratigraphic evidence, we can exclude affinities of this femur to the most commonly occurring aquatic reptiles: the Eosauropterygia. The histology of a femur of aff. *Pachystropheus* from Aust Cliff, Gloucestershire, UK, is also described here for the first time and compared to the bone from Slovakia. However, a precise taxonomical assignment of the Rhaetian femur from Slovakia is not possible. The bone shows strong osteosclerosis that points to an inhabitant of a shallow marine environment. On the basis of morphological and histological characters, affinities to a cyamodontoid placodont, *Endennasaurus*-like thalattosaur or a rhynchocephalian are conceivable. The morphology of the Slovak find does not fully exclude choristoderan affinity, but the rare histological data available for comparison do not support such a statement. For all these reasons, we allocated this bone as Diapsida indet. The bone described here sheds the first, although limited light on the possible faunal composition of the Rhaetian tetrapod assemblage in the Western Carpathians. We can assume that the bone, which shows marks of transport, either represents an allochthonous component in this marine environment, transported postmortem and most likely from nearby dry land (i.e., in the case of rhynchocephalian affinities), or it belonged to an inhabitant of this shallow coastal biotope (e.g., cyamodontoid placodont affinities).

Keywords: Triassic, vertebrate, femur, histology, Slovakia.

Introduction

The Late Triassic is a particularly interesting period. The break-up of Pangaea initiated very important changes in global climate evolution. This event was accompanied by changes in distribution of climate zones in the northern hemisphere (Simms & Ruffell 1990; Parrish 1993; Sellwood & Valdes 2006). During the Triassic, the central West Carpathian area was situated on the south-western margin of the North European shelf. Sedimentation in this area was influenced by the opening of the Penninic Rift and by simultaneous closure of the Meliata Ocean during the latest Triassic (Michalík 1993, 1994). Siliciclastic influx into the Tatric, Fatric and partly also Veporic units was controlled by climate. Eustatic and tectonic events caused non-deposition and erosion responsible for sedimentary gaps in the Tatric, Hronic and Silicic zones. Although uppermost Triassic sediments are often missing due to an emergence in the marginal Tatric Unit, the continental Tomanová Formation represents this time (Michalík et al. 1976, 1988; Lintnerová et al. 2013).

Although the Triassic represents one of the greatest transitions in the evolution of life after the end-Permian mass extinction, fossil vertebrates are, unfortunately, extremely rare in the deposits of the Western Carpathians. In fact, only a few Mesozoic tetrapods have been reported from Slovakia till today (Čerňanský et al. 2018). These include Upper Triassic dinosaur tracks from the Tomanová Formation of the High Tatra Mountains (Michalík et al. 1976; Michalík & Kundrát 1998; on footprints from this formation, see also Niedźwiedzki 2005, 2011), Middle Triassic pachypleurosaur remains from Demänovská dolina valley (Čerňanský et al. 2018) and isolated teeth of Jurassic thalattosuchians (Čerňanský et al. 2019). Thus, there are large discontinuities in our knowledge of the Mesozoic evolution of amniotes in this area. In southern Poland to which the Tatra Mountains continue, the Middle Triassic labyrinthodont amphibian (*Tatrasuchus kulczyckii*) has been described from the Partnach Beds (Maryańska & Shishkin 1996). In contrast, many Late Triassic localities with vertebrate assemblages are known in the regions close to the Carpathians, such as

Silesia (Dzik & Sulej 2007; Dzik et al. 2008; Sulej et al. 2011).

Because of the scarcity of Mesozoic vertebrates in the Western Carpathians, every find of this age can help us to fill the gap in the tetrapod distribution in this territory during this geological era. For this reason, we treat here in detail the morphology, microanatomy, and histology of an isolated femur from the shallow marine Upper Triassic (Rhaetian) sediments of the Úbočka locality near Čičmany village in the Strážov Highlands, in the north-western part of Slovakia and discuss its possible taxonomical affinities.

Material and methods

The find described here is the left femur of a diapsid reptile. It was found by one of us (M. S.) during geological field work in 2018. The specimen is housed in the Slovak National Museum in Bratislava and inventoried as Z 28224. It was scanned using the micro-computed tomography (μCT) facility at the Slovak Academy of Sciences in Banská Bystrica, using a Phoenix mikro-CTv|tome|x L240. The images were recorded over 360°. Data were analysed using Avizo 8.1 on a high-end computer workstation in the Department of Ecology (Comenius University in Bratislava). For comparison, we also studied a right femur of aff. *Pachystropheus,* a possible choristoderan from the Rhaetian Westbury Formation of South-West England (Storrs 1992; Storrs & Gower 1993; Storrs et al. 1996). It is also housed in the Slovak National Museum in Bratislava and inventoried as Z 28225. Both femora were cut along a transverse plane at the narrowest point of the midshaft, which usually preserves the most complete growth record. The samples were processed into standard petrographic thin sections (Klein & Sander 2007; Padian & Lamm 2013). The thin sections were studied under a Leica DM2500LP polarizing microscope. Digital photomicrographs were taken with a Leica DFC420 mounted colour camera and edited using the 2007 Leica Image Access EasyLab 7 software. The bone histological terminology used in this study follows Francillon-Vieillot et al. (1990). The surface ratio between medullary and cortical region as well as bone compactness was measured with a pixel counting computer program (© P. Göddertz, IGPB). Photographs of both femora were taken prior to cutting by a Nikon D3Xcamera.

Geological setting

The Úbočka locality (48°56'20.95"N, 18°30'0.08"E) is a small outcrop in meadows close to the village of Čičmany in the Strážov Highlands (in north-western Slovakia; Fig. 1). It exposes shallow marine carbonates (28–30 m thick) of the Rhaetian Fatra Formation, deposited in the intrashelf Zliechov Basin (belonging to the Fatric Unit). The sequence (with sedimentation rate of 50–175 mm/ka) is arranged in

shallowing-upward cycles (Michalík 2007). Nine long eccentricity cycles (á 400 ka; Michalík et al. 2013) indicate that the marine transgression of the Fatra Fm. started 1 Ma after the beginning of the Rhaetian Stage (if we accept the duration of the Rhaetian Stage as 4.14±0.39 Ma according to Wotzlaw et al. 2014; note that the problem of when Rhaetian stage started is still being discussed, see e.g., Lucas 2017).

Dolomites and dolomicrite mudstones directly covered terrigenous Upper Triassic Carpathian Keuper in rapidly subsiding parts of the basin (Michalík et al. 2013; Fig. 2). They contain plant fragments, ostracod tests, agathamminid foraminifers, shells of bivalves, linguloid brachiopods, shark teeth, and ichnofossils indicating a mixed, brackish environment. A bone-bed layer with fish and shark teeth closing the cycle indicate condensation and temporal winnowing.

Tempestite beds built of biomicritic to oomicrobiosparitic wackestone/packstone with load casts and/or *Thalassinoides* burrows contain two different bivalve associations: the soft-bottom infaunal *Gervillaria* association, and the solid bottom *Placunopsis* dominated one (Golej in Michalík et al. 2013). Sea storms, which dominate this part of the sequence, are subsequently replaced by terrestrial dust storms bringing fine quartz debris.

The Fatra Formation (Michalík 1982; Michalík & Jendrejáková 1978) with mollusc shells, crinoid ossicles, foraminifers (*Triasina hantkeni*, etc.; see Michalík & Jendrejáková 1978; Gaździcki 1983), and infaunal *Thalassinoides* burrows, with coral fragments (*Rhaetiophyllia paraclathrata*; Roniewicz 1974; Roniewicz & Michalík 1998), *Asteriacites* traces, calcareous sponges and algae, and brachiopods (*Rhaetina gregaria, Rh. pyriformis*, *Zugmayerella uncinata*, and *Austrirhynchia cornigera*), bears signs of a stabilized marine regime. Although the exact provenance of the bone described here is not known, it probably comes from this part of the sequence.

Terrigenous quartz grain support and ferruginous content increase upwards (Michalík et al. 2007, 2010). They record monsoon-like maxima of terrigenous flux in 100 ka periodicity. Bivalves are represented by *Placunopsis* sp., *Lopha haidingeriana,* and *Chlamys valoniensis*. Submarine slumping affected the topmost beds. The contact with overlying non-carbonate shaly Kopieniec Formations is sharp.

Systematic paleontology

Eureptilia Olson, 1947
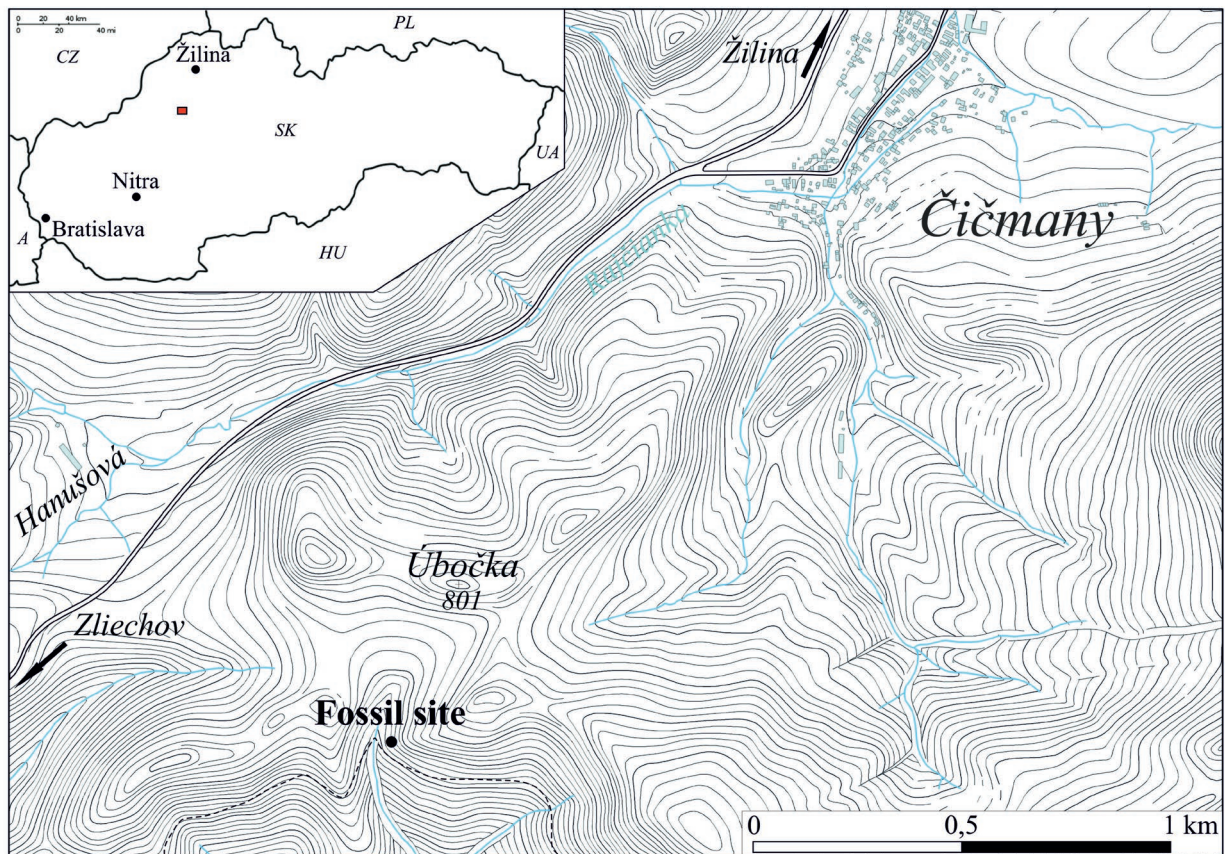Diapsida Osborn, 1903

Diapsida indet.
(Figs. 3, 4)

Referred Specimen: An isolated left femur, Z 28224.
Horizon: Upper Triassic (Rhaetian), Fatra Formation.
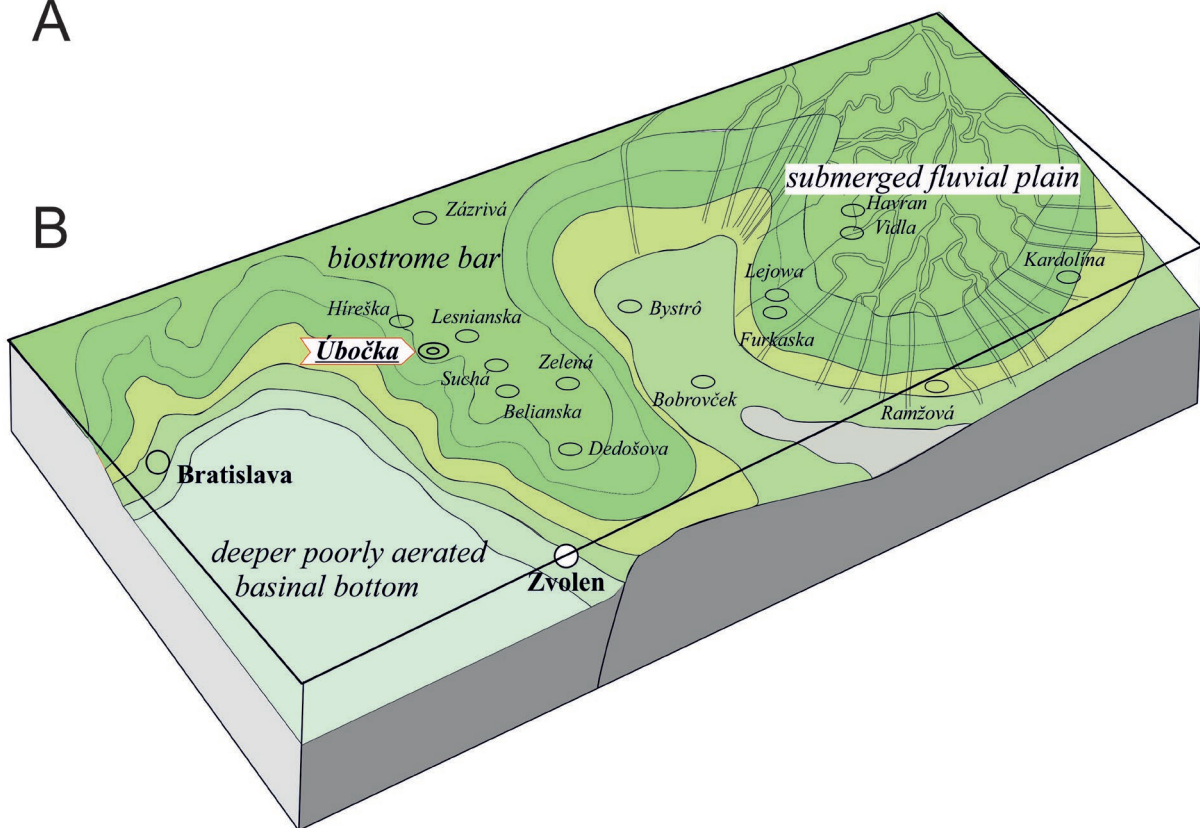**Locality:** Úbočka near Čičmany, Strážovské Mountains (Slovakia).

Fig. 1. A — Localization of the finding site within Slovakia. **B** — 3D reconstruction of the Zliechov Basin (length of the block diagram is about 300 km).

Fig. 2. Correlation of the Fatra Fm. sequence in seven sections from the Zliechov Basin (compare with block diagram in Fig. 1).

Description

Morphology: Z 28224 has the typical elongated shape of a femur. The bone has a slightly sigmoid appearance, with a slender and relatively straight, constricted midshaft, a thick proximal and a flat distal portion (Fig. 3). The proximal portion displays a pronounced internal trochanter and a flat dorsal side. The internal trochanter is located distal to the proximal head. It is expanded ventromedially and gradually diminishes distally. It most likely marks the attachment of a strong pubo-ischio-femoralis externus muscle. A shallow, but distinct ventral intertrochanteric fossa is present posterior to it. The fossa has a rough insertional surface and becomes less distinct distally. The ridge that borders the fossa posteriorly (the posterior ridge) is mostly damaged in the proximal region, but it continues distally to form a longitudinal adductor ridge. Near the distal end of the fossa there is a prominent rugose area, to which plausibly attached the caudifemoral musculature. A small rounded prominence on the dorsal portion of the head (the upperside of the head) is present. It is most likely a muscle rugosity (Fig. 3B,C). In pre-postaxial view

the proximal head is concave (due to the bulged internal trochanter). Most of the distal region is broken off and missing, although it was originally found together with the rest of the bone. However, this portion was left at the locality by the finder and is lost now. A photograph exists that can give us an approximate estimation of the flattened character of the distal end and its gradual widening (see Fig. 3G). In addition to the recent damage, the femur suffered from damage during transport resulting in an eroded proximal end. The proximal and distal end are not angled with respect to each other. The maximum length of the preserved portion is 83 mm. The maximum width of the proximal end is 12.6 mm, that of the midshaft is 9.4 mm, and that of the preserved distal end is 14.6 mm. The mid-section of the bone is oval in cross-section, but it becomes more antero-posteriorly compressed proximally (Fig. 4).

Microanatomy, histology and growth record: Primary bone tissue of Z 28224 is obscured by diagenesis, which is most obvious in polarized light (Fig. 4B,D,F,G). In addition, the cross section is crossed by numerous small cracks (Fig. 4 A–D). A small free medullary cavity, which occupies
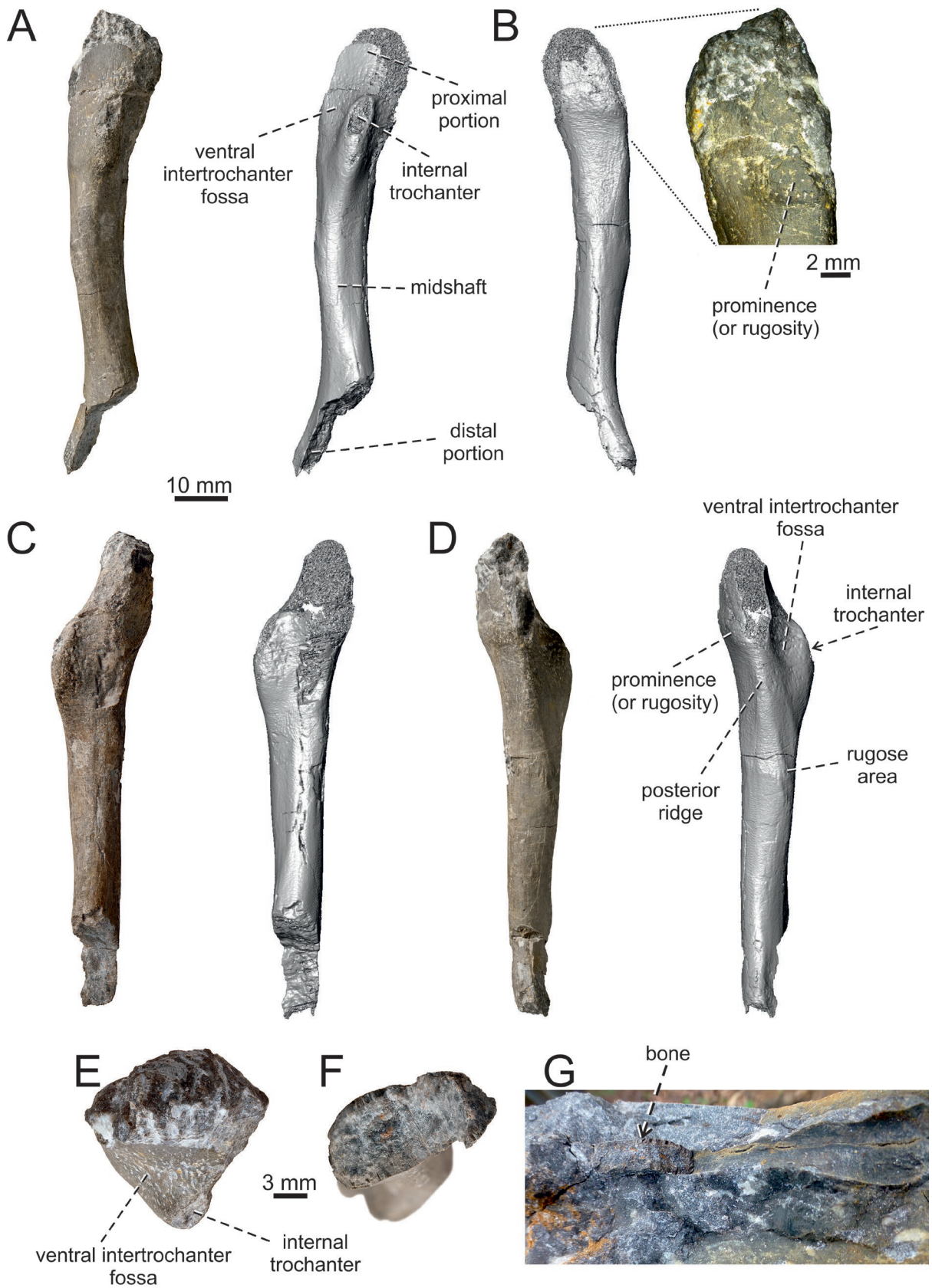
Fig. 3. The left femur Z 28224 from Rhaetian deposits of the locality Úbočka in the Strážov Highlands in: **A** — ventral, **B** — dorsal with a detail of the proximal portion, **C** — anterior, **D** — posterior, **E** — proximal, and **F** — distal aspects. **G** — The photography of the missing distal part of the bone in situ.
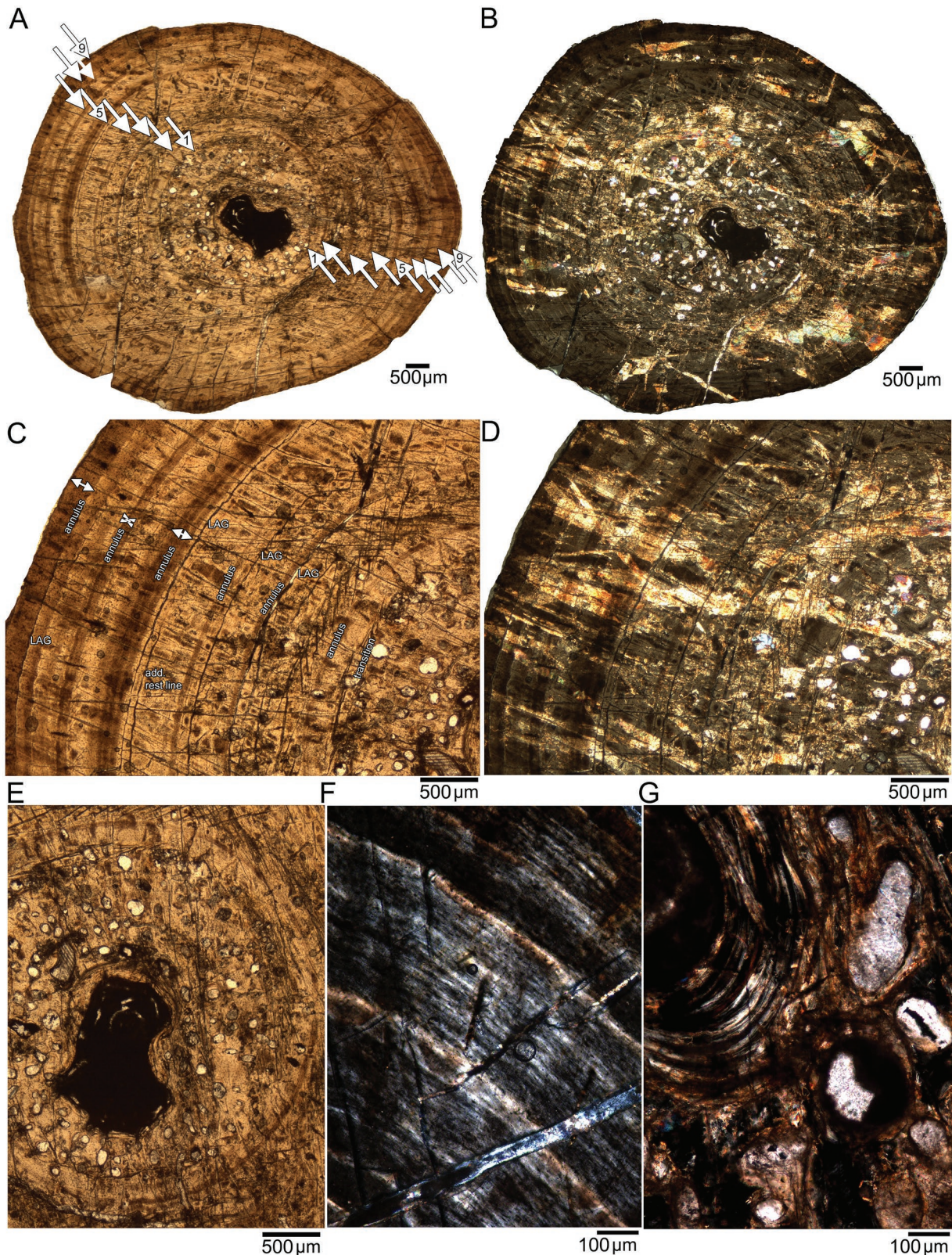
Fig. 4. Histology and microanatomy of femur Z 28224 from the Rhaetian of Slovakia. **A** — femoral cross section in normal light. Arrows indicate growth marks. **B** — Same section in polarized light. Note the small medullary cavity surrounded by scattered erosion cavities in the inner cortex. **C** — Detail of growth record in normal light. The cortex is evenly stratified by LAGs closely followed by bright lines interpreted as annuli, although clear zones are missing. **D** — Same section in polarized light. **E** — Detail of the small medullary cavity surrounded by the remodelling zone, which largely occupies the 1st inner growth cycle. **F** — Detail of highly organized avascular parallel-fibred tissue in polarized light. **G** — Detail of endosteal bone lining the small medullary cavity and scattered erosion cavities.

only 1.94 % of the surface area when compared to the cortex, is located somewhat off-centre (Fig. 4A,B,E). The medullary cavity is lined by an irregularly thick layer of endosteal bone (Fig. 4E,G) and surrounded by a remodelling zone in which mainly round-oval erosion cavities are scattered (Fig. 4E,G). The compact cortex, which consists – as far as can be said due to diagenesis – of highly organized parallel-fibred tissue, is avascular (Fig. 4). Osteocytes are numerous but small. Bone compactness is 96.35 % (ratio of the small medullary cavity and the erosion cavities of the inner remodelling zone to the periosteal cortex). Thus, the femur can be considered highly osteosclerotic.

The entire cortex is regularly stratified by distinct growth marks (Fig. 4A,C,F). Stratification is indicated by changes in colour but not by changes in tissue organization or vascularization. Growth marks are deposited as thin annuli (Fig. 4C). Some annuli are accompanied by lines of arrested growth (LAG) that can also be embedded into the annulus. The first visible growth cycle is the largest one and encompasses most of the remodelling zone, which means the area where erosion cavities are most densely scattered (Fig. 4E). The possibility cannot be entirely excluded that inner growth marks were destroyed by remodelling, but it seems unlikely. Subsequent growth cycles are evenly spaced. Nine growth cycles can be followed all around the cross section, indicating an advanced ontogenetic stage (i.e. adult) of the individual (Fig. 4A).

<div align="center">

Archosauromorpha von Huene, 1946
Choristodera Cope, 1884
Pachystropheidae Kuhn, 1961
Pachystropheus von Huene, 1935

aff. *Pachystropheus*
(Figs. 5, 6)

</div>

Referred Specimen: An isolated right femur, Z 28225.
Horizon: Upper Triassic (Rhaetian), Westbury Formation.
Locality: Aust Cliff, Gloucestershire (United Kingdom).

Description

Morphology: The femur is proximally and distally incomplete due to damage. It has a rather simple morphology. The bone has a slightly thicker proximal head when compared to the flat distal end (Fig. 5). The region, where the internal trochanter is usually located in the femur, is damaged. However, some bone protrusion can be identified here based on the edge of the bone, forming a ridge which gradually diminishes distally. A small portion of the shallow indistinct fossa (or depression) appears to be present posterior to it. It can probably be interpreted as the ventral intertrochanteric fossa – a presence of the rough insertional surface supports such interpretation. The shaft of the bone is straight, slender, and constricted (Fig. 5A). The curved proximal head is ventrally convex and dorsally straight to convex (Fig. 5C,D).

The proximal and distal ends are angled to each other. The maximum length of the preserved portion is 54.4 mm. The maximum width of the proximal end is 11 mm, that of the midshaft is 6.7 mm, and that of the distal end 11.7 mm, as far as preserved. The mid-section of the bone is oval in cross-section (Fig. 6).

Remarks: The long bone sample Z 28225 is tentatively interpreted as a femur of aff. *Pachystropheus*. The bone originates from the classic Rhaetian exposure at Aust Cliff (numerous assemblages of *Pachystropheus* are known from this locality, see Storrs 1994). Although its proximal and distal ends are incomplete, we identified it as a femur because of its similarities to a femur of *Pachystropheus* figured by Storrs et al. (1996: text-fig. 12). Note that the proximal half in Z 28225 is more curved when compared to femora figured by Storrs et al. (1996), but this can be interpreted as intraspecific variation. We are also convinced that we have a femur here because humeri are usually asymmetrically curved, generally more massive and distally broadened (Storrs & Gower 1993: fig. 2; Romer 1956). Zeugopodial elements also differ in morphology and are usually asymmetrical (Romer 1956). Fibulae are often strongly curved, as Z 28225 is, but they are usually slenderer and show a rather simple morphology. Tibiae are much more robust with a massive proximal head. The morphology of the proximal articulation facets of radius and ulna is more complex as this is indicated by the incomplete proximal part of Z 28225.

Microanatomy, histology and growth record: The midshaft section has an irregularly shaped free central cavity that is locally invaded by a few endosteal trabeculae, indicating that the endosteal area had been actively expanding (Fig. 6A, C,E). The free cavity makes up 11.7 % of the surface area of the cross section. Remodelling of the periosteal bone by erosion cavities is not visible. The cortex consists of parallel-fibred tissue (Fig. 6F,G). Osteocytes are numerous but small. A few longitudinal and radial simple vascular canals are scattered around (Fig. 6A,B). Vascular density is low, resulting in a bone compactness of 86.5 %. Thus, the femur can also be considered as osteosclerotic when compared to a standard terrestrial tetrapod.

The cortex is stratified by distinct growth marks. Growth marks mainly consist of thin annuli (Fig. 6A,C). Annuli and zones can be divided by changes in colour and also by changes in tissue organization and vascularization. Some annuli are accompanied by or contain rest lines. The first visible growth cycle is the largest one. By the time of death, it was already largely replaced by the expansion of the medullary cavity. The possibility cannot entirely be excluded that inner growth marks were destroyed by the expansion of the medullary cavity, but it seems unlikely. A short distance from the end of the 1st growth cycle, two closely spaced rest lines are deposited, which are considered as one single annual growth cycle (2nd growth cycle). The next growth cycle (3rd) is the widest in the entire cross section. The two following growth cycles (4th and 5th) are again closely spaced. The end of the 5th growth cycle is indicated by a broad annulus and several closely

spaced rest lines. The last deposited growth mark is followed by highly organized and nearly avascular parallel-fibred tissue, indicating that the individual was still growing, although its growth rate had decreased. Altogether 5 growth cycles are counted where the cortex is thickest, indicating that the animal died in its 6 year of life. On the opposite side of the bone where the cortex is thinner, only three growth marks are visible, which is due to merging of growth marks here.

Discussion

Taxonomic assignment of Z 28224

In the following, we compare the morphology and histology of femur Z 28224 to femora of Middle and Upper Triassic reptiles that are well known, to address the possible taxonomic affinities of the unique find from Slovakia.

Sauropterygia: Sauropterygia is a diverse group of diapsid marine reptiles that ranged from the Lower Triassic until the end of the Cretaceous (Rieppel 2000). The Triassic radiation includes predominately shallow marine forms such as the Eosauropterygia (Pachypleurosauria, Nothosauria, Pistosauria) as well as the Placodontia (Rieppel 2000). Most Triassic representatives were restricted to epicontinental seas of the Tethys Ocean. Triassic Sauropterygia are notable for having a large variety of ecologies, life histories and feeding strategies, which enabled them to live contemporaneously in the same habitats (Klein et al. 2015a,b, 2016). Taxonomic affinities of Z 28224 to marine eosauropterygians can be excluded due to differences in stratigraphic range, morphology, microanatomy, and tissue type. Pachypleurosauria and Nothosauria are so far not documented after the Ladinian, at least in the western Tethyan province (Rieppel 2000) and younger occurrences in the eastern Tethyan province are questionable due to the uncertain stratigraphic range of the sediments (see Rieppel
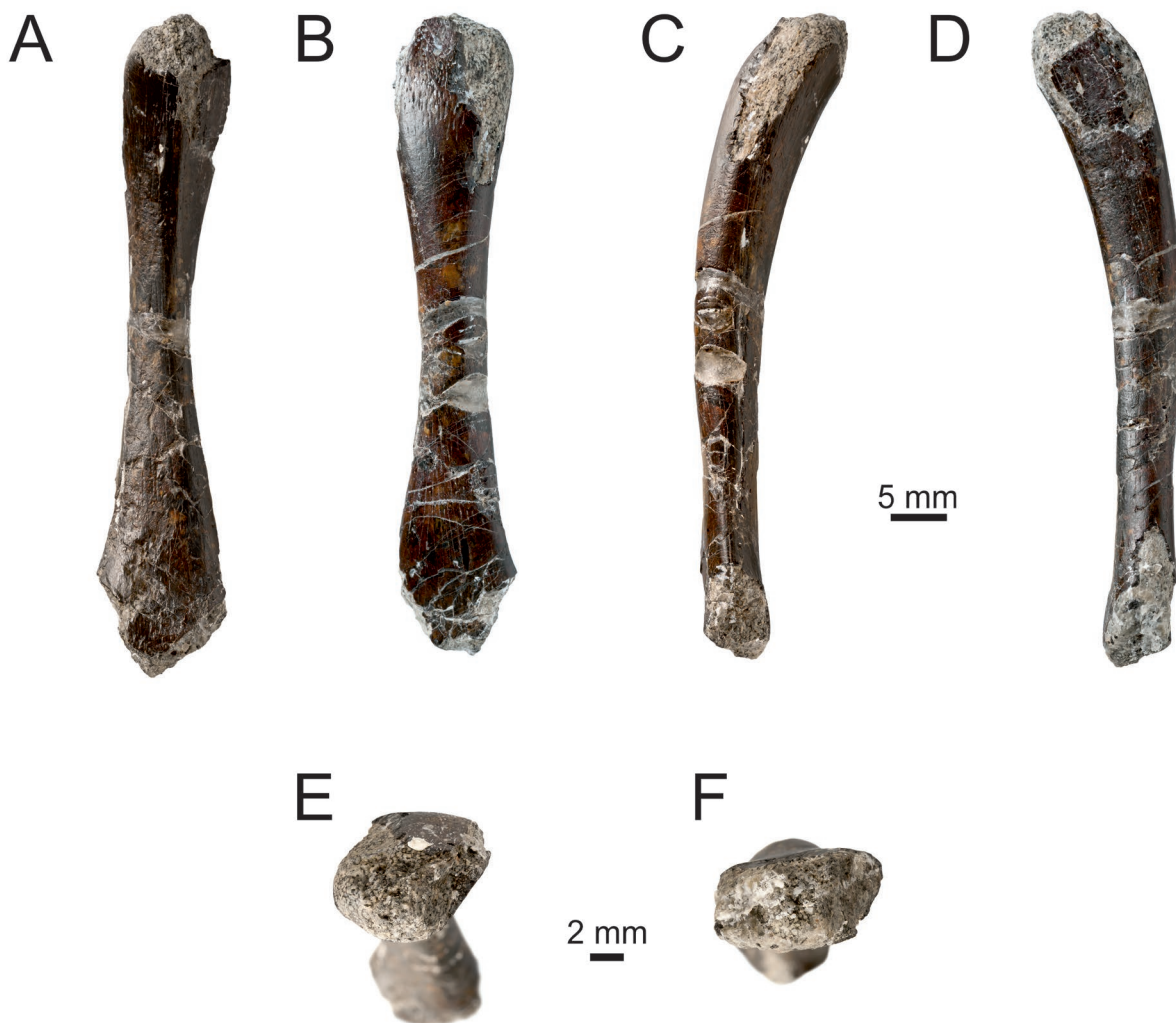
Fig. 5. The right femur Z 28225 of aff. *Pachystropheus* from Rhaetian deposits of the locality Aust Cliff, Gloucestershire, UK in: **A** — ventral, **B** — dorsal, **C** — anterior, **D** — posterior, **E** — proximal, and **F** — distal aspects.
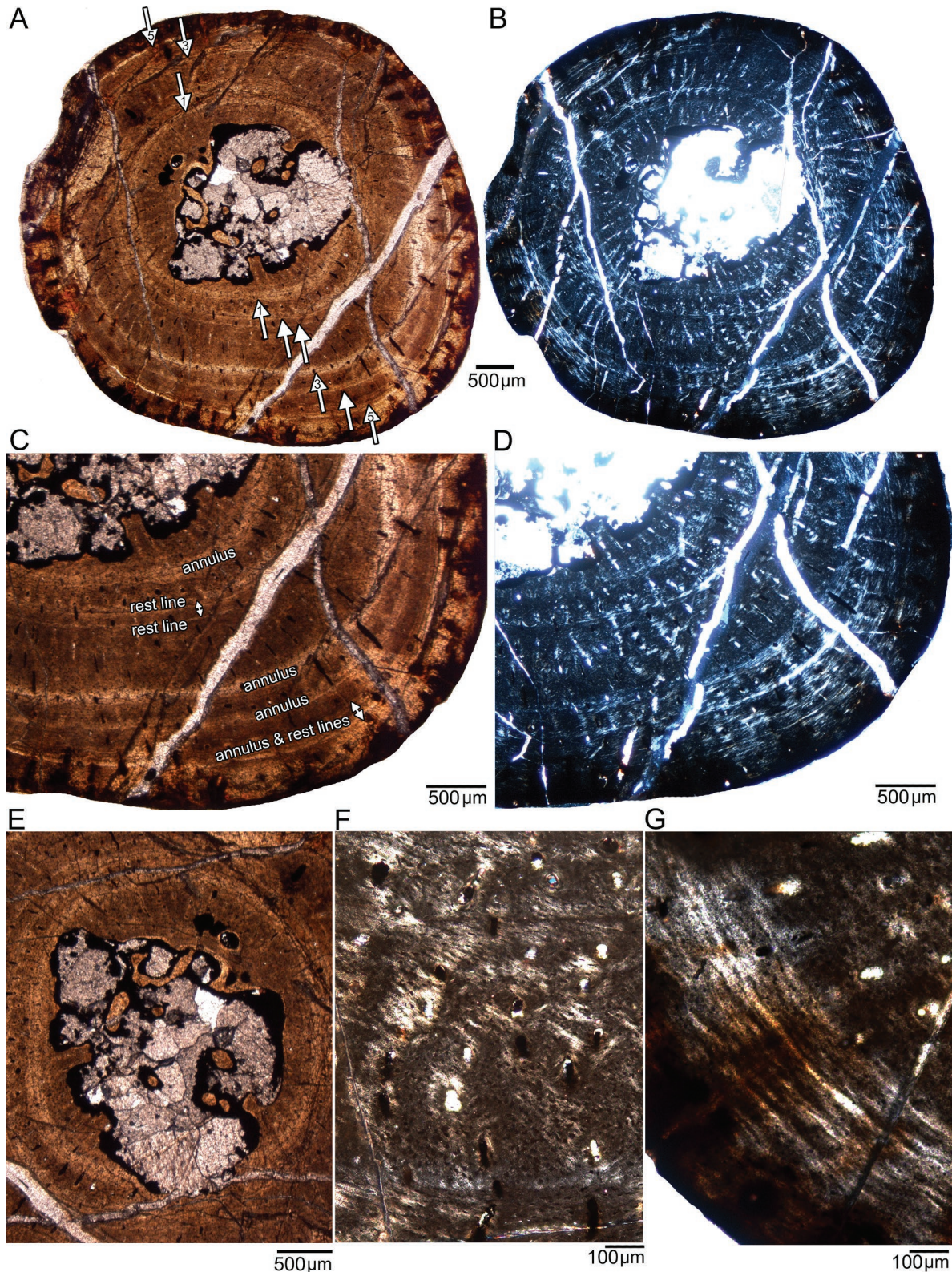
Fig. 6. Histological and microanatomy of femur Z 28225 aff. *Pachystropheus* from Rhaetian deposits of the locality Aust Cliff, Gloucestershire, UK. **A** — femoral cross section in normal light. Arrows indicate growth marks. **B** — Same section in polarized light. Note the relatively large expanding medullary cavity. **C** — Detail of growth record in normal light, depicting widely spaced growth marks in form of bright lines (i.e. annuli) and occasionally rest lines, which are not very distinct and cannot be followed all around the cross section. **D** — Same section in polarized light. **E** — Detail of the medullary cavity with few endosteal trabeculae. The medullary cavity largely occupies the 1st inner growth cycle. **F** — Detail of parallel-fibred tissue with simple longitudinal and radial vascular canals in polarized light. **G** — Detail of parallel-fibred tissue followed by highly organized parallel-fibred bone which forms the broad 5th annulus.

2000; Liu et al. 2011; Zou et al. 2015; Sun et al. 2016). Pachy-pleurosaurian affinities can additionally be excluded due to size differences. Anisian nothosaurs and pistosauroids are within the size range of the femur from Slovakia (Klein et al. 2015c), but most Ladinian taxa are larger (Sues 1987; Rieppel 2000; Klein et al. 2016). An internal trochanter, which is pronounced in Z 28224, is also present in eosauropterygians but modified and differs in size, shape, and location from that of Z 28224. Femur Z 28224 differs further from eosauropterygian femora in the morphology of the proximal and distal head (Klein 2010; Klein et al. 2015c). The division into two condyles is in the eosauropterygian femur already visible in the distal midshaft area. This area is also preserved in Z 28224 but no division into two condyles is obvious. The distal end is in Z 28224 more set off from the midshaft and is flatter when compared to an eosauropterygian femur. Bone histology of eosauropterygians differs from that of Z 28224 in having a moderately to highly vascularized cortex and poorly organized parallel-fibred tissues, which is interspersed in some taxa even with woven bone (Klein 2010; Hugi et al. 2011; Krahl et al. 2013; Klein & Griebeler 2016, 2018; Klein et al. 2016).

Several taxa of cyamodontoid placodonts are described from the Upper Triassic (Rieppel 2000). However, morphological comparison is difficult since most of these taxa are only incompletely known, and usually only a skull or parts of their dermal armour is diagnostic; postcranial material such as long bones often cannot be reliably assigned. *Macroplacodus* and *Psephoderma* are so far the only placodonts documented in Rhaetian sediments by diagnostic material (Rieppel 2000, 2001). *Placochelys* was also in the past considered to occur in Rhaetian deposits, but according to Rieppel (2000) this cannot be established on the basis of diagnostic material. So far as is known, femoral morphology is in general in cyamodontoid placodonts not as complex as in Z 28224 (see e.g., Jaekel 1907: plate VIII). An internal trochanter is developed in placodonts (Rieppel 2000), although it is less pronounced in *Psephoderma* and *Placochelys* when compared to the stratigraphically much older *Placodus*, where it is distinctly offset (Romer 1956). Humerus and femur histology of the cyamodontoid placodont *Psephoderma* from the Rhaetian of Switzerland was studied by Klein et al. (2015a,b), and some similarities with Z 28224 can be found, although the morphology and microanatomy differ (Pinna & Nosotti 1989; but see Jaekel 1907). *Psephoderma* and Z 28224 share a highly organized, nearly avascular parallel-fibred tissue regularly interrupted by closely spaced growth marks and both have a small medullary cavity surrounded by a remodelling zone. However, remodelling of the periosteal bone is distinctly higher in the *Psephoderma* femur indicated by numerous large, scattered erosion cavities reaching beyond the middle cortex (Klein et al. 2015a: fig 2D, 2015b: fig. 2B).

Choristodera: Choristoderes are a clade of extinct diapsid reptiles with an exclusively Laurasian occurrence. The oldest known choristoderes are from the Ladinian of southern Germany (Schoch 2015) and surprisingly, the youngest records are reported from the Oligocene and Miocene of Europe (Hecht 1992; Evans & Klembara 2005). Choristoderes are usually regarded as freshwater inhabitants (Storrs et al. 1996; Matsumoto & Evans 2010).

The femur of the choristoderes *Khurendukhosaurus* from the Lower Cretaceous (Aptian) of Khuren Dukh, Mongolia, has a different morphology of the proximal head and of the internal trochanter. The femoral midshaft is curved in *Khurendukhosaurus* (Matsumoto et al. 2009: fig. 2l-p), when compared to Z 28224. Skutschas & Vitenko (2017) studied bone histology of a Lower Cretaceous choristodere from Siberia, which has affinities to *Khurendukhosaurus*. The only studied long bone in that study is a humerus, which was not cut at midshaft due to the large medullary region depicted and the elongated oval shape of the cross section. Tissue is highly organized avascular parallel-fibred tissue or even lamellar tissue. However, because of the non-midshaft sampling location microanatomical comparison is not reliable.

In an unpublished master's thesis (Toljagic 2012), which is available online, choristodere-like femora from the Upper Triassic (Norian, see Kowal-Linka 2019) of a locality close to the Lisowice village in Poland are described and their histology studied. Size but mainly morphology of the femora from Poland differ from that of the femur from Slovakia. For example, the internal trochanter is more proximally located and not set off, whereas the distal end is much more massive in the femora from Poland. In regards to histology, the femora from Poland share with Z 28224, a relatively highly organized and poorly vascularized parallel-fibred tissue. Vascular canals seem to be represented only by small longitudinal simple vascular canals. The centre has a small free cavity which is surrounded by an actively expanding medullary region indicated by endosteal trabeculae and scattered large erosion cavities in the innermost cortex. Three growth marks identifiable in the Polish specimen are widely spaced, which is also different from Z 28224.

Rib samples of the large choristoderan *Champsosaurus* from the Late Cretaceous of North America had been studied by Nopcsa & Heidsieck (1934). The ribs show highly organized avascular tissue with numerous scattered erosion cavities, indicating remodelling of periosteal bone.

Pachystropheus

The taxon *Pachystropheus* is problematic because the holotype of *Pachystropheus rhaeticus* (E. von Huene 1935) consists of a fragmentary and disarticulated bone assemblage distributed over a small slab, interpreted as associated bones of a single individual. The assignment of many bones by v. Huene were labelled by a question mark (v. Huene 1935) and thus, except maybe for vertebrae, the bones of the holotype are not diagnostic. E. v. Huene referred in her work (v. Huene 1935) to figures and descriptions of two older publications (F. v. Huene 1902; v. E. v. Huene 1933), including the sketch of an incomplete femur (E. v. Huene 1933: fig. 45),

which also present no diagnostic features. Since then abundant material from Rhaetian bone beds from England and Germany had been assigned to *Pachystropheus* (e.g., Storrs & Gower 1993; Storrs 1994; Storrs et al. 1996; Mears et al. 2016; Sander et al. 2016), leaving the taxon as a waste bin taxon. *Pachystropheus* certainly requires a detailed revision in regards of its clear apomorphic features. Choristoderan affinities of *Pachystropheus* had already been proposed by Huene (1935; at that time considered to be rhynchocephalians) and were later continued by Storrs & Gower (1993) and Storrs et al. (1996). Renesto (2005) suggested that *Pachystropheus* could be an *Endennasaurus*-like thalattosaur. However, both allocations are problematic, because of the largely undiagnostic holotype and the lack of skull material, except for an isolated ectopterygoid assigned to *Pachystropheus* by Storrs et al. (1996).

This femur from the Rhaetian deposits of Aust Cliff (Z 28225) differs from the femur from Slovakia (Z 28224) by (1) size – the length of the femur of the holotype of *Pachystropheus* (63 mm) is equal to the size of our Aust Cliff bone (Z 28225) and thus, smaller than the femur from Slovakia. However, Storrs et al. (1996: text-fig. 13, BRSUG 7010.4) figured a femur of around 10 cm length, which is within the size range of Z 28224 and they interpreted this femur as belonging to an adult individual; (2) differences in the location and expression of the internal trochanter; (3) a curved proximal head (note that this curvature is, however, not as pronounced in the femora of *P. rhaeticus* figured by Storrs et al 1996: text-fig. 12-13); and (4) the proximal and distal end are angled to each other in the femur of aff. *Pachystropheus*, which is not the case in the bone from Slovakia.

Based on these morphological, as well as on micro-antomical (size of medullary cavity) and histological (i.e., size of remodelling zone, spacing pattern of growth cycles, vascular density) differences, we came to the conclusion that the find from Slovakia is not comparable to femora from the Rhaetian of England assigned to *Pachystropheus*. However, choristoderan affinities cannot be fully excluded for Z 28224.

Thalattosauria: *Endennasaurus* is a reptile described from the prolific Upper Triassic Zorzino Limestone of northern Italy and is referred to the thalattosaurs (Renesto 1992, Müller et al. 2005), a group of aquatic diapsids that are known exclusively from the Triassic (*Thalattosaurus*, *Hescheleria*, *Askeptosaurus*, *Clarazia*, *Nectosaurus*, and others). This group is known from North America, Europe and China, showing its cosmopolitan distribution (Merriam 1905; Peyer 1936a,b; Kuhn 1952; Renesto 1984; Nicholls & Brinkman 1993; Nicholls 1999; Rieppel et al. 2000; Liu & Rieppel 2001). A thalattosaur is also described from Austria (the Kössen Formation, outcrop near Salzburg; see Müller 2007).

Both known *Endennasaurus* specimens (Renesto 1992; Müller et al. 2005) show some degree of flattening, but they are preserved on stone slabs, so some features of the bones cannot be detailed with the same accuracy as in isolated, three-dimensionally preserved bones. The femur of *Endennasaurus* is proportionally longer and slenderer than in other known thalattosaurs (see Rieppel 1987; Liu & Rieppel 2001; Müller 2005). The proximodistal length of the femur of the holotype of *Endennasaurus* is 58 mm. The proximal head is moderately expanded and slightly flattened, the shaft is slender and shows a small degree of sigmoid curvature, with a slight constriction at midshaft, the distal head is less expanded than the proximal one and is also less flattened. The articular surfaces for the tibia and fibula are convex. The proximal and distal heads are only slightly angled to each other. A strong proximal trochanter is present, separated from the proximal head, showing a medioventral expansion that diminishes distally, as in Z 28224.

No data on the bone histology of thalattosaurs have been published so far.

Rhynchocephalia: Rhynchocephalia are a clade of lepidosaurs (Rhynchocephalia+Squamata) that exist from the Middle Triassic till today (Jones et al. 2013; Schoch 2015). Note however, that Simões et al. (2018) suggest that lepidosaurs and most other diapsids originated before the Permian/Triassic extinction event and thus, the Triassic might be seen as a period of radiation, not origin, for several diapsid lineages. Extant members of rhynchocephalians are represented only by the single genus *Sphenodon*. This taxon is restricted to a few small islands off the coast of New Zealand. However, the clade was very diverse and widely distributed across Pangea during the early Mesozoic (Fraser 1982, 1986, 1988, 1993; Whiteside 1986; Fraser & Benton 1989; Sues et al. 1994; Wu 1994; Sues & Reisz 1995; Evans et al. 2001). Their fossil record is restricted due to their usually terrestrial life style (except for Jurassic Pleurosauridae) and their relatively small size. Thus, femora for comparison are rare because usually only cranial and dental material is found and/or described as diagnostic. This clade is also known from the Upper Triassic of Poland (e.g., Kowalski et al. 2019).

Early members form the extinct clade Clevosauridae, which is currently thought to include several species allocated to three genera: *Clevosaurus*, *Brachyrhinodon*, and *Polysphenodon*. They are known from Britain (Swinton 1939; Fraser & Benton 1989; Säilä 2005; Keeble et al. 2018), Germany (Jaekel 1911; von Huene 1929; Fraser & Benton 1989), southern Africa (Gow & Raath 1977; Sues & Reisz 1995), China (Wu 1994), North America (Sues et al. 1994), and South America (Bonaparte & Sues 2006) during the Late Triassic to Early Jurassic. Among the clevosaurid taxa, as far as known, *Clevosaurus*, which is extremely similar to the modern *Sphenodon,* is the most species-rich and widely distributed (Asia, Europe, North America, South America, Africa; see Wu 1994; Sues et al. 1994; Reynoso 1996; Hsiou et al. 2015).

The femur Z 28224 indeed appears to exhibit generalized lepidosaurian morphology. With *Clevosaurus*, which has femoral morphology very similar to that of *Sphenodon*, it

shares a prominent internal trochanter and a slender, constricted midshaft. The femur of *Clevosaurus* retains a sigmoid flexure of the shaft (see Fraser 1988). It is difficult to completely evaluate this character in Z 28224, because the distal portion is broken off. Although a sigmoid appearance can be recognized, it appears not to be so pronounced, at least compared to Fraser`s specimen (see Fraser 1988: fig. 33). Moreover, the femur of *Clevosaurus* (based on described available specimens) is much smaller than Z 28224. According to Keeble et al. (2018), the complete left femur of *Clevosaurus* is approximately 25 mm long. This is in a sharp contrast with the Slovak find (the complete length of Z 28224 might reach approximately 100 mm). The much smaller length of the femur relative to Z 28224 is seen in *Brachyrhinodon*, *Polysphenodon*, *Homeosaurus* and even extant *Sphenodon* (see Fraser & Benton 1989: table 1). If Z 28224 represents a lepidosaurian, it would plausibly point to an insular gigantism or might indicate an invasion of the aquatic environment by rhynchocephalians/lepidosaurs long before pleurosaurids appeared in the Early Jurassic (see below).

Unfortunately, no histological data are available for these taxa, except for the modern *Sphenodon*, the bone histology and skeletochronology of which were studied by Castanet et al. (1988) in detail. A femur (NHMW 8108:2; 4.2 cm in length) of *Sphenodon punctatus* from the Natural History Museum of Vienna (Austria) was thin sectioned at the IGPB (Schucht 2018, unpublished master thesis). The cross section displays a moderately sized but actively expanding medullary cavity that is surrounded by a thin layer of endosteal bone. The bone is made of avascular lamellar tissue that contains a high number of osteocytes. The cortex is regularly stratified by relatively closely and evenly spaced growth marks. Osteocytes are very numerous and regularly distributed through the cortex. The femur of *Sphenodon* (Fig. 7C, D) differs from femur Z 28224 in the presence of a larger medullary cavity and in the lack of periosteal resorption in the inner cortex by scattered erosion cavities (Fig. 7A, B). However, the avascular tissue, spacing of growth marks, and relatively high number of growth marks (9 in Z 28224 and 16 in NHMW 8108:2) is very similar in both specimens (Fig. 7).

The clade Rhynchocephalia includes also a marine radiation. The extinct Pleurosauridae from the Lower Jurassic of Germany is such a marine piscivorous rhynchocephalian. Despite a much smaller size and a gracile appearance the femoral morphology of *Paleopleurosaurus* fits quite well, including the shape and location of the internal trochanter (Carroll 1985). Bone histology of the pleurosaurid *Paleopleurosaurus* was studied by Klein & Scheyer (2017). The sampled femur (Fig. 7E, F) measured ~5.2 cm and depicts a microanatomy that is quite different compared to Z 28224. The femur of *Paleopleurosaurus* is not osteosclerotic but has a huge free central cavity, more closely resembling terrestrial than aquatic conditions. Tissue is in both femora highly organized, but the femur of *Paleopleurosaurus* show at least some vascularization (Klein & Scheyer 2017) and is not avascular as in Z 28224. Also, the spacing of growth marks differs and
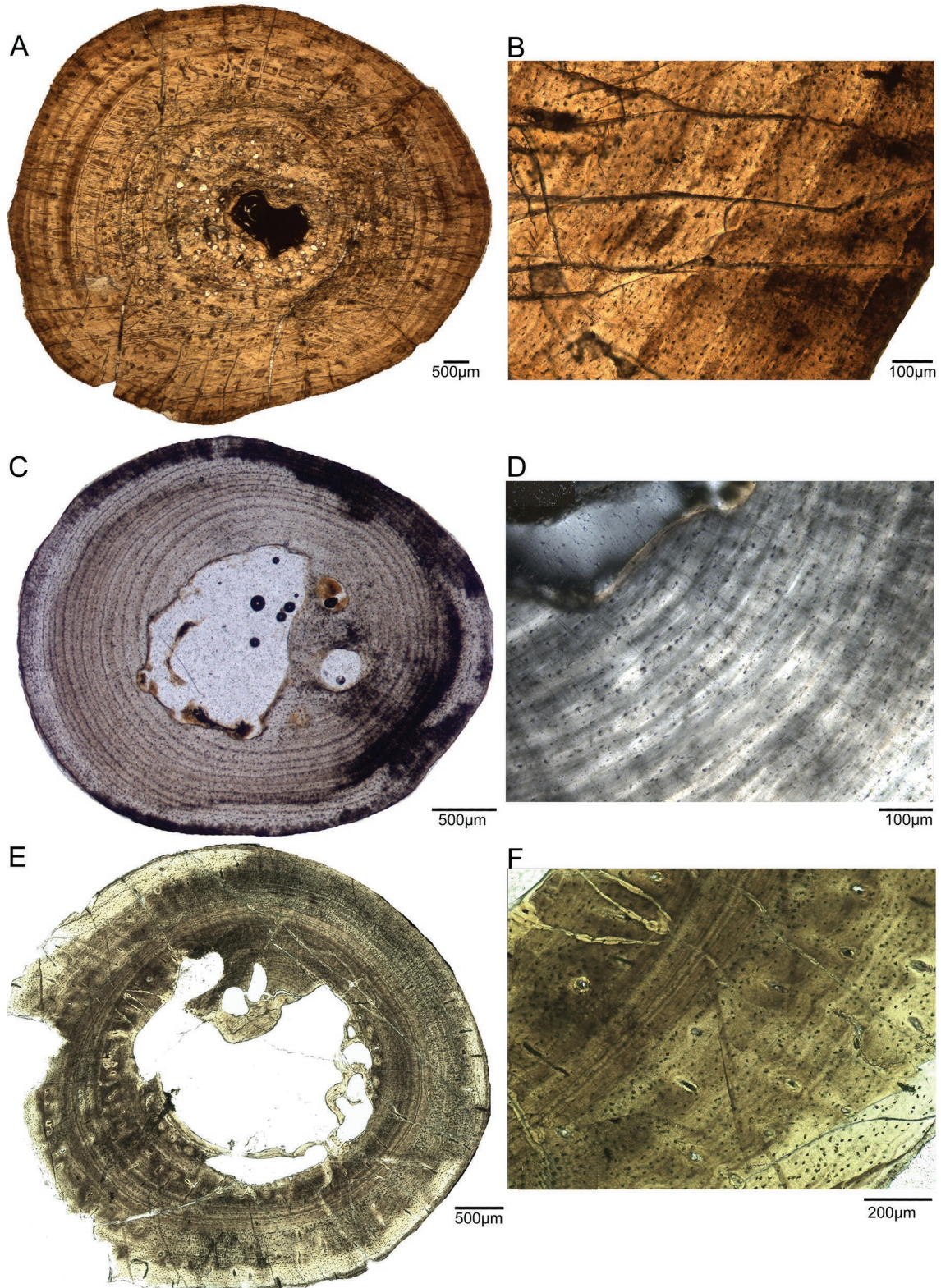
the pattern of remodelling of periosteal bone (few small scattered erosion cavities in the femur from Slovakia vs. intensive and active expansion of the medullary cavity in *Paleopleurosaurus*).

Conclusion

On the basis of morphological, histological and stratigraphic evidence, we can exclude affinities of the bone from Slovakia to Eosauropterygia. A taxonomical assignment of the Rhaetian femur Z 28224 from Slovakia to a cyamodontoid placodont, an *Endennasaurus*-like thalattosaur, or a rhynchocephalian (lepidosaurian) might be conceivable. Whereas the femur from Slovakia is likely within the size range of a placodont, it is more-or-less double in length when compared to *Edennasaurus* and to most lepidosaurs/rhynchocephalians (but note that the diversity of Triassic lineages is surely not completely known). The morphology of the Slovak find might also point to a presence of an undetermined choristoderan, but the histology of Z 28224 does not support such a statement because its histological and microanatomical features differ from that of other so far known choristoderes. In general, it is difficult to make reliable determinations on the basis of isolated limb bones and thus, all interpretations of an isolated femur need to be met with caution. For all these reasons, we allocate this bone here only as Diapsida indet.

Although a precise taxonomical assignment is not possible, the bone described here from the Úbočka opens a window on the Upper Triassic Western Carpathian faunal assemblage. Previously, dinosaur footprints (see Michalík et al. 1976) from High Tatra Mountains and fish teeth and scales (Zahradníková in Michalík et al. 2013) were the only evidence of vertebrates from this time period in this region. We can assume that the bone either represents an allochthonous component in this marine environment, transported postmortem and most likely from nearby dry land (i.e., rhynchocephalian affinities) or it belonged to an inhabitant of this shallow coastal environment (e.g., cyamodontoid – placodont affinities or rhynchocephalian affinities). In any case, the femur shows indication of transport. Only further, more complete material from this locality might shed light to this problem.

Fig. 7. Comparison of microanatomy and histology of Z 28224 with rhynchocephalian femora of the modern *Sphenodon punctatus* and the Jurassic *Paleopleurosaurus*. **A** — Femur (Z 28224, approximately about 10 cm in total length) from the Rhaetian of Slovakia in normal light. **B** — Detail of bone tissue of Z 28224 in normal light. **C** — Femur of *Sphenodon punctatus* (NHMW 8108:2, 4.2 cm) in normal light (Schucht 2018, unpublished master's thesis). **D** — Detail of bone tissue of NHMW 8108:2 in normal light. **E** — Femur of *Paleopleurosaurus* (SMNS 81774, 5.2 cm) in normal light (from the study of Klein & Scheyer 2017). **F** — Detail of bone tissue of femur of *Paleopleurosaurus* in normal light.

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