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A Middle Triassic pachypleurosaur (Diapsida: Eosauropterygia) from a restricted carbonate ramp in the Western Carpathians (Gutenstein Formation, Fatric Unit): paleogeographic implications

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Abstract: An eosauropterygian skeleton found in the Middle Triassic (upper Anisian) Gutenstein Formation of the Fatric Unit (Demänovská dolina Valley, Low Tatra Mountains, Slovakia) represents the earliest known occurrence of marine tetrapods in the Western Carpathians. The specimen represents a partly articulated portion of the postcranial skeleton (nine dorsal vertebrae, coracoid, ribs, gastral ribs, pelvic girdle, femur and one zeugopodial element). It is assigned to the Pachypleurosauria, more precisely to the *Serpianosaurus–Neusticosaurus* clade based on the following combination of features: (1) small body size; (2) morphology of vertebrae, ribs and femur; (3) tripartite gastral ribs; and (4) microanatomy of the femur as revealed by µCT. Members of this clade were described from the epicontinental Germanic Basin and the Alpine Triassic (now southern Germany, Switzerland, Italy), and possibly from Spain. This finding shows that pachypleurosaur reptiles attained a broader geographical distribution during the Middle Triassic, with their geographical range reaching to the Central Western Carpathians. Pachypleurosaurs are often found in sediments formed in shallow, hypersaline carbonate-platform environments. The specimen found here occurs in a succession with vermicular limestones in a shallow subtidal zone and stromatolitic limestones in a peritidal zone, indicating that pachypleurosaurs inhabited hypersaline, restricted carbonate ramps in the Western Carpathians.

Keywords: Reptilia, osteology, Gutenstein Limestone, Low Tatra Mountains, Mesozoic.

Introduction

Occurrences of vertebrates are extremely rare in the Triassic deposits of the Western Carpathians. With the exception of the late Triassic dinosaur tracks from the Tomanová Formation of the Tatra Mountains (Michalík et al. 1976; Michalík & Kundrát 1998; Niedźwiedzki 2011), no tetrapod remains were described until now. Therefore, the paleogeographic and paleoenvironmental distribution of Mesozoic reptiles in this region is poorly documented. Here, we describe an eosauropterygian skeleton, which represents an earliest Triassic vertebrate skeleton found in the Western Carpathians. The specimen was found in the Gutenstein Formation of the locality Štefanová Cave (Fig. 1; Demänovská dolina Valley, the Low Tatra Mountains). The deposits are of Late Anisian age (e.g., Bystrický 1970; Havrila in Biely et al. 1997; the age is based on brachiopods, echinoderms, conodonts and dasycladacean algae, see below).

Sauropterygia represent a diverse group of marine reptiles that existed from the late Early Triassic until the end of the Cretaceous (Rieppel 2000; Motani 2009). The Triassic radiation consists of shallow marine Placodontia, Pachypleurosauria, and Nothosauria as well as the more open marine Pistosauria. In contrast, the Jurassic and Cretaceous seas were ruled by the open marine Plesiosauria. Pachypleurosauria, Nothosauria and Pistosauria form the Eosauropterygia (Rieppel 2000). Their monophyly has been challenged due to the description of several new taxa from the Middle Triassic of China (e.g., Jiang et al. 2008; Shang et al. 2011; Wu et al. 2011), which exhibit a mosaic of pachypleurosaurian and nothosaurian characters, questioning the monophyly of pachypleurosaurs and nothosaurs (Wu et al. 2011; Ma et al. 2015). Isolated bones of Sauropterygia are the most common skeletal elements in the Muschelkalk bone beds of the Germanic Basin and are numerous in the Alpine Triassic. They are also quite common in the Middle Triassic of the eastern Tethyan (now South

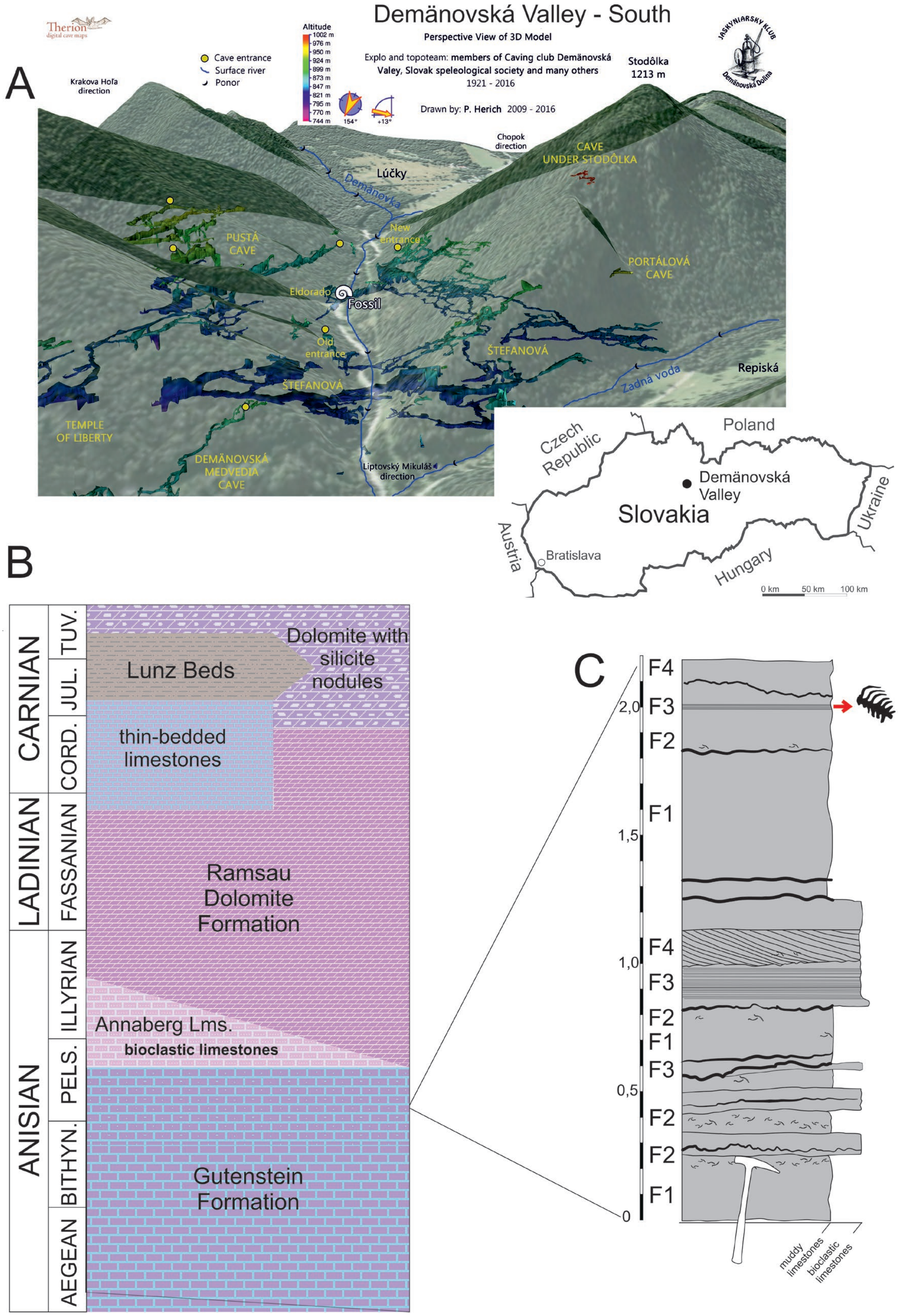

Fig. 1. Štefanová Cave in the Low Tatra Mts. **A** — Location of the cave in Slovakia and the find location. **B** — Lithostratigraphy of Middle–Upper Triassic formations of the Fatric Unit (Krížna Nappe) in the Low Tatra Mts. **C** — Lithological log of the Gutenstein Formation in the Štefanová Cave section. The pachypleurosaur find is indicated, and facies types of limestones are marked in the section (F1–F4 facies types are spelled out in Fig. 3 caption).

China) faunal provinces. Sauropterygia have never been documented from the Western Carpathians.

Pachypleurosauria are small (<120 cm) and have a long neck and tail as well as an elongated trunk region. They are interpreted as anguilliform swimmers, preferring hypersaline habitats and most likely feeding on small invertebrates/arthropods (e.g., Sues 1987; Rieppel 1989). Some pachypleurosaurs were viviparous [(Cheng et al. 2004); it should be noted that although the tiny specimen of *Neusticosaurus* was identified as an embryo by Sander (1988), the direct evidence for viviparity is restricted to the chinese taxon *Keichousaurus*, which is, however, frequently considered closer to nothosaurs (see Holmes et al. 2008)]. Pachypleurosaurs from the Alpine Triassic of Monte San Giorgio and China show morphological adaptations for swimming such as trunk shape, body ratios (e.g., neck, trunk, and tail lengths), simplification of limb bones, reduction of carpal and tarsal bones, and pronounced pachyostosis of vertebrae and ribs. Their long bones are pachyosteosclerotic (Hugi et al. 2011). Members of the *Serpianosaurus–Neusticosaurus* clade (Alpine Triassic; Sander 1989; Rieppel 1989, 2000) and *Keichousaurus* (Guizhou province; Lin & Rieppel 1998; Cheng et al. 2009; Xue et al. 2015) were highly abundant (with hundreds of complete skeletons found in the Alps and China).

The aims of this paper are: (1) an anatomical description of the skeleton; (2) its taxonomical allocation based on morphology, including data revealed from µCT; and (3) the paleogeographic and paleoecological implications of this find for the distribution of pachypleurosaurs during the Middle Triassic in the Western Carpathians.

Material and methods

The fossil skeleton (for measurements, see Table 1) was found in Štefanová Cave (Demänovská dolina Valley, Slovakia) within the Gutenstein Limestone. The find was made by cavers from the P. H. group (Demänovská dolina Valley Caving Club) and was excavated by the authors A. Č., M. O. and J. Š. The studied specimen is housed in the Slovak Museum of Nature Protection and Speleology, Liptovský Mikuláš (Slovakia) and prefixed by P15136. Standard anatomical orientation is used throughout this article. The specimen 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 with the following settings: VxSize=0.05978500; Current=220; Voltage=220; Inttime=20000; Average=3; Steps360=2400. The images were recorded over 360°. Data were analysed using Avizo 8.1 on a high-end computer workstation at the Department of Ecology (Comenius University in Bratislava). The photography of the fossil is from a D610 Nikon camera. The paleogeographic map was modified using modified data from several authors (Michalík & Kováč 1982; Häusler et al. 1993; Michalík 1993, 1994; Stampfli 1996; Diedrich 2009; Renesto 2010; Stockar et al. 2012; Beardmore & Furrer 2016).

Geological setting

The cave system of the Demänovská dolina Valley is located in the region of the Low Tatra Mountains in north-central Slovakia (Fig. 1A). The remains of the skeleton were recovered from dark grey bedded limestones inside the Štefanová Cave (in the part of the cave called “Eldorádo”), 26 metres directly below the river Demänovka (GPS 48°59’25.398 N, 19°35’21.32 E). These limestones belong to the Gutenstein Formation, which is well known from the Middle Triassic sequence of Austroalpine and Central Western Carpathian units. This formation was defined by Hauer (1853) and intended as a dark to grey-black bedded limestones with white carbonate veins, which alternated in their lower part with schists of the Werfen Formation and in their upper part (Annaberg Limestone *sensu* Tollmann 1966) with dolomites of the Ramsau Formation. In the Western Carpathians, similar limestones were also named as the Vysoká Formation (Vetters 1904), which is characterized by the presence of oolitic, biostromal, tempestite and sebkha-type carbonates (Michalík et al. 1992; Michalík 1997).

Table 1: Measurements and dimensions of P 15136 in millimeters.

Length of articulated part of the trunk column	49
Length/width/height of preserved vertebrae I-IX (measured in anteroposterior direction)	3.3/9.8/4.5 – 5.7/9.3/6.3 – 5.4/9.5/6.8 – 5.4/9.6/7 – 5.4/9.1/6.6 – 5.3/9.2/6.8 – 5.3/8.8/6.8 – 5.3/8.4/6.4 – 4.8/7.5/6.6
Length of complete ribs (measured in anteroposterior direction)	25
Length of gastralia	12
Length and width of incomplete coracoid	10
Length / width of incomplete right and left pubis	12.6/14.2 - 13/17
Length of incomplete femur	19
Midshaft width of femur	3.3
Width/thickness of proximal femur head	4.2
Length and width of incomplete zeugopodial element	12

The Middle Triassic carbonates of the Demänovská Dolina Valley are divided into the Gutenstein Formation, Annaberg Limestone and Ramsau Formation (Fig. 1B). They were already studied by Štúr (1868). He considered that they belonged to the Muschelkalk. The sequence described by Štúr (l.c.) comprises dark dolomitic limestones, crinoidal limestones with *Encrinus lilliformis* and coquina limestones with brachiopods and bivalves (e.g., *Decurtella decurtata*, *Spiriferina fragilis*, *Sp. mentzelii*, *Terebratulla vulgaris*, *Pecten discites*). These fossils proved the Anisian age of the Gutenstein Limestone (Kettner 1927; Matějka & Andrusov 1931). Bioclastic limestones below the base of the Ramsau Dolomite Formation also contain the Anisian dasycladacean algae, such as *Physoporella dissita*, *Ph. praealpina*, *Diplopora annulatissima* (Bystrický 1970; Biely et al. 1997). Diplopora-bearing limestones were recorded at several sites in the vicinity of the Demänovská Dolina Valley (e.g., Lúčky and Siná hill — Biely et al. 1997; Demänovská Cave of Liberty — Volko Starohorský 1950). In the uppermost part of the Gutenstein Formation, bioclastic limestones with cherts are also present. They contain holothurian sklerites *Theelia immisorbicula* and *Theelia* sp., as well as the conodonts *Prionidina mülleri*, *Gondolella* cf. *constricta*, *Neohindonella* sp., *Gondolella excelsa*, and *Gondolella hanbulogi* (Havrila in Biely et al. 1997). These microfossils indicate that the transition between the Gutenstein Limestone Formation and the Ramsau Dolomite Formation corresponds to the Pelsonian/Illyrian boundary (i.e. Middle to early Late Anisian).

The reptile skeleton was found in peritidal facies of the Gutenstein Formation in the Štefanová Cave section (Fig. 1C). Similarly as in other successions of the Gutenstein Formation in the Alps and Carpathians, they were deposited on muddy tidal flats affected by episodic high-energy storm events (Mišík 1968, 1972; Michalík et al. 1992; Michalík 1997; Hips 1998, 2007; Rüffer & Bechtädt 1998; Bechtel et al. 2005; Rychliński & Szulc 2005; Gaál 2016). These facies reveal sedimentary environments of the Anisian carbonate platform, which was developed in the Western Carpathian area (Fig. 2).

Facies analysis of sedimentary environments

The Štefanová Cave section is composed of shallow subtidal to peritidal facies types, with vertical stacking implying

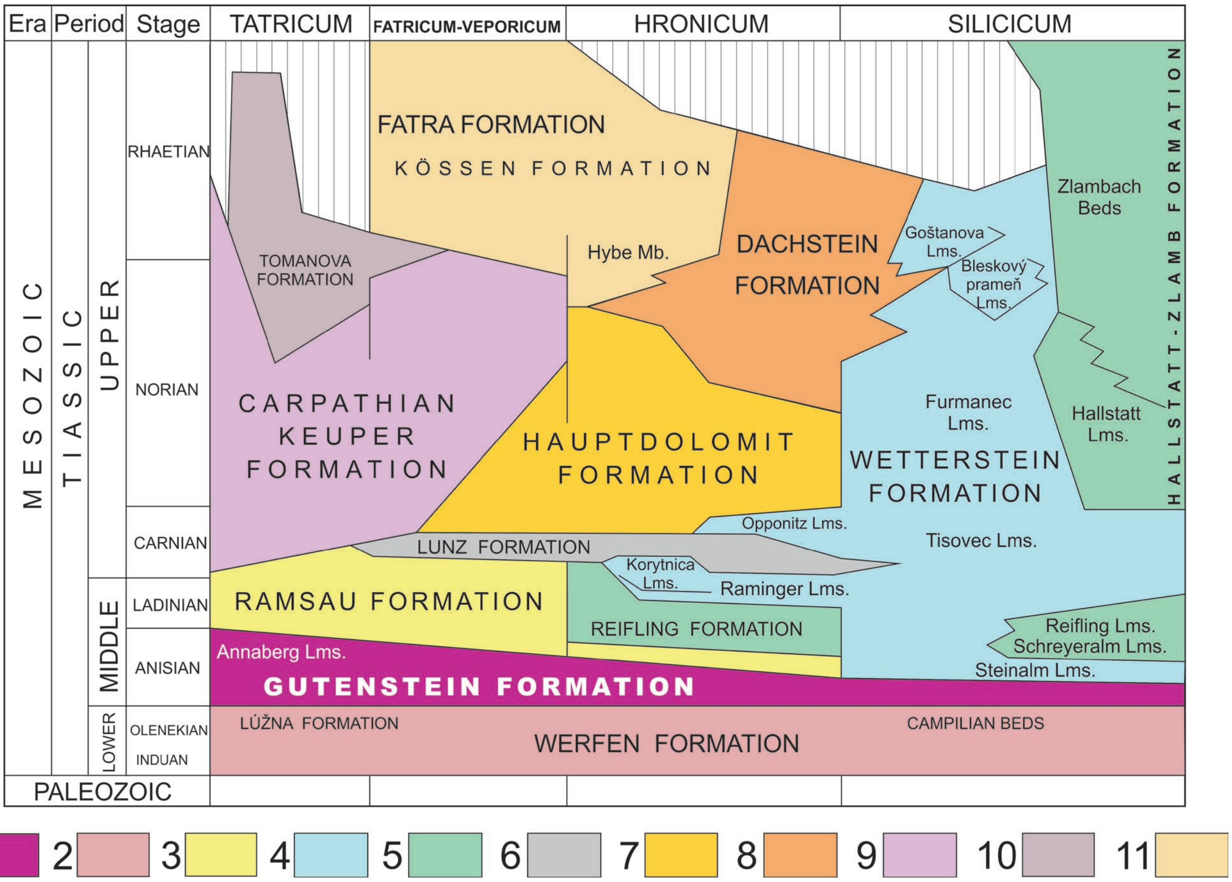

Fig. 2. Monoclinal carbonate ramp of the Gutenstein Formation within Triassic platform-basin system of the Central Western Carpathians. Explanation: 1 — carbonate ramp facies; 2 — continental facies; 3 — lagoonal hypersaline dolomites; 4 — reefal facies of rimmed platforms; 5 — basinal facies; 6 — pluvial terrigenous facies; 7 — sebkha-type dolomite facies; 8 — lagoonal peritidal facies; 9 — terrigenous red-bed facies; 10 — swamp and estuarine facies; 11 — biostrome intra-platform facies (adapted from Michalík 1977 and completed by facies types of lithostratigratigraphic formations).

a cyclic nature of deposition. Subtidal facies are formed by dark-grey bedded limestones (Fig. 3A) with mudstone to wackestone microfacies, evaporate pseudomorphs (so-called birdseyes — Fig. 3B), pellets (coprolites) and thick-walled ostracods. The rare species *Meandrospira deformata* (Fig. 3C) belongs to the foraminifers with ecological adaptation to hypersaline facies (Salaj & Polák 1978). Subtidal facies indicate a low-energy hypersaline environment on a restricted carbonate ramp.

Shallow subtidal facies were colonized by burrowing organisms (Fig. 3D). The limestones are heavily bioturbated by *Thalassinoides* (Fig. 3E), the burrows of which are sometimes truncated by erosional surfaces and dispersed to worm-like structures known as vermicular limestones. It seems that bioturbated lime mud sediments were eroded by ephemeral storm currents. Trace fossil abundance was probably related to the hypersaline conditions of the Anisian carbonate ramp (see Jaglarz & Uchman 2010).

The subtidal facies are overlain by intertidal facies with cryptalgal lamination (Fig. 3F). The limestones exhibit a microbial wrinkle structures of algal muds, fenestral structures and desiccative pores. The presence of these microbial and subaerial structures indicates shallow-water tidal flat environments of restricted lagoons with intermittently exposed conditions.

Intertidal flat deposits are bounded by erosional scours and overlain by cross-stratified beds of bioclastic limestones (Fig. 3F–I). These limestones are rich in birdseye particles, intraclasts, peloids, skeletal grains of crinoids, foraminifers (e.g., *Glomospirella lampangensis*, *Pilamminella* cf. *gemerica*) and ostracod shells (Fig. 3G, H, J). Cross-stratified beds in the Gutenstein Limestone could be interpreted as deposits of shallow tidal channels or sedimentary lags filled by tempestites. Their ripple cross-stratification also resembles imbricated structures from storm-dominated Anisian carbonate ramps in the Central Western Carpathians (Malé Karpaty Mts., Michalík et al. 1992; Michalík 1997; High Tatra Mountains, Jaglarz & Szulc 2003), Aggtelek-Rudabánya Mountains (Hips 1998) and the Germanic Basin (Schwarz 1975).

The Gutenstein Formation at the Štefanová Cave section was deposited in shallowing-upward cycles that capture a transition from shallow subtidal to peritidal zones and from low-energy to high-energy environments. The fossil skeleton of the pachypleurosaur was found in the shallowest part of the peritidal sequence, where gradual shoaling led to formation of intertidal algal mats in restricted hypersaline lagoons (Fig. 1C — F3 facies type of cryptalgal limestones). Vermicular limestones from shallow subtidal environments can also indicate a higher salinity, which suggest that pachypleurosaurs inhabited as swimmers hypersaline waters of the shallow carbonate ramp.

Systematic paleontology

It should be noted that some authors (Wu et al. 2011; Ma et al. 2015) did not find support for the clade Pachypleurosauria rather than Eosauropterygia. The taxa previously included in the Pachypleurosauria were found to be scattered in the pectinate basal part of the Eosauropterygian tree. According to these authors, Sauropterygia includes the Placodontia and the Eosauropterygia, the latter containing the “pachypleurosaur-grade” taxa, and the monophyletic Nothosauroidea and Pistosauroidea (comprising plesiosaurs). Other recent phylogenetic hypotheses, however, with discordant results have been published (e.g., Lee 2013). The resolving of these conflicts between results from data sets is beyond the aim of this paper and we choose to retain Pachypleurosauria as a valid taxon here.

Sauropterygia Owen,1860
Eosauropterygia Rieppel, 1994
Pachypleurosauria Nopcsa, 1928

Pachypleurosauria indet. aff. *Serpianosaurus* Rieppel, 1989/
Neusticosaurus Seeley, 1882
(Figs. 4–7)

Referred specimen: partly articulated skeleton comprising associated parts of the posterior trunk region P 15136

Horizon: Gutenstein Limestone Formation of the Demänovská Cave system in the Low Tatra Mountains, middle to early late Anisian, lower Middle Triassic.

Locality: Štefanová Cave (Demänovská dolina Valley, Slovakia), 48°59‘25.398 N, 19°35‘21.32 E.

Description

Dorsal vertebrae: Nine articulated dorsal vertebrae are preserved in anatomical position (Figs. 4, 5). In dorsal view they appear swollen (pachyostotic). The anteroposteriorly elongated centra are shallowly amphicoelous. In lateral aspect, the centrum is constricted and slightly concave (Fig. 6C). The synapophyses are large and protrude strongly laterally (Fig. 6). The neural canal is small and rounded. The neural spine, which is most completely preserved on the 4th vertebra (counted from posterior; see Fig. 6A–E) is rectangular in shape and longer than high. Pre- and postzygapophyses are small, only slightly inclined from a horizontal plane. They possess articulation areas that are not laterally expanded, but more-or-less directed anteroposteriorly.

Ribs: Seven ribs are well preserved on the left side (Fig. 5). They are robust and curved. The curvature is especially distinct in the anterior ones, where the ribs are markedly bent in the proximal third of their length. The last two posteriorly located ribs are slightly smaller relative to the others. Rib thickness is largest along the proximal articulation area. They are single-headed. Distally the ribs end bluntly.

Gastral ribs: The preserved gastral ribs are well ossified (Fig. 4). These elements are only preserved in the posterior section of the specimen. They consist of three parts, gradually diverging posterolaterally (see Rieppel 2000). There is a broad

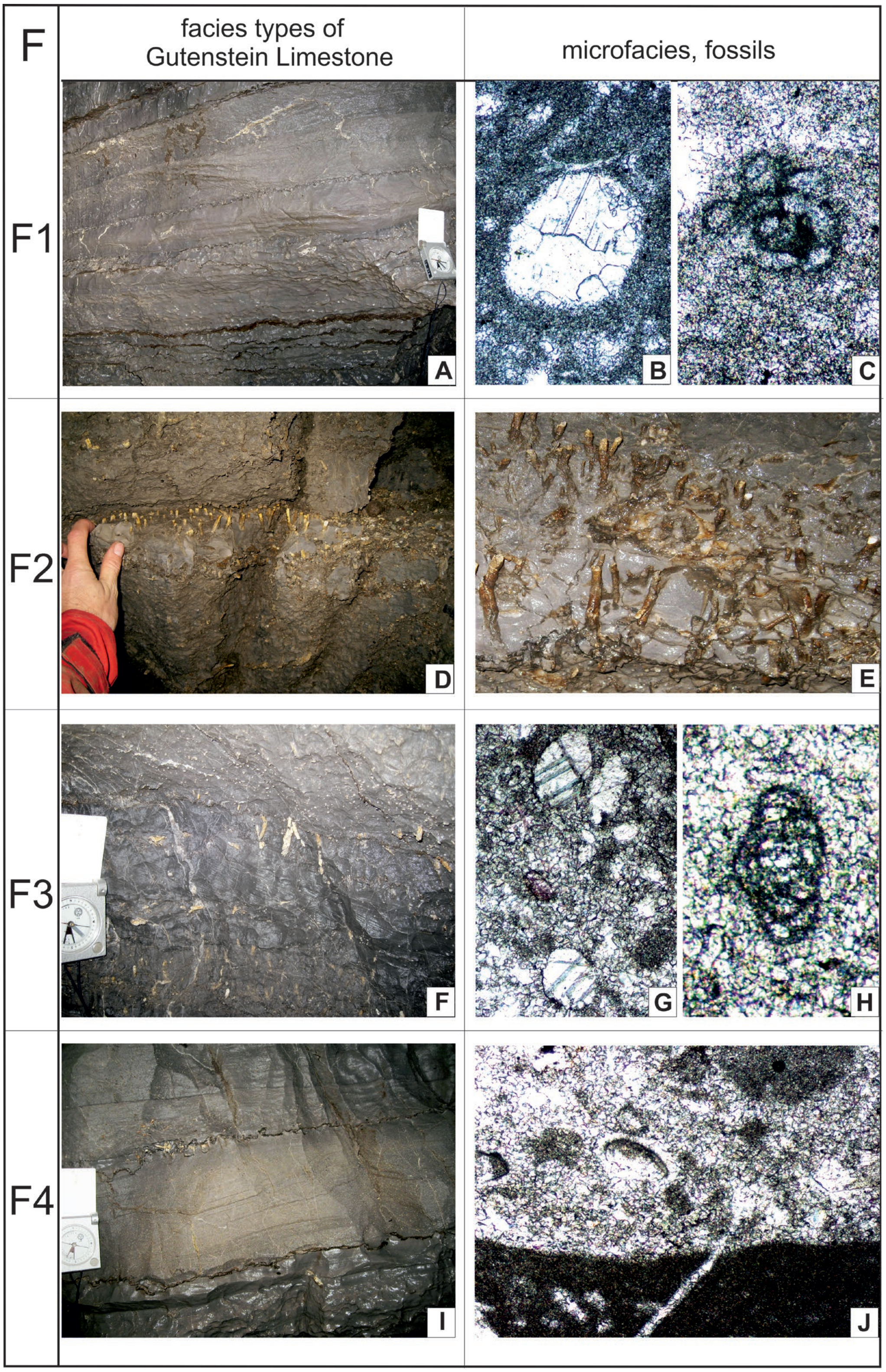

Fig. 3. Limestone facies of the Gutenstein Formation at the Štefanová Cave section. Four limestones facies (F1–F4) are outlined on the basis of their microfacies, microfossils, stratification, bio-erosion and sedimentary environments. F1: dark grey well-bedded micritic limestones (**A**) with sparitic vugs after anhydrite — birdseye structures (**B**) and foraminifers *Meandrospira deformata* (**C**) from shallow subtidal hypersaline environments; F2: densely burrowed limestones (**D**) with crustacean trace fossils — ?*Thalassinoides* sp. (**E**) from shallow subtidal storm-influenced environments; F3: laminated cryptalgal limestones and grainstone tempestites (**F**) with reworked particles of evaporate pseudomorphs (**G**) and foraminifers *Glomospirella lampangensis* (**H**) from intertidal environments; F4: cross-stratified bed of bioclastic limestones (**I**) and erosional base of tempestite with skeletal grains, ooids and peloids (**J**) from tidal channels or storm-influenced environments.

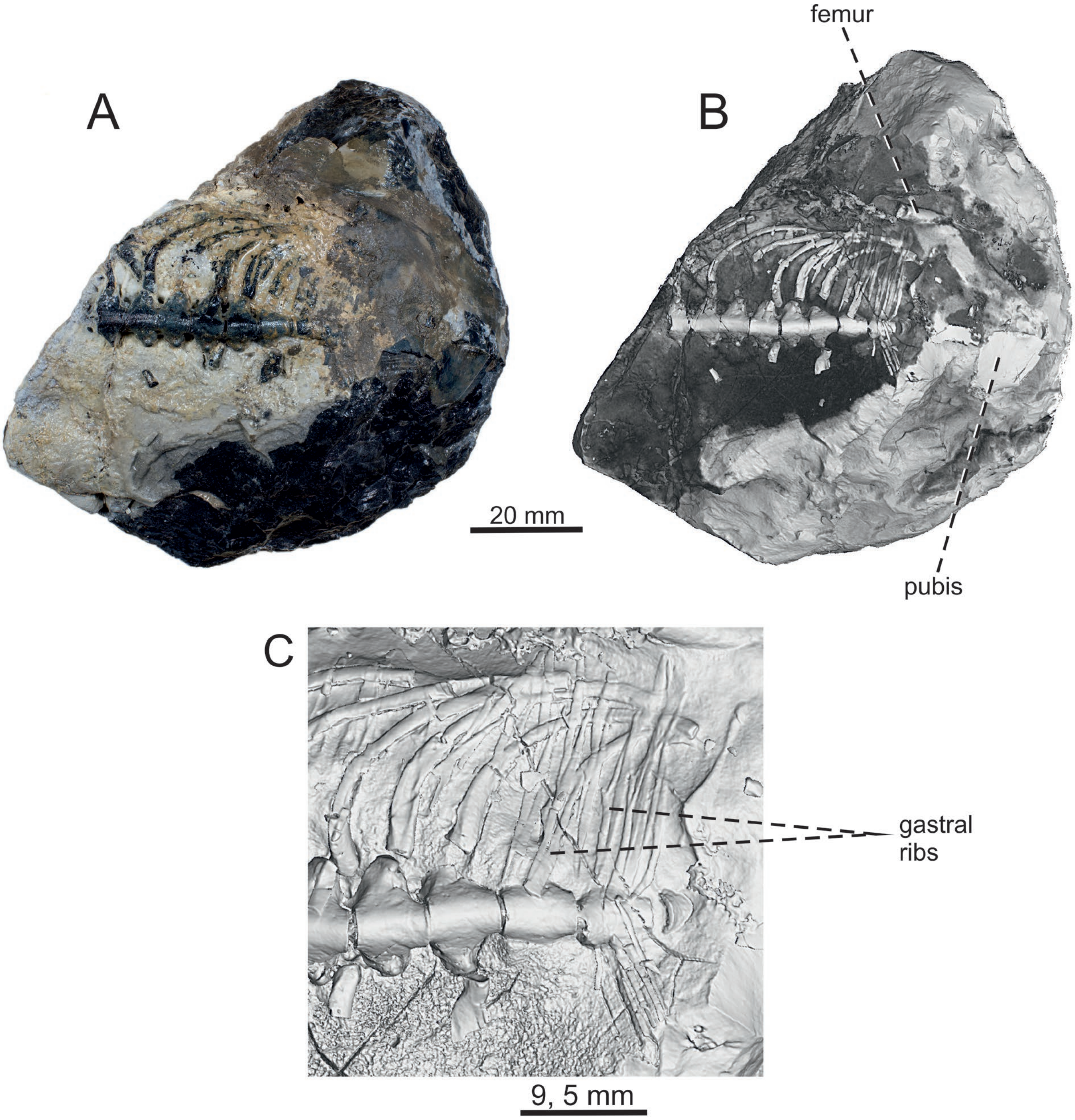

Fig. 4. A — The pachypleurosaur skeleton P 15136 from Štefanová Cave in Gutenstein Limestone. **B** — CT visualization of the find. **C** — detail of visible gastral ribs.

medioventral element, possessing an anterior projection and a slender lateral element on either side of it.

Coracoid: The element occupying the anterior region of the preserved skeleton is interpreted here as a coracoid (Fig. 5). Unfortunately, this element is badly preserved — heavily weathered and damaged. It is flat but robustly built. The middle portion is typically constricted, which is expressed especially on one side. This side is regarded as the medial margin, because according to Rieppel (1989), this margin is typically more concave than the lateral one.

Pelvic girdle: The pubis is preserved on both sides, although its original shape is difficult to determine because its margins are damaged (Fig. 7A–C). The bone is essentially a flat element. Its thickness gradually decreases medially, whereas it is more robust around the acetabulum. It is slightly constricted in its mid-region, however, this is preserved only on one side. The dorsal side is weakly angulated. The ventral side of both right and left elements possesses grooves (two in the left and one in the right pubis). However, these grooves were most likely caused by postmortem and fossilization processes (they may be, e.g., bore holes of clionid sponges). The bone is pierced by a small obturator foramen in its posterior margin, where it contacts the ischium, which is close to the elliptical acetabulum. The obturator foramen is almost fully enclosed in the pubis, although a small shallow notch on the ventral surface runs from the foramen to the margin. The bony septum,

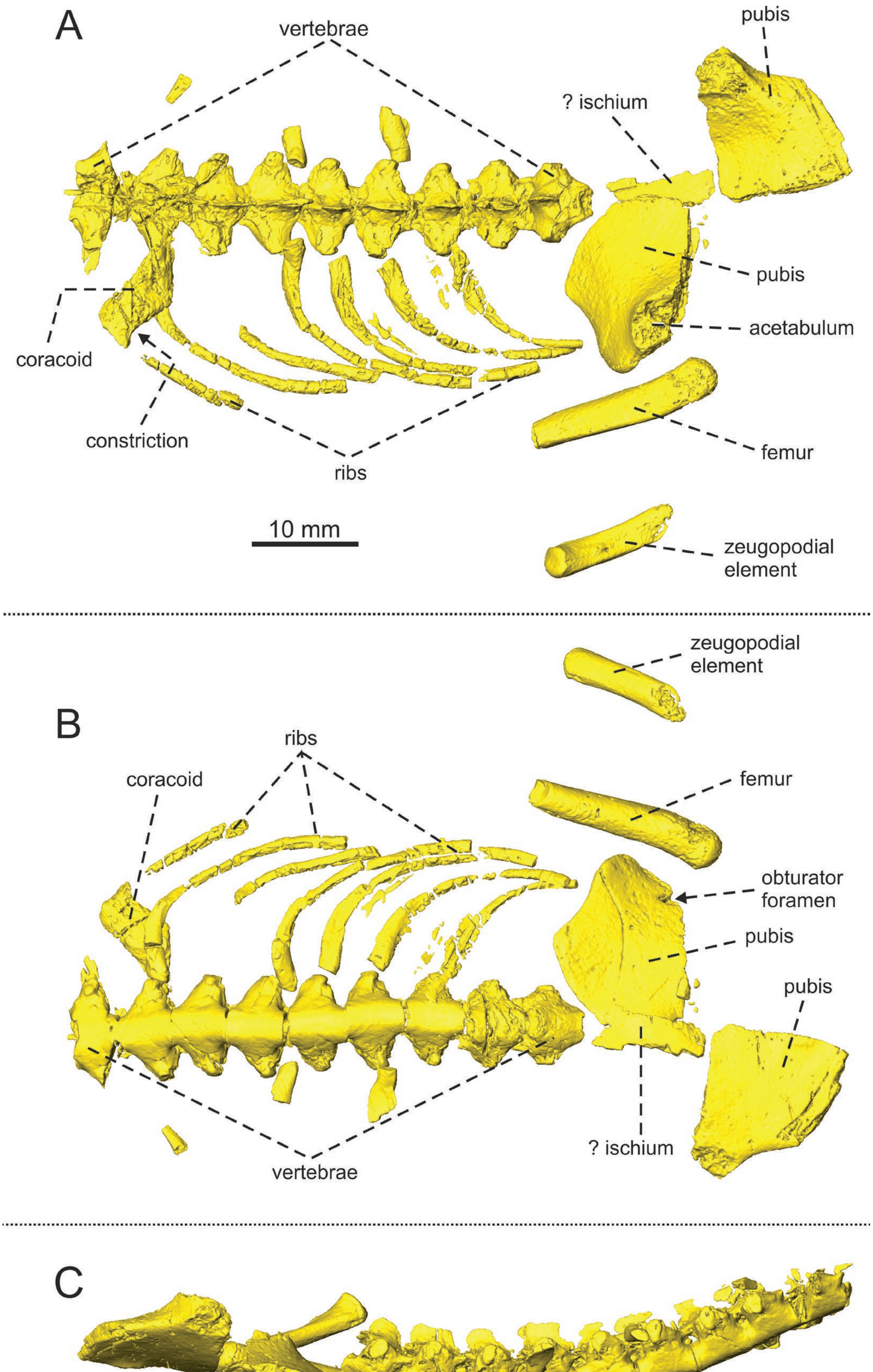

Fig. 5. The pachypleurosaur skeleton P15136 from Štefanová Cave. Segmented skeletal preserved elements (except the gastral ribs) in: **A** — dorsal, **B** — ventral, and **C** — lateral views.

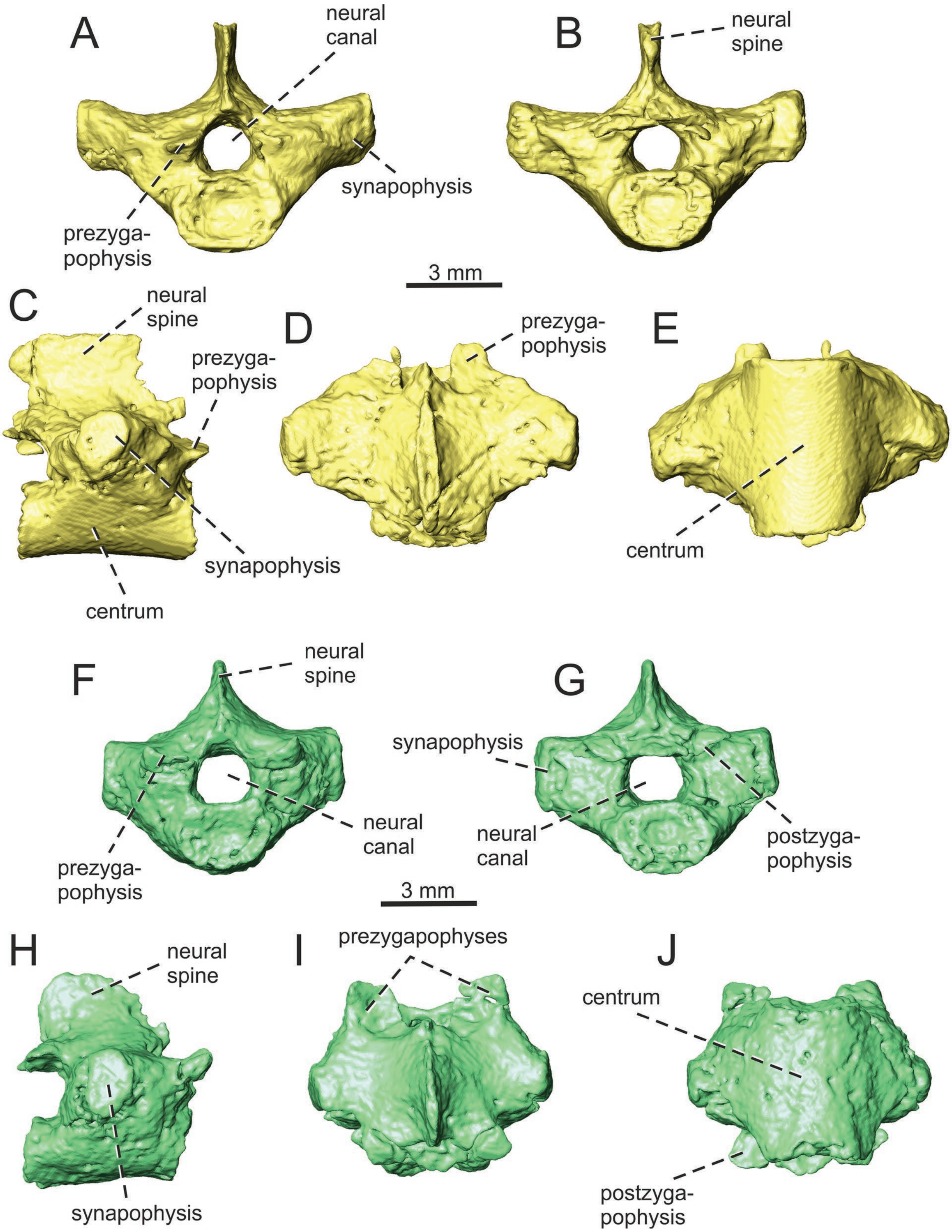

Fig. 6. The Triassic pachypleurosaur P15136 from Štefanová Cave. Vertebrae in: **A, F** — anterior; **B, G** — posterior; **C, H** — lateral; **D, I** — dorsal; and **E, J** — ventral views.

which surrounds the foramen is porous. Incomplete remains of another element, which are located medially between the right and left pubis, is interpreted here as the ischium.

Femur: Only the proximal to midshaft part of the femur is preserved. The diaphysis is elongated and nearly straight, the proximal head not offset. In the region close to the proximal region, rugosities on the surface are present. The midshaft cross section is typically round (Fig. 7D).

CT data revealed microanatomical information from the oval cross section of midshaft area (Fig. 7D). The femur has a central large medullary region that is filled by tissue and scattered with few erosional cavities appearing as dark spots in Fig. 7D. Thus, the femoral cross sections reveal osteosclerosis. The medullary region is surrounded by a distinct dark ring, which is most likely the sharp line of Klein (2010) and Hugi et al. (2011) representing the border between endosteal and periosteal domains. Details of the bone tissue and of the vascular system cannot be made out.

Zeugopodial bone: A fragment of a zeugopodial element is preserved. It is compressed, resulting in a markedly elliptical cross-section. Due to the size of the element (Table 1) in comparison to the femur, it could well represent the tibia.

Discussion

Taxonomic assignment

The small size and the morphology of the preserved elements such as the pachyostotic vertebrae and proximal ribs, as well as the tripartite gastral ribs clearly point to affinities with the pachypleurosaur *Neusticosaurus*, or at least with the *Neusticosaurus*+*Serpianosaurus* clade (Rieppel 1989, 2000; Sander 1989). In the specimen P15136, the number of gastral ribs is estimated on the basis of the preserved portion. In any case, even if the total number of elements would be five, this would be not in contrast with our assignment to the pachypleurosaurs, since gastral ribs are composed of five elements each in primitive pachypleurosaurs such as *Serpianosaurus* as well (see Rieppel 1989). However, the incorporation of five elements in a gastral rib is regarded as representative of the plesiomorphic condition and thus cannot be diagnostic (Rieppel 1989; e.g., the nothosaur *Lariosaurus*, which also includes small representatives, has 5-part gastral ribs as well). The shape and preserved morphology of the girdle elements, although all highly incomplete, and of the femur support our assignment.

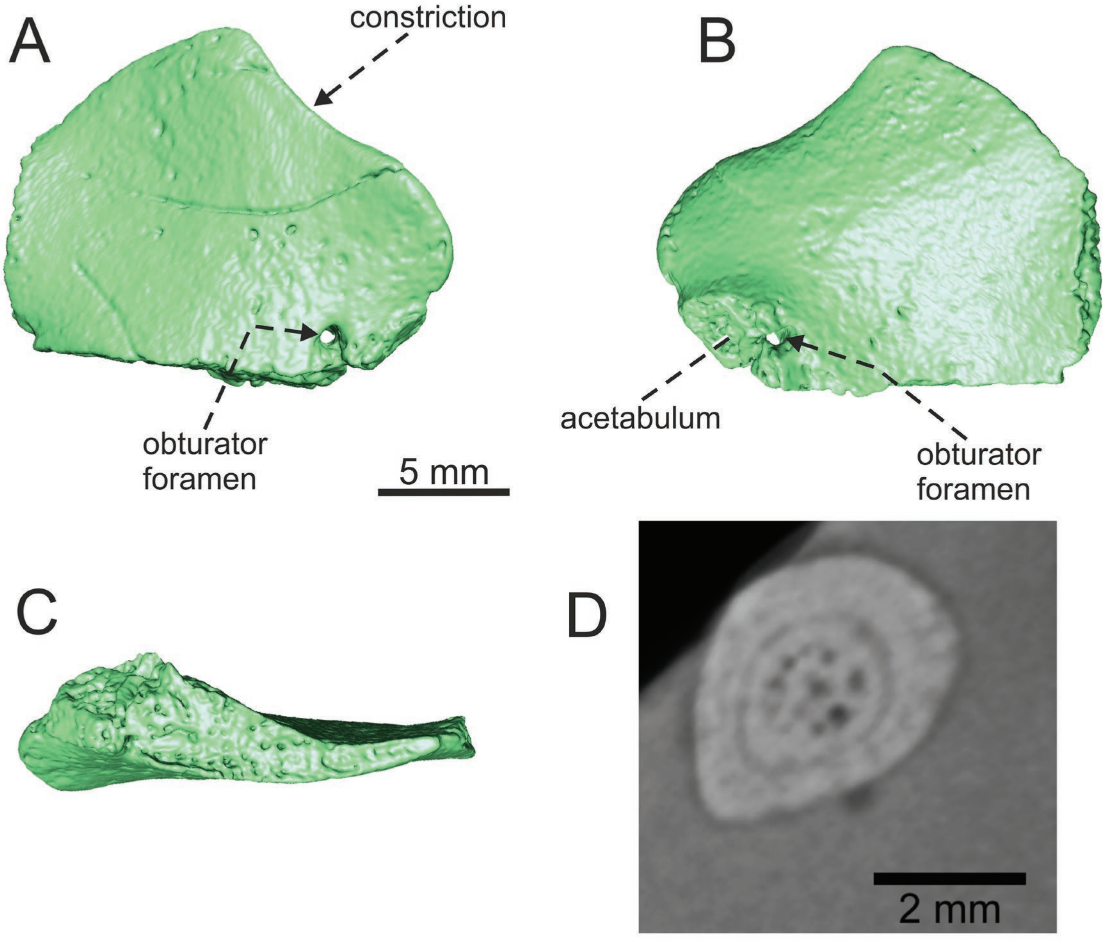

Fig. 7. The Triassic pachypleurosaur P15136 from Štefanová Cave. Pubis in: **A** — dorsal; **B** — ventral and **C** — posterior view. **D** — femur in cross-section revealed from µCT.

The femoral cross sections reveals a compact medullary region resulting in osteosclerosis similar to what was described for *Neusticosaurus* and *Serpianosaurus* (Hugi et al. 2011) and contrary to the condition in the pachypleurosaur *Anarosaurus heterodontus* and *Nothosaurus* spp., which have a free cavity at femur midshaft (Klein 2012; pers. obs. of N.K.).

A more precise identification is not possible due to the incompleteness of P 15136 and due to the general lack of diagnostic characters in the postcranial skeleton of Pachypleurosauria. An unambiguous assignment to Eosauropterygia is often only possible when a skull is preserved on which alpha taxonomy is usually solely based (e.g., Rieppel 2000; Klein 2012; Klein et al. 2016a).

According to Rieppel & Hagdorn (1997, 1998), the *Serpianosaurus–Neusticosaurus* clade originated in the Alpine Triassic at a time around the Anisian–Ladinian boundary and diversified in the southern Alpine intraplatform basin from where hundreds of complete individuals are known (e.g., Sander 1989; Rieppel 2000). Whereas *Serpianosaurus* was restricted to the Alpine Triassic of Monte San Giorgio (Italy and Switzerland), *Neusticosaurus* spp. was more widespread and is also documented in southern Germany (early Ladinian/Lettenkeuper of Hoheneck; Seeley 1882; Rieppel & Lin 1995). A possible member of the *Serpianosaurus–Neusticosaurus* clade was also reported from Spain (Rieppel & Hagdorn 1998). Other eosauropterygians, however, have been collected in Israel and Saudi Arabia (Rieppel 2000).

Our find now proves that the *Serpianosaurus–Neusticosaurus* clade was even more widely distributed in Europe during the Middle Triassic than previously thought and that they inhabited the marine environments of the Western Carpathians already during the late Anisian.

Paleogeographic and paleoecological implications

Pachypleurosaurs were typically near-shore inhabitants, sticking to shallow marine environments (Sues 1987; Rieppel 1989; Rothschild & Storrs 2003). They show few morphological adaptations to swimming and seem not to have been very efficient swimmers or divers (Carroll & Gaskill 1985;

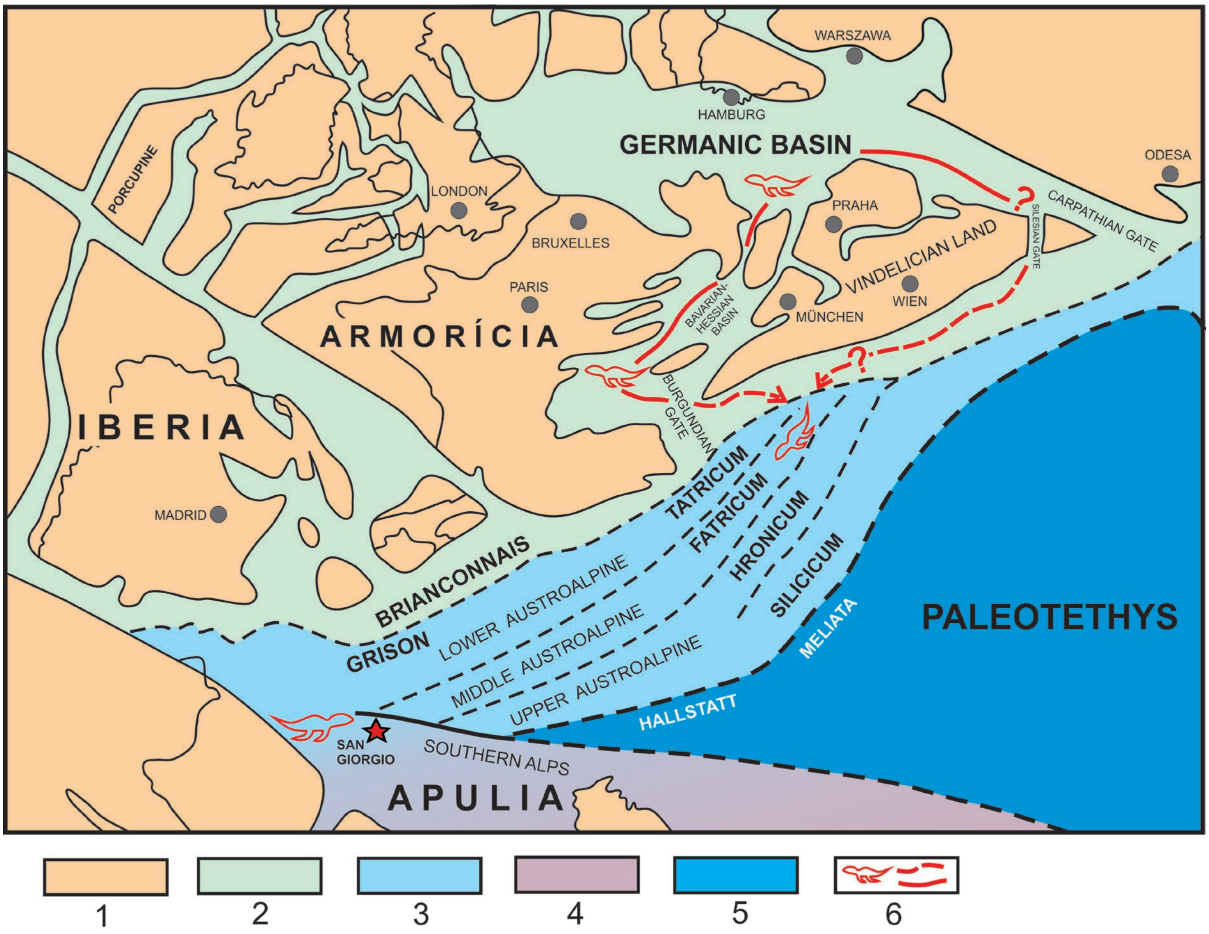

Fig. 8. Paleogeographic sketch map of the European–western Tethyan realm in the Middle Triassic period (after Michalík & Kováč 1982; Häusler et al. 1993; Michalík 1993, 1994; Stampfli 1996; Diedrich 2009; modified). 1 — dry land; 2 — epicontinental sea; 3 — carbonate platforms of the Alpine–Carpathian shelf; 4 — carbonate platforms of the Apulia shelf; 5 — Paleo-Tethyan oceanic basin; 6 — pachypleurosaurs and their possible migratory routes from Germanic basin to Carpathian basins (full red line indicates more presumable route than that of dashed line). Asterisk — indication of Monte San Giorgio locality with abundant fossil record of pachypleurosaurs in Southern Alps (see Renesto 2010; Stockar et al. 2012; Beardmore & Furrer 2016).

Hugi et al. 2011), in contrast to other members of Sauropterygia that lived at the same time (e.g., Rieppel 2000; Klein et al. 2015, 2016b). At localities from the eastern Tethyan faunal provinces (now South China), the environments that yielded high numbers of pachypleurosaurs are interpreted as hypersaline (Wang et al. 2008). It should be noted that terrestrial land was close to all these localities.

A preference for shallow marine and hypersaline habitats fits well with the paleoenvironmental conditions suggested for the Gutenstein Formation, which is interpreted as a monoclinal carbonate ramp (Michalík et al. 1992; Hips 1998), with sedimentological, ichnological, and geochemical evidence for hypersaline conditions (Mišík 1972; Spötl 1988, Jaglarz & Uchman 2010). Birdseye, stromatolitic and vermicular facies at the Štefanová Cave section indicate that pachypleurosaurs inhabited environments with hypersaline conditions. The preservation of associated elements of the incomplete skeleton P15136 rules out long-distance transport and indicates that the specimen is not allochthonous.

The interpretation of the Gutenstein Formation of Demänovská dolina Valley (shallow marine carbonate ramp, sedimentation in a shallow subtidal to peritidal environment) as well as the presence of a marine reptile in this layer can indicate the presence of a coast nearby and/or at least some elevated areas such as small islands. The European pachypleurosaurs are assumed to be anguiliform swimmers (e.g., Caroll & Gaskill 1985; Lin & Rieppel 1998; Houssaye 2012), but with the inability to dive deeply (Rieppel 1989). Moreover, it has been suggested that the forelimbs of small European pachypleurosaurs are also used for terrestrial locomotion (Sander 1989; Lin & Rieppel 1998). Although sedimentological evidence from the Anisian formations in the Central Carpathian units does not indicate any presence of terrestrial habitats (Fig. 8), presence of small islands (peritidal environments are typically associated with barrier islands, channels) can be rather inferred from facies differentiation and shallowing upward cyclicity generated by migrating islands.

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