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Taxonomical and palaeoecological investigations of the chondrichthyan and osteichthyan fish remains from the Middle-Late Triassic deposits of the Villány Hills (Southern Hungary) [☆]

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Abstract

Two sites in the Villány Hills, Hungary, have yielded rich fish assemblages from Middle to Late Triassic shallow marine deposits. The collected material comes from the Ladinian Templomhegy Dolomite Member and from the Carnian Mészhegy Sandstone Formation. The ichthyofauna is composed of both chondrichthyans (Hybodontidae indet., *Palaeobates angustissimus*, ‘*Polyacrodus*’ sp., ?*Lissodus* sp.) and osteichthyans (*Gyrolepis* sp., *Birgeria* sp., and further indeterminate actinopterygians). Despite the large sample size, no remains of neoselachians have been found. The Ladinian Templomhegy Dolomite is dominated by durophagous hybodontiforms (*Palaeobates angustissimus*, ?*Lissodus* sp.), but the piscivorous hybodontid and the generalist ‘*Polyacrodus*’ sp. are missing, while in the fish fauna collected from the Carnian Mészhegy Formation indeterminate piscivorous hybodontids are the most common elements and durophagous forms are much less abundant. The dominance of piscivorous hybodontids in the Carnian Mészhegy Sandstone could be related to the global decrease of diversity of marine fish-eating reptiles (e.g., nothosaurs) or to a change of paleoenvironmental conditions. The present study improves our knowledge on the poorly known Triassic vertebrate faunas of the Tisza Mega-unit, which formed a segment of the passive Neotethys margin of the European Plate and shows an important example of a potential vertebrate faunal shift during the Middle to Late Triassic.

Keywords: Hybodontidae

Palaeobates

Gyrolepis

Birgeria

Neotethys

Muschelkalk

Keuper

1. Introduction

The current knowledge of the diversity of Mesozoic marine fishes of Hungary (i.e., Transdanubian Range and the Tisza Megaunit) is scarce and incomplete, although Triassic and Jurassic sediments exposed in the country are predominantly marine (Haas, 2001) and at least fish teeth are relatively abundant microfossil elements in these sediments. Ósi et al. (2013) reported a diverse Triassic vertebrate assemblage from the Villány Hills (Southern Hungary), including various fish (see below) and marine reptile (e.g., *Nothosaurus*, cf. *Cyamodus*) taxa, which has been collected in two localities from the Middle Triassic (Ladinian) Templomhegy Dolomite Mb. and from the Upper Triassic (Carnian) Mészhegy Sandstone Fm. However, the paleoenvironmental origin of these Triassic formations remains poorly known, because of the lack or poor preservation of hard-shelled invertebrate fossils. Since this first report (Ósi et al., 2013), an intensive screen-washing activity has been carried out at the Villány vertebrate locality, resulting in the discovery of thousands of isolated tooth remains, scales, and other skeletal remains of fishes and reptiles from both Triassic sites, which provide useful information on the paleoenvironment of these bone-bearing successions.

The present study focuses on the fish remains unearthed from the Ladinian Templomhegy Dolomite Mb. of the Csukma Dolomite Fm., and the overlying Carnian Mészhegy Sandstone Fm., characterized by different depositional environments. Here we give a systematic description of these fish remains, and the ichthyofaunal composition of the two formations is compared to each other, and also to other Middle and Late Triassic fish faunas around Europe. The possible paleoecological consequences of the identified fish fauna is also discussed.

2. Locality and geological background

2.1. Regional palaeogeography and geological setting

The studied area is situated in the Southern Pannonian Basin of Hungary, 200-300 m northwest of the village of Villány (Villány Hills, Southern Hungary; Fig. 1(A)). The Lower Triassic section of the Villány-Bihor Unit is predominantly characterized by clastic sedimentation (Alpine Buntsandstein facies), which is gradually substituted by carbonatic Middle Triassic deposits (Muschelkalk facies). Both deposits show a close genetic relationship with the Germanic-type Triassic sediments (Török, 1997). In contrast to the Lower and Middle Triassic sequences, the thin, coastal-continental Upper Triassic succession of this unit shows close affinities to the Carpathian Keuper facies of the European shelf of the Tethys (Bleahu et al., 1994).

The Triassic sedimentary sequence of Southern Hungary was deposited in a homoclinal carbonate ramp, which succeeded a clastic-covered terrain of Early Triassic (Buntsandstein) siliciclastic ramp phase (Török, 1997, 2000). The ramp morphology is characterized by a relatively uniform subsidence rate of the passive continental margin and by a high production of carbonate mud and lack of reef biota (Török, 1998). Geotectonic setting and related slow subsidence suggest that eustatic sea-level changes were one of the major controls over sediment deposition on this ramp (Török, 2000), resulting in three Middle Triassic deepening-upward and shallowing-upward cycles in Villány Hills (Götz and Török, 2008). The first cycle corresponds to the ramp initialisation and the onset of carbonate sedimentation in southern Hungary (Hetvehely Anhydrite Fm. and Rókahegy Dolomite Fm.), coinciding with the early Anisian global sea-level rise (Götz et al., 2003; Götz and Török, 2008), while the second depositional cycle is detectable from the middle to the late Anisian carbonates (Zuhánya Fm.), showing striking similarities with the first Muschelkalk cycle of the Central European Basin (Török, 2000; Götz and Török, 2008). The third cycle (including the latest Anisian to early Ladinian sediments) is poorly documented in the Muschelkalk of the Villány Hills, but the Ladinian Csukma Dolomite Fm. could correspond to the general shallowing of the basin (Haas, 2001).

The Csukma Dolomite Fm. consists of grey, thick bedded, sometimes laminated dolomicrites, sucrosic dolomites with rare relicts of ooids as well as micro-tepee and fenestral structures (Török, 2000), indicating that the depositional environment of these sediments was the subtidal to peritidal zone of the inner ramp environment (Rálich-Felgenhauer and Török, 1993; Török, 2000). The uppermost part of the Csukma Dolomite Fm. is made up by the alternation of yellowish grey dolomite and marl layers representing the Templomhegy Dolomite Mb. of this formation (Fig. 1(B)). Based on the preliminary paleogeographical, stratigraphical and paleontological investigations, the sediments of the Templomhegy Mb. of the Csukma Dolomite Fm. were deposited in a flat tidal shelf or shelf-lagoon environment which most probably connected with the open marine province (Török, 1998, 2000; Haas, 2001; Bérczi-Makk et al., 2004; Ósi et al., 2013; Botfalvai et al., 2019). The Templomhegy Dolomite Mb. represents the most important part of the Ladinian succession in the Villány Hills, because it yielded a relatively diverse material of marine reptile and fish (Ósi et al., 2013).

The Templomhegy Mb. is covered by the Carnian Mészhegy Sandstone Fm. composed of variegated conglomerate, sandstone, pelite and dolomitic limestone (Vörös, 2009, 2010; Pozsgai et al., 2017; Fig. 1(B)). This thin, siliciclastic unit also contains

vertebrate remains (mostly microvertebrate remains, see below), while marine invertebrate fossils are completely absent from these layers.

The Upper Triassic siliciclastic layers are covered by the shallow marine Pliensbachian Somssichhegy Limestone Fm., with a rich invertebrate assemblage indicating a clearly marine depositional environment (Vörös, 2009).

The Villány Hills belong to the Villány-Bihar Unit of Tisza Mega-unit, which was situated on the passive margin of the European Plate southwards to the Bohemian Massif during the Triassic period (Haas and Péro, 2004; Pozsgai et al., 2017; Fig 1(C)). The Triassic vertebrate sites of the Villány Hills investigated in the present paper are exposed in two different sections (see below), but both of them represent the uppermost part of the Muschelkalk carbonate ramp and a short interval of Keuper typical of the Villány Hills (Vörös, 2009; Ósi et al., 2013).

2.2. Vertebrate sites of Villány Hills

The two studied, fossil-bearing sites are exposed in two sections: (i) the Ladinian Construction site on the Somssich Hill, and (ii) the abandoned Carnian Road-cut site on Templom Hill, where productive and continuous excavations have been carried out between 2012 and 2018. Fieldworks resulted in a diverse assemblage of marine animals including isolated cranial and postcranial remains of Sauropterygia (e.g., *Nothosaurus*, cf. *Cyamodus*), few vertebrae of *Tanystropheus*, and several bony fish teeth (Ósi et al. 2013; 2018; Segesdi et al. 2017). we provide below a brief overview on the sedimentary section of these vertebrate sites based on available sedimentary data and field observations (see Botfalvai et al., 2019 for detailed sedimentary descriptions and the interpretation of the depositional environments).

2.2.1. Construction site

The excavated fossiliferous section is made up of an alternation of grey dolomite and yellowish dolomarl layers of the Templomhegy Dolomite Mb. of the Csukma Dolomite Fm. (Fig. 2). Its stratigraphic position (situated between the late Anisian Zuhány Limestone Fm. and the Carnian Mészhegy Sandstone Fm.) and the abundant occurrence of *Nothosaurus* sp. in various bone-yielding horizons indicate a Middle Triassic, most probably Ladinian age (Török, 1998, 2000; Ósi et al. 2013). Three lithofacies were recognized using a classification based on color, grain size, bedding, paleontological content and sedimentary structures.

The most dominant lithofacies of the bonebeds is composed of yellowish to grey dolomarl with pale reddish colored mottles. The thickness can vary from 10 to 50 cm. The clay content and the degree of cementation vary considerably among the variegated calcareous marl layers. The vertebrate fossils are more common in those horizons of

dolomarl, which are characterized by a high clay content. The vertebrate fossils are predominantly isolated, but one associated partial skeleton of a small-sized eosauropterygian was also recovered from bed 14 of the bone-bearing section (Segesdi et al., 2017). Bed 14 is the most important horizon in terms of chondrichtyan and osteichthyan fish remains of the Construction site (Fig. 2), providing more than six hundred fish tooth remains from the enclosing sediment of the eosauropterygian partial skeletons (Table S1; Appendix A). The dolomitization, mud dominated lithologies and lack of grainstone textures suggest that this sediment was deposited in a low energy, restricted shallow marine environment (Botfalvai et al., 2019).

The second lithofacies is a greyish-white, hardly cemented dolomite, being less common in the bonebed section of the Construction site. The thickness of dolomite beds varies from 10 to 30 cm and occur within the succession of dolomitic marl. This lithofacies also contains teeth and bones of sauropterygians (Ósi et al., 2013), but fish teeth cannot be detected from them, because the sediment was strongly cemented and screen-washing was impossible to conduct during the fieldwork. The dolomitic fabric suggests a limemud precursor sediment indicating that this lithofacies can be interpreted as a carbonate mud deposited in a low-energy, shallow, restricted lagoonal environment (Botfalvai et al., 2019).

The third lithofacies, represented by only one horizon of red mudstone with purple to green-colored mottles is present in the observed section. Its reddish color, mineral content and diverse macrofeatures including root traces and mottles indicate that this claystone was better drained than the above mentioned lithofacies and can be interpreted as a calcic paleosol (Pozsgai et al., 2017). The thickness of this thin red mudstone layer does not exceed 10 cm and vertebrate fossils are completely missing from this horizon.

Only a few poorly preserved casts of hard-shelled invertebrate fossils are known from the bonebeds of the Templomhegy Mb., which currently cannot be used for more detailed paleoenvironmental reconstruction (the carbonate shelled fossils probably were destroyed due to dolomitization). However, results of earlier sedimentological works (Török, 1998, 2000; Haas, 2001; Bérczi-Makk et al., 2004) as well as the newly discovered vertebrate remains including well-preserved and unworked sauropterygian remains (Ósi et al., 2013; and see below) suggest that the depositional environment was a tidal flat shelf or a lagoon environment, connected with the open marine province (Török, 1998; Bérczi-Makk et al., 2004; Ósi et al., 2013).

2.2.2. Road-cut site (“Siklóbevágás”)

The Road-cut site (“Siklóbevágás” in Hungarian) is a nearly 30 m-long and 3–5 m-high section, where three different formations are exposed (Fig. 3). The first formation is situated in the northern half of the Road-cut site (*ca.* 10 m-long section) and represents the uppermost part of the Templomhegy Dolomite Mb. of the Csukma Dolomite Fm., including alternating layers of dolomite and yellowish dolomarl. The water-screened residue of the Templomhegy Mb. at the Road-cut site was not productive for fish fossils, but a few sauropterygian bones were discovered from different horizons (Ósi et al., 2013).

The amount of siliciclastic content increases upwards in the section and the Templomhegy Mb. is overlain by an almost 15 m-thick sequence of the Mészhegy Sandstone Fm. (Vörös, 2010; Fig. 3). This part of the section consists of cycles of weakly cemented, greyish, yellowish, purplish or greenish sandstone, siltstone and reddish, purplish or variegated clay strata, with subordinate amounts of greyish dolomite and yellowish dolomarl (Pozsgai et al., 2017). The palynological investigations indicate a Carnian age for the formation and its observed phytoclast assemblage suggests that the sediments were deposited in a nearshore depositional environment characterized by a high input of land-derived organic matter (Ósi et al. 2013). Different layers of the Mészhegy Sandstone Fm. were sampled for screen-washing, but only three brownish-greyish sandstone beds (L3, L4, L5) were productive for fish remains (Fig. 3), which are investigated in this paper. Screen-washing of these three brownish-greyish sandstone beds of the Road-cut site has provided a relatively rich and diverse assemblage of marine fishes (see below), that might serve as a good indicator of the depositional environment, suggesting a marine rather than a fluviolacustrine origin for this bone-bearing succession. The richest fish material was recovered from the uppermost sandstone bed (L5 in Fig. 3(B)), which provided almost three hundred teeth from different fish taxa (Table S1; Appendix A). The Triassic sequences of the Road-cut site on Templom Hill are covered by the Pliensbachian (Early Jurassic) Sommsichhegy Limestone Fm. (Fig. 3).

Sedimentological and petrographical examinations of the Carnian sandstones exposed at the Road-cut section have been already conducted by several authors (Rálich-Felgenhauer, 1985; Vörös, 2009, 2010; Pozsgai et al., 2017). However, the depositional environment of this succession has been interpreted in different ways such as shallow marine or littoral (Rálich-Felgenhauer, 1981; Török, 1998) or as fluviolacustrine (Vörös, 2010). The depositional environment was difficult to define, because these authors actually did not find any fossils useful for more detailed paleoenvironmental reconstruction.

3. Material and methods

The present study focuses on the chondrichthyan and osteichthyan remains unearthed from the Middle Triassic (Ladinian) Templomhegy Dolomite Mb. and the Upper Triassic (Carnian) Mészhegy Sandstone Fm. The uppermost member of the sequence is the Lower Jurassic (Pliensbachian) Somssichhegy Limestone Fm. (Fig. 3), which also yielded a large number of vertebrate remains. Because these are reworked Triassic elements (Ősi et al., 2013), we have decided to exclude them from our study.

All of the described fish remains were unearthed during excavations carried out between 2013 and 2018; the collected material is housed in the vertebrate paleontological collection of the Department of Paleontology and Geology of the Hungarian Natural History Museum (Budapest; abbrev.: NHMUS).

In the first round of screen-washing, we sampled a total of 25 kg of bulk rock from several layers of the Templomhegy Dolomite Mb. at the Construction site, but only four layers (beds 14, 18, 20, 22; Fig. 2(A)) were productive for fish fossils. Among them, bed 14 was the most productive, thus in the summer of 2018, *ca.* 250 kg of additional samples have been screen-washed from this bed. We used tap water and 5% acetic acid during the procedure, which resulted in thousands of fish microremains.

Three beds (L3, L4, L5; Fig. 3) of the Mészhegy Sandstone Fm. exposed in the Road-cut site were productive for microvertebrate remains, among which layer L5 was the most productive for microvertebrate remains.

Specimens were gold-coated and photographed under a Hitachi S-2600N scanning electron microscope. The observed Villány material is highly fragmented, mostly due to the screen-washing procedure. Therefore, we tentatively interpreted the number of referable remains per taxa as the number of identified specimens (maximum number of individual; NISP), following the methods mentioned by Lyman (2008) and Cannon (2013). The number of identified specimens is the most popular and simplest measure of taxonomic abundances and therefore it is commonly used by palaeontologists. The NISP value includes the number of tooth remains, which were identified taxonomically at least at the family level in the Villány vertebrate assemblages.

Classification of chondrichthyans follows Cappetta (2012), while that of osteichthyans mainly follows Böttcher (2015). Chondrichthyan tooth terminology mainly follows Cappetta (2012), while tooth and scale terminology for osteichthyans follows Allard et al. (2015), Delsate and Duffin (1999), Lakin et al. (2016), Landon et al. (2017), and Romano et al. (2017). Mesial, distal, labial and lingual sides were distinguished by general morphological features (e.g., the inclination of the cusps).

4. Systematic paleontology

Class Chondrichthyes Huxley, 1880

Cohort Euselachii Hay, 1902

Order Hybodontiformes Maisey, 1975

Family Hybodontidae Owen, 1846

Hybodontidae indet.

Fig. 4(A-F)

Referred material: 194 isolated cusps (NHMUS VER 2013.22.1-126., VER 2018.2305.-2307., and VER 2018.2318.) from the Mészhegy Sandstone Fm. of the Road-cut site.

Description: All of the referred tooth remains are isolated cusps showing convex labial and lingual crown faces. The cutting edges are smooth all along; the tip is blunted or pointed, depending on wear. The specimens referred as main cusps are slender and high, bearing apicobasal striation reaching the crown tip region. The labial surface is less convex and usually less striated than the lingual one. The main cusps are upright and lingually bent to weakly sigmoid on supposed anterior files, whereas they are distally inclined on inferred lateral files. Some cusps are conical and lower than others and are therefore considered as possible lateral cusplets.

Remarks: Compared to dental remains of other Late Triassic euselachians from Europe, the preserved dental characteristics listed above refer these remains with close relation to Hybodontidae. Figured types of the hybodontid *H. minor* (Agassiz, 1837: pl. 23, figs. 23, 24) possess the strong apicobasal striation, with the weak sigmoid curvature of the main cusp, flanked by lateral cusplets. Although the majority of hybodontid species have been described from isolated teeth (Cappetta, 2012), it is not possible to determine the presently described teeth below family level. Here, several problems render a generic assignment for hybodontid sharks difficult, and include the absence of association between cusps and roots, and possible heterodonty.

Family Polyacrodontidae Glikman, 1964

Genus *Palaeobates* Meyer, 1849

Palaeobates angustissimus (Agassiz, 1838)

Fig. 4(G-R)

Referred material: 81 teeth, incomplete teeth and tooth fragments (NHMUS VER 2013.23.1-46., VER 2013.42., VER 2018.2304., VER 2018.2316.) from the Mészhegy Sandstone Fm. at Road-cut site; 1275 teeth, incomplete teeth and tooth fragments (NHMUS

VER 2018.2323., VER 2018.2330., VER 2018.2334., VER 2018.2337.-2343.) from the Templomhegy Dolomite Mb. of the Construction site.

Description: Most of the here-referred specimens are fragmentary and, except for a few, poorly preserved rootless portions. The teeth represent various stages of wear. Inferred anterior teeth (Fig. 4(G-L)) possess a convex crown in profile view. In profile view, the highest point of the crown is bulge-like (or cusp-like), and positioned near the midline of the mesiodistal axis. This could differ in anteriormost files, where the central bulge is weakly shifted mesially. In apical (or “occlusal”) view, these teeth become narrow toward their extremities, resulting in a lentoid shape. When unworn, the apical surface bears a mixture of reticulations and vertical ridges along the crown base. Inferred anterior teeth could have a weak transversal crest (Fig. 4(J)). Inferred lateral teeth (Fig. 4(M-P)) are mesiodistally elongated with rounded to weakly angled extremities. The crown surface is reticulated, with vertical folds at the periphery of the crown. Inferred posterior files (Fig. 4(Q, R)) possess teeth of simple morphology. They are roundish in occlusal view, some with weakly angled outline. In profile view, the crown is flat, even if unworn. The apical surface is also ornamented.

Remarks: *Palaeobates* remains are well known from Lower to Upper Triassic deposits of Europe and North America (Romano and Brinkmann, 2010; Cappetta, 2012). The genus is mainly known from isolated teeth and fin spines, however, some skeletal remains are also known from Spitsbergen (Romano and Brinkmann, 2010; Cappetta, 2012). The generally small size of the Villány *Palaeobates* teeth, together with the low cusped anterior files, the richly and finely pitted apical (or “occlusal”) surface (especially that of teeth from lateral files), and the simple, roundish and low morphology of teeth from posterior files, make them referable to the type species *P. angustissimus* (Delsate and Duffin, 1999; Schultze and Kriwet, 1999; Chrzastek, 2008; Diedrich, 2009; Dalla Vecchia and Carnevale, 2011; Cappetta, 2012; Pla et al., 2013; Böttcher, 2015), which was originally described by Agassiz (1834) as ‘*Strophodus angustissimus*’. Teeth of *Acrodus* are morphologically similar, but this taxon has larger, more robust teeth with a higher crown in lateral view, and with different apical ornamentation, than teeth of *Palaeobates* (see figures in Cappetta, 2012 and Böttcher, 2015).

Genus *Polyacrodus* Jaekel, 1889

‘*Polyacrodus*’ sp.

Fig. 5(A-F)

Referred material: Ten incomplete teeth (NHMUS VER 2013.24.3-6., VER 2018.2310., VER 2018.2311., VER 2018.2321., VER 2018.2322.) from the Mészhegy Sandstone Fm. of Road-cut site.

Description: All ‘*Polyacrodus*’ tooth remains from Villány Hills are rootless, fragmentary crowns consisting mainly of the principal cusp. A distinctive transversal crest extends along the apical tooth surface mesiodistally, from which several smaller, weakly arched crests run to the edge of the tooth. A well-defined apron is present on the labial base of the principal cusp (e.g., NHMUS VER 2018.2322., Fig. 5(E)).

Remarks: The validity of the genus *Polyacrodus* is a complex subject as well as its differentiation from other members of the family Hybodontidae (Dorka, 2003; Rees, 2008; Cappetta, 2012; Koot et al., 2013). Compared to the Villány hybodontid teeth, ‘*Polyacrodus*’ tooth remains have a lower and more robust main cusp, without distinct cutting edges, but with an ornamentation of massive ridges far less in number, and with a distinct labial apron. According to these characters, we provisionally refer these teeth to *Polyacrodus* (Dorka, 2003; Cappetta, 2012).

The type species of the genus is *P. polycyphus* (originally described from the Muschelkalk of Lunéville, France as *Hybodus polycyphus* by Agassiz (1837)). Teeth of this species possess a massive, but low and pyramidal main cusp with a distinct labial apron. However, teeth of *P. polycyphus* are larger, with a more complex crown ornamentation, than the Villány specimens (see Agassiz, 1837; Dorka, 2003; Böttcher, 2015).

The dentition of the genus is typically heterodont. Complete teeth are massive and mesiodistally expanded with a high, lingually displaced root. The crown typically has a large principal (or central) cusp, laterally the heels could bear up to four lateral cusplets (Cappetta, 1987, 2012). The Villány teeth are poorly preserved (rootless and fragmentary) and low in number, therefore, due to the problematic synonymy of the genus, we refer our material to as ‘*Polyacrodus*’ sp. until more complete material helps to clarify its taxonomic position.

Polyacrodus remains are known from around Europe, Russia and Greenland, ranging from the Lower Triassic to the Upper Cretaceous (Cappetta, 2012).

Family Lonchidiidae Herman, 1977

Genus *Lissodus* Brough, 1935

?*Lissodus* sp.

Fig. 5(G-L)

Referred material: 56 incomplete teeth (NHMUS VER 2018.2326., VER 2018.2344.-2347.) from the Templomhegy Dolomite Mb. of Construction site; 13 incomplete teeth (NHMUS VER 2013.21.1-12., VER 2018.2320.) from the Mészhegy Sandstone Fm. of Road-cut site.

Description: All Villány *Lissodus* teeth are rootless and show various stages of wear. Inferred anterior and lateral teeth are generally long, but low crowned. They are characterised by a strong, well-developed, sharp transversal crest. The teeth are narrowing to their mesial and distal extremities, resulting in a triangular to lentoid shape in apical view. If unworn, the apical surface is ornamented with a few fine ridges extending from the lower third of the crown height to the transversal crest (with some ridges reaching the crest). A pronounced labial protuberance (or labial peg) is present, which is positioned at the basal midline of the teeth. Inferred distal teeth (Fig. 5(K, L)) are flattened, bearing an occlusal crest, with no distinctive surface sculpting.

Remarks: Based on the small, mesiodistally expanded, low crowned, lentoid to triangular teeth with folded surface and a labial protuberance, here we tentatively assign these remains to *Lissodus* (Rees and Underwood, 2002; Cappetta, 2012). Due to the problematic taxonomy, complex synonymy of the genus (e.g., Rees and Underwood, 2002; Rees, 2008; Cappetta, 2012; Koot et al., 2013) and the low number and poor preservation of the here-referred Villány material, more specific determination is currently not possible.

Lissodus is known by more or less complete skeletons and by isolated teeth. The genus ranges from the Lower Triassic to the Upper Cretaceous of Europe, North America and South Africa (Cappetta, 2012).

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii Klein, 1885

Order Palaeonisciformes Hay, 1902

Family Palaeoniscidae Vogt, 1851

Genus *Gyrolepis* Agassiz, 1833

Gyrolepis sp.

Fig. 6(A-H)

Referred material: 13 teeth (NHMUS VER 2018.2328., VER 2018.2348., VER 2018.2349.) and 167 scales (NHMUS VER 2018.2327., VER 2018.2350.-2354.) from the Templomhegy Dolomite Mb. of Construction site; 7 scales (NHMUS VER 2013.24.1., VER 2013.24.2., VER 2018.2308., VER 2018.2317.) from the Mészhegy Sandstone Fm. of the Road-cut section.

Description: These teeth (Fig. 6(A-C)) are slender, apically tapering and pointed with a gentle curvature. The teeth show a near circular cross-section, with basally increasing diameter. The tooth-base bears faint apicobasal ridges. The microsurface of the base bears a fusiform ornamentation made up by vertical, lentoid units covering the entire tooth base, but not the cap (Fig. 6(C)).

The referred scales are flat and rhomboid in shape (Fig. 6(D-H)). They have a relatively thick, bony base, bearing laterally a shiny layer of ganoine. The ganoine cover displays a pattern made up of straight to slightly sinuous enamel ridges running in the inferred antero-posterior direction. The surface of the ganoine possesses well-preserved ganoine tubercles (Fig. 6(E)). Due to the general preservation of the scales, no traces of peg-and-socket articulation is visible.

Remarks: Minute, slender, gently curved, long and tapering teeth with a shiny, translucent cap and finely ridged base are characteristic of *Gyrolepis* (see *Gyrolepis albertii* in Delsate and Duffin, 1999; Allard et al., 2015; Korneisel et al., 2015; Lakin et al., 2016; Landon et al., 2017) as well as the fusiform ornamentation of *Gyrolepis* teeth has been noted by several authors (Delsate and Duffin, 1999; Duffin, 1999). Scales with a rhomboid outline, thick bony base and ridged ganoin are widely referred to *Gyrolepis* (Böttcher, 2015; Lakin et al., 2016). Following parsimony, we attribute the Villány scales to *Gyrolepis* sp., until further remains lead us to reassess our conclusion.

The genus *Gyrolepis* is widely represented in the Triassic sediments of Europe by isolated scales and teeth (Korneisel et al., 2015; Lakin et al., 2016), and even by associated skeletal remains (Schultze and Kriwet, 1999; Böttcher, 2015).

Order Birgeriiformes Heyler, 1969

Family Birgeriidae Aldinger, 1937

Genus *Birgeria* Stensiö, 1919

***Birgeria* sp.**

Fig. 7

Referred material: 29 teeth (NHMUS VER 2018.2329., VER 2018.2355.-2357.) from the Templomhegy Dolomite Mb. of Construction site; 16 teeth (NHMUS VER 2013.29.1-14., VER 2018.2312.) from the Mészhegy Sandstone Fm. of Road-cut site.

Description: The here-referred teeth preserve a relatively high root and an acrodin cap. The teeth have a circular base in cross-section, and an overall conical to blade-shaped cap. Fine, longitudinal striae, running apicobasally, are present on the tooth base. The enamel cap is weakly flattened (presumably in labiolingual direction), shiny and slightly translucent with

fine vertical ridges, which do not reach the very tip. Both anterior and posterior cutting edges are present on the tooth cap. A strong neck is present, separating the two parts of the tooth.

Two size groups are separable, representing the two tooth row types: the lingual tooth row is represented by larger, robust teeth (represented by a single tooth, NHMUS VER 2018.2356.), while teeth in the labial row are smaller and minute (represented by all other Villány *Birgeria* tooth remains).

Remarks: Conical teeth with ridged base and striated enamel cap are characteristic for this Triassic predatory fish genus (see *Birgeria acuminata* in Savage and Large, 1966; *B. americana* in Romano et al., 2017; and *B. mougeoti* in Böttcher, 2015), which is widely known by articulated skeletons. Following the low number of the isolated Villány material, here we refer these specimens as *Birgeria* sp.

Aldinger (1937) erected the family Birgeriidae without a diagnosis. Later on, Nielsen (1949) provided an extensive diagnosis. *Birgeria* is known from Triassic marine deposits worldwide (Romano and Brinkmann, 2009).

Actinopterygii indet.

Fig. 8

Referred material: 18 teeth (NHMUS VER 2018.2324., VER 2018.2331., VER 2018.2332., VER 2018.2335., VER 2018.2358., VER 2018.2359.) and 282 scales (NHMUS VER 2018.2325., VER 2018.2333., VER 2018.2336., VER 2018.2360.-2362.) from the Templomhegy Dolomite Mb. of Construction site; 14 teeth (NHMUS VER 2013.25.1-10., VER 2013.26., VER 2018.2313.-2315.) and 2 scales (NHMUS VER 2018.2309., VER 2018.2319.) from the Mészhegy Sandstone Fm. of Road-cut section.

Description: The here referred Villány fish teeth represent two morphotypes:

- **Morphotype 1** (Fig. 8(A-F)) is circular in occlusal view, and conical to hemispherical in profile view (depending on functional wear). The acrodin surface is shiny and smooth. If unworn, the tooth bears a central papilla in the middle of the apical surface;
- **Morphotype 2** (Fig. 8(G, H)) is apicobasally high, with a rounded tip, and flattened labiolingually. This morphotype is represented by only one tooth, found in Layer 14 of the Templomhegy Dolomite Mb.

A high number of ganoid scales have been sampled from the residues (Fig. 8(I, J)). The most complete specimens have a rhomboidal outline in lateral view. They all bear a shiny layer of ganoine, different from those of *Gyrolepis* scales (see above) in being simple and continuous. Due to their poor preservation, a peg-and-socket articulation cannot be observed.

Remarks: Triassic fish teeth with a general morphology similar to that of the Villány indeterminate actinopterygian teeth of morphotype 1 have been referred to as “*?Paralepidotus* or *?Heterolepidotus*” by Godefroit et al. (1998) and “*?Sphaerodus*” by Dalla Vecchia and Carnevale (2011). The Villány teeth are also similar to the wart-like crushing teeth of *Colobodus* Agassiz, 1844, despite their missing striation (Sun et al., 2008; Diedrich, 2009; Böttcher, 2015; Nordén et al., 2015). Isolated teeth of *Bobasatrania* White, 1932 are also similar to morphotype 1 in their generally simple morphology (Böttcher, 2014, 2015). Teeth of the various semionotiform and dapediiform genera also resemble morphotype 1 in being hemispherical with a central papilla (Chalupová, 2009; Bermúdez-Rochas and Poyato-Ariza, 2015; Korneisel et al., 2015; Nordén et al., 2015; Mears et al., 2016; Landon et al., 2017).

Morphotype 2 is similar to Triassic fish teeth referred to as *?Felberia* sp. by Böttcher (2015: fig. 8.22) in being high and having a smooth, unornamented crown with a rounded, labiolingually flattened tip. Attributing the Villány indeterminate actinopterygian teeth to any of the aforementioned fish taxa requires further skeletal elements (e.g., skull remains), therefore the here-referred teeth are described as Actinopterygii indet. until more complete material may allow for a more precise determination.

Various Triassic actinopterygians are characterized by simple ganoid scales (e.g., certain dapediiform and semionotiform taxa). This suggests the presence of further actinopterygian taxa in the Villány ichthyofauna. Here we describe these scale remains as ganoid scales of indeterminate actinopterygians, until further remains help us to a more accurate description. Since they are all isolated elements, it cannot be decided whether the Villány indeterminate actinopterygian dental and non-dental elements belong to the same species or not.

5. Discussion

5.1. Feeding habits and habitat preferences of the Villány fish

Altogether four chondrichthyan (Hybodontidae indet., *Palaeobates angustissimus*, ‘*Polyacrodus*’ sp., *?Lissodus* sp.) and at least three osteichthyan taxa (*Gyrolepis* sp., *Birgeria* sp., Actinopterygii indet.) have been identified in the two fossil-bearing formations of the Triassic Villány Hills vertebrate sites. All of them are predatory animals with various feeding strategies.

There are two primary dentition types recognized in Hybodontidae: clutching-type and tearing-type, suggesting various diets. The high number of isolated, well-developed lateral cusplets suggests that the Villány Hybodontidae indet. represents a piscivorous feeder with teeth adapted for catching fast prey, such as various cephalopods and smaller fish (Dica and

Codrea, 2006). The dentition of *Palaeobates* is composed of specialized, slender and generally flat-crowned teeth, suggesting that it fed on a wide variety of hard-shelled prey (Romano and Brinkmann, 2010). *Polyacrodus* has low crowned, mesiodistally elongated teeth with well-expressed principal and laterals cusps, and an occlusal surface ornamented with numerous crests. This made *Polyacrodus* a generalist predator, capable of feeding both on fish and shelled prey (Blanger, 2005). The general crushing-type dentition of *Lissodus* refers to hard-shelled, benthic prey (Korneisel et al., 2015); however, according to Cuny and Benton (1999), dental characteristics of *Lissodus* indicate a more opportunistic feeding behaviour than the specialized grinding dentition of *Palaeobates*. The elongate, piercing-type teeth of *Gyrolepis* imply that these fishes were predators, most probably feeding on smaller fish and invertebrates (Korneisel et al., 2015; Mears et al., 2016). Members of *Birgeria* were large predatory fishes with large pointed teeth and massive jaws (Romano et al., 2017; Ni et al., in press). The small-sized bony fishes (represented by a large number of scales and teeth, as Actinopterygii indet.) could have provided a food source for piscivorous and generalist forms too.

Because the Villány hybodontid taxon is not referable at the genus or species level, it is insignificant for a more precise paleoenvironmental reconstruction of the Mészhegy Sandstone Fm. in the Road-cut site. However, the genus *Hybodus*, most similar to the Villány hybodontid, is mainly marine, but there are some reports of *Hybodus* from brackish and freshwater environments from Europe, Asia, Africa and North America (Dica and Codrea, 2006; Klug et al., 2010; Cuny, 2012). Except for the brackish lower Keuper (Hagdorn and Mutter, 2011; Böttcher, 2015) and the layers of Schöningen, Germany, with varied salinity (Dorka, 2001), *Palaeobates angustissimus* is typically reported from marine sediments of Europe (Schultze and Kriwet, 1999; Diedrich, 2003, 2009; Chrzastek, 2008; Dalla Vecchia and Carnevale, 2011; Pla et al., 2013; Ferrón et al., 2014). Teeth referred to *Polyacrodus* from the Late Triassic of Europe have been unearthed from brackish (Dorka, 2001) to fully marine sediments (Diedrich, 2003, 2009), thus either the Triassic representatives of the genus were able to tolerate brackish ecosystems (Böttcher, 2015), or more likely *Polyacrodus* is polyphyletic (Rees, 2008). Therefore, similarly to the indeterminate Villány hybodontid, without specific identification, *Polyacrodus* is not informative for paleoenvironmental reconstruction. The same can be said for ?*Lissodus*, as remains of this genus have been found in freshwater and brackish deposits, but are also known from marine sediments (Brough, 1935; Fischer and Schneider, 2008; Cappetta, 2012). This means that without specific determination, the Villány ?*Lissodus* teeth are not informative for paleoenvironmental

reconstruction. *Gyrolepis* has been found in sediments of marine coastal environment (Tintori et al., 2001); Whiteside et al. (2016: table 2) also regarded *Gyrolepis* as a marine fish genus.

Following the habitat preferences of the Villány fish taxa, the general picture of the ichthyofauna points to a marine depositional environment for all the bone-bearing successions in the two formations. Nevertheless, Hybodontidae indet., '*Polyacrodus*' sp. and ?*Lissodus* sp. are less significant in determining the Villány paleoenvironment, because of their variable habitat preferences depending on species and also because of the taxonomic problems related to these taxa.

5.2. Faunal composition of the Templomhegy Dolomite Member and the Mészhegy Sandstone Formation

Despite the large sample size and the large number of sampled microvertebrate fossils, no remains of neoselachians and sarcopterygians have been found. Both taxa are reported elements of Middle and Late Triassic vertebrate faunas; however, neoselachians were reported in Europe only from the Erfurt Fm. (Ladinian) in Germany (Table S1; Appendix A). Their absence in the Villány fauna is worth noting and could be related to the fact that the Villány assemblage is rather poorly diversified. Regarding the absence of neoselachians, another reason is also worth of consideration. Neoselachians are attested by low-diversity assemblages in the Late Triassic, then they underwent a rapid diversification throughout the Jurassic and Cretaceous periods, up to diverse assemblages containing representatives of most extant clades by the end of the Cretaceous (Underwood, 2006). In this interpretation, their absence in the Villány fauna could reflect their under-representation in the Middle to Late Triassic global fossil record.

The sedimentary sequence exposed in the two Villány Hills sites shows a major difference in the composition of the discovered fish faunas (Fig. 9). The Ladinian Templomhegy Dolomite Mb. of Construction site yielded a fish fauna dominated by durophagous hybodontiforms (*Palaeobates* and ?*Lissodus*; ca. 72 % of the complete Templomhegy Dolomite Mb. fish fauna), while no remains of piscivorous Hybodontidae and generalist '*Polyacrodus*' have been found in this site. On the other hand, the Carnian Mészhegy Sandstone Fm. of the Road-cut site shows an ichthyofaunal composition different from that of the Construction site: it is dominated by fish-eating Hybodontidae indet. (> 50% of the Mészhegy Sandstone Fm. fish fauna).

The variation in apparent dominance (as well as presence or lack of different taxa) do not seem to reflect sampling bias, because the differences can be firmly established based on representative sample size of screen-washed material from various bone-yielding successions.

The absence of piscivorous Hybodontidae and the generalist '*Polyacrodus*' from the Templomhegy Dolomite Mb. is unusual, since these forms are widespread in Triassic shallow marine sediments across Europe (Cappetta, 2012; Böttcher, 2015). Moreover, remains of potential prey animals (e.g., *Gyrolepis* and further indeterminate actinopterygians) are abundant in the Templomhegy Dolomite Mb. (Fig. 9). This phenomenon might be explained by two different causes or the combination of these scenarios. The relatively great abundance of fish-eating marine reptiles, such as the heterodont nothosaurs in the Ladinian Villány environment, could have been an important factor in the observed faunal differences between the two sites (Ósi et al., 2013). These predators could have been major competitors for piscivorous hybodontids (Rieppel, 2002) and the generalist '*Polyacrodus*' in exploiting available fish prey sources. Diversity and disparity of marine reptiles suffered a major decrease during the Carnian (Renesto and Dalla Vecchia, 2018) that might reflect the occurrence of fish-eating sharks in the Carnian Mészhegy Sandstone Fm. (Fig. 9). Alternatively, the change of depositional environment (from tidal flat shelf or lagoon to nearshore environment) could also have been a simple cause, resulting in the faunal differences between the two fossil-bearing sites.

6. Conclusion

There are two recently discovered Triassic vertebrate sites in the Villány Hills, southern Hungary, which were situated on the passive margin of the European Plate southwards to Bohemian Massif (western Tethys Ocean) during the Triassic period. Bone-bearing beds of the Ladinian Templomhegy Dolomite Mb. and the Carnian Mészhegy Sandstone Fm. have resulted in (among various reptile bones and teeth) at least seven different chondrichthyan and osteichthyan fish taxa, including an indeterminate hybodontid, *Palaeobates angustissimus*, '*Polyacrodus*' sp., ?*Lissodus* sp., *Gyrolepis* sp., *Birgeria* sp., and further indeterminate actinopterygians.

The fish fauna from the Ladinian Templomhegy Dolomite Mb. is dominated by durophagous hybodontiforms, while no remains of piscivorous hybodontids and the generalist '*Polyacrodus*' have been discovered. On the other hand, fish remains of the Carnian Mészhegy Sandstone Fm., deposited in a shallow marine (siliciclastic) environment, show a markedly different faunal composition. In these layers, the dominant group was the indeterminate Hybodontidae, with an inferred piscivorous diet. Differences in the taxonomic compositions between the two successions might be related to the global decrease in diversity of marine fish-eating reptiles (e.g., nothosaurs) or to the change of paleoenvironmental conditions (from tidal flat shelf or lagoon to nearshore environment).

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Appendix A. Supplementary information

Supplementary information (including Table S1) associated with this article can be found, in the online version, at:

References

- Agassiz, L., 1833–43. *Recherches sur les Poissons Fossiles*, Tome III – Atlas. Neuchâtel, 432 p.
- Aldinger, H., 1937. Permische Ganoidfische aus Ostgrönland. *Meddelelser om Grønland* 102(3), 1–392.
- Allard, H., Carpenter, S.C., Duffin, C.J., Benton, M.J., 2015. Microvertebrates from the classic Rhaetian bone beds of Manor Farm Quarry, near Aust (Bristol, UK). *Proceedings of the Geologists' Association* 126, 762–776.
- Bérczi-Makk, A., Konrád, Gy., Rálich-Felgenhauer, E., Török, É., 2004. Tisza Mega-unit. In: Haas, J. (Ed.), *Geology of Hungary, Triassic*. ELTE Eötvös Press, Budapest, pp. 303–360. (in Hungarian)
- Bermúdez-Rochas, D.D., Poyato-Ariza, F.J., 2015. A new semionotiform actinopterygian fish from the Mesozoic of Spain and its phylogenetic implications. *Journal of Systematic Palaeontology* 13, 265–285.
- Blanger, K. de, 2005. The effect of the Permian mass extinction on shark faunas. Ph.D. Thesis, University of Bristol, 250 p. (unpubl.).
- Bleahu, M., Bordea, S., Panin, Ş., Ştefănescu, M., Šikić, K., Haas, J., Kovács, S., Péró, Cs., Bérczi-Makk, A., Konrád, Gy., Nagy, E., Rálich-Felgenhauer, E., Török, Á., 1994.

- Triassic facies types, evolution and paleogeographic relations of the Tisza Megaunit. *Acta Geologica Hungarica* 37, 187–234.
- Botfalvai, G., Györi, O., Pozsgai, E., Farkas, I.M., Sági, T., Szabó, M., Ósi, A., 2019. Sedimentological characteristics and palaeoenvironmental implication of Triassic vertebrate locality in Villány (Villány Hills, southern Hungary). *Geologica Carpathica* 70, 135–152.
- Böttcher, R., 2014. Phylloidont tooth plates of *Bobasatrania scutata* (Gervais, 1852) (Actinoperygii, Bobasatraniiiformes) from the Middle Triassic (Longobardian) Grenzbonebed of southern Germany and eastern France, with an overview of Triassic and Palaeozoic phylloidont tooth plates. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 274, 291–311.
- Böttcher, R., 2015. 8. Fische des Lettenkeupers. In: Hagdorn, H., Schoch, R., Schweigert, G. (Eds.), *Der Lettenkeuper – Ein Fenster in die Zeit vor den Dinosauriern. Palaeodiversity, Sonderband*, pp. 141–202.
- Brough, J., 1935. On the structure and relationships of the Hybodont sharks. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 79, 35–49.
- Bürgin, T., Rieppel, O., Martin Sander, P., Tschanz, K., 1989. The Fossils of Monte San Giorgio: An ancient sea provides a rich assemblage of vertebrates from the Triassic period. *Scientific American* 260,74–81.
- Cannon, M.D., 2013. NISP, Bone Fragmentation, and the Measurement of Taxonomic Abundance. *Journal of Archaeological Method and Theory* 20, 397–419.
- Cappetta, H., 1987. Chondrichthyes II. Mesozoic and Cenozoic elasmobranchii. In: Schultze, H.-P. (Ed.), *Handbook of Paleoichthyology, Vol. 3B*, Gustav Fischer Verlag, Stuttgart, New York, 193 p.
- Cappetta, H., 2012. *Handbook of Paleoichthyology, Vol. 3E: Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth*. Verlag Dr. Friedrich Pfeil, 512 p.
- Carroll, R.L., 1988. *Vertebrate Paleontology and Evolution*. W.H. Freeman and Company, New York, 698 p.
- Chalupová, B., 2009. Rétske žraloky a ryby z fatranského súvrstvia (profil Kardolína, Belianske Tatry, Slovensko [Rhaetian Chondrichthyes and Osteichthyes remains from the Fatra Fm. (Kardolína section, Belianske Tatry Mts., Slovenia)]. *Mineralia Slovaca* 41, 283–290. (In Slovenian)
- Chrzastek, A., 2008. Vertebrate remains from the Lower Muschelkalk of Raciborowice Górne (North-Sudetic Basin, SW Poland). *Geological Quarterly* 52, 225–238.

- Cuny, G., 2012. Freshwater hybodont sharks in Early Cretaceous ecosystems: a review. In: Godefroit, P. (Ed.), *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, Bloomington, pp. 518-529.
- Cuny, G., Benton, M.J. 1999. Early radiation of the neoselachian sharks in Western Europe. *Geobios* 32, 193–204.
- Dalla Vecchia, F.M., Carnevale, G., 2011. Ceratodontoid (Dipnoi) calvarial bones from the Triassic of Fúsea, Carnic Alps: the first Italian lungfish. *Italian Journal of Geosciences* 130, 128–135.
- Delsate, D., Duffin, C.J., 1999. A new fish fauna from the Middle Triassic (Upper Muschelkalk) of Moersdorf (Grand Duchy of Luxembourg). *Travaux Scientifiques du Musée National d'Historie Naturelle de Luxembourg* 32, 5–53.
- Dica, E.P., Codrea, V., 2006. On the *Hybodus* (Euselachii) from the Early Jurassic of Anina (Caraş Severin district, Romania). *Studia Universitatis Babeş-Bolyai, Geologia* 51, 51–54.
- Diedrich, C. (2003). Die Wirbeltier-Fauna aus einer Bonebed-Prospektionsgrabung in der *enodis/posseckeri*-Zone des Oberen Muschelkalkes (Unter-Ladin, Mitteltrias) von Lamerden (NW-Deutschland). *Philippia* 11, 133–150.
- Diedrich, C., 2009. The vertebrates of the Anisian/Ladinian boundary (Middle Triassic) from Bissendorf (NW Germany) and their contribution to the anatomy, palaeoecology, and palaeobiogeography of the Germanic Basin reptiles. *Palaeogeography, Palaeoclimatology, Palaeoecology* 273, 1–16.
- Dorka, M., 2001. Shark remains from the Triassic of Schöningen, Lower Saxony, Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 221, 219–247.
- Dorka, M., 2003. Teeth of *Polyacrodus* Jaekel, 1889 from the Triassic of the Germanic Basin. *Mitteilungen aus dem Museum für Naturkunde in Berlin* 6, 147–155.
- Dzik, J., Sulej, T., 2007. A review of the early Late Triassic Krasiejów Biota from Silesia, Poland. *Palaeontologica Polonica* 64, 3–27.
- Duffin, C.J., 1999. Chapter 14, Fish. In: Swift, A., Martill, D.M. (Eds.), *Fossils of the Rhaetian Penarth group*. The Palaeontological Association, Field guide to fossils 9, pp. 191-222
- Fischer, J., Schneider, J.W., 2008. Palaeobiogeography of *Lissodus* (Hybodontoida) during the Carboniferous and Permian in freshwater of Central Europe. 5th Symposium on Permo-Carboniferous Faunas, pp. 7–11.

- Felber, M., 2005. Il Monte san Giorgio. Dai fossili alla lavorazione artistica della pietra: una storia di 300 milioni di anni. (con la collaborazione di Furrer H. & Tintori A.). Ed. Casagrande, 222 p.
- Ferrón, H., Pla, C., Martínez-Pérez, C., Escudero-Mozo, M.J., Botella, H., 2014. Morphometric Discriminant Analysis of isolated chondrichthyan scales for palaeoecological inferences: the Middle Triassic of the Iberian Chain (Spain) as a case of study. *Journal of Iberian Geology* 40, 87–97.
- Glikman, L.S., 1964. Sharks of Paleogene and their stratigraphic significance. Nauka Press, 229 p. (In Russian)
- Godefroit, P., Cuny, G., Delsate, D., Roche, M., 1998. Late Triassic vertebrates from Syren (Luxembourg). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 210, 305–343.
- Götz, A.E., Török, Á., 2008. Correlation of Tethyan and Peri-Tethyan long-term and high-frequency eustatic signals (Anisian, Middle Triassic). *Geologica Carpathica* 59, 307–317.
- Götz, A.E., Török, Á., Feist-Burkhardt, S., Konrád, Gy., 2003. Palynofacies patterns of Middle Triassic ramp deposits (Mecsek Mts., S Hungary): A powerful tool for high-resolution sequence stratigraphy. *Geoaustria-Mitteilungen der Gesellschaft der Geologie und Bergbaustudenten in Österreich* 46, 77–90.
- Haas, J., 2001. Tisza Mega-unit. Alpine evolution. In: Haas, J. (Ed.), *Geology of Hungary*. Eötvös University Press, Budapest, pp. 168–193.
- Haas, J., Péró, Cs., 2004. Mesozoic evolution of the Tisza Mega-unit. *International Journal of Earth Sciences* 93, 297–313.
- Hagdorn, H., Mutter, R.J., 2011. The vertebrate fauna of the Lower Keuper Albertibank (Erfurt Formation, Middle Triassic) in the vicinity of Schwäbisch Hall (Baden-Württemberg, Germany). *Palaeodiversity* 4, 223–243.
- Hay, O.P., 1902. Bibliography and catalogue of fossil vertebrata of North America. *Bulletin of the United States Geological Survey* 179, 1–868.
- Herman, J., 1977. Les sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. *Eléments d'une biostratigraphie intercontinentale. Mémoires pour servir à l'explication des cartes géologiques et minières de la Belgique*, 1975 15, 401 p.
- Heyler, D., 1969. Vertébrés de l'Autunien de France. *Cahiers de Paléontologie*, CNRS, Paris, 259 p.

- Huxley, T.H., 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880, 649–662.
- Jaekel, O., 1889. Die Selachier aus dem oberen Muschelkalk Lothringens. Abhandlungen Geologische Spezialkarte Elsass-Lothringen, Ser. 3(4), 273–332.
- Klein, E.F., 1885. Beiträge zur Bildung des Schädels der Knochenfische. 2 Jahreshefte Vereins Vaterländischer Naturkunde in Württemberg 42, 205–300.
- Klug, S., Tütken, T., Wings, O., Pfretzschner, H.-U., Martin, T., 2010. A Late Jurassic freshwater shark assemblage (Chondrichthyes, Hybodontiformes) from the southern Juggar Basin, Xinjiang, Northwest China. Palaeobiodiversity and Palaeoenvironments 90, 241–257.
- Korneisel, D., Gallois, R.W., Duffin, C.J., Benton, M.J., 2015. Latest Triassic marine sharks and bony fishes from a bone bed preserved in a burrow system, from Devon, UK. Proceedings of the Geologist's Association 126, 130–142.
- Koot, M.B., Cuny, G., Tintori, A., Twitchett, R.J., 2013. A new diverse shark fauna from the Wordian (Middle Permian) Khuff Formation in the Interior Haushi-Huqf Area, Sultanate of Oman. Palaeontology 56, 303–343.
- Lakin, R.J., Duffin, C.J., Hildebrandt, C., Benton, M.J., 2016. The Rhaetian vertebrates of Chipping Sodbury, South Gloucestershire, UK, a comparative study. Proceedings of the Geologists' Association 127, 40–52.
- Landon, E.N.U., Duffin, C.J., Hildebrandt, C., Davies, T.G., Simms, M.J., Benton, M.J., 2017. The first discovery of crinoids and cephalopod hooklets in the British Triassic. Proceedings of the Geologist's Association 128, 360–373.
- Lombardo, C., Tintori, A., Tona, D., 2012. A new species of *Sangiorgioichthys* (Actinopterygii, Semionotiformes) from the Kalkschieferzone of Monte San Giorgio (Middle Triassic; Meride, Canton Ticino, Switzerland). Bollettino della Società Paleontologica Italiana 51, 203–212.
- López-Arbarello, A., Bürgin, T., Furrer, H., Stockar, R., 2016. New holostean fishes (Actinopterygii: Neopterygii) from the Middle Triassic of the Monte San Giorgio (Canton Ticino, Switzerland). PeerJ 4, e2234.
- Lyman, R.L., 2008. Quantitative Paleozoology. Cambridge University Press, New York, 374 p.
- Maisey, J.G., 1975. The interrelationships of phalanthous selachians. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1975, 553–567.

- Maxwell, E.E., Romano, C., Wu, F., Furrer, H., 2015. Two new species of *Saurichthys* (Actinopterygii: Saurichthyidae) from the Middle Triassic of Monte San Giorgio, Switzerland, with implications for character evolution in the genus. *Zoological Journal of the Linnean Society* 173, 887–912.
- Mears, E.M., Rossi, V., MacDonald, E., Coleman, G., Davies, T.G., Arias-Riesgo, C., Hildebrandt, C., Thiel, H., Duffin, C.J., Whiteside, D.I., Benton, M.J., 2016. The Rhaetian (Late Triassic) vertebrates of Hampstead Farm Quarry, Gloucestershire, UK. *Proceedings of the Geologist's Association* 127, 478–505.
- Meyer, H., 1849. Fische, Crustaceen, Echinodermen und andere Versteinerungen aus dem Muschelkalk Oberschleisens. *Palaeontographica* 1, 216–242.
- Nagy, E., Nagy, I., 1976. Triasbildungen des Villányer Gebirges. *Geologica Hungarica Series Geologica* 17, 113–227.
- Ni, P., Tintori, A., Sun, Z., Lombardo, C., Jiang, D., in press. Postcranial skeleton of *Birgeria liui* (Osteichthyes, Actinopterygii) from the Longobardian (Ladinian, Middle Triassic) of Xingyi, Guizhou Province, South China. *Swiss Journal of Geosciences*, DOI: 10.1007/s00015-018-0329-0.
- Nielsen, E., 1949. Studies on Triassic fishes from East Greenland 2. *Australosomus* and *Birgeria*. *Palaeozoologica Groenlandica* 3, 1-309.
- Nordén, K.K., Duffin, C.J., Benton, M.J., 2015. A marine vertebrate fauna from the Late Triassic of Somerset, and a review of British placodonts. *Proceedings of the Geologists' Association* 126, 564–581.
- Owen, R., 1846. Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals. Part 1. Fishes. Longman, Brown, Green and Longmans, London, 304 p.
- Ósi, A., Pozsgai, E., Botfalvai, G., Götz, A.E., Prondvai, E., Makádi, L., Hajdu, Zs., Csengődi, D., Czirják, G., Sebe, K., Szentesi, Z., 2013. First report of Triassic vertebrate assemblages from the Villány Hills (Southern Hungary). *Central European Geology* 56, 297–335.
- Ósi, A., Szabó, M., Segesdi, M., Botfalvai, G., 2018. A new Triassic (Ladinian/Carnian) vertebrate locality from Villány, Southern Hungary. Abstracts of the XVIth EAVP, p. 140.
- Pla, C., Márquez-Aliaga, A., Botella, H., 2013. The chondrichthyan fauna from the Middle Triassic (Ladinian) of the Iberian Range (Spain). *Journal of Vertebrate Paleontology* 33, 770–785.

- Pollerspöck, J., Straube, N., 2018. Bibliography database of living/fossil sharks, rays and chimaeras (Chondrichthyes: Elasmobranchii, Holocephali). www.shark-references.com, World Wide Web electronic publication, Version 2018 [accessed 01/12/2018].
- Pozsgai, E., Józsa, S., Dunkl, I., Sebe, K., Thamó-Bozsó, E., Sajó, I., Dezső, J., von Eynatten, H., 2017. Provenance of the Upper Triassic siliciclastics of the Mecsek Mountains and Villány Hills (Pannonian Basin, Hungary): constraints to the early Mesozoic paleogeography of the Tisza Megaunit. *International Journal of Earth Sciences* 106, 2005–2024.
- Rálisch-Felgenhauer, E., 1981. Templomhegyi Dolomit Formáció (Templomhegy Dolomite Formation). MÁFI Jelentés villányi-hegységi alapszelvények vizsgálatáról. [Geological Institute of Hungary report about the study of key sections of the Villány Hills.] MÁFI, 40 p.
- Rálisch-Felgenhauer, E., 1985. Road-cut section in Templom Hill (Villány Hills). *Magyarország geológiai alapszelvényei*, MÁFI, Budapest, 5.
- Rálisch-Felgenhauer, E., Török, A., 1993. Mecsek and Villány Mountains. In: Haas J. (Ed.): *Triassic lithostratigraphic units of Hungary*. Hungarian Geological Survey-MOL Ltd. Budapest, pp. 232-260. (In Hungarian)
- Rees, J., 2008. Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology – preliminary results. *Acta Geologica Polonica* 58, 217–221.
- Rees, J., Underwood, C.J., 2002. The status of the shark genus *Lissodus* Brough, 1935, and the position of nominal *Lissodus* species within the Hybodontoida (Selachii). *Journal of Vertebrate Paleontology* 22, 471–479.
- Renesto, S., Dalla Vecchia, F.M., 2018. Late Triassic marine reptiles. In: Tanner, L.H. (Ed.): *The Late Triassic World: Earth in a Time of Transition*. Springer Nature, Switzerland, pp. 263–314.
- Rieppel, O., 2002. Feeding mechanics in Triassic stem-group sauropterygians: the anatomy of a successful invasion of Mesozoic seas. *Zoological Journal of the Linnean Society* 135, 33–63.
- Romano, C., Brinkmann, W., 2009. Reappraisal of the lower actinopterygian *Birgeria stensioei* Aldinger, 1931 (Osteichthyes; Birgeriidae) from the Middle Triassic of Monte San Giorgio (Switzerland) and Besano (Italy). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 252, 17-31.

- Romano, C., Brinkmann, W., 2010. A new specimen of the hybodont shark *Palaeobates polaris* with three-dimensionally preserved Meckel's cartilage from the Smithian (Early Triassic) of Spitsbergen. *Journal of Vertebrate Paleontology* 30, 1673–1683.
- Romano, C., Jenks, J.F., Jattiot, R., Scheyer, T.M., Bylund, K.G., Bucher, H., 2017. Marine Early Triassic Actinopterygii from Elko County (Nevada, USA): implications for the Smithian equatorial vertebrate eclipse. *Journal of Paleontology* 91, 1025–1046.
- Savage, R.J.G., Large, N.F., 1966. On *Birgeria acuminata* and the absence of labyrinthodonts from the Rhaetic. *Palaeontology* 9, 135–141.
- Skrzycki, P., 2015. New species of lungfish (Sarcopterygii, Dipnoi) from the Late Triassic Krasiejów site in Poland, with remarks on the ontogeny of Triassic dipnoan tooth plates. *Journal of Vertebrate Paleontology* 35, e964357.
- Schultze, H.-P., Kriwet, J., 1999. Die Fische der Germanischen Trias. In: Hauschke, N., Wilde, V. (Eds.), *Trias eine ganz andere Welt. Europa im frühen Erdmittelalter*. Pfeil Verlag, München, pp. 239–250.
- Segesdi, M., Ósi, A., Botfalvai, G., 2017. New eosauropterygian remains from the Middle Triassic of Villány, Hungary. *Abstracts of the 8th SATLW*, p. 47.
- Stensiö, E.A. 1919. Einige Bemerkungen über die systematische Stellung von *Saurichthys mougeoti* Agassiz. *Senckenbergiana* 1, 177–181.
- Sun, Z., Tintori, A., Lombardo, C., Dayong, J., Weicheng, H., Yuanlin, S., Feixiang, W., Rusconi, M., 2008. A new species of the genus *Colobodius* Agassiz, 1844 (Osteichthyes, Actinopterygii) from the Pelsonian (Anisian, Middle Triassic) of Guizhou, South China. *Rivista Italiana di Paleontologia e Stratigrafia* 114, 363–376.
- Tintori, A., 1998. *Ctenognathichthys bellotti* (De Alessandri, 1910): Nomenclatural problems and stratigraphical importance of this Middle Triassic actinopterygian fish. *Rivista Italiana di Paleontologia e Stratigrafia* 104, 417–422.
- Tintori, A., Posenato, R., Kustatscher, E., Wachtler, M., 2001. New Triassic fish remains from paralic environments in the Alps. *Abstract of III Int. Meeting on Mesofishes*, p. 66.
- Török, Á., 1997. Triassic ramp evolution in Southern Hungary and its similarities to Germano-type Triassic. *Acta Geologica Hungarica* 40, 367–390.
- Török, Á. 1998. Controls on development of Mid-Triassic ramps: examples from southern Hungary. In: Wright V.R., Burchette, T.P. (Eds.), *Carbonate Ramps*. Geological Society, London 149, 339–367.

- Török, Á., 2000. Muschelkalk carbonates in southern Hungary: an overview and comparison to German Muschelkalk. *Zentralblatt für Geologie und Paläontologie, Teil I.* 9, 1085–1103.
- Underwood, C.J., 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology* 32, 215–235.
- Vogt, C., 1851. *Zoologische Briefe. Naturgeschichte der lebenden und untergegangenen Thiere, für Lehrer, höhere Schulen und Gebildete aller Stände II: Frankfurt am Main, Literarische Anstalt*, 640 p.
- Vörös, A., 2009. Tectonically-controlled Late Triassic and Jurassic sedimentary cycles on a peri-Tethyan ridge (Villány, southern Hungary). *Central European Geology* 52, 125–151.
- Vörös, A., 2010. A villányi mezozóos rétegsor: visszatekintés új nézőpontból. [The Mesozoic sedimentary sequences at Villány.] *Földtani Közlöny* 140, 3–30.
- Whiteside, D.I., Duffin, C.J., Gill, P.G., Marshall, J.E.A., Benton, M.J., 2016. The Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: Stratigraphy and setting. *Palaeontologia Polonica* 67, 257–287.

Figure captions

Fig. 1. **A.** Locality map of the Villány site (modified after Botfalvai et al., 2019). **B.** Schematic stratigraphic section of the Triassic vertebrate sites in the Villány Hills. **C.** Paleogeographical map of the Tisza Megaunit in the Late Triassic (compiled by Pozsgai et al., 2017).

Fig. 2. **A.** Schematic stratigraphic section of the Construction site showing the main lithofacies and the positions of the productive microvertebrate samples. **B.** Picture of the bone-bearing beds of the Construction site.

Fig. 3. **A.** Stratigraphic section of the Road-cut site (modified after Botfalvai et al., 2019). **B.** Picture of the Carnian fossiliferous horizons of Mészhegy Sandstone Formation showing the beds providing paleontological data. P, palynological sample; L3-L4-L5, vertebrate paleontological samples.

Fig. 4. A-F. Hybodontidae indet., tooth remains from the Mészhegy Sandstone Formation. A-C: main cusp (NHMUS VER 2018.2306) in lingual (A), profile (B) and lingual (C) views; D-F: ?lateral cusplet (NHMUS VER 2018.2307) in lingual (D), profile (E) and labial (F) views. **G-R.** *Palaeobates angustissimus* tooth remains from the Templomhegy Dolomite Member. G-I: anterior tooth (NHMUS VER 2018.2341) in apical (G), ?labial (H) and distal (I) views; J-L: anterior tooth (NHMUS VER 2018.2340) in apical (J), ?lingual (K) and mesial (L) views; M, N: lateral tooth (NHMUS VER 2018.2338) in apical (M) and ?labial (N) views; O, P: lateral tooth (NHMUS VER 2018.2337) in apical (O) and ?lingual (P) views; Q, R: posterior tooth (NHMUS VER 2018.2342) in apical (Q) and profile (R) views. Scale bars: 1 mm.

Fig. 5. A-F. '*Polyacrodus*' sp. teeth from the Mészhegy Sandstone Formation. A-C: tooth (NHMUS VER 2018.2311) in apical (A), ?labial (B) and ?lingual (C) views; D-F: tooth (NHMUS VER 2018.2322) in apical (D), labial (E) and lingual (F) views. **G-L.** ?*Lissodus* sp. teeth from the Templomhegy Dolomite Member. G, H: anterior-anteriolateral tooth (NHMUS VER 2018.2344) in occlusal (G) and labial (H) views; I, J: anterior-anterolateral tooth (NHMUS VER 2018.2345) in occlusal (I) and labial (J) views. K, L: posterior tooth (NHMUS VER 2018.2346) in occlusal (K) and labial (L) views. Scale bars: 500 μ m.

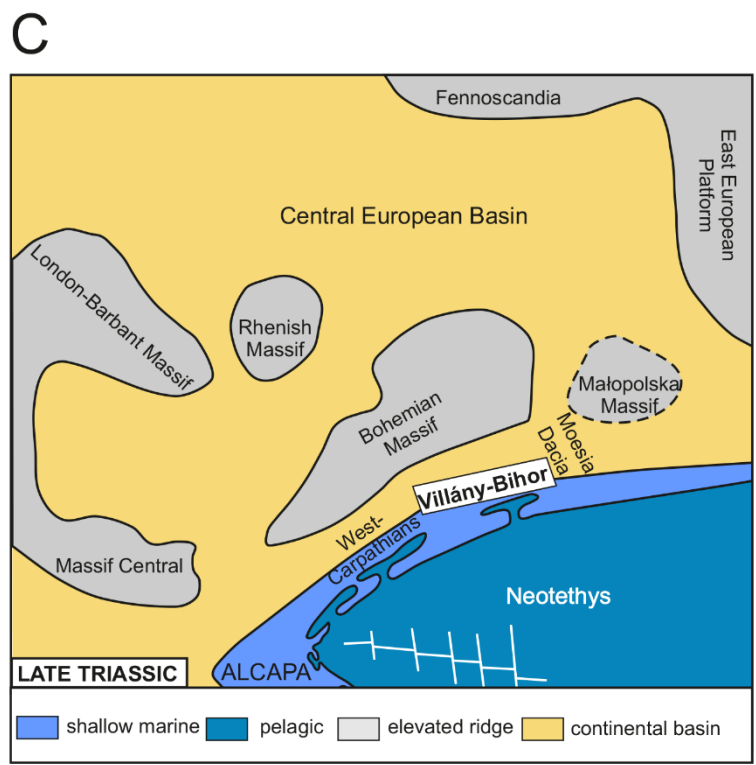
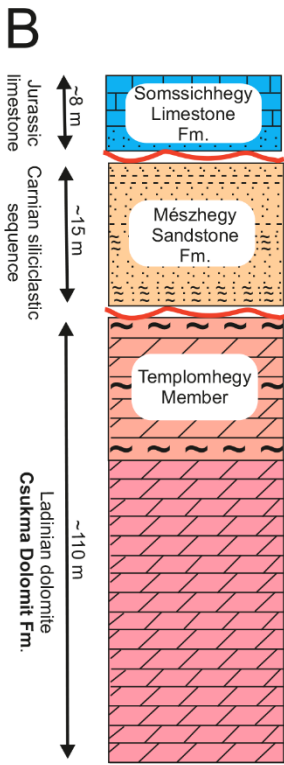
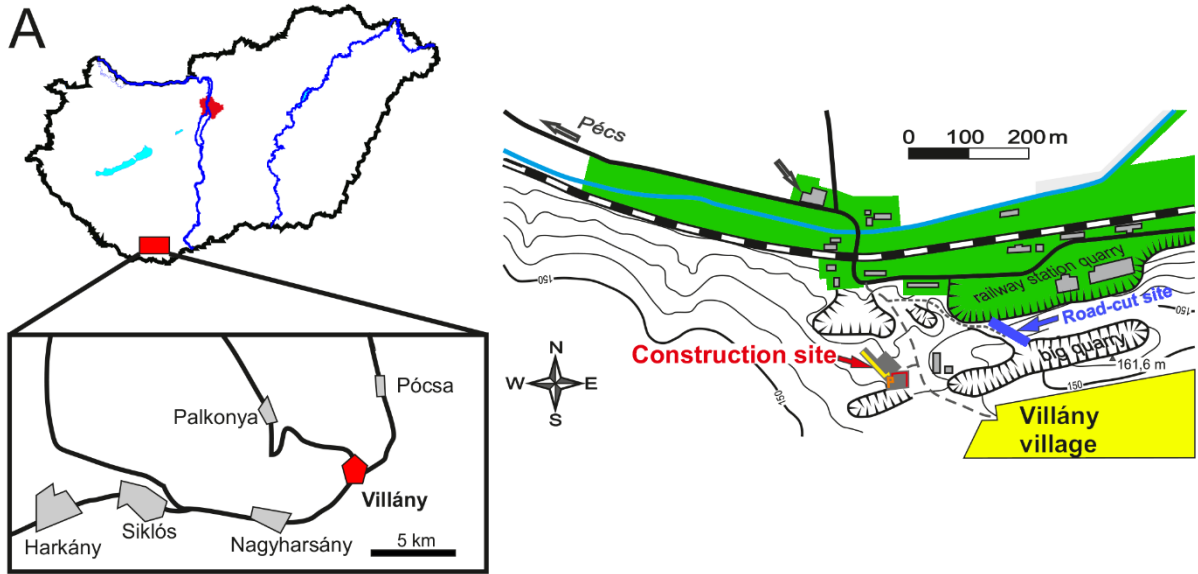
Fig. 6. *Gyrolepis* sp. remains from the Templomhegy Dolomite Member. **A, B.** Tooth (NHMUS VER 2018.2348) in two different views. **C.** Close-up view of the tooth surface. **D.** scale (NHMUS VER 2018.2350) in lateral view. **E.** Close-up view of the ganoid covering of D. **F-H.** Scales (NHMUS VER 2018.2351, NHMUS VER 2018.2352, NHMUS VER 2018.2353) in lateral view. Scale bars: 1 mm (A, B, D, F-H), 100 μ m (C, E).

Fig. 7. *Birgeria* sp. from the Templomhegy Dolomite Member. **A-D.** Tooth (NHMUS VER 2018.2356) in labial (A), profile (B) and lingual (C) views. D: Close-up view of the acrodin cap surface. **E, F.** Tooth (NHMUS VER 2018.2355) in labial or lingual (E) and profile (F) views. Scale bars: 5 mm (A-C), 1 mm (E, F).

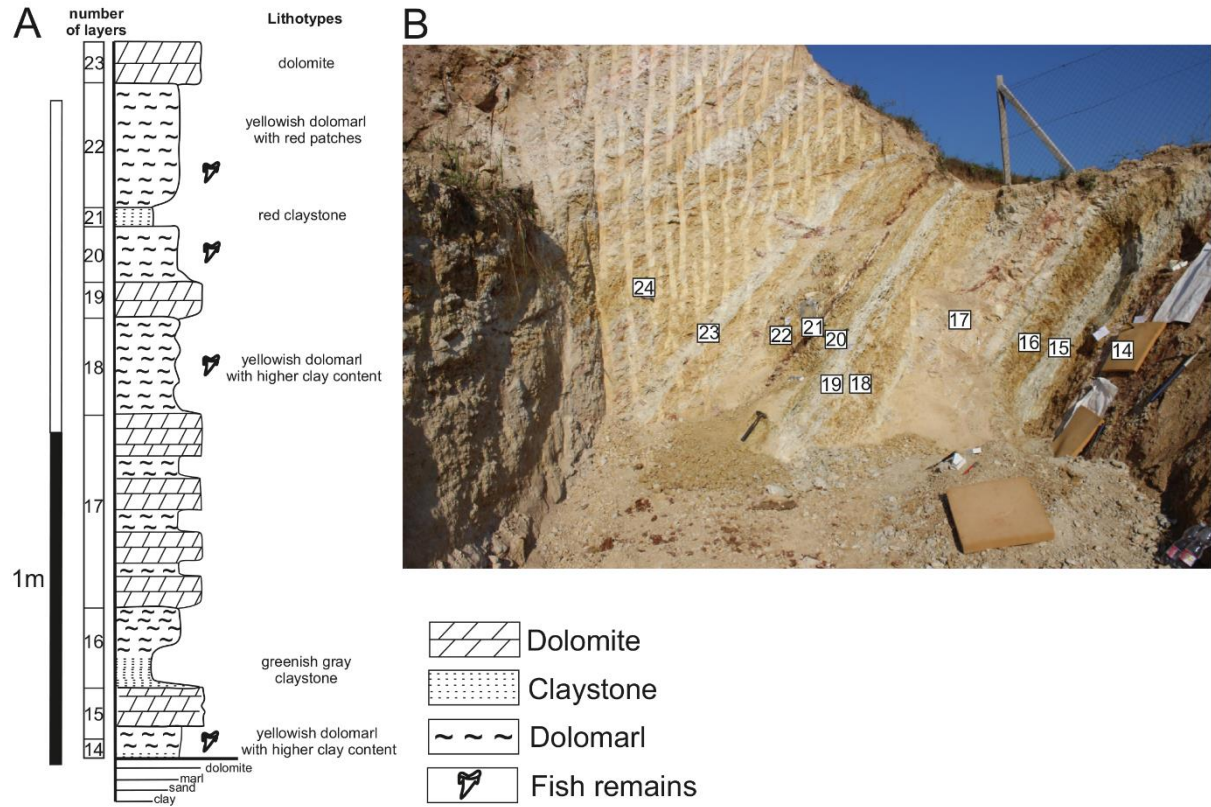
Fig. 8. *Actinopterygii* indet. elements from the two fossil-yielding formations of the Villány locality: Mészhegy Sandstone Formation (A-F) and Templomhegy Dolomite Member (G-J). **A, B.** Tooth morphotype 1 (NHMUS VER 2013.25.1) in occlusal (A) and profile (B) views. **C, D.** Tooth morphotype 1 (NHMUS VER 2018.2314) in occlusal (C) and profile (D) views. **E, F.** Tooth morphotype 1 (NHMUS VER 2018.2315) in occlusal (E) and profile (F) views. **G, H.** Tooth morphotype 2 (NHMUS VER 2018.2358) in labial or lingual (G) and profile (H) views. **I.** scale (NHMUS VER 2018.2360) in lateral view. **J.** Scale (NHMUS VER 2018.2361) in lateral view. Scale bars: 500 μm .

Fig. 9. Faunal composition of the two fossil-bearing exposures in Villány. Numbers of remains per taxa are interpreted here as maximum number of individuals (NISP; after Lyman, 2008; Cannon, 2013).

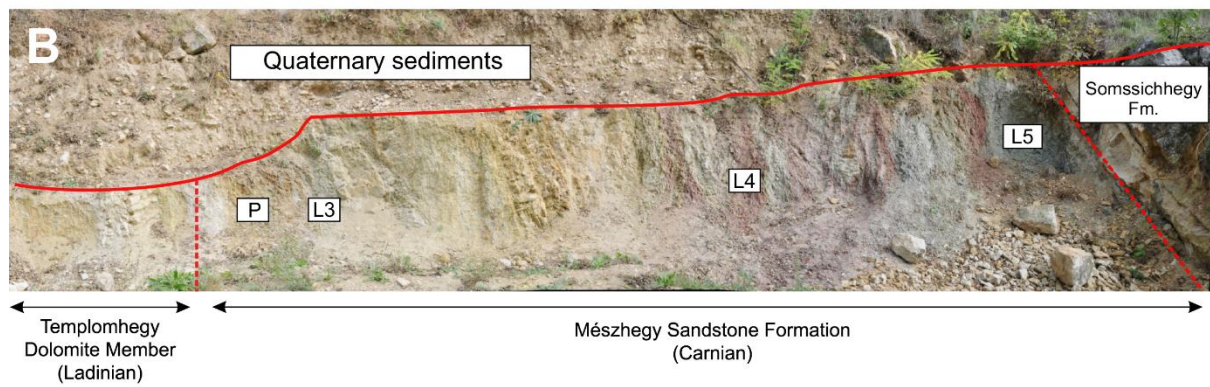
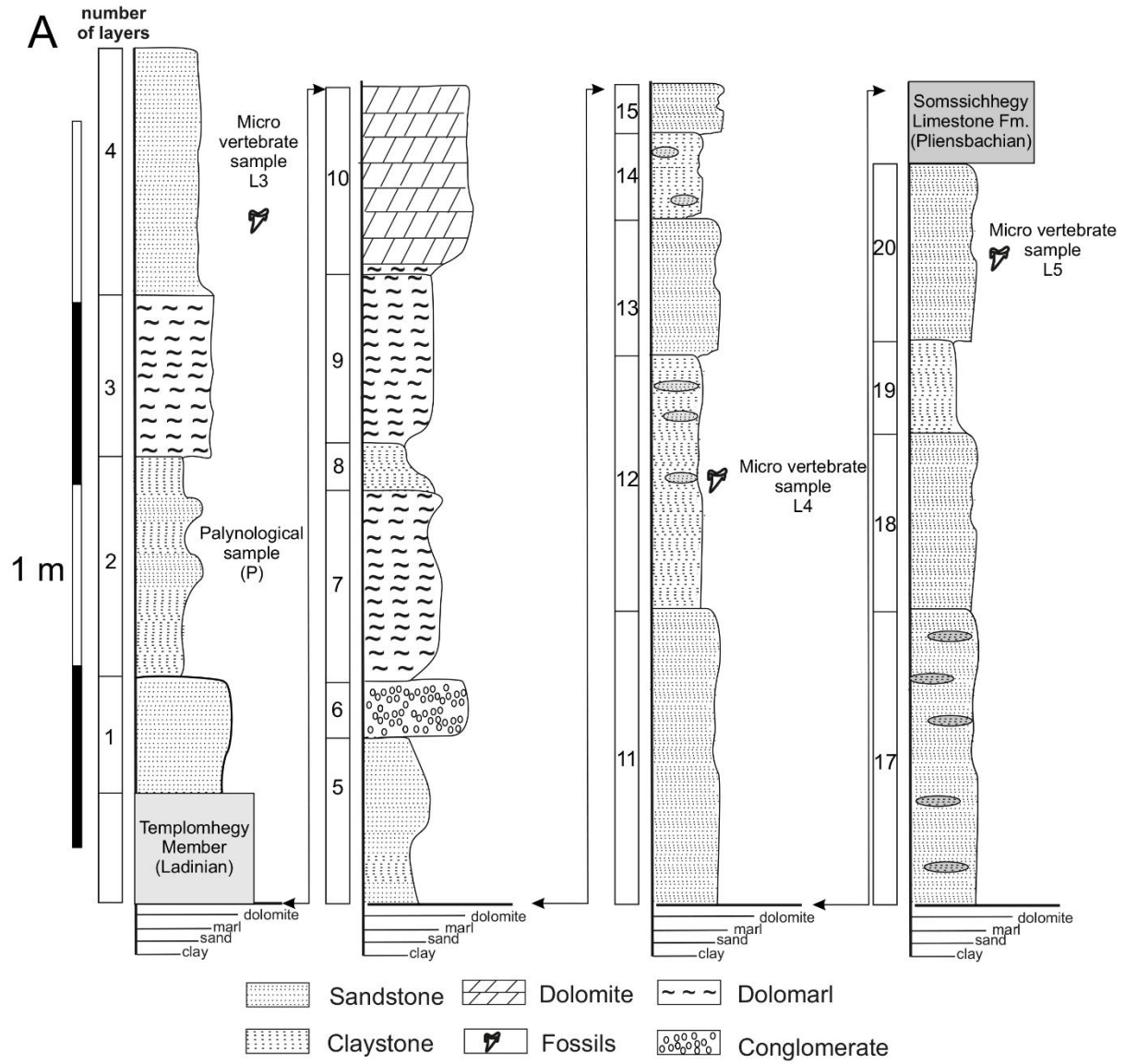
Figr-1



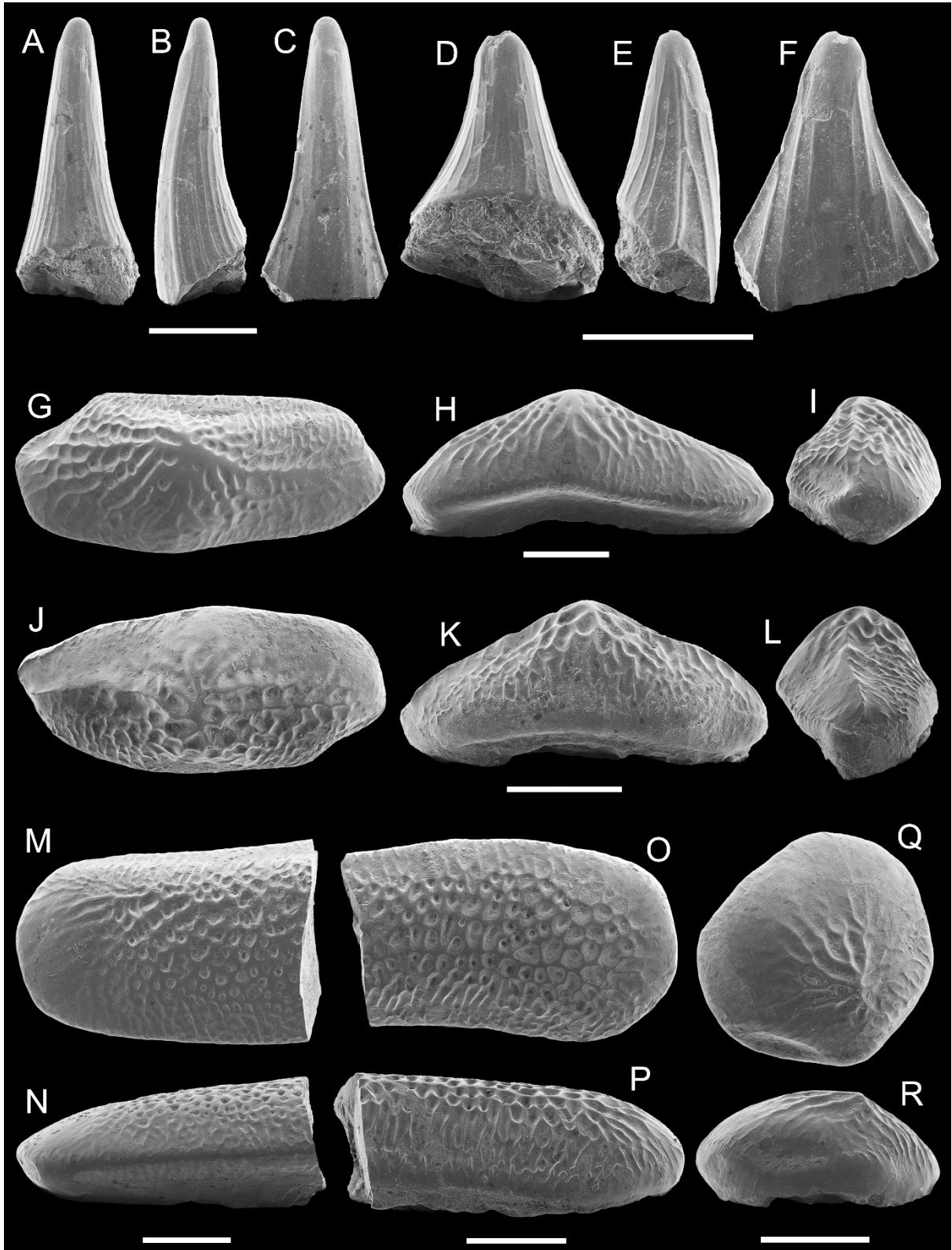
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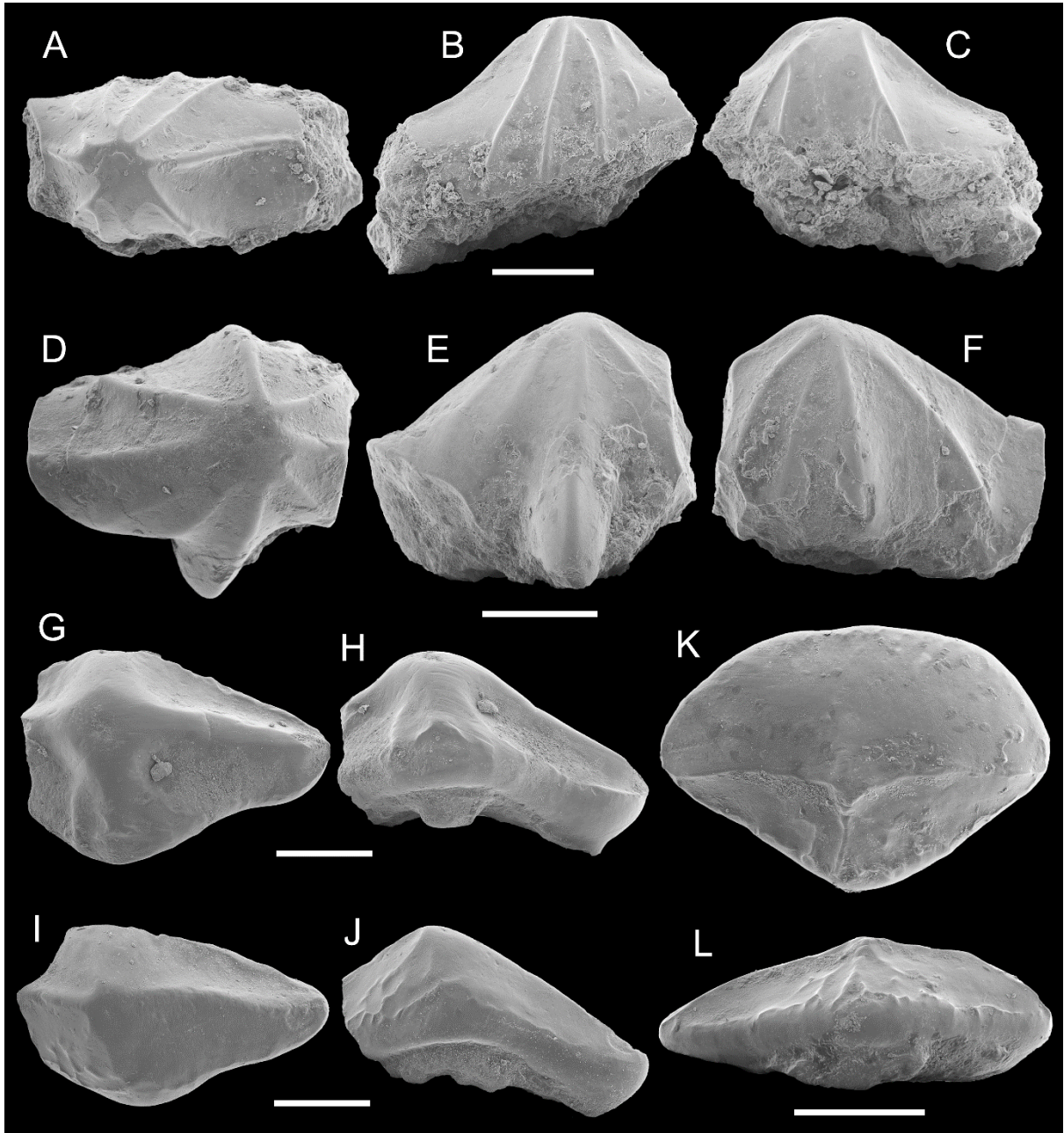
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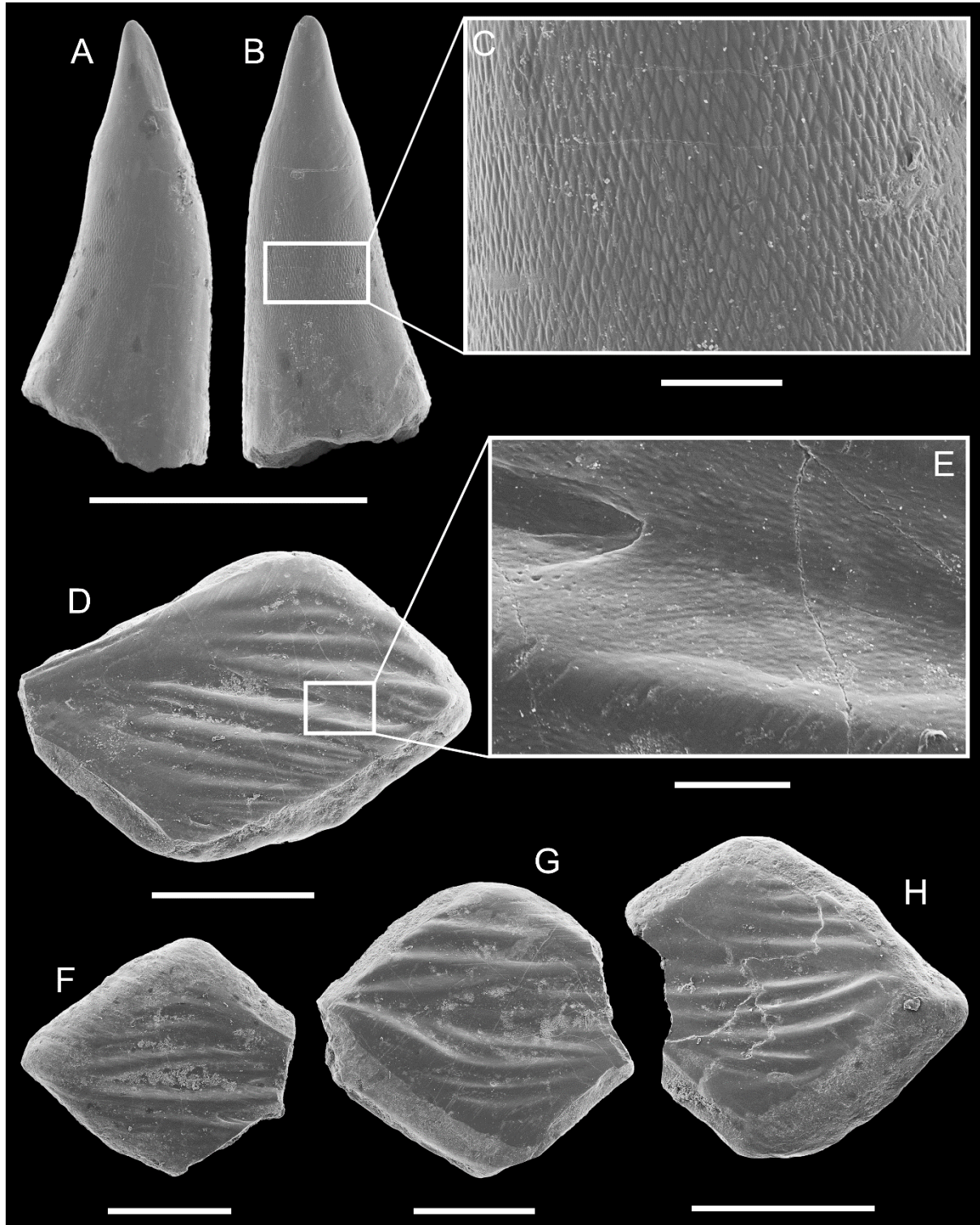
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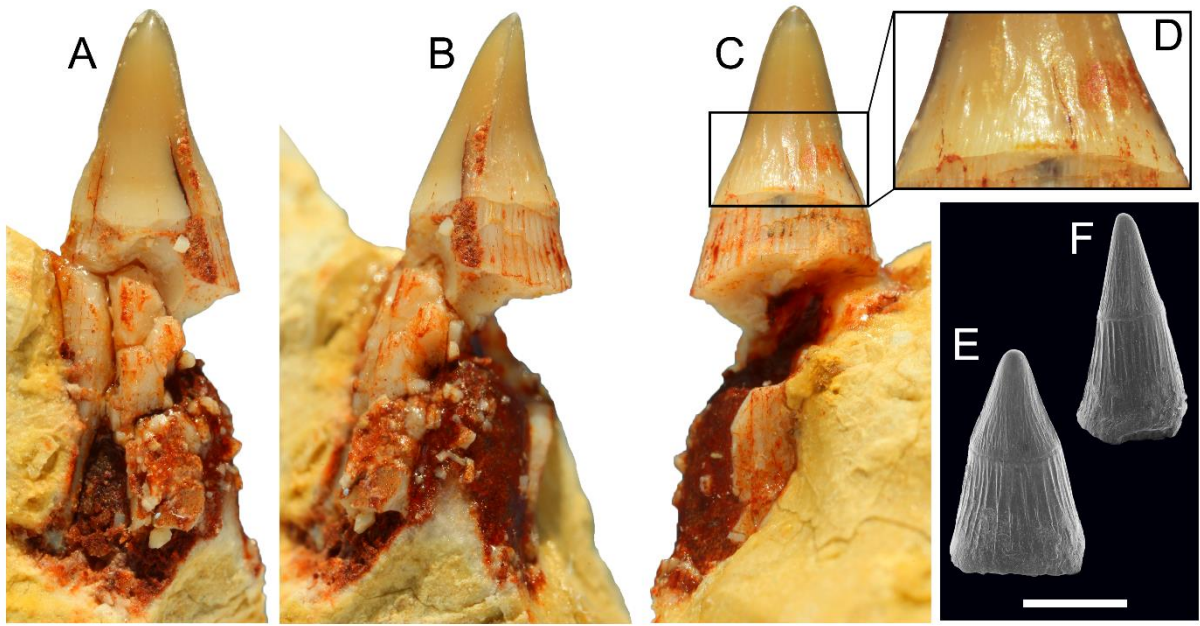
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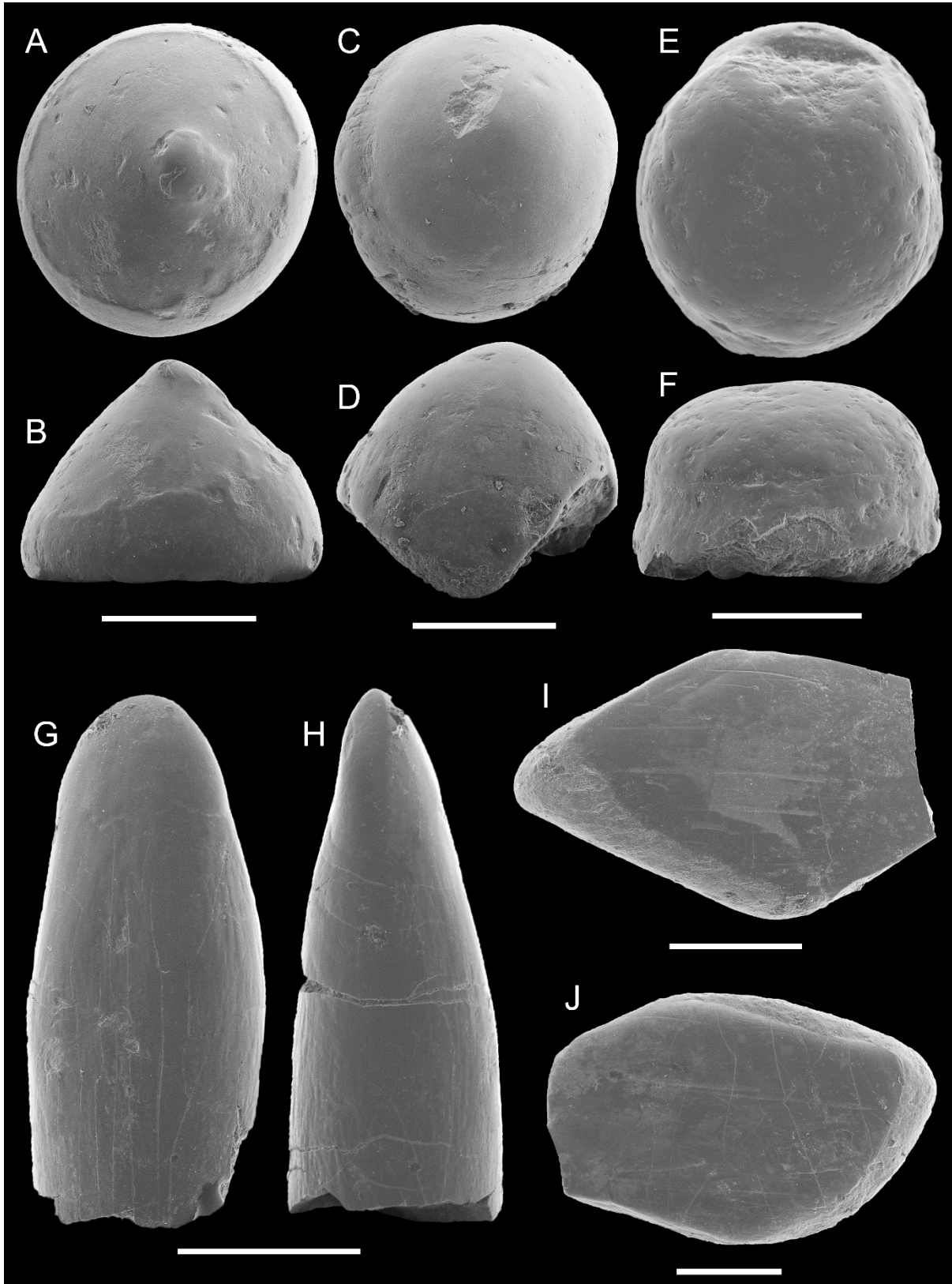


Figr-7



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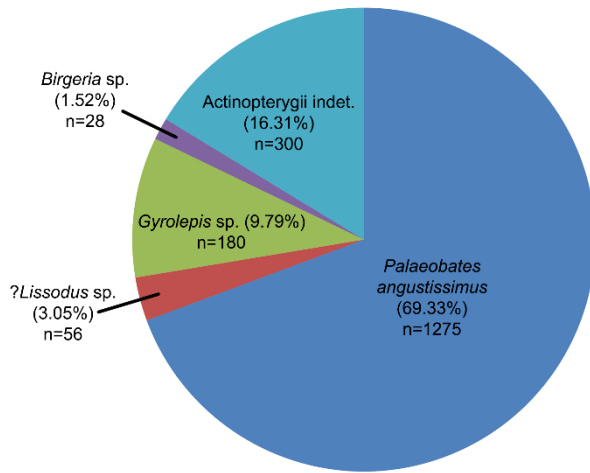
Figr-8



Figr-9

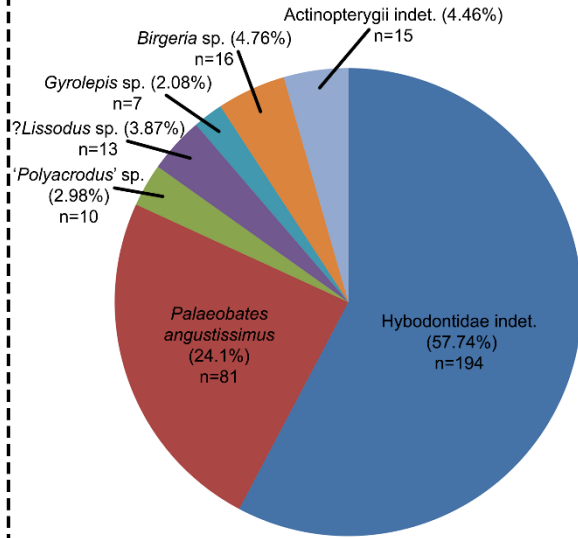
Templomhegy Dolomite Member (Ladinian)

Taxon	Layer 22	Layer 20	Layer 18	Layer 14	Σ
<i>Palaeobates angustissimus</i>	1	4	1	1269	1275
? <i>Lissodus</i> sp.	0	1	0	55	56
<i>Gyrolepis</i> sp.	0	7	0	173	180
<i>Birgeria</i> sp.	0	2	0	26	28
Actinopterygii indet.	2	31	4	263	300



Mészhegy Sandstone Formation (Carnian)

Taxon	L3	L4	L5	Σ
Hyodontidae indet.	3	0	191	194
<i>Palaeobates angustissimus</i>	17	1	63	81
' <i>Polyacrodus</i> ' sp.	2	0	8	10
? <i>Lissodus</i> sp.	1	0	12	13
<i>Gyrolepis</i> sp.	4	0	3	7
<i>Birgeria</i> sp.	0	0	16	16
Actinopterygii indet.	1	0	14	15



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