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Tanystropheus and other archosauromorph reptile remains from the Middle and Late Triassic of Villány (Villány Hills, Hungary)

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Abstract: *Tanystropheus* and other possible archosauromorph fossils have been discovered from Middle to Upper Triassic shallow marine sedimentary sections in Villány (Villány Hills, southern Hungary). Four fragmentary cervical vertebrae can be assigned to *Tanystropheus* sp. based on characteristic features including the strongly elongate and hollow vertebral body with extremely reduced neural spine. Besides the cervicals, various teeth, classified into four different morphotypes including longitudinally striated, carinated and ziphodont ones, are thought to belong to archosauromorphs, since they markedly differ from the frequently found teeth of fish and sauropterygians. In addition, three enigmatic cranial bones that might represent some circumorbital elements, have been found as well, and are referred to here as Sauropsida indet. These fossils, originated from the same tectonic unit as those from the Anisian of Bihor (Romania), are of great importance for a better understanding of the poorly known semi-aquatic to terrestrial vertebrate fauna of the Middle to Late Triassic of central Europe.

Keywords: *Tanystropheus*, Archosauromorpha, teeth, vertebrae, Ladinian, Carnian, Hungary.

Introduction

Triassic vertebrate fossils from Villány have been known since the early 1900's (Lőrenthey 1907; Lóczy 1912; Rálisch-Felgenhauer 1981, 1985), but their systematic excavation and documentation only started in 2012, when a rich bone-bearing sedimentary section was discovered thanks to a new construction in the city of Villány (see as Construction site below) and the area was recognized as a potential Triassic vertebrate locality (Ősi et al. 2013). Currently two outcrops are known in Villány that produced Triassic vertebrates.

One of them, the Construction site (Fig. 1C) is located on the Somssich Hill where continuous excavations have been carried out in the last six years resulting in thousands of macro- and microvertebrate remains of fishes and reptiles in several beds of the Middle Triassic Templomhegy Dolomite.

The other vertebrate site, the Road-cut site (local name: Siklóbevágás, Fig. 1C) on the northern side of the Templom Hill, where a relatively thick sequence of Carnian siliciclastic sediments (Mészhegy Sandstone Formation) are exposed including diverse microvertebrate assemblages. The paleontological and sedimentological importance of the Road-cut site have been recognized for a long time (Rálisch-Felgenhauer 1985; Vörös 2009, 2010), but the detailed petrographical and paleontological descriptions of its bone yielding horizons have begun only recently (Pozsgai et al. 2017; Botfalvai et al. 2019).

The fish fauna of these Triassic beds has recently been documented (Szabó et al. 2019), and the diverse assemblage of placodonts and nothosaurs have been published (Segesdi et al. 2017; Ősi et al. 2018). Although the vertebrate fauna is composed of dominantly marine elements, some semi-aquatic to possibly terrestrial forms also occur in the assemblage. Among these are the remains of the enigmatic *Tanystropheus* which has a highly complicated taxonomic history and poorly known paleobiogeography (Spiekman & Scheyer 2019) thus every fossil belonging to this form, especially from still un- or poorly represented paleogeographical areas, is of great importance. In this paper the archosauromorph fossils discovered from the Middle Triassic (Ladinian) Templomhegy Dolomite and the Carnian Mészhegy Sandstone Formation are described and compared in detail.

Locality, geology and age

Villány city is in the eastern margin of the Villány Hills, southern Hungary (Fig. 1). This region is situated in the Southern Pannonian Basin and stratigraphically belongs to the Villány–Bihor Unit of the Tisza Megaunit which formed part of the passive southern shelf of the European Plate southwards to the Bohemian Massif during the Triassic (Csontos & Vörös 2004; Haas & Péró 2004; Pozsgai et al. 2017).

Most of the vertebrate fossils, described below, came from the Ladinian Templomhegy Dolomite Member of the Csukma Dolomite Formation, the sediments of which were formed in a protected inner ramp lagoon and connected tidal flat depositional environment (Török 1998, 2000; Botfalvai et al. 2019).

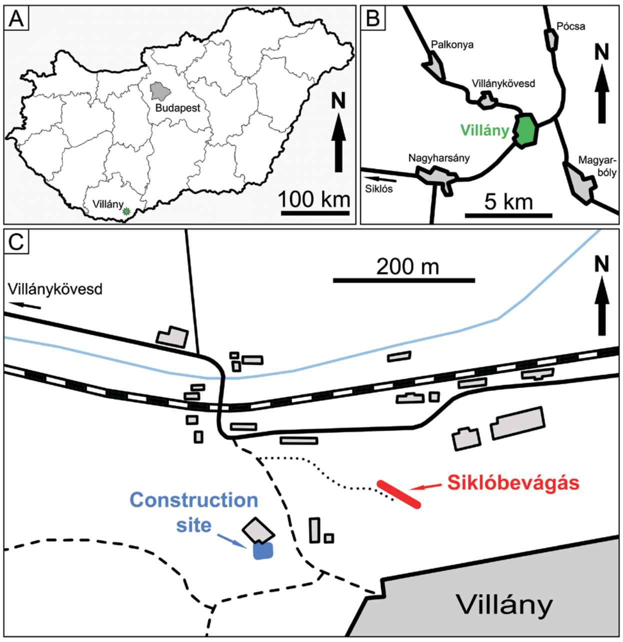

Fig. 1. Locality map of the Triassic vertebrate sites in Villány.

The bone-bearing layers of the Teplomhegy Dolomite Member, exposed in the Construction site (Fig. 2A), represent an alternation of yellowish grey dolomite and dolomarl beds with subordinate reddish paleosol intercalations (Fig. 2B). Detailed sedimentological investigation suggests that the depositional environment was a nearshore (subtidal to pertidal) zone of a ramp, where the sedimentation was controlled by climatic and sea-level changes (see details in Botfalvai et al. 2019). The Ladinian age for the Construction site is mainly based on its stratigraphical position (the Teplomhegy Dolomite Member is situated between the Middle-Upper Anisian Zuhánya Limestone and the Carnian Mészhegy Sandstone Formations), since index fossils of ammonites and conodonts are absent in this shallow marine sequence (Botfalvai et al. 2019).

Macrofossils have been discovered from the 14th–23th beds of the Templomhegy Dolomite of the Construction site by systematic, layer by layer excavations between 2012–2019, where the layer 14 and 18 were the most productive for vertebrate remains (Fig. 2A).

Only one tooth (MTM PAL 2020.16.1.), belonging to morphotype 1 (see below), has been found in the Carnian siliciclastic sediments of the Mészhegy Sandstone Formation of the Road-cut site (Fig. 2B). This formation consists of cycles of weakly cemented, sandstone, siltstone and variegated clay strata, with subordinate amounts of dolomite and dolomarl (Vörös 2010; Pozsgai et al. 2017). Sedimentological and paleontological investigations of the Carnian deposits of the Road-cut section indicate a near-shore, shallow marine depositional environment characterized by high siliciclastic input from the mainland (Botfalvai et al. 2019). Samples for microvertebrates were taken and screen-washed from various beds of the Road-cut site (Szabó et al. 2019), where the above mentioned single archosauromorph tooth came from bed L5 (Fig. 2B). The siliciclastic sequence of Mészhegy Sandstone Formation has been considered Upper Triassic and has been frequently correlated with the “Carnian Pluvial Event” (Vörös 2009; Pozsgai et al. 2017). The Carnian age was supported by palynological investigation for the lower part of the formation (Ősi et al. 2013).

Material and methods

The fossils described here were unearthed during excavations carried out in 2012–2019, and all of them are housed in the vertebrate paleontological collection of the Hungarian Natural History Museum. The exact stratigraphic position of the specimens is indicated on Fig. 2.

Broken parts of macroscopic specimens collected by careful hand preparation from beds 14–23th were fixed by cyanoacrylate (superglue). Besides focusing on specimens visible to the naked eye, samples from five beds (22th, 20th, 18th, 14th and 10th) of the Templomhegy Dolomite Member at the Construction site have been also taken for screen-washing. After sorting the collected and screen-washed samples, the 14th bed was by far the most productive, thus in the Summer of 2018, approximately 250 kilograms of sediment from this layer have been screen-washed by using tap water and 5 % of acetic acid. This process resulted in thousands of fish and sauropterygian remains and a few archosauromorphs as well. Screen-washing of the Mészhegy Sandstone Formation was quite similar and has been described in detail by Szabó et al. (2019).

For scanning electron microscopic photography, we used a Hitachi S-2600N scanning electron microscope.

Institutional abbreviations: MFSN – Museo Friulano di Scienze Naturali, Udine, Italy; MOR – Muzeul Ţării Crişurilor Oradea, Romania; MPUM – Museum of the Dipartimento di Scienze della Terra ‘A. Desio’ of Milano University, Milano, Italy; MSNM – Museo di Storia Naturale, Milan, Italy; MTM – Hungarian Natural History Museum, Budapest, Hungary; PIMUZ – Paläontologisches Institut und Museum der Universität Zürich, Zurich, Switzerland; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany.

Description and comparisons

Archosauromorpha Huene, 1946
Tanystropheidae Gervais, 1859
Tanystropheus Meyer, 1852
Tanystropheus sp.

Material: Four cervical vertebrae (MTM PAL 2020.8.1.–PAL 2020.11.1.)

Description and comparison: Altogether four vertebrae, referred here to *Tanystropheus* sp., are known from Villány. Though they are poorly preserved and mostly compressed lateromedially, on the broken surfaces it is possible to observe that

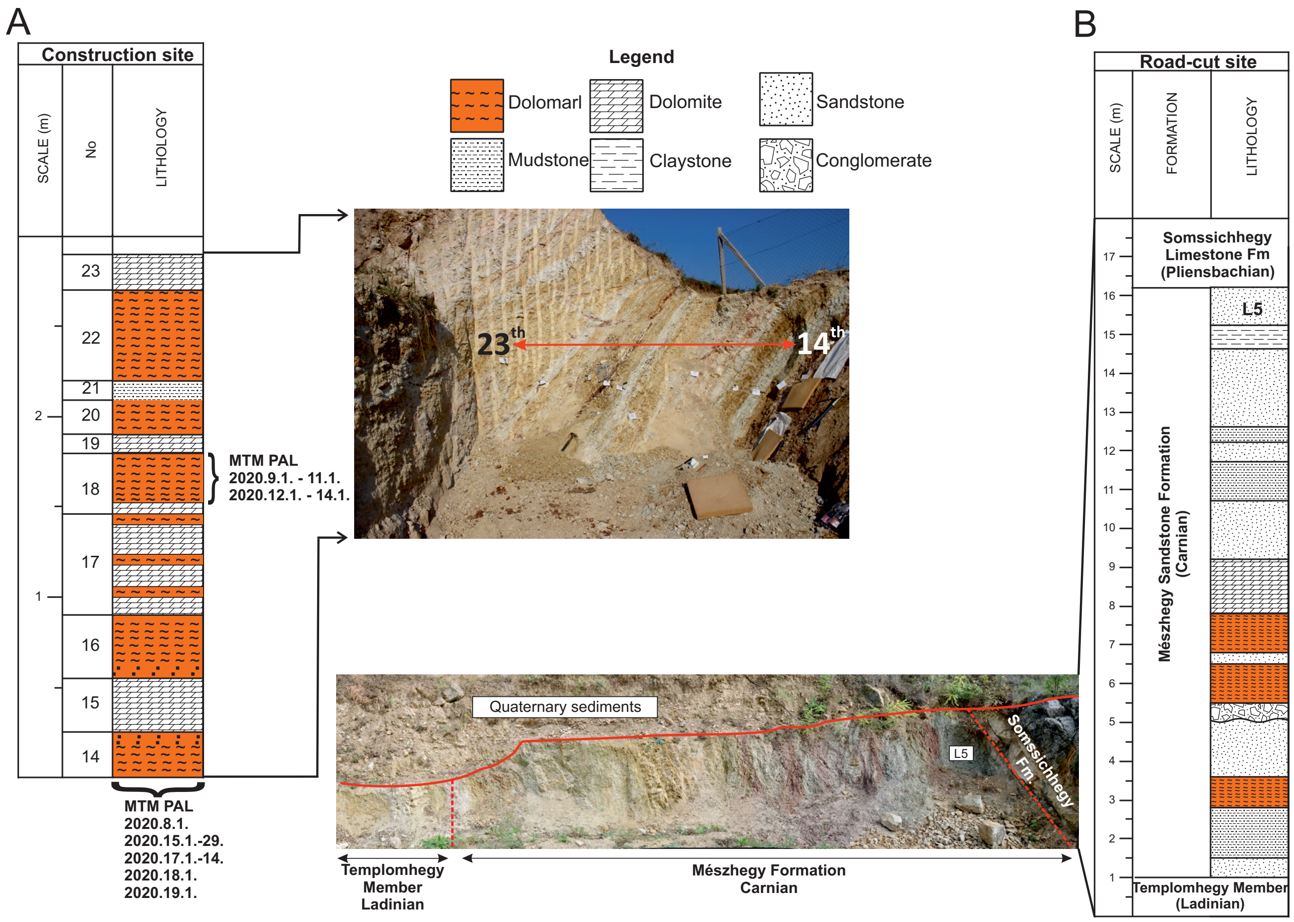

Fig. 2. Schematic stratigraphic sections of the Triassic vertebrate sites in Villány with the exact position of the fossils described here. **A** — Bone-bearing layers of the Construction site (in orange). **B** — Stratigraphic section of the Road-cut (Siklóbevágás) site (L5=paleontological sample contains MTM PAL 2020.16.1.). For more details, see Botfalvai et al. (2019).

the vertebral body of all specimens is hollow inside. The ventral side of the centrum is flat with distinct, keel-like lateral edges and it bends very slightly anteroposteriorly that is not the result of taphonomic deformation (Fig. 3B). A shallow, centrally positioned, longitudinal keel extends on this ventral surface on the anterior and posterior thirds of the centrum, like that seen on some specimens of *Tanystropheus longobardicus* from Monte San Giorgio (Wild 1973) and *Tanystropheus conspicuus* (considered a nomen dubium by Spiekman & Scheyer 2019, and possibly indistinguishable from *T. longobardicus*) from the Muschelkalk of Germany (e.g., SMNS 16364, SMNS 54644). Close to the centre of specimens MTM PAL 2020.8.1. and MTM PAL 2020.9.1., two foramina, most probably the foramina venae vertebralis (sensu Wild 1973), open into the hollow centrum as it can be observed, for example, in SMNS 16364 and on the well-preserved cervical (MOR 88) from the Bihor Mountains, Romania (Jurcsák 1975).

Neural spine is only a few millimetres high at the posterior end in all vertebrae, and in the mid-third of the centrum it is just a dorsally oriented shallow crest (Fig. 3A, D). The posterior end of the neural spine is only a short, rounded protuberance (apparently not broken), while that of the Monte San Giorgio (e.g., PIMUZ T 2819) specimens bears a posterodorsally pointed process.

Whereas in MTM PAL 2020.8.1. the posterior articular surface of the centrum is slightly concave with its margin apparently eroded (Fig. 3C), in another specimen (MTM PAL 2020.9.1.) the articular surfaces are deeply concave, a phenomenon that is partly the result of lateromedial compression (Fig. 3F). Both in MTM PAL 2020.8.1. and MTM PAL 2020.9.1. the posterior end of the vertebral centra is not as abruptly widened lateromedially as that of the cervical from Bihor (MOR 88) or that of the cervical (MFSN 31579) from the Aupa Valley (Dalla Vecchia 2006), both identified as *Tanystropheus* sp. Preserved postzygapophyses extend well (with 1–1.5 cm in MTM PAL 2020.8.1. and MTM PAL 2020.9.1.) beyond the articular surfaces of the centrum with an angle ranging between 20–40º relative to the horizontal plane (Fig. 3A, D).

Although discovered in the same tectonic unit, the vertebra (MOR 88) from Bihor slightly differs from the Villány specimens in having much more ventrally curved ends of the vertebral body. In the case of MOR 88 this curvature is definitely not the result of taphonomic deformation since every part of the specimen is in a wonderful, unbroken, three-dimensionally preserved condition. The degree of curvature of the ventral margin of the centrum is, however, quite variable in some taxa (Spiekman & Scheyer 2019), preventing the taxonomical use of this character. Another potential difference is that the concave articulation surfaces of the Bihor vertebra are wider than high, which is most probably not the case in the Villány specimens. However, in the latter even the best-preserved specimen is compressed laterally (Fig. 3C). Spiekman & Scheyer (2019: 22) listed five morphological characters of the cervical vertebrae of *Tanystropheus* to assess the variation occurring in cervical vertebrae assigned to *Tanystropheus* spp. Unfortunately, however, the poor preservation of the Villány specimens severely hampers the observation and comparison of these characters.

Compared to the well-preserved cervical series of the Monte San Giorgio specimens (Wild 1973; Nosotti 2007), all the Villány cervicals, though they differ in relative size, represent vertebrae of the mid-section (4th to 11th positions) of the cervical series.

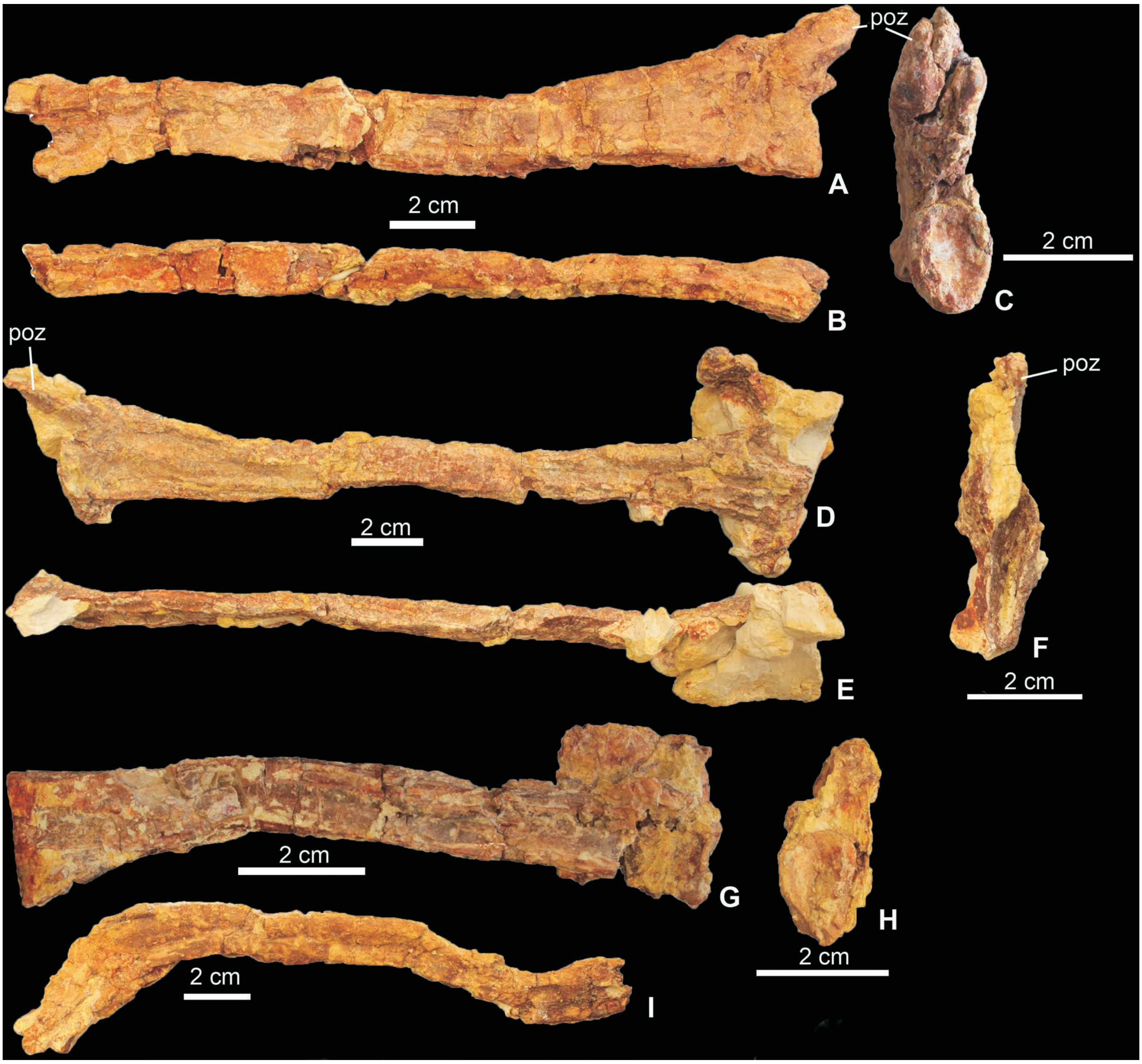

Fig. 3. *Tanystropheus* sp. fossils from the Middle Triassic (Ladinian) Templomhegy Dolomite of Villány. **A–C** — Cervical vertebra of *Tanystropheus* sp. (MTM PAL 2020.8.1.) in lateral (A), ventral (B) and posterior (C) view. **D–F** — Cervical vertebra of *Tanystropheus* sp. (MTM PAL 2020.9.1.) in lateral (D), ventral (E) and posterior (F) view. **G, H** — Cervical vertebra of *Tanystropheus* sp. (MTM PAL 2020.10.1.) in lateral (G) and ?anterior (H) view. **I** — Cervical vertebra of *Tanystropheus* sp. (MTM PAL 2020.11.1.) in lateral view. Anatomical abbreviation: poz — postzygapophysis.

Archosauromorpha indet.

Material: Isolated teeth: morphotype 1 (MTM PAL 2020.15.1.–MTM PAL 2020.15.29., MTM PAL 2020.16.1.), morphotype 2 (MTM PAL 2020.17.1.–MTM PAL 2020.17.14.), morphotype 3 (MTM PAL 2020.18.1.), morphotype 4 (MTM PAL 2020.19.1.)

Description and comparison: Of the teeth, four morphotypes are present. Morphotype 1 (MTM PAL 2020.15.1.–MTM PAL 2020.15.29., MTM PAL 2020.16.1.) has relatively short, pointed, labiolingually slightly compressed and lingually curved crown (Fig. 4A–I). The mesial side of the crowns is strongly convex basally and, in some specimens, it is slightly constricted (Fig. 4B,E). Labiolingually and distally they bear apicobasally oriented, shallow enamel ridges, but these ridges are not as sharp and regular as those on the teeth of nothosaurs (Schoch 2015). Mesiodistally the teeth are void of well-developed carinae, but in the case of larger specimens two well-developed, non-serrated ridges extend on the mesiolabial and mesiolingual sides, bordering a smooth, convex mesial surface (Fig. 4G,H). Weak apical and labiolingual wear is present on some of the teeth (Fig. 4A).

These teeth are similar to the striated, distally curved premaxillary and anterior dentary teeth of *Tanystropheus longobardicus* (Wild 1973). Similar, distally strongly curved, slightly ornamented anterior teeth are present in specimen MSNM BES SC 1018 and in MSNM BES SC 265, but their teeth lack the prominent, mesiolabial and mesiolingual ridges present on some of the Villány teeth. Anterior teeth of larger *Tanystropheus longobardicus* specimens (e.g., MSNM V 3663, PIMUZ T 2818) are more different in being only slightly curved distally and bearing more prominent apicobasal ridges on the enamel (Nosotti 2007). Ridges are basically like those on the teeth of *Tanystropheus* sp. from Italy (Dalla Vecchia 2006) and Germany (Schoch 2015). Dalla Vecchia (2006) noted shallow, secondary ridges present on the teeth of *Tanystropheus* sp. from Italy to distinguish them from the teeth of nothosaurs. Similar secondary ridges on the basal half of the crown are, however, also present in some other archosauromorph teeth, such as *Jaxtasaurus* (Schoch & Sues 2013). However, these less developed, secondary ridges are not present in morphotype 1, and these teeth are more curved distally and relatively shorter than the nothosaur teeth. Furthermore, nothosaur teeth differ from morphotype 1 in having more developed and regular longitudinal ridges, and crowns have a circular cross-section. Compared to pachypleurosaurs, they usually have much smaller teeth, in some forms rather mesiodistally wide (Rieppel & Lin 1995), whereas in others they are semicircular in cross-section and have longitudinal ridges without carinae (Sander 1989).

The second morphotype (MTM PAL 2020.17.1.–MTM PAL 2020.17.14.) is labiolingually flattened, triangular and, in some specimens, slightly curved distally (Fig. 4J–S). Cross-section is oval (Fig. 4L,O). Shallow apicobasal ridges are present on the enamel, among which those on the lingual side are slightly more prominent than those of the labial side. Mesially and distally the ridges form weak, non-serrated carinae (Fig. 4K,M). In contrast to morphotype 1, secondary ridges are present on the basal half of the crowns. Crowns are only very slightly constricted at their base. Some specimens show well-developed distal curvature that is recognizable by the distal orientation of striae (Fig. 4N). This morphotype is similar to the unserrated teeth of some archosauromorphs, such as the maxillary and dentary teeth of the larger specimens of *Tanystropheus longobardicus* (e.g., MSNM V 3663a, PIMUZ T 2818, 2819) in having labiolingually flattened, triangular teeth with longitudinal ridges. Similar *Tanystropheus* sp. teeth were also figured by Dalla Vecchia (2006: fig. 5B,C). The maxillary teeth of *Jaxtasaurus* from the Ladinian of Germany are also reminiscent of the teeth from Villány in having similar general shape, ornamentation and smooth mesial and distal carinae, though carinae are more prominent in *Jaxtasaurus* (Schoch & Sues 2013; Schoch 2015). In addition, Schoch (2015: fig. 10.13g–h) illustrated an additional archosauromorph tooth (SMNS 91230) that is very similar to morphotype 2 from Villány, though SMNS 91230 seems to have finely serrated carinae.

Morphotype 3 (MTM PAL 2020.18.1.) is represented by a single apical region of a tooth crown (Fig. 4T,U). It is labiolingually compressed, slightly bent distally, and avoids the developed, parallel, apicobasally oriented enamel ridges present in morphotypes 1 and 2. The enamel surface is, however, not smooth but very shallow, apicobasally oriented, slightly irregular ridges are present that bend very slightly mesially or distally, most probably reaching the edge of the carinae (Fig. 4T). Mesial and distal carinae seem to be non-ziphodont in contrast with morphotype 4 (see below), though pseudoziphodont carinae cannot be excluded since carinae are mostly eroded. Only a short section of the mesial carina is complete, showing the mesially extending enamel ridges. The lingual side of the crown is slightly concave and shelf-like along the mesial and distal carinae (Fig. 4U). This feature together with the mesiodistally extending ridges are quite reminiscent of those of the teeth of much later neosuchian crocodyliforms (Martin et al. 2010; Ősi et al. 2016, 2019), though it is clear that this tooth does not belong to that group. Nevertheless, this tooth clearly differs from all the sauropterygian teeth known from the locality and is also different from the three other morphotypes of archosauromorph teeth presented here. It also does not correspond to any of the archosauromorph teeth from the Ladinian Lettenkeuper of Germany (Schoch 2015). Similar shelf-like structures along the carinae can be observed on one of the archosauromorph teeth (MPUM 9154) from the Norian of Italy (Renesto et al. 2005: fig. 4B), though this tooth is distinctly serrated.

Morphotype 4 (MTM PAL 2020.19.1.) is represented by a basal fragment of a tooth crown (Fig. 4V). The complete crown should have been labiolingually slightly compressed to have an oval cross section. It preserves a very short section of a serrated carina with equidimensional and mesially rounded denticles, though it has to be noted that two of the denticles are partly eroded (Fig. 4V). Based on the preserved four denticles

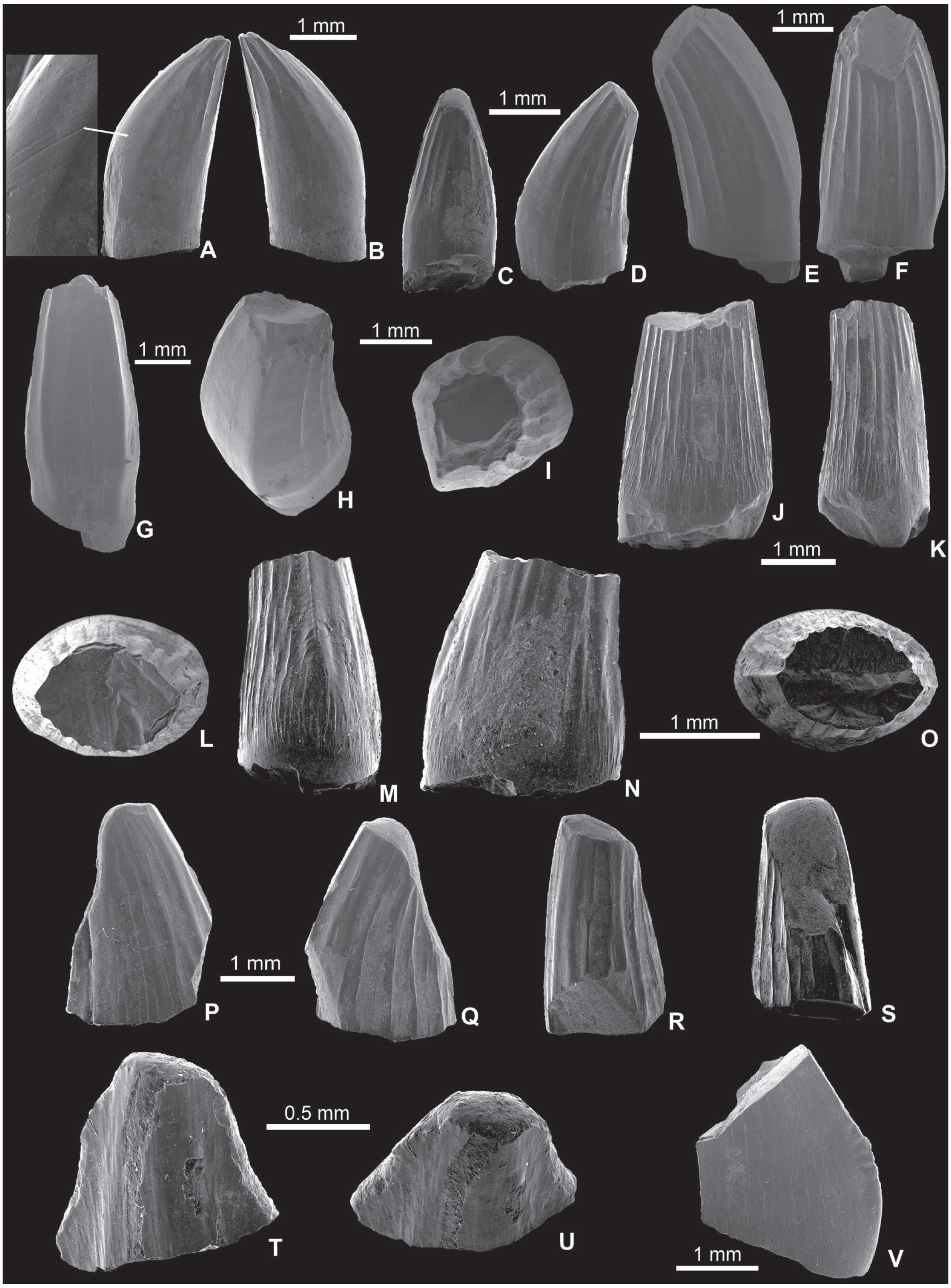

Fig. 4. Archosauromorpha indet. teeth from the Middle and Late Triassic of Villány. **A, B** —Morphotype 1, lingually curved fang tooth (MTM PAL 2020.16.1.) with oblique striae on tooth wear (left) from the Carnian Mészhegy Sandstone Formation in ?mesial (A) and ?distal (B) view. **C, D** — Morphotype 1, lingually curved fang tooth (MTM PAL 2020.15.1.) from the Ladinian Templomhegy Dolomite in lingual (C) and ?mesial (D) view. **E–I** — Morphotype 1, lingually curved fang tooth (MTM PAL 2020.15.2.) from the Ladinian Templomhegy Dolomite in ?mesial (E), lingual (F), labial (G), oblique (H) and apical (I) view. **J–L** — Morphotype 2, lateral tooth (MTM PAL 2020.17.1.) from the Ladinian Templomhegy Dolomite in lingual (J), ?distal (K) and apical (L) view. **M–O** — Morphotype 2, distally curved lateral tooth (MTM PAL 2020.17.2.) from the Ladinian Templomhegy Dolomite in mesial (M), labial (N) and apical (O) view. **P–S** — Morphotype 2, distally curved lateral tooth (MTM PAL 2020.17.3.) from the Ladinian Templomhegy Dolomite in lingual (P), labial(Q), mesial (R) and distal (S) view. Note the deep longitudinal groove distally (S) that might be pathological. **T, U** — Morphotype 3, labiolingually flattened tooth crown fragment (MTM PAL 2020.18.1.) from the Ladinian Templomhegy Dolomite in lingual (T), oblique-apical (U) view. **V** — Morphotype 4, ziphodont tooth fragment (MTM PAL 2020.19.1.) from the Ladinian Templomhegy Dolomite in ?lingual view.

the number of denticles per mm is estimated to be 5.5–6. This character, together with denticle shape and dimensions are most like that of the archosauromorph teeth from Italy (Renesto et al. 2005). Compared to the teeth of 'rauisuchians', including *Teratosuchus* (Benton 1986), *Batrachotomus* (SMNS 91653; Gower 1999) and some teeth from the Late Triassic of South Africa (Tolchard et al. 2019), the Villány specimen is similar in its smooth surface and the presence of serrated carinae. The outer cutting edge of the individual denticles is, however, slightly different in being more rounded than, for example, on the teeth from South Africa (Tolchard et al. 2019: fig. 4). Renesto et al. (2005) compared the Norian specimens from Italy with the teeth of early theropod dinosaurs. Based on its Ladinian age, however, the Villány specimen is most probably not from this group.

Sauropsida indet.

Material: Three cranial elements (MTM PAL 2020.12.1., MTM PAL 2020.13.1., MTM PAL 2020.14.1.),

Description and comparison: Two of the cranial elements are reminiscent of a circumorbital bone; MTM PAL 2020.12.1. is slightly smaller (preserved length: 59 mm) than MTM PAL 2020.13.1. (preserved length: 63 mm), but is better preserved. This element is flattened and slightly bent lateromedially resulting in a slightly convex lateral and concave medial surface (Fig. 5A–C). The external surface of the bone is smooth, without ornamentation (grooves and/or ridges appear to be absent). The inner side does not show any crest or lamina either, only a shallow ridge extends longitudinally. On one side, it shows an asymmetrical forked articulation surface (Fig. 5A). On the other side of the bone, a bar-like, mediodorsally bent process bears a deep groove on its outer surface accepting the neighbouring bone. Between these processes the shorter side is a thin edge that might have formed the margin of one of the cranial openings.

MTM PAL 2020.13.1. is similar in shape and features to MTM PAL 2020.12.1., but it is slightly compressed and damaged (Fig. 5D, E). The only feature to be mentioned is that the forked articulation is relatively longer than in MTM PAL 2020.12.1.

A third cranial element (MTM PAL 2020.14.1.) is a flattened bone (preserved length: 47 mm) showing the original, slightly bent shape (Fig. 5F–H). It is roughly similar to the aforementioned two other cranial elements, but it differs from them in some features. Whereas one bar-like process is preserved showing a slightly eroded articulation surface, the opposite end of the bone is missing. One edge of the bone is slightly concave and most probably formed the margin of one of the cranial openings. On the other side, there is a rounded process with a shelf-like outer margin that is similarly present in the previous cranial bones (Fig. 5F–H).

In spite of the good preservation of these cranial elements, their anatomical and even taxonomic assignment is still dubious. In placodonts and nothosaurs, as frequent elements of the Villány vertebrate assemblage, the bones marginating the cranial openings are in many cases not as flattened and more bar-like, and many of the bones are slightly or markedly ornamented (Rieppel & Wild 1996; Rieppel 2000, 2001a). In the three-dimensionally preserved skull of *Nothosaurus mirabilis* (PIMUZ A/III 0780) bones of the dorsal rostrum and those of the circumorbital region are thicker, and neither of them shows the rounded, shelf-like margin as seen in the Villány elements. More similar, roughly triradiate elements with a bar-like process appear in the skull of archosauromorphs, such as the postorbital or the postfrontal of *Tanystropheus longobardicus*. Although Wild (1973) gave a detailed description of many *Tanystropheus longobardicus* specimens, the illustration of the individual cranial elements is quite simple, perhaps due to the compressed preservation of many specimens. The specimens described here are reminiscent of the circumorbital bones of *Tanystropheus longobardicus* (Nosotti 2007) but none of them shows unambiguous similarities. Whereas the forked articulation surface is also present as in the jugal and the postorbital (Nosotti 2007), the Villány bones do not have the concave shelf marginating the bones around the supratemporal fenestra (well seen e.g., PIMUZ T 2819). The most characteristic part of these cranial elements is the convex, shelf-like margin (Fig. 5A, F: sma). This slightly concave shelf-like surface does not correspond to an articular surface for an overlapping bone, nor to the inner rim of a temporal fenestra. It rather looks to be a reduced process, such as the reduction of the lower temporal arcade of later lepidosauromorphs.

These elements might have bordered some cranial openings (perhaps the orbit and/or temporal fenestrae) in a sauropsid skull, but until now we have not been able to identify their more precise anatomical position, thus we refer to them here as Sauropsida indet., until more complete specimens shed light on their affinities.

Discussion and conclusions

The diagnostic four cervicals, presented here, clearly indicate the most probably Ladinian occurrence of *Tanystropheus* in the Villány area and extend the spatial range of this bizarre form. The new remains represent the second and richest occurrence of the genus in the Carpathian-Balkan region indicating that *Tanystropheus* might have been a frequent faunal element of the coastal margins of this part of the northern Tethyan shelf already from the late Anisian (Jurcsák 1975; Patrulius et al. 1979) until most probably the Ladinian. This scenario fits well into the global paleobiogeography of *Tanystropheus*, namely that this animal had a Tethys-wide occurrence (Rieppel 2001b; Rieppel et al. 2010; Spiekman & Scheyer 2019). The outlined anatomical differences between the vertebrae from Bihor and those from Villány, however, might suggest some taxonomical differences as well, that might also be related to their suggested different ages. Co-occurrence of different species of *Tanystropheus* on a single landmass has previously been suggested for the assemblage from Israel (Rieppel 2001b), and

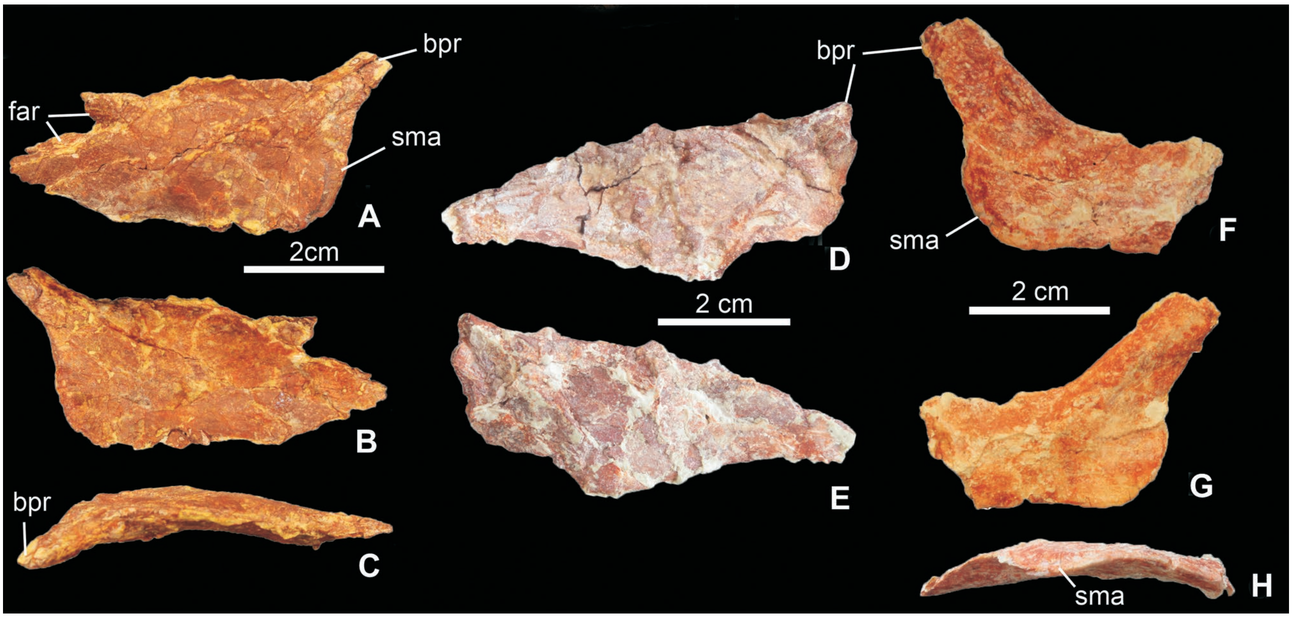

Fig. 5. Sauropsida indet. fossils from the Middle Triassic (Ladinian) Templomhegy Dolomite of Villány. **A–C** — Cranial element (MTM PAL 2020.12.1.) in outer (A), inner (B) and ?dorsal (C) view. **D, E** — cranial element (MTM PAL 2020.13.1.) in outer (D) and inner (E) view. **F–H** — cranial element (MTM PAL 2020.14.1.) in outer (F), inner (G) and ?ventral (H) view. Anatomical abbreviations: bpr — bar-like process; far — forked articulation; sma — shelf-like margin.

might possibly be the case for Monte San Giorgio, if the small and large morphotypes represent separate species (Spiekman & Scheyer 2019).

Of the teeth, morphotypes 1 and 2 might belong to this taxon as well, though they are not completely identical with those from the Middle Triassic of the German and Alpine basins. Morphotype 1 with its strongly distally curved crown probably represents teeth of a widely spaced anterior tooth series, as is indicated by the labiolingual wear features (Fig. 4A). On these slightly worn surfaces, elongated, parallel scratches are present suggesting the side-to-side occlusion of the upper and lower fangs, frequently seen in vertebrates with procumbent, widely-spaced teeth such as crocodyliforms (Ősi 2014) and pterosaurs as well (AŐ, pers. observation).

Morphotype 2 perhaps represents the lateral teeth of *Tanystropheus*, though they also strongly resemble some other archosauromorph teeth described from the German Lettenkeuper (Schoch 2015). Interestingly, no tricusped teeth, characteristic elements of the European *Tanystropheus* assemblages (Wild 1973; Nosotti 2007; Schoch 2015), have been found in the screen-washed material from Villány, despite thousands of teeth, including the dozens belonging to the four described archosauromorph morphotypes, having been unearthed. Morphotype 1 and 2 share two features: the pointed apex and the longitudinal striae along the crown. Although the taxonomic assignment of these teeth is still problematic, these common features strongly suggest a piscivorous habit of their owners (Massare 1987).

Morphotype 3 might represent either a pseudoziphodont or ziphodont tooth crown, but it clearly differs from the teeth of sauropterygians and *Tanystropheus*. On the other hand, morphotype 4 is clearly ziphodont indicating the rare occurrence of meat-eater archosauromorphs in the assemblage. The question, if morphotype 4 represents a rauisuchian, a dinosauriform, or another lineage of Middle Triassic archosauromorph reptiles, remains to be unsolved until more complete material is unearthed.

The depositional environment in the Villány area during the Middle–Late Triassic was a shallow marine lagoon with fluctual terrestrial influx (Török 2000; Botfalvai et al. 2019). Accordingly, fossils of marine animals including fish (Szabó et al. 2019), nothosaurs, and placodonts are the dominant elements, whereas archosauromorphs, representing semi-aquatic to terrestrial forms, are comparatively rare. Hopefully, further excavations and more material will shed light on the details of this poorly known non-marine fauna.

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