

First report of Triassic vertebrate assemblages from the Villány Hills (Southern Hungary)

Attila Ósi*

*MTA–ELTE Lendület Dinosaur Research Group
Budapest*

Gábor Botfalvai

*MTA–ELTE Lendület Dinosaur Research Group
Budapest*

*Department of Applied and Physical Geology
Eötvös Loránd University, Budapest*

Edina Prondvai

*MTA–ELTE Lendület Dinosaur Research Group
Budapest*

Zsófia Hajdu

*Department of Applied and Physical Geology,
Eötvös Loránd University, Budapest*

Gábor Czirják

*Department of Applied and Physical Geology
Eötvös Loránd University, Budapest*

Zoltán Szentesi

*Hungarian Academy of Sciences – Hungarian Natural
History Museum – Eötvös Loránd University,
Paleontological Research Group, Budapest*

Emília Pozsgai

*Department of Geology
University of Pécs, Pécs*

Annette E. Götz

*Department of Geology
Rhodes University, Grahamstown*

László Makádi

*MTA–ELTE Lendület Dinosaur Research Group
Budapest*

*Department of Geology and Paleontology, Hungarian
Natural History Museum, Budapest*

Dóra Csengődi

*MTA–ELTE Lendület Dinosaur Research Group
Budapest*

Krisztina Sebe

*Department of Geology
University of Pécs, Pécs*

Addresses: A. Ósi, G. Botfalvai, E. Prondvai, L. Makádi, Zs. Hajdu, D. Csengődi, G. Czirják,

Z. Szentesi: H-1117 Budapest, Pázmány P. sétány 1/c, Hungary,

*Corresponding author e-mail: hungaros@gmail.com

E. Pozsgai, K. Sebe: H-7624 Pécs, Ifjúság u. 6, Hungary

A. E. Götz: P.O. Box 94, Grahamstown 6140, South Africa

Received: January 25, 2013; accepted: July 9, 2013

Remains of Triassic vertebrates discovered in the Villány Hills (SW Hungary) are described here. After the well-documented Late Cretaceous Iharkút locality, this material represents the second systematically collected assemblage of Mesozoic vertebrates from Hungary. Fossils were collected from both the classical abandoned road-cut at Templom Hill (Templom-hegy) and a newly discovered site at a construction zone located 200 meters west of the road-cut. Macrofossils of the construction site are mainly isolated bones and teeth of nothosaurs from the Templomhegy Dolomite, including a fragmentary mandible referred to as *Nothosaurus* sp. and placodont teeth tentatively assigned here to cf. *Cyamodus* sp. Affinities of these fossils suggest a Middle Triassic (Ladinian) age of these shallow marine deposits.

New palynological data prove for the first time a Late Triassic (Carnian) age of the lower part of the Mészhegy Sandstone Formation. Vertebrate remains discovered in this formation clearly represent a typical Late Triassic shallow-marine fauna including both chondrichthyan (*Lissodus*, *Palaeobates*, *Hybodus*) and osteichthyan (cf. *Saurichthys*, ?*Sphaerodus* sp.) fish fossils. The presence of reworked nothosaur and placodont tooth fragments as well as of possible archosauriform teeth, suggest an increase of terrestrial influence and the erosion of underlying Triassic deposits during the Late Triassic.

A belemnite rostrum collected from the lowermost beds of the Somssichhegy Limestone Formation proves that this Lower Jurassic (Pliensbachian) layer was deposited in a marine environment. Most of the vertebrate remains (nothosaurs, placodonts, hybodont shark teeth, perhaps *Palaeobates*, *Lissodus*) recovered from these beds are also reworked Triassic elements strongly supporting an erosive, nearshore depositional environment.

Key words: Villány, Triassic, Templomhegy Dolomite, Mészhegy Sandstone, vertebrates, Sauropterygia

Introduction

Vertebrate remains from the Mesozoic of Hungary are very rare and they are mostly isolated finds from different stratigraphic levels. A few of these fossils are associated or even articulated remains of marine sauropsids, such as the holotype of the Late Triassic (Carnian) placodontian *Placochelys placodonta* (Jaekel 1901, 1902a, 1902b, 1907; Rieppel 2001b) from the Bakony Mountains, the thalattosuchian crocodile referred to as *Steneosaurus* sp. (Ósi et al. 2012), or the recently discovered Temnodontosaurus-like ichthyosaur, the latter two of which were found in the Lower Jurassic (Toarcian) of the Gerecse Mountains (Dunai 2012). Up to now the only known systematically-collected vertebrate site in the country is the Late Cretaceous (Santonian) Iharkút locality (Bakony Mts, Western Hungary), which provided a rich and diverse assemblage of freshwater and terrestrial vertebrates (Ósi et al. 2012).

Except for the nicely-preserved cranial and postcranial material of *Placochelys* mentioned above, Triassic vertebrate fossils are restricted to isolated bones and teeth, mostly of fishes and marine sauropsids. Among these are some articulated ichthyosaur vertebrae unearthed by I. Szabó from the limestone beds of the Middle Triassic Vászoly Formation (Balaton Highland). In the same formation, but at the well-known Felsőörs outcrop, a nothosaur mandible fragment was found by A. Vörös. In addition some ichthyosaur vertebrae are also known from the Middle Triassic Felsőörs Limestone Formation close to Mencshely (A. Vörös, pers. comm.).

Regarding fishes, Jaekel (1902b) briefly described some isolated fish remains from the Upper Triassic of the Bakony Mountains. Beside the isolated fish teeth from some Triassic formations, articulated fish remains are known in the Upper Triassic finely laminated-limestone of the Sándorhegy Limestone Formation (Nosztor Valley, Balaton Highland) (A. Galács, pers. comm.).

Triassic remains from the southern part of Hungary (i.e. from the Mecsek and Villány Hills) are even fewer than from the Triassic beds of the Transdanubian Range. Some isolated nothosaur teeth have been found in different stratigraphic levels of the Mecsek Mountains. Lőrenthey (1907) and a few years later Lóczy (1912) mentioned *Nothosaurus* sp. remains from the quarry close to the railway station at Villány. The beds exposed in this quarry belong to the Csukma Dolomite Formation (of which the uppermost beds form the Templomhegy Dolomite Member). Furthermore, unidentified sauropsid bones have been reported from the Upper Triassic Mészhegy Sandstone Formation in the abandoned road-cut of Templom Hill of the Villány Hills (Rálich-Felgenhauer 1981). However, the beds providing these remains are now considered to belong to the underlying Templomhegy Dolomite (Vörös 2010 and this article); the sauropsid remains have never been studied in detail.

In the spring of 2012 a new, artificial outcrop (a construction site owned by Zs. Maul) of the Templomhegy Dolomite and the Mészhegy Sandstone Formation was discovered by T. Budai, A. Vörös and A. Ősi on Somssich Hill, a few hundred meters west of the classical abandoned road-cut of Templom Hill at Villány. During the detailed stratigraphic mapping, one of the authors (E. Pozsgai) found a few tiny remains including a tooth, vertebrae, and some limb elements. Later on, additional excavations and intensive screen washing of material were carried out both in the new outcrop and the abandoned road-cut, which resulted in the discovery of several hundred bones and teeth from different stratigraphic levels. The well to moderately-preserved fossils of the construction site are relatively abundant and represent a significant assemblage of sauropterygians. Our fieldwork rediscovered the bone-yielding horizon of the abandoned road-cut from which a few fragmentary bones were collected and reported more than three decades ago (Rálich-Felgenhauer 1981). Furthermore, five additional beds (both Triassic and Jurassic, L1, L3–L6 in Fig. 2) provided isolated vertebrate microfossils (small bone fragments and teeth). Most of these new remains are fragmentary, poorly preserved and do not provide any taxonomic information. At least 30% of the bones and especially of the teeth, however, can be referred to different genera or suprageneric taxa (osteichthyan and chondrichthyan fishes, nothosaurs, placodontians, possible archosauromorphs). This assemblage represents the first systematically collected assemblage of Triassic vertebrates from Hungary. These fossils play a crucial role in the dating and paleoenvironmental reconstruction of the poorly-known Mészhegy Sandstone Formation and provide insight into the changes of the vertebrate fauna during the deposition of the Templomhegy Dolomite and the Mészhegy Sandstone

Formation. In addition our discoveries help to clarify the facies interpretation of the most basal layers of the Early Jurassic Somssichhegy Limestone Formation.

The current study presents new palynological data from the Mészhegy Sandstone Formation and provides a preliminary description of the newly discovered vertebrate remains from Triassic and Jurassic beds, of which a more detailed description will be published separately. Based on these new findings, the age, stratigraphic position and depositional environment of the Templomhegy Dolomite and the Mészhegy Sandstone is discussed.

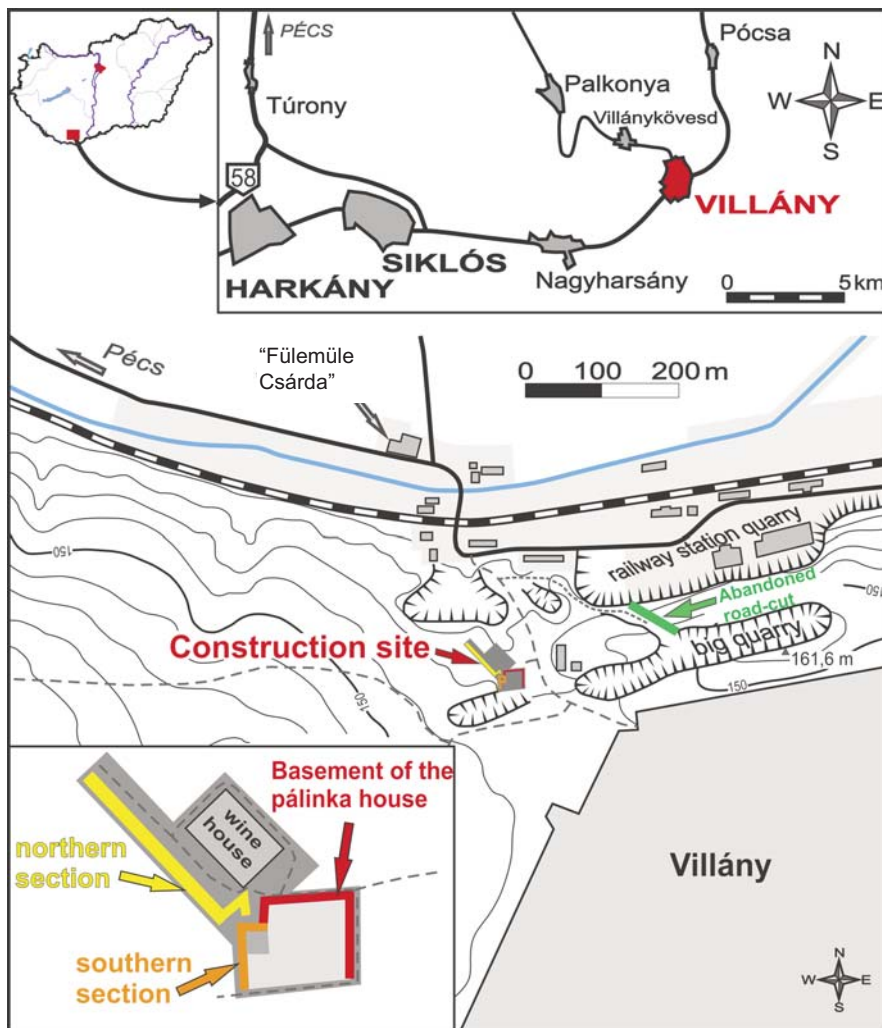


Fig. 1
Location of the two vertebrate sites at Villány. The lower left map shows the details of the construction site

Materials and methods

The vertebrate remains described here were collected during various field campaigns in 2012 in the Villány Hills, southern Hungary, in the new, artificial outcrop (construction site) and the classical abandoned road-cut of Templom Hill. All the remains collected from these localities (see Table 1 for the list of specimens) are housed in the Hungarian Natural History Museum (MTM). All elements were recovered as isolated specimens from different beds of the two outcrops. Specimens were prepared mechanically in the technical labs of the Hungarian Natural History Museum. The bones are generally poorly preserved and pink, purple or white in color.

Most of the teeth were discovered by screen-washing of sediments from four different stratigraphic levels of the abandoned road-cut. Approximately 90% of the washed material is from grayish green sand and weakly cemented sandstone from the top of the Triassic sequence exposed in the abandoned road-cut. During this process more than 1.5 tons of excavated matrix was dried and the samples were spread on tarps prior to washing. We used a composite of three different sieves with mesh sizes of 2 mm, 1 mm, and 0.5 mm. After drying, the residue was sorted under a stereo microscope.

Transversal thin sections of an unidentified bone fragment were acquired following standard methods (Wells 1989). Histological features were studied under a Nikon LV 100 polarized light microscope, pictures of the sections were taken with a QImaging MP5.0 digital microscope camera and processed with Image Pro Insight software.

Additionally, samples from a claystone interval at the base of the Mészhegy Sandstone Formation exposed in the abandoned road-cut section at Templom Hill were studied with respect to the sedimentary organic matter content and age-diagnostic palynomorphs. All samples were prepared using standard palynological processing techniques, including HCl (33%) and HF (73%) treatment for the dissolution of carbonates and silicates, and saturated ZnCl₂ solution (D ≈ 2.2 g/ml) for density separation. Residues were sieved at 15 μm mesh size. Slides were mounted in Eukitt, a commercial resin-based mounting medium.

Localities and geologic setting

Localities

The studied area is located in the Villány Hills (Southern Hungary), about 200–300 meters northwest of the town of Villány (Fig. 1). The investigated formations are exposed in two sections: 1) in the famous Templom Hill sequence, on the way up to the quarry in an abandoned road-cut (Fig. 2) and 2) about 200 meters westward, at an active construction site (Figs 3–5) on Somssich Hill.

Table 1
List of vertebrate specimens published in this study

Catalogue number	Taxon	Specimen(s)	Number of specimens	Age	Locality and stratigraphic unit
VER 2013.1.	<i>Nothosaurus</i> sp.	fragmentary mandible	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb.
VER 2013.2.	Vertebrata indet.	hollow bone	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.3.	Nothosauria indet.	vertebral centrum	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.4.	Nothosauria indet.	vertebral centra	65	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.5.	Nothosauria indet.	neural arch	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.6.	Nothosauria indet.	neural arch	3	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.7.	Nothosauria indet.	coracoid	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.8.	Nothosauria indet.	coracoid	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.9.	Nothosauria indet.	scapula	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.10.	Nothosauria indet.	scapula	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.11.	Nothosauria indet.	humerus(?)	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.12.	Sauropterygia indet.	limb bone	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.13.	Nothosauria indet.	ischium	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.14.	Nothosauria indet.	ischium	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.15.	cf. <i>Cyamodus</i> sp.	grinding tooth	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.16.	Placodontia indet.	tooth/osteoderm(?)	5	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.17.	Sauropterygia indet.	vertebral centrum	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.18.	Sauropterygia indet.	osteoderm	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.19.	Nothosauria indet.	tooth	2	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.20.	Sauropterygia indet.	rib fragment	1	Middle Triassic	Villány, construction site, Templomhegy Dolomite Mb
VER 2013.43.	Nothosauria indet.	teeth and vertebra	10	Middle Triassic	Villány, Road-cut, Templomhegy Dolomite, Layer 1
VER 2013.21.1.	<i>Lissodus</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.21.2.	<i>Lissodus</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.21.3-12.	<i>Lissodus</i> sp.	tooth	10	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.22.1.	<i>Hybodus</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.22.2.	<i>Hybodus</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.22.3.	<i>Hybodus</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.22.4.	<i>Hybodus</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.22.5-126.	<i>Hybodus</i> sp.	tooth	122	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.42.	? <i>Palaeobates</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 4
VER 2013.23.1.	? <i>Palaeobates</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.23.2.	<i>Palaeobates</i> sp.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.23.3-46.	<i>Palaeobates</i> sp.	tooth	44	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.24.1.	Chondrichthyes indet.	dermal scale	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.24.2.	Chondrichthyes indet.	dermal scale	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.24.3-6.	Chondrichthyes indet.	dermal scale	4	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.25.1.	Osteichthyes indet. (?Sphaerodus sp)	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.25.2.	Osteichthyes indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.25.3.	Osteichthyes indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.25.4-10.	Osteichthyes indet.	tooth	7	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5
VER 2013.26.	Vertebrata indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészegyhégy Sandstone Fm., Layer 5

Table 1 (cont.)

Catalogue number	Taxon	Specimen(s)	Number of specimens	Age	Locality and stratigraphic unit
VER 2013.27.	Vertebrata indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.28.	Vertebrata indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.29.1.	? <i>Saurichthys</i>	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.29.2.	? <i>Saurichthys</i>	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.29.3.	? <i>Saurichthys</i>	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.29.4-14.	? <i>Saurichthys</i>	tooth	11	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.30.1.	Archosauriformes indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.30.2.	Archosauriformes indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.30.3.	Archosauriformes indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.30.4.	Archosauriformes indet.	tooth	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.31.1.	Nothosauria indet.	tooth (reworked)	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.31.2-15.	Nothosauria indet.	tooth (reworked)	14	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.32.1.	Placodontia indet.	tooth (reworked)	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 3
VER 2013.32.2.	Placodontia indet.	tooth (reworked)	1	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.32.3-4.	Placodontia indet.	tooth (reworked)	2	Late Triassic	Villány, Road-cut, Mészhegy Sandstone Fm., Layer 5
VER 2013.33.	? <i>Saurichthys</i>	tooth (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.34.1.	<i>Hyodus</i> sp.	tooth (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.34.2.	<i>Hyodus</i> sp.	tooth (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.34.3-18.	<i>Hyodus</i> sp.	tooth (?reworked)	16	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.35.1.	<i>Palaeobates</i> sp.	tooth (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.35.2.	<i>Palaeobates</i> sp.	tooth (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.35.3-23.	<i>Palaeobates</i> sp.	tooth (?reworked)	21	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.36.1.	<i>Lissodus</i> sp.	tooth (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.36.2-5.	<i>Lissodus</i> sp.	tooth (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.37.1.	Chondrichthyes indet.	dermal scale (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.37.2.	Chondrichthyes indet.	dermal scale (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.37.3-4.	Chondrichthyes indet.	dermal scale (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.38.1.	Nothosauria indet.	tooth (reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.38.2.	Nothosauria indet.	vertebra (reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.38.3-18.	Nothosauria indet.	bone fragment (reworked)	16	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.39.1.	Placodontia indet.	tooth (reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.39.2-8.	Placodontia indet.	tooth (reworked)	7	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.40.	?Pisces indet.	tooth (?reworked)	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6
VER 2013.41.	Belemnites indet.	rostrum	1	Early Jurassic	Villány, Road-cut, Somssichhegy Limestone Fm., Layer 6

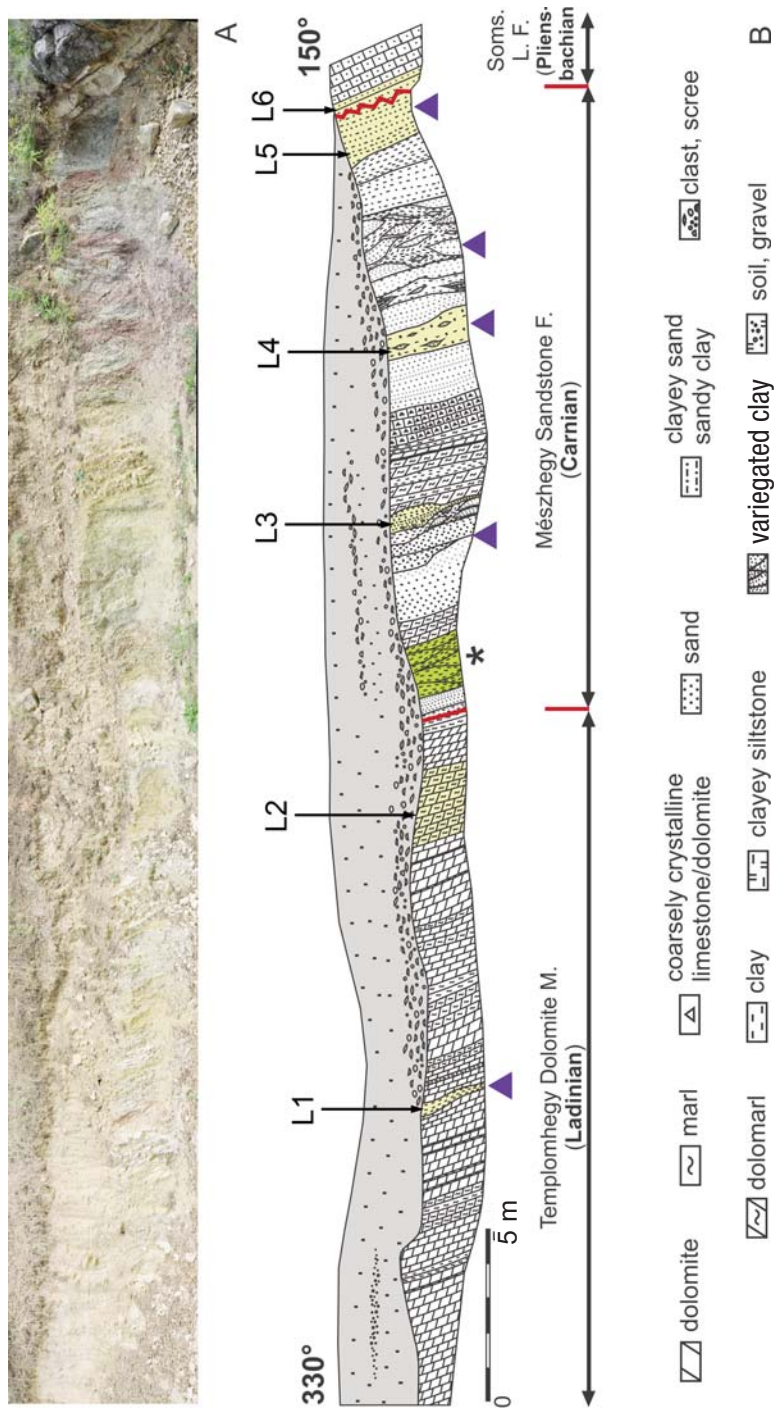


Fig. 2
 Stratigraphic section of the abandoned road-cut at Templom Hill, Villány. Light yellow color indicates fossiliferous beds, L1–L6 marks the six fossiliferous layers (Layer 1–Layer 6), asterisk marks the bed providing palynological data indicating the Carnian age, blue triangles indicate the screened horizons

Geologic setting

The present-day Villány Hills used to be part of the southern passive margin of the European Plate during the first half of the Mesozoic. This unit was located on the Tethyan shelf, in the proximity of the Germanic Basin (Haas and Péro 2004; Csontos and Vörös 2004). The Middle Triassic sedimentation was primarily carbonatic. Tectonic differentiation of the area due to rifting processes began in the late Middle Triassic; by the Upper Triassic, carbonate sedimentation switched to mostly detrital. In the late Middle Triassic – early Late Triassic the Villány Zone became an elevated ridge compared to the adjacent domains (Vörös 2012). Although the extensive Middle Triassic carbonates resemble the Germanic Muschelkalk succession (Török 1998), the paleogeographic and paleo-environmental setting of the overlying Upper Triassic detrital sequence is debated: it shows closer similarities to the Carpathian Keuper than to the classical Keuper of the Germanic realm (Bleahu et al. 1994; Feist-Burkhardt et al. 2008). The

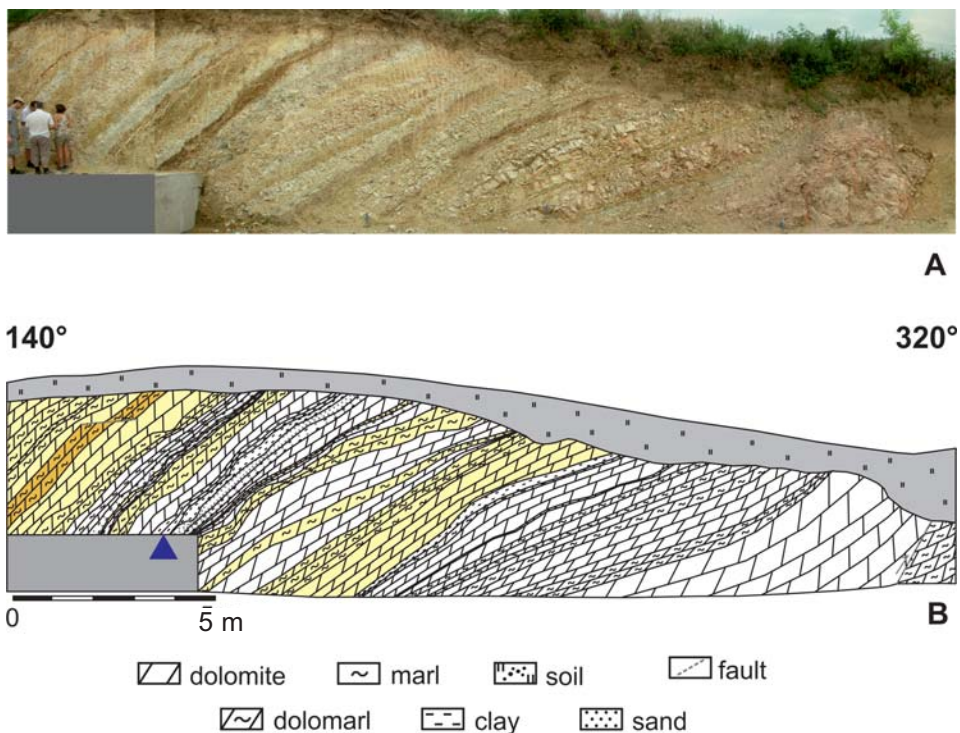


Fig. 3
Stratigraphic section of the northern part of the construction site in Villány. Light yellow color indicates fossiliferous beds and blue triangle refers to the screen-washed horizon. Among these, the dolomarl bed indicated with dark yellow color was the most productive one. This bed continues in the southern section (see Fig. 5)



Fig. 4
An overview of the southern part of the construction site. Red circle indicates the place where the *Nothosaurus* sp. (see in Fig. 6) mandible (VER 2013.1.) was found

sedimentary succession investigated in the present paper represents the uppermost part of the Muschelkalk carbonate ramp deposits and the very thin interval of clastic "Keuper" typical of the Villány Hills (Bérczi-Makk et al. 2004; Vörös 2009).

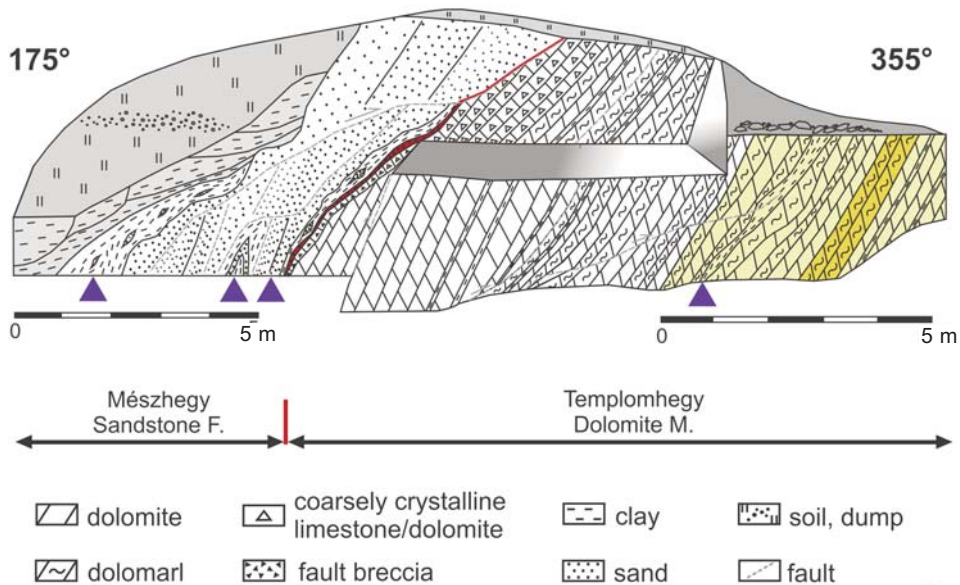
Road-cut ("Siklóbevágás")

After a long period of inaccessibility, the classical sequence has been made available for study again since April 2012. This 30 meter-long, three to five meter-high, northwest to southeast-oriented section comprises three formations of the early Mesozoic. In an approximately 15 meter-long interval in its northern part, the uppermost part of the Templomhegy Dolomite Member is exposed, characterized by thin-bedded, usually grayish-white to yellowish-gray dolomite, marly dolomite or calcareous dolomite and yellowish dolomarl, showing an upward increase of pelitic content. Variegated clay and silt interlayers become increasingly frequent upsection. The deposits of this formation indicate a shallow marine, subtidal (Nagy and Nagy 1976), intertidal (Török 1998) or supratidal (Bérczi-Makk et al. 2004), possibly lagoonal (Rálich-Felgenhauer 1981) paleoenvironment. No fossils of chronostratigraphic significance are known from this formation and its uppermost 30 meters have been reported as barren so far, apart from some Reptilia incertae sedis bone fragments (Lórenthey 1907; Lóczy 1912; Rálich-Felgenhauer 1981). Based on its stratigraphic position its age is probably Ladinian (Nagy and Nagy 1976; Vörös 2010).

Above a sharp boundary, probably an erosional unconformity, the Templomhegy Dolomite is overlain by a thin clastic sequence, the Mészhegy Sandstone. The latter consists of fining-upward cycles of weakly cemented, usually grayish, yellowish, purplish or greenish sandstone, siltstone and reddish, purplish or variegated clay strata, with subordinate amounts of grayish dolomite and yellowish dolomarl (Vörös 2010). Its facies has been interpreted as shallow marine or littoral (Rálich-Felgenhauer 1981; Török 1998) or as fluvio-lacustrine (Vörös 2010). It has been reported to be barren, apart from some unidentified plant remnants, which have been mentioned in the literature (Bleahu et al. 1994) but could not be found during our fieldwork. Based on the stratigraphic position



A



B

Fig. 5 Stratigraphic section of the southern part of the construction site in Villány. Light yellow color indicates fossiliferous beds and blue triangles refer to the screen-washed horizons. Among these, the dolomarl bed indicated with dark yellow color was the most productive one. This bed continues in the northern section (see Fig. 3)

and lithological appearance, its age has been thought to be Late Triassic by the above-mentioned authors. Its deposition is assumed to have been controlled by climatic changes such as the 'Carnian pluvial event' and thus to be of probable Carnian age (Vörös 2009). Vörös (2010) put forward the idea that the three distinguished sedimentary cycles may correspond to different time intervals, namely to the Carnian, Norian and Rhaetian ages. In the last three meters of the section, at the southern end of the road-cut, the Mészhegy Sandstone is overlain with a sharp boundary by the lowermost, grayish-yellowish calcareous sandstone beds of the Pliensbachian (Vörös 1972, 2010) Somssichhegy Limestone Formation.

The construction site

An active construction site opened in 2011 exposes the same Triassic formations as those known from the road-cut. This locality has two parts. In its northern part, a winery is being built, from which approximately five meters to the west a 30 meter-long, four to five meter-high, approximately northwest to southeast-oriented section is exposed (Fig. 3). This section includes the uppermost strata of the Templomhegy Dolomite (dolomite and dolomarl with clay and silt interlayers) similar to the road-cut section. However, the construction site section represents a more complete exposure of the upper part of the formation. During our first field campaign in March 2012, these layers (dipping to south) were also exposed at the base of the winery, a few meters below the surface, but shortly thereafter this exposure became a cellar.

Over the southern part a brandy shop will soon be built (Fig. 4), but it was possible to study its excavated basement until the end of the year 2012. This basement covers a surface of nearly 25×25 meters and is three to four meters deep. Its northwestern (Fig. 5) and eastern walls also expose the Templomhegy Dolomite. In its southwestern part (Fig. 5), a 10 meter-long and six meter-high section of the Mészhegy Sandstone Formation, a thinner sequence than in the road-cut, could be investigated. This sequence is characterized by reddish to grayish sandstone and reddish-purplish clay; it unconformably overlies the Templomhegy Dolomite.

Results

Palynology of the Mészhegy Sandstone Formation

The sedimentary organic matter of the basal Mészhegy Sandstone Formation is characterized by a high amount of plant debris, mostly opaque phytoclasts of different size and shape. Translucent phytoclasts are mainly large particles. This phytoclast assemblage indicates a nearshore, proximal depositional environment characterized by a high input of land-derived organic particles. The palynomorph association includes *Patinasporites densus*, *Infernopollentia* sp., *Aratrisporites* spp., *Ovalipollis* spp., and *Triadispora* spp. indicating a Carnian age.

Vertebrate remains from the construction site

Although three different sandstone levels of the Mészhegy Sandstone Formation exposed in the southern part of the construction site were subjected to screen-washing, no fossils were encountered. Vertebrate remains are most abundant in the yellowish, partly reddish marl of the uppermost beds of the Templomhegy Dolomite exposed in both parts of the construction site. Rarely, bones were also found in the white and more calcareous beds. Most of the fossils are only bone chips or incomplete, compressed specimens but some of them are complete. Postcranial elements of different groups are more abundant, but isolated teeth were also discovered. The vertebrate assemblage contains approximately 400 isolated specimens representing at least two groups of sauropterygians (placondonts and nothosaurs) and an undetermined bone, most probably of a terrestrial animal.

Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994
Nothosauridae Baur, 1889
Nothosaurus Münster, 1834
Nothosaurus sp.

Nothosaurian remains are relatively abundant in the locality, being represented by both cranial and postcranial remains. Besides various isolated teeth, a probable skull fragment (part of the skull roof) and a fragmentary but well-preserved mandible (VER 2013.1.) with *in situ* teeth have been discovered (Fig. 6). The mandible specimen consists of the anterior part of both dentaries that are fused in a lateromedially wider than anteroposteriorly long symphysis (maximal length/width ratio is 0.86) representing the plesiomorphic condition within *Nothosaurus* (Albers and Rieppel 2003). The left dentary is more complete posteriorly than the right one. Dorsolaterally, the symphyseal region bears five pairs of enlarged alveoli. As in most nothosaurs (see Rieppel and Wild 1996) these alveoli possess labially, anterolabially oriented and slightly lingually curved fang teeth (the left 2nd and 4th and the right 3rd are preserved). Whereas the first three alveoli are separated by a short diastema, the fourth and fifth are separated only by a thin bony septum. The fangs are followed by four to five times smaller, widely spaced, slightly curved and pointed teeth that are, similarly to the larger fang teeth, ornamented by longitudinal enamel wrinkles. Posteriorly the dentaries are not complete; thus the total number of teeth cannot be determined. The medial side of the mandibles is slightly compressed; thus the anterior extension of the splenial cannot be seen (Fig. 6).

Based on the features of the symphyseal region, the Villány specimen is most similar to that of *Nothosaurus* in having a relatively elongate, "spoon"-shaped symphysis that bears enlarged and distinctly procumbent fangs, behind which the dentary carries a palisade of distinctly smaller teeth (Rieppel 2000:69).

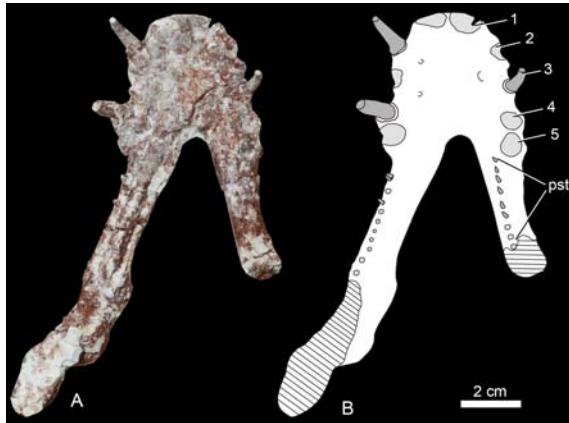
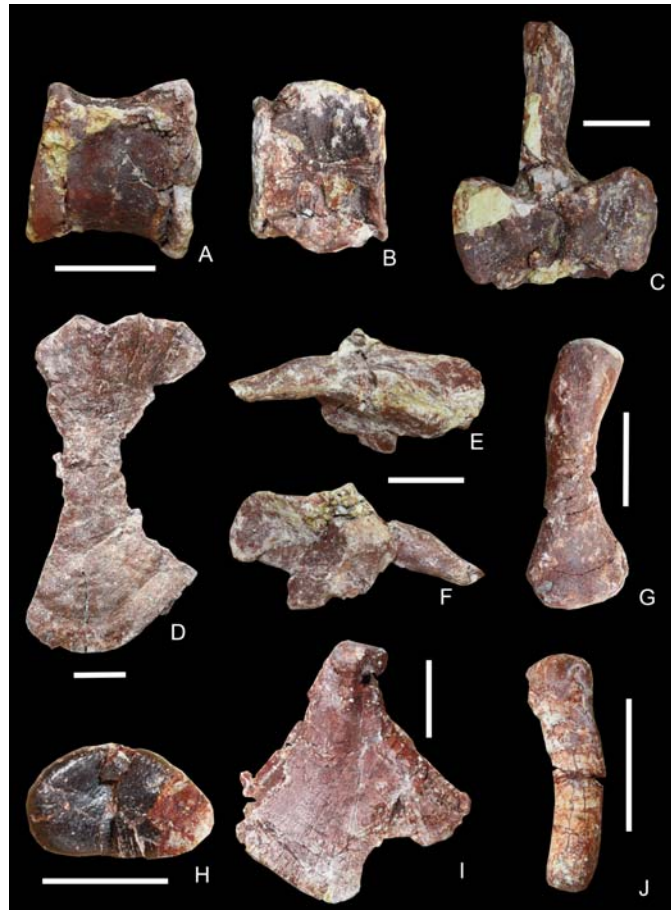


Fig. 6
Nothosaurus sp. fragmentary mandible (VER 2013.1.) from the Templomhegy Dolomite exposed in the southern part of the construction site. Photograph (A) and its technical drawing (B) in occlusal view. Abbreviations: pst, palisade of smaller teeth; 1–5, alveolus/tooth

Simosaurus differs from the Villány specimen in the lack of an anteroposteriorly elongated, massive symphysis (Rieppel 1994). The mandibles of *Lariosaurus* and *Nothosaurus mirabilis* and *N. jagisteus*, each having a longer than wide symphysis (Rieppel 2000, 2001a), and *N. youngi* with four fang teeth in the symphyseal region (Li and Rieppel 2004) are different from the Hungarian specimen. The fifth fang tooth, being completely behind the level of the posterior end of the symphysis (VER 2013.1., Fig. 6B), is most similar to *Nothosaurus giganteus* and *N. marchicus* in this respect. *N. giganteus* is more similar to the Villány specimen, with the fourth and fifth alveoli being separated only by a thin alveolar septum (in *N. marchicus* the five fangs are separated by a diastema of approximately the same length). The main difference between the mandibles of the Villány form and *N. giganteus* is their size; the mandible of the latter form is 1.5 to 2 times larger than the Villány specimen (Fig. 6). It is important to note, however, that the ontogenetic status of the latter specimen is unknown, so it may represent a skeletally immature, still actively growing animal, and its total adult length could have been larger. Whereas in more primitive nothosaurs the rostrum, together with the length of the mandibular symphysis, is short, providing a length/width ratio of the mandibular symphysis below or around 1.0, in more advanced forms this ratio is higher (e.g. 1.0–1.3 in *N. giganteus*, 1.5–1.6 in *N. mirabilis*). Rieppel and Wild (1996:74) noted that "the trendlike development of these characteristics is, to some degree, mirrored by the stratigraphic distribution of the taxa in question". This suggests that the Villány specimen, with a ratio of 0.86, is not among the latest and more developed forms with elongate rostrum and symphysis, but it is closer to *N. marchicus*. However, we must keep in mind that this ratio may have changed during ontogeny. Unfortunately, in *Germanosaurus* and *Cymatosaurus*, and in several species of *Nothosaurus* (*N. edingeri*, *N. juvenilis*, *N. haasi*, *N. rostellatus*, *N. winkelhorsti*, *N. jagisteus*, *N. winterswijkensis*) the mandible or the symphyseal region of the mandible is not preserved; thus no comparison can be made with VER 2013.1.

Postcranial material is represented by several dozens of isolated vertebral centra (VER 2013.3., VER 2013.4.) with maximum central width ranging from 5 to 35 mm, some neural arches (VER 2013.5., VER 2013.6.) (as typically seen in nothosaurs, the vertebral centra and neural arches are not fused; thus they are frequently found as separated elements), fragmentary ribs (VER 2013.20.), two coracoids (VER 2013.7., VER 2013.8.), two scapulae (VER 2013.9., VER 2013.10.), two ischia (VER 2013.13., VER 2013.14.) and some limb bones including a humerus (VER 2013.11., VER 2013.12., Fig. 7). These bones show the morphology typical of nothosaurs and they are particularly similar to the postcranial elements described in the different *Nothosaurus* species. The best preserved neural arch (Fig. 7C) is most similar to that of *Nothosaurus* cf. *N. juvenilis* described recently from the Italian side of the Monte San Giorgio fossiliferous area (Renesto 2010; S. Renesto pers. comm. 2013), although the Italian specimen is half the size. Following the principle of parsimony we tentatively refer to these postcranial elements as *Nothosaurus* sp. until more complete, associated material helps to clarify their taxonomic status.

Fig. 7
Isolated sauropterygian remains from the Templomhegy Dolomite exposed in the southern part of the construction site. A, nothosaur vertebral centrum (VER 2013.3.) in lateral, B, dorsal view. C, nothosaur dorsal neural arch (VER 2013.5.) in anterior view. D, nothosaur coracoid (VER 2013.7.) in ventral view. E, nothosaur scapula (VER 2013.9.) in lateral, F, medial view. G, nothosaur ?humerus (VER 2013.11.) in ?anterior view. H, placodont grinding tooth (VER 2013.15.) referred to cf. *Cyamodus* sp. I, nothosaur ischium (VER 2013.13.) in ?lateral view. J, undetermined sauropterygian limb bone (VER 2013.12.). Scale bars equal 2 cm



Placodontia Gürich, 1884
 Cyamodontidae Nopcsa, 1923
Cyamodus Meyer, 1863
 cf. *Cyamodus* sp.

At least six teeth (VER 2013.15., VER 2013.16.) can be assigned to placodontians. Although varying in size and shape, all of them could have had a more or less rounded, non-rectangular shape with low and flat crowns (Fig. 7H). All teeth are fragmentary; thus the thickness of the enamel coat can be observed in cross-section. It ranges between 0.7 to 1.0 mm, representing one fourth or one fifth of the total crown height. The two largest specimens (VER 2013.15., VER 2013.16) are rather kidney-shaped with one of the longitudinal (?lingual) margins being straight and not as rectangular as those of the palatal teeth of *Placodus* (Sues 1987; Rieppel 1995). The shape and size of the largest teeth show great similarities with those of cyamodontids. The length/width (in mm) ratio of the two largest teeth are $31.8/19.0=1.67$ and $39.2/23.7=1.65$, the latter of which is based on estimated values. These ratios are higher than those documented in the case of the palatal teeth of any of the five species of *Cyamodus* but they are closer to the ratio measured in *Placocheylanus stoppanii* (1.73; Rieppel 2001b: Table 7). The enlarged palatal teeth of the latter species are, however, oval-shaped with convex margins (Pinna 1976: Fig. 1). Based on their large size, these teeth are from the second palatal or the last dentary tooth positions. Similarly large (e.g. *Cyamodus muensteri*) or even larger (e.g. *Macroplacus raeticusi*) palatal teeth are present in some species of cyamodontids (Rieppel 2001b). Their elongated shape resembles much more the teeth of *Cyamodus* sp. described from the Late Ladinian to Early Carnian of Slovenia (Buffetaut and Novak 2008) than those of the different *Cyamodus* species listed by Rieppel (2001b). In the latter forms all margins of these teeth are convex and usually neither a straight nor slightly concave margin is present. *Macroplacus* has rather deltoid-shaped palatal teeth. The Hungarian teeth are also similar to the distinctly elongated posterior palatal teeth of *Psephoderma* (Pinna and Nosotti 1989). However, *Psephoderma* is known only from Norian-Rhaetian deposits; thus the affinity of the Hungarian specimens (Fig. 7H) with the teeth of the Ladinian-aged *Cyamodus* genus is more reasonable.

At least the largest teeth show indication of wear. In some parts of the crown the slightly irregular enamel surface is smooth, indicating the presence of dental wear.

Undetermined terrestrial bone

A fragmentary hollow bone (VER 2013.2., Fig. 8A–C) is the only possible evidence for the presence of a terrestrial amniote in the Mesozoic of Villány. This specimen is a 10 cm-long diaphyseal part of an elongate bone fragment with an average width of 1.3 cm. Although the specimen is compressed due to diagenetic events, in cross-section it can be observed that it is hollow with an average

thickness of the bony wall of 2 mm (Fig. 8C). The preserved cross-section of the bone indicates that originally it had an oval or flattened rather than circular cross-section. This is further supported by the thickened bony wall in the bending edges of the bone. None of the epiphyses are preserved, and it seems that at least one of the ends of the bone was broken off well before burial. The medullar cavity is filled with grayish-brownish clay (Fig. 8C). This sediment is completely

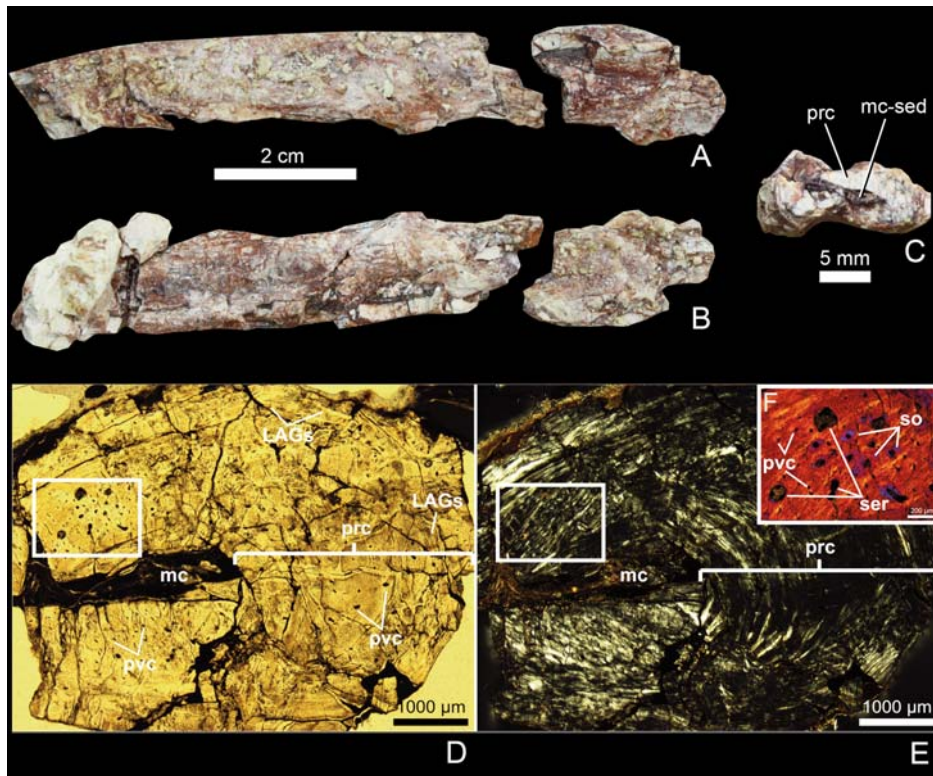


Fig. 8
Morphology (A–C) and histology (D–F) of the unidentified bone fragment (VER 2013.2.). Gross morphology (A, one side; B, opposite side; C, cross-section view) of this poorly preserved, slightly compressed specimen implies a genuinely elongate, slender shaped bone with oval cross-section and distinct bone cortex and medullar cavity. The medullar cavity is filled in with characteristic brownish sediment (mc-sed) that has not been encountered in any other specimen found at the locality so far. Transversally cut histological thin sections of this bone fragment (D, under single plane polarizer; E, under crossed plane polarizers; F, under crossed plane polarizers with $\frac{1}{4}\lambda$ -plate) show predominantly parallel-fibred primary cortex (prc) with low overall vascularity and some, locally concentrated lines of arrested growth (LAGs). Vascular density appears higher in the inner than in the outer cortex. The outermost cortex is missing. Secondary osteons (so) are sparse but some also occur in the outer half of the preserved cortex. Neither trabeculae in the medullar cavity, nor traces of extensive remodeling activity in the perimedullar region of the cortex can be observed. White rectangle in D and E locates the magnified area presented in F. Further abbreviations: mc, medullar cavity; pvc, primary vascular canals; ser, secondary erosion rooms

different from the matrix (yellowish dolomarl) surrounding the outer surface of the bone, suggesting its terrestrial origin. These taphonomic features imply that this bone had been exposed to terrestrial conditions for a long time before burial. Due to its fragmentary nature the taxonomic assignment of this bone is problematic.

Although fragmentary and morphologically poorly preserved, its histological features are still discernible. Due to the intense compression, the medullary cavity is crushed; thus neither its original extent nor its microanatomical structures can be unequivocally discerned. However, the cortex appears relatively thick, without any considerable increase in number and size of erosion rooms toward the innermost cortex, and the medullary cavity seems to be devoid of trabeculae. The bony fragments present in the cavity appear primary in origin implying that these fragments are in fact broken-off pieces of the primary cortex. The outermost cortex is not preserved in the sectioned part of the bone (Fig. 8D, E).

The majority of the cortex is composed of parallel-fibred primary bone, although some scattered secondary osteons are also observable in the outer half of the cortex. The primary vascular canals are almost exclusively longitudinal with very few transversal anastomoses. Vascular density is higher in the inner two thirds than in the outer one third of the cortex but there are also regional differences within the inner and peripheral cortex. Nevertheless, vascularity is generally low in the entire preserved cortex (10–35 nr/mm²). Furthermore the sparse vascular canals have narrow lumens, indicating their fairly mature state. Fine lamellation is visible throughout the cortex with some outer cortical layers exhibiting more distinct and densely packed growth marks. These latter can be interpreted as lines of arrested growth (LAGs), the presence of which points to temporal interruptions in the diametrical bone growth. The scarcity of narrow vascular canals, along with the presence of more expressed LAGs in the outer cortex, suggests that this specimen had passed the faster growing juvenile phase of its ontogeny. On the other hand, there is no unambiguous sign of considerable slowing down of growth in the outer third of the cortex, which would characterize a skeletally mature, fully-grown individual. However, the apparent lack of the original outer cortical surface prevents the identification of the skeletal maturity state of this specimen.

Vertebrate remains from the abandoned road-cut of Templom Hill

The road-cut exposure of Templom Hill consists of both Triassic (Templomhegy Dolomite Member of the Csukma Dolomite Formation and the Mészhegy Sandstone Formation) and Jurassic sediments (Somssichhegy Limestone Formation); vertebrate remains have been found in six stratigraphic horizons (see L1–L6, see Fig. 2). Macroscopic specimens are rare and the discovery of most fossils (dominantly teeth and bone fragments under 5 mm) is the result of extensive screen-washing or preparation of the rock pieces under a stereo microscope.

Fossils from the Middle Triassic dolomite-dolomarl beds (Templomhegy Dolomite)

The first vertebrate remains discovered in the classical road-cut outcrop during the early 1980s were some fragmentary bones (probably sauropsid bones [L. Kordos pers. comm.] perhaps including a vertebra [E. Rálich-Felgenhauer pers. comm.]), but since that time the specimens have been lost. The detailed description of the beds of this locality by Rálich-Felgenhauer (1981:30) indicates that these bones are from the 25th bed made up of yellowish dolomarl located approximately in the middle of the outcrop (Layer 2, 'L2' in Fig. 2). After re-cleaning the site in April of 2012, based on her work the fossiliferous bed could be identified; also, some additional, reddish bones have been found including some isolated vertebral centra. These vertebrae, being simple platycoel rounded elements without a neural arch, are identical to those found in the marly beds of the construction site. Based on their similar morphology and the equivalent stratigraphic position compared to those of the construction site these remains can be tentatively referred to as *Nothosaurus* sp.

Beside collecting macrofossils, intensive screen-washing was also carried out on material from five different levels of the outcrop, including some beds of the Templomhegy Dolomite (Fig. 2). One of these beds is a reddish clay layer seven meters below the yellow, bone-yielding dolomarl bed (Layer 1, 'L1' in Fig. 2) mentioned above. Similarly to the other fossiliferous horizons of the formation, this reddish clay bed yielded fragmentary nothosaur remains, including small teeth and vertebral centra (VER 201343).

Fossils from the Upper Triassic Mészhegy Sandstone Formation

Four different layers of the Mészhegy Sandstone Formation were sampled for screen-washing (see Fig. 2). Of the three lower beds 20 to 50 kg of sediment were sieved, of which only the second one (Layer 4, 'L4' in Fig. 2) provided a single hybodont (VER 201342.) (*?Palaeobates* sp.) tooth fragment. Teeth with similar morphology (pitted and relatively thick, rounded enamel surface) are relatively abundant in the uppermost bed of the Mészhegy Sandstone and the lowermost bed of the Somssichhegy Formation (see below).

Between these two sampled beds (Layer 2 and Layer 4, 'L2' and 'L4' in Fig. 2, respectively) a brownish-greyish sandstone bed with embedded large, rounded, reworked clay and sandstone clasts (Layer 3, 'L3' in Fig. 2) is present, from which a large piece of reworked sandstone provided a 2 cm-wide placodont tooth fragment (VER 2013.32.1., Fig. 9A). This tooth, although fragmentary and worn occlusally, shows great similarity both in size and morphology with those found in the uppermost beds of the Templomhegy Dolomite.

The most productive bed of the formation is the uppermost layer (greyish-greenish sandstone, Layer 5, 'L5' in Fig. 2), which provided more than a hundred teeth and bone fragments. These vertebrate remains can be assigned to the following taxa:

Chondrichthyes Huxley, 1880
 Hybodontoida Owen, 1846
 Polyacrodontidae Glückman, 1964
Lissodus Brough, 1935
Lissodus sp.

Twelve tooth fragments (VER 2013.21.1., VER 2013.21.2., VER 2013.21.3-12.) can be referred to this genus. Specimens indicate a mesiodistal length of the crowns from 2 to 5 mm. The root cannot be observed in any specimen. The crown is elongate and angular; the coronal profile is low and a prominent occlusal crest is present (VER 2013.21.1., VER 2013.21.2., Fig. 9A, B). The central cusp is low and no ridge is present on its surface. The labial peg is shallow or in some cases moderate and no longitudinal ridge is present labially. If present, lateral cusplet pairs are only incipient. Occlusally the labial grinding surface is strongly concave. Most of the crown surface is smooth; only the labial side (mostly the margin) is ornamented by shallow ridges and cusplets.

The specimens of this assemblage show some similarity with the teeth of *Lissodus angulatus* (Stensiö 1921) but the labially present longitudinal ridge and the developed labial peg (Duffin 2001; Blazejowski 2004) clearly distinguish the mentioned Early Triassic species from the Villány specimens. The most similar teeth of the genus *Lissodus* appear to be those of *L. nodosus* from the Anisian to Norian of Germany and Poland (Seilacher 1943; Duffin 1985, 2001). Among the similarities of the above-listed features the very weak labial peg (on the posterodorsal teeth of *L. nodosus*) and the ridged and ornamented labial side are of great importance.

Fig. 9 →

Microvertebrate fossils from the Upper Triassic Mészhegy Sandstone Formation exposed in the abandoned road-cut at Villány. A, *Lissodus* sp. tooth fragment (VER 2013.21.1.) in occlusal view. B, *Lissodus* sp. tooth fragment (VER 2013.21.2.) in occlusal view. C, *Hybodus* sp. tooth (VER 2013.22.1.). D, *Hybodus* sp. tooth (VER 2013.22.2.). E, *Hybodus* sp. tooth (VER 2013.22.3.). F, *Hybodus* sp. tooth (VER 2013.22.4.). G, ?*Palaeobates* sp. tooth in occlusal view (VER 2013.23.1.). H, *Palaeobates* sp. tooth in occlusal view (VER 2013.23.2.). I, selachian scale fragment (VER 2013.24.1.). J, selachian scale fragment (VER 2013.24.2.). K, undetermined osteichthyan (possibly ?*Sphaerodus* sp.) tooth (VER 2013.25.1.) in occlusal, L, lateral views. M, undetermined carinate tooth (VER 2013.26.) in occlusal, N, ?medial view. O, undetermined osteichthyan tooth (VER 2013.25.2.) in occlusal view. P, undetermined osteichthyan tooth (VER 2013.25.3.) in occlusal view. Q, undetermined pointed tooth (VER 2013.27.). R, undetermined carinate tooth (VER 2013.28.). S–V, Saurichthys-type teeth (VER 2013.29.1., VER 2013.29.2., VER 2013.29.3.). W, ?*Archosauriformes* indet. tooth (VER 2013.30.1.) in ?mesial, X, ?labial view. Y, ?*Archosauriformes* indet. tooth (VER 2013.30.2.). Z, reworked nothosaur tooth (VER 2013.31.1.). A', reworked placodont tooth (VER 2013.32.1) in occlusal view. B', reworked placodont tooth fragment (VER 2013.32.2.) in cross section. Scale bars of A–Z and B' equal 500 μ m, and 5 mm in A'



Hybodontidae Owen, 1846

Palaeobates Meyer, 1849

Palaeobates sp.

Four tooth fragments (VER 2013.23.1., VER 2013.23.2., VER 2013.23.3-46.) can be referred tentatively to *Palaeobates* sp. (Fig. 9G, H). The teeth have an oval and rounded shape in occlusal view. The occlusal crest is poorly developed or in some specimens cannot be seen. Occlusally, the crown surface shows a marked reticulate ornamentation and mesiodistally short, parallel ridges appear. The mesiodistal extremities of the crowns are rounded instead of being angular. None of the teeth preserve the root.

The mesial or distal extremities of these specimens show a more rounded margin compared to those of *Reticulodus synergus* from the Norian of the southwestern United States (Murry and Kirby 2002) and based on the number and size of the small pits on the occlusal surface, the teeth from Villány are more reminiscent of that of *Palaeobates angustissimus* (see e.g. Dorka 2001).

Hybodus Agassiz, 1837

Hybodus sp.

Pointed, slightly flattened teeth (VER 2013.22.1., VER 2013.22.2., VER 2013.22.3., VER 2013.22.4, VER 2013.22.5-126, Fig. 9C–F) are among the most frequent remains in the uppermost layer of the Mészhegy Sandstone Formation. These teeth represent the largest, central cusp of the multicusped teeth of hybodont sharks. Whereas on some teeth the mesial surface is slightly convex and in some cases devoid of any parallel enamel ridges (VER 2013.22.1., VER 2013.22.2., Fig. 9C, D), the distal side is more convex and ornamented by finer or more developed vertical ridges (VER 2013.22.3., VER 2013.22.4, Fig. 9E, F). Some teeth have a lower, more robust triangular central cusp and the vertical enamel ridges are prominent. These latter teeth are very similar both in size and morphology to the central cusp of *Hybodus minor* (Duffin 1993).

Chondrichthyes indet.

Beside the teeth, three indeterminate, most probably selachian scales (VER 2013.24.1., VER 2013.24.2., VER 2013.24.3-6., Fig. 9I, J) were also found. These fragmentary specimens ranging between 2 and 4 mm have a convex surface ornamented by developed parallel or sub-parallel ridges. Their ornamentation is quite similar to those of the selachian scales published by Duffin (1993: Text-fig. 14) or to those illustrated by Delsate et al. (2002: Plate 10) and Cuny et al. (2000: Fig. 3 E–F), though the Villány specimens are three to four times larger.

Osteichthyes Huxley, 1880
Acipenseriformes Agassiz, 1843
Saurichthidae Goodrich, 1909
Saurichthys Agassiz, 1834
cf. *Saurichthys* sp.

Fourteen teeth (VER 2013.291., VER 2013.292., VER 2013.293., VER 2013.294-14.) with a total height ranging from 0.8 to 2.5 mm have a simple conical shape. The base of the tooth, if preserved, is not covered with acrodine but ornamented by vertical grooves. The apical half of the tooth is a smooth, conical, slightly transparent acrodine cusp that is devoid of any vertical ridges or carinae (VER 2013.291., VER 2013.292., VER 2013.293., Fig. 9S–V) similar to the teeth of *Saurichthys* reported from other localities (see e.g. Cuny and Ramboer 1991; Chhabra and Mishra 2002).

Osteichthyes indet.

Ten cusp-like teeth (VER 2013.251., VER 2013.252., VER 2013.253., VER 2013.254-10.) ranging from 0.8 to 1.5 mm in diameter are hemispherical (Fig. 9K, L, O, P). Their crown is smooth, slightly transparent and lack vertical ridges or carinae. They are similar to the tooth crowns preserved on the undetermined tooth plates from the Upper Triassic Chinle Group which were previously referred to Colobodontidae/Perleididae (Mutter and Heckert 2006). One tooth differs from the other specimens in having a pointed apical cap (VER 2013.251., Fig. 9K, L). Similar teeth (both the simple hemispherical and the one with an apical cap) have been described from the uppermost Ladinian of northeastern Italy as ?*Sphaerodus* sp. (Dalla Vecchia and Carnevale 2011: Fig. 5N, O).

Reworked sauropterygian teeth

Beside the different fish teeth, a few undetermined teeth (see below) and small bone chunks, fifteen fragmentary nothosaurian teeth (conical, slightly curved teeth with parallel vertical enamel ridges, VER 2013.31.1., VER 2013.31.2-15., Fig. 9Z) and four placodont tooth fragments (covered with extremely thick [ca. 2 mm] enamel, VER 2013.32.1., VER 2013.32.2., VER 2013.32.3-4., Fig. 9A', B') were also discovered. These specimens, although broken in many cases, frequently show abraded surfaces, suggesting that they are not *in situ* fossils but were reworked from the underlying deposits, most probably from the Middle Triassic Templomhegy Dolomite.

?Archosauriformes Gauthier, Kluge and Rowe 1988
 ?Archosauriformes indet.

Two teeth may represent some archosaurian sauropsids (Fig. 9W–Y). One of them (VER 2013.30.2.), being 2.7 mm long, has a massive root with well-developed pulp cavity opening basally (Fig. 9Y). There is no constriction between the crown and the root. The crown has only its basal part preserved that is ornamented by very fine vertical enamel ridges.

The other tooth (VER 2013.30.1.) is larger, with a total height of 3 mm (Fig. 9W, X). The enamel cover of this conical tooth bears vertically-oriented sub-parallel ridges that merge in some cases with each other, so this tooth differs from the teeth of nothosaurs in this respect. The crown is relatively robust, slightly curved, most probably distally, and is not rounded on its mesial side but more keel-like (but does not bear a carina) that indicates a rather drop-like than oval or subcircular cross section.

Vertebrata incertae sedis

The screen-washed material of the uppermost beds of the Mészhegy Sandstone Formation provided some unidentified teeth or tooth fragments. Among these specimens two teeth (VER 2013.26.) with a total height between one and two mm possess a conical crown that is slightly compressed labiolingually, so their cross-section is not circular as the teeth of *Saurichthys* but oval or subcircular, resembling rather the teeth of various archosaurian groups (Fig. 9M, N). They bear two unserrated carinae, probably positioned mesiodistally, and the rest of the crown is not smooth but ornamented by very fine vertical enamel ridges. These ridges are not as developed as those seen on the teeth of nothosaurs.

Two other teeth (VER 2013.27., VER 2013.28.) have more flattened crowns with some keel-like carinae mesiodistally. One of them has an asymmetrical pointed main cusp and some vertical grooves on its basal part (Fig. 9Q). The other tooth is symmetrical, triangular-shaped and has a smooth enamel surface (Fig. 9R).

Fossils from the Lower Jurassic Somssichhegy Formation

Vertebrate remains in the basal, coarse sandy layers of the Lower Jurassic (Pliensbachian) Somssichhegy Limestone (Layer 6, 'L6' in Fig. 2) have been known for years, but up to now nobody collected and published any vertebrate material. On the other hand, invertebrate fossils, such as ammonites or belemnites, much more useful for dating stratigraphic units (Doyle and Bennett 1995), have not been known from the lowermost beds of this formation (only some bivalves have been reported from these strata). Intensive prospecting by our team in the approximately 50 cm-thick most basal yellowish conglomerate and sandstone layers of the formation resulted in the discovery of, among others, a belemnite rostrum (VER 2013.41., Fig. 10M). This specimen clearly supports the Lower

Jurassic and most probably Pliensbachian age indicated by ammonites and brachiopods collected from a somewhat higher part of the formation (Ager and Callomon 1971). In addition we collected a few hundred isolated and in several cases fragmentary bones and teeth (Fig. 10). Besides autochthonous fossils such as fish teeth of different taxa, a significant part of the remains, including nothosaur



Fig. 10
Microvertebrate fossils from the Lower Jurassic Somssichhegy Limestone Formation exposed in the abandoned road-cut at Villány. A, fragmentary *Saurichthys*-type tooth (VER 2013.33). B, *Hybodus* sp. tooth (VER 2013.34.1). C, *Hybodus* sp. tooth (VER 2013.34.2). D, *Palaeobates* sp. tooth in occlusal view (VER 2013.35.1). E, *Palaeobates* sp. tooth in occlusal view (VER 2013.35.2). F, *Lissodus* sp. tooth (VER 2013.36.1) in occlusal view. G, hybodont tooth fragment (VER 2013.37.1). H, multicusped selachian scale fragment (VER 2013.37.2). I, reworked nothosaur tooth (VER 2013.38.1). J, undetermined fragmentary ?fish tooth (VER 2013.40). K, reworked nothosaur vertebral centrum (VER 2013.38.2) in oblique view. L, reworked placodont tooth fragment (VER 2013.39.1) in a piece of conglomerate from the lowermost beds of the Somssichhegy Limestone Formation. M, fragmentary belemnite rostrum (VER 2013.41) in a piece of conglomerate from the lowermost beds of the Somssichhegy Limestone Formation. Scale bars of A–J equal 500 μ m, and 5 mm in K–M

(Fig. 10I, K) and placodont remains (Fig. 10L), and perhaps some fish teeth as well (Fig. 10C, J), had been reworked from underlying Triassic rocks. These specimens are usually broken and heavily worn due to their accumulation in an abrasive environment.

Since most of these remains do not represent taxonomically different forms compared to the remains of the uppermost beds of the Mészhegy Sandstone Formation, we do not repeat their description, and we describe only those specimens which differ from the taxa mentioned above, thereby possibly representing different taxa.

The taxonomically informative vertebrate material prepared mechanically from the lowermost beds of the Pliensbachian Somssichhegy Limestone includes tooth fragments of *Palaeobates* sp. (VER 2013.35.1., VER 2013.35.2., Fig. 10D, E), *Hybodus* sp. (VER 2013.34.1., VER 2013.34., Fig. 10B, C), reworked nothosaur teeth (VER 2013.38.3-18., VER 2013.38.1., Fig. 10I) and small rounded vertebral centra (VER 2013.38.2., Fig. 10K), placodont tooth fragments (VER 2013.39.2-8., VER 2013.39.1., Fig. 10L), and two types of possibly selachian dermal scales (VER 2013.37.1., VER 2013.37.2., Fig. 10 H). One of the few complete teeth can be referred to as *Lissodus* sp. (VER 2013.36.1., Fig. 10F), quite similar to the fragments collected from the Mészhegy Sandstone Formation. VER 2013.37.1. (Fig. 10G) is a fragment of a large sized hybodont shark tooth. VER 2013.37.2. is a multicusped scale having two main cusps and smaller cusps surrounding the larger ones. The cusps are ornamented by prominent radial ridges extending from the apex to the base of the cusp (Fig. 10H).

A single fragmentary, most probably fish tooth (VER 2013.40.1) shows different morphology from the teeth from the Mészhegy Sandstone. It has a low, triangular and flattened cusp preserved that is slightly curved and has a smooth surface (Fig. 10J).

Depositional environment and taphonomic processes

The vertebrate fossil assemblage recovered from the two sites at Villány has not yet allowed detailed taphonomic studies. However, the dispersion of the bone assemblage may yield important information about the depositional environment.

All elements of the fossil material are isolated bones. However, small, localized concentrations of some bones have been observed in some cases. These were mostly caudal vertebrae, they were found close to each other but the bones were not associated. Bones have been found inside the layers and on bedding surfaces as well in equal preservation state. The ribs and vertebrae are the most abundant bone elements (about 80%) in the assemblages by far, and are usually poorly preserved but not abraded. The original bone surface is well defined in many cases and usually bones have well or moderately-preserved articulation surfaces. Furthermore, an almost complete lower jaw (including left and right sides as well)

of a nothosaur was found at the construction site, and contains several well-preserved *in situ* teeth. The above-described preservation characters indicate that the bone elements were not exposed to abrasion; however, they have undergone scattering before burial. This suggests that the remains of the carcass had been transported prior to burial, resulting in the disarticulation of the skeletal elements. The embedding sediments (dolomarl, sandstone and to a minor extent clay) have not been a good preservative matrix for the bones because fluids moving in the sediment could destroy the bone structure; thus the bones show poor preservation.

The fossil assemblages collected from the sites in small quantities show significant dispersion and may be sorted according to bone size and/or type. It must be noted that preburial taphonomic processes cannot be reconstructed in detail because of the limited number of available bones. However, the already-discussed taphonomic characters may help to interpret the environment prevailing during the deposition of the bones. Previous studies examined the disarticulation of skeletons in marine (Beardmore et al. 2012a), terrestrial (Hill 1979; Behrensmeyer 1982), fluvial (Dodson 1973) and lacustrine (Davis and Briggs 1998) environments, but the process of disarticulation in a shallow marine environment is less studied (Soares 2003). Furthermore, many experiments have been conducted on the transport of disarticulated skeletons in flow because it has been recognized that the different segments of the same skeleton show variations in their transportability depending on size, shape and density of individual bones (Dodson 1973; Behrensmeyer 1975; Kaufmann et al. 2011). Usually, if an assemblage is sorted and dispersed and the articulated elements are of limited number or missing, then these features generally indicate that bones of the assemblage were transported for a shorter or longer distance and/or time before their burial (Behrensmeyer 1988; Britt et al. 2009). Up to now, the Villány assemblage contains exclusively isolated bones that are poorly sorted according to bone size and/or type; thus it is assumed that the material was exposed to transport before the burial. Terrigenous sediment present in the carbonatic sedimentary environment indicates that periodically significant sediment influx occurred from the hinterland, the currents of which could have caused dispersion of bones of skeletons at the sediment-water interface after the breakdown of soft tissues.

The taphonomic history of the Villány vertebrate assemblage may be described as follows: The individuals died in the water column; then, after a short floating phase they were transferred to the sediment-water interface where decay and disarticulation of the carcasses began. The carcasses became disassociated by decay and scavengers; a process which might have been relatively rapid and efficient because there was a potential for aerobic decomposition (Soares 2003; Beardmore et al. 2012b). There are two potential explanations for the observed high frequency of the vertebrae and ribs: 1. Recognition of these elements is easier than that of other types of bones (such as skull elements) in poorly-preserved

assemblages; 2. Pachyostotic bones of nothosaurs exhibit a greater density and more compact bone tissue than the other bones of the carcass; thus they might have been more resistant against pre- and postburial destructive processes (Soares 2003).

The taphonomic history presented above is far from being complete because more bones and more taphonomic data (e.g. orientation of bones, bone surface texture, etc.) are necessary to interpret the taphonomic processes occurring between death and burial of these animals.

Discussion

Age and paleoenvironment

Templomhegy Dolomite

The age of the Templomhegy Dolomite has been considered Ladinian based on its stratigraphic position. Some specimens of brachiopods (*Lingula* sp., *Lingula christomani*), sponges, foraminifers (*Glomospira* sp.), bivalves and *Neocalamites incertae sedis* have been found in its lower part, none of them age-diagnostic. The upper 30 m of the formation proved to be barren (Nagy and Nagy 1976), apart from the unidentified sauropsid bones reported from the Mészhegy Sandstone (Rálich-Felgenhauer 1981) but originating from beds that are now classified as part of the Templomhegy Dolomite. The new vertebrate remains (cf. *Cyamodus* sp., *Nothosaurus* sp., Figs 6, 7) discovered in the upper section of the formation suggest, though do not unambiguously prove, the late Middle Triassic age. The fragmentary mandible (VER 2013.1.) assigned to *Nothosaurus* sp. shows some similarities with that of *N. marchicus* but in most anatomical aspects of the symphyseal region it is most similar to that of *N. giganteus*.

The postcranial nothosaur remains support the presence of relatively large animals. A complete dorsal neural arch with strongly elongate neural spine (VER 2013.5., Fig. 7C) has a total transverse width of 66 mm and a total height of 85 mm. It is quite similar in size to that of a dorsal vertebra described from Ladinian sediments of northern Italy (Dalla Vecchia and Carnevale 2011: Fig. 5G), although the latter, referred to as *Nothosaurus* cf. *N. giganteus*, has a much lower neural spine that is a characteristic feature of this species (Rieppel and Wild 1996). Strongly elongated neural spines are characteristic of *N. mirabilis*. This species has, however, a strongly elongated mandibular symphysis that is quite different from that of the Villány specimen. If the most parsimonious hypothesis is assumed, namely that the fragmentary mandible and the postcranial remains represent the same species of *Nothosaurus*, then a species with short mandibular symphysis and elongate dorsal neural spines is identified, being different in this respect from *N. marchicus*, *N. giganteus* and *N. mirabilis*. Another hypothesis is that there are two different taxa in the locality, which, however, cannot be supported yet.

Most species of *Nothosaurus* are known from Middle Triassic deposits, although a few of them have been recorded from uppermost Lower and lower Upper Triassic sediments (Rieppel 2000). *Nothosaurus marchicus* is known from the latest Olenekian to the lowermost Ladinian, *N. giganteus* from the latest Anisian to latest Ladinian, and *N. mirabilis* from the late Anisian to late Ladinian (Rieppel and Wild 1996). To sum up, the Villány specimen cannot be assigned to a certain species, but its symphyseal morphology indicates close affinity with Middle Triassic (probably Ladinian) species.

The size and shape of the cyamodont placodontian teeth (VER 2013.15.) referred here to as cf. *Cyamodus* sp. clearly distinguish the Villány specimens from the teeth of *Placochelys* or *Psephoderma* known from the Upper Triassic of Central Europe (Rieppel 2001a). The similarity in shape and size with the teeth of some species of *Cyamodus* (Rieppel 2001a), and with the teeth of *Cyamodus* sp. described from the late Ladinian to early Carnian of Slovenia (Buffeteau and Novak 2008) further supports the Ladinian age of this vertebrate assemblage.

The frequent occurrence of *Nothosaurus* sp. could help to clarify the depositional environment of the Templomhegy Dolomite: it supports a tidal flat environment, connected with the open marine province, as supposed by Nagy and Nagy (1976), Török (1998) and Bérczi-Makk et al. (2004), against a lagoonal one (proposed by Rálich-Felgenhauer 1981). Fossils of hard-shelled invertebrates (gastropods, brachiopods, bivalves, ammonites) are almost entirely absent from the dolomite and dolomarl beds; therefore the presence of cyamodontid placodonts, generally regarded as durophagous forms feeding dominantly on small to large sized, epibenthic and sessile hard shelled invertebrates (Rieppel 2002), is remarkable. Preliminary results of the taphonomic features of the sauropterygian fossils from the Templomhegy Dolomite show that most specimens are complete (e.g. the preserved part of the nothosaur mandible with complete *in situ* teeth) or only deformed, in several cases due to diagenetic and tectonic effects, but they were not abraded by water currents. This indicates relatively low-energy conditions and that these fossils had not been transported too long.

Mészhegy Sandstone Formation

The age and depositional environment of the Mészhegy Sandstone Formation are among the most intensively discussed problems of the Mesozoic of the Villány Hills. Vörös (2010) gave an overview on the previous work and the hypotheses regarding these questions; thus here we only briefly summarize the most recent interpretations. Bérczi-Makk (1986) and Bleahu et al. (1994) described this formation as reminiscent of the Carpathian Keuper in the Bihor Mountains (Scarița Formation), while Rálich-Felgenhauer (1981) and Török (1998) supposed a shallow-water, nearshore, coastal plain environment during its deposition. In contrast, Vörös (2009, 2010) regarded this formation as an Upper Triassic fluvio-

lacustrine succession deposited in a tectonically-controlled local half-graben and composed of three sedimentary parasequences, one definitely Carnian, and two others, possibly Norian and Rhaetian in age. The palynological results, described above, represent the first precise data for the age of this unit, indicating a Carnian age for the lower part (the first parasequence) of the formation. However, the age of the upper part (containing most of the vertebrate microfossils) is still not clear (it can be Carnian or even younger). The thinness of the formation and the seemingly continuous succession rather suggest a Carnian age for the whole formation, but this hypothesis cannot be supported by the fossil content. The predominance of chondrichthyan fish remains and the few reworked nothosaur and placodont teeth suggest a marine rather than a fluvio-lacustrine depositional environment for the uppermost beds of the Mészhegy Sandstone Formation. On the other hand, the reworked nothosaur and placodont tooth fragments show a continuous terrestrial influence and erosion of underlying Triassic deposits during the Late Triassic (Vörös 2009, 2010). The possible archosauriform teeth, belonging to a semi-aquatic animal, point to neighboring dry lands, which were only partly inundated.

Somssichhegy Limestone Formation

The vertebrate assemblage collected from the coarse sandy, basal layers of the Somssichhegy Limestone does not show significant differences compared to those screen-washed from the uppermost greyish-greenish sandstone layer of the Mészhegy Sandstone.

The *Palaeobates*-like crushing teeth, the rhomboidal *Lissodus* teeth, the *Saurichthys*-like pointed, conical teeth, the pointed, flattened central cusps of hybodont teeth, and the possible hybodont scales, along with the certainly reworked nothosaur and placodont remains are present in both formations (Figs 9, 10). If the teeth of *Palaeobates* and *Lissodus*, and the *Saurichthys*-like and hybodont-like tooth fragments are not reworked elements, then they may represent different species compared to those from the Mészhegy Sandstone Formation. The hiatus between the upper part of the Upper Triassic (probably Carnian) Mészhegy Sandstone and the Pliensbachian Somssichhegy Limestone is almost 30 million years and includes the Triassic/Jurassic boundary. It seems that most of the vertebrate remains recovered in the coarse basal layers of the Somssichhegy Limestone Formation were reworked from underlying Triassic and possibly Lower Jurassic (Hettangian–Sinemurian) deposits; they do not represent a Pliensbachian vertebrate fauna. A few teeth and a multicusped hybodont scale are the only fossils which are morphotypes not present among the remains of the Triassic beds. However, these fossils are not sufficiently age-diagnostic to unambiguously support an Early Jurassic age. All the vertebrate remains, along with the fragmentary belemnite rostrum, support the hypothesis that these

lowermost beds of the formation were accumulated in a nearshore, shallow marine environment.

Remarks on the enigmatic, possibly terrestrial bone

Based on gross morphological features of long bones of sauropsids and synapsids that inhabited the Middle Triassic terrestrial environments, the undetermined bone (VER 2013.2.) could have belonged to a number of different archosauriforms (e.g. lagerpetids [Sereno and Arcucci 1993], rauisuchids [Chatterjee 1985], dinosauriforms [Nesbitt et al. 2012]) and cynodonts (Botha and Chinsamy 2004), which are all characterized by relatively lightly built and hollow bones (Nesbitt 2011).

Since the preservation state of this bone fragment (Fig. 8) is very poor, it is very hard to identify which element of the skeleton it might represent, let alone its taxonomical assignment. Nevertheless, based on its gross morphological and histological features along with taphonomic observations, some hypotheses can be excluded and others given more support.

If this specimen is a fragment of a limb bone, it is very unlikely that it belonged to an aquatic animal. Aquatic Triassic amniotes, such as nothosaurs or placodonts had short and stocky humeri, the general morphology of which does not correspond with the more elongate and slender morphology of the unidentified bone fragment. Although the femur of these aquatic animals is more elongate, it has a circular cross section unlike the obviously oval cross section of the fragmentary specimen. Based purely on morphology, our specimen could still represent an antebrachial bone (radius or ulna) or bone of the lower leg (tibia or fibula) of any of the latter aquatic groups. However, its microanatomical features contradict this interpretation. Sauropterygians generally show pachyostotic (outer bone hyperplasy), osteosclerotic (inner bone compaction) and/or pachyosteosclerotic (thickening of trabecular bone along with pachyostosis) limb bones, ribs and vertebrae as secondary aquatic adaptations (Buffrénil et al. 2010; Houssaye 2013). None of these features can be observed in the fragmentary bone under discussion.

On the other hand, there is an array of terrestrial Triassic sauropsids and synapsids, the limb bones of which may show very similar morphologies as well as microanatomical traits. However, considerable differences appear at the histological level. Basal archosauromorphs and archosauriforms such as rhynchosaurids, proterosuchids, erythrosuchids, euparkeriids etc. all have higher vascular density and generally more extensive medullar cavity in their limb bones (de Ricqlés et al. 2008; Botha-Brink and Smith 2011) than those observable in the fragmentary specimen. Moreover, the former groups exhibit large perimedullary erosion rooms in the long bone cortex (de Ricqlés et al. 2008; Botha-Brink and Smith 2011), features that are almost completely absent in the unidentified bone. Unlike in our specimen, limb bone histology in Triassic pseudosuchians can be

characterized by very frequent and much more distinct, cyclical LAG deposition throughout the entire cortex (de Ricqlés et al. 2003). In addition, similar to more basal archosauriforms, the inner cortex of the limb bones of Triassic pseudosuchians shows more extensive secondary erosion rooms and osteons with high perimedullar density (de Ricqlés et al. 2003). In general, the long bones of Late Permian and Triassic therapsids such as gorgonopsians, therocephalians, dicynodonts and non-mammalian cynodonts are also characterized by much higher vascular density and different vascular architecture, with numerous transversally-oriented canals compared to what we see in the bone fragment from Villány (Botha and Chinsamy 2000, 2004; Ray and Chinsamy 2004; Ray et al. 2004). Nevertheless, there are some examples for therapsid limb bones with relatively low vascularity. The fibula of the dicynodont *Endothiodon* is sparsely vascularized; however, the cortex also shows some radiating canals and there are large, irregular perimedullar resorption cavities (Ray et al. 2009). The radius of *Tritylodon*, an Early Jurassic non-mammalian cynodont, is of very similar general appearance to the undetermined bone with low vascularity and no perimedullary erosion rooms, but it also shows a thick endosteal layer (Ray et al. 2004), a feature that is not discernible in the fragmentary specimen.

On the other hand, if we discard the assumption that this bone fragment represents a long bone, other skeletal elements that may come into question are girdle elements and ribs. The ribs of most Permian and Triassic therapsids have very similar microstructure to our element; however, there are some remarkable differences. The most common one is the presence of extensive secondary remodeling and perimedullar resorption cavities in the ribs of some members of the latter groups (e.g. *Pristerognathus*, *Procynosuchus* [Ray et al. 2004]; *Lystrosaurus*, *Wadiasaurus* [Ray et al. 2009]). The clavicle of *Procynosuchus* has the same characteristic histological features (Ray et al. 2004) that are in contrast to the predominantly primary cortex with some scattered secondary osteons observed in the undetermined bone. Nevertheless there is a striking similarity in the histology of our specimen and that of the rib of the Triassic cynodont *Trirachodon* (Botha and Chinsamy 2004: Fig. 4B). Unfortunately, in the absence of a figure showing the entire cross section of the *Trirachodon* rib, a more detailed comparison is not possible.

The above-described histological similarities, along with the oval shaped cross section, suggest that the discussed specimen might well represent a fragment of a rib rather than that of a limb bone. Furthermore, the microanatomical features of this bone fragment support a terrestrial origin. However, its taxonomical assignment is still impossible even at the level of the major amniote dichotomy (i.e. sauropsids vs. synapsids) as there is not enough comparative histological material of the ribs and different girdle elements of various representatives of these clades. Even if there were, skeletal elements of the representatives of these two major amniote clades might not bear any taxon-specific histological characters at all.

Similar Triassic faunas from Europe

The Middle Triassic and Late Triassic vertebrate faunas discovered in the Villány Hills are from two different paleoenvironments and represent different paleocommunities. The Middle Triassic (Ladinian) assemblage from the Templomhegy Dolomite reveals the typical Muschelkalk-Lettenkeuper vertebrate faunal composition dominated by sauropterygians. The co-occurrence of cyamodontoid placodonts and nothosaurs is most frequent in the classical localities of the Germanic Triassic of Western Europe (Rieppel and Wild 1996; Rieppel and Hagdorn 1997; Rieppel 2000, 2001a, b and references therein), but similar assemblages have been also reported from localities of the Alpine Middle Triassic. For example, both *Cyamodus* and nothosaurs have been reported from the uppermost Ladinian of the Carnic (Fusea site; Dalla Vecchia and Carnevale 2011) and the Julian Alps (Dalla Vecchia 1994), northeastern Italy. Although slightly older, among others nothosaur and placodontian bones have been described from Anisian deposits of the Bihor Mountains, Romania (Jurcsák 1987). Remains of Middle Triassic *Nothosaurus* (probably *N. giganteus* Rieppel 2000) have been documented in Bulgaria (Rieppel and Wild 1996), in the southern Alpine Triassic (Peyer 1939; Renesto 2010), and in localities along the northern Gondwana shelf and the eastern Pacific region (Rieppel 1997; Rieppel et al. 1999; Vickers-Rich et al. 1999). Beside the classical localities of the Germanic Triassic (see Diedrich 2011 for an overview), *Cyamodus* sp. was described among others from the late Ladinian to early Carnian of Slovenia (Buffeteaut and Novak 2008). The teeth of *Cyamodus* appear to be most similar to the cyamodontoid teeth from Villány, and support, both temporally and spatially, the more widespread occurrence of stem-group sauropterygians (e.g. nothosaurs, placodonts) in Europe than previously thought (Rieppel 2000).

The Upper Triassic Mészhegy Sandstone Formation shows a significant terrestrial influence; accordingly, the fragmentary nothosaur teeth and placodont tooth fragments do not seem to be in situ fossils but rather transported or perhaps reworked from older deposits. The fish fauna includes both chondrichthyan (*Lissodus*, *Palaeobates*, *Hybodus*) and osteichthyan (cf. *Saurichthys*, undetermined forms, ?*Sphaerodus* sp.) forms but with the dominance of hybodontoids strongly resembling the typical Late Triassic (Carnian to Rhaetian) vertebrate fish faunas of the Germanic Basin (e.g. Delsate 1992; Duffin 1993, 2001; Cuny et al. 1998) and that of the Alpine Triassic (Dalla Vecchia and Carnevale 2011; Krainer et al. 2011), respectively.

Conclusions

Excavations and screen-washing of sediments of the Middle Triassic Templomhegy Dolomite Member, the Upper Triassic Mészhegy Sandstone and the Lower Jurassic Somssichhegy Limestone Formations resulted in the first documentation of a rich and diverse Triassic vertebrate fossil assemblage from two

different localities in the Villány Hills. Hundreds of fossil sauropterygian remains in the newly discovered construction site highlight this locality as a significant Triassic vertebrate site in Central Europe. The remains of *Nothosaurus* sp. and cf. *Cyamodus* sp. show great similarities with sauropterygians of the Germanic and Alpine late Middle Triassic, and suggest a Ladinian age for the formation. A single undetermined, hollow bone representing a terrestrial animal indicates that terrestrial influence was relatively significant and the discovery of more material of land vertebrates can be expected.

Our studies provided the first palynological data from the Mészhegy Sandstone Formation indicating an Upper Triassic (Carnian) age for the lower part of the sequence exposed in the abandoned road-cut. The microvertebrate remains collected from the upper part of the Mészhegy Sandstone Formation represent a typical Late Triassic shallow marine fauna including both chondrichthyan (*Lissodus*, *Palaeobates*, *Hybodus*) and osteichthyan (cf. *Saurichthys*, ?*Sphaerodus* sp.) fishes.

A belemnite rostrum collected from the bone-yielding lowermost beds of the Somssichhegy Limestone Formation proves that this Early Jurassic (Pliensbachian) layer was deposited in a marine environment. Most of the vertebrate remains (nothosaurs, placodonts, hybodont shark teeth, perhaps *Palaeobates*, *Lissodus*) recovered from these beds appear to have been reworked from underlying Triassic rocks. In accordance with the lithology of these beds, the preservation of these fossils indicates an erosive, nearshore environment and a possible subaerial/emergence period preceding the deposition of the Somssichhegy Limestone.

The vertebrate material recovered from the Triassic and Jurassic rocks of Villány are of great importance for the stratigraphic and paleoenvironmental interpretation of the Mesozoic successions in southern Hungary. In addition it clearly demonstrates that further prospecting and excavation in this area are promising and essential to document more details of these early Mesozoic vertebrate faunas.

Acknowledgements

We are grateful to Attila Vörös and Silvio Renesto for their constructive comments and suggestions that highly improved the manuscript. The authors are eminently thankful to Attila Vörös, Erzsébet Rálich-Felgenhauer, Gyula Konrád, Tamás Budai, József Pálffy, László Kordos, István Szente, Piroska Pazonyi and Orsolya Sztanó for useful discussions and consultations. Zsolt Dallos, Veronika Iván, Tibor Pecsics, Jennifer Sarrang and Martin Segesdi are acknowledged for their assistance in the field. Attila Németh (construction supervisor), Zsolt Maul (Maul Winery, Villány) and Antal Domokos kindly allowed us to conduct field work at the construction site. Special thanks go to the Fülemlé Restaurant (Villány) for logistical help. Our work was supported by: Hungarian Academy of Sciences Lendület Program; Hungarian Scientific Research Fund; Hungarian

Natural History Museum; Eötvös Loránd University, Department of Applied and Physical Geology; University of Pécs, Doctoral School of Earth Sciences (especially by Zoltán Dövényi), and the Danube-Dráva National Park (especially by Ildikó Havasi).

References

- Agassiz, L. 1833–1843: Recherches sur les poissons fossiles. Tome 3 concernant l'histoire de l'ordre des Placoïdes. – Imprimerie de Petitpierre. 390+34 p.
- Ager, D.V., J.H. Callomon 1971: On the Liassic age of the "Bathonian" of Villány (Baranya). – *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös nominatae, Sectio Geologica*, 14, pp. 5–16.
- Albers, P.C.H., O. Rieppel 2003: A new species of the sauropterygian genus *Nothosaurus* from the Lower Muschelkalk of Winterswijk, The Netherlands. – *Journal of Paleontology*, 77/4, pp. 738–744.
- Baur, G. 1889: Palaeohatteria Credner, and the Proganosauria. – *American Journal of Science, Series 3*, 37, pp. 310–313.
- Beardmore, S.R., P.J. Orr, T. Manocchi, H. Furrer 2012a: Float or sink: modelling the taphonomy pathway of marine crocodiles (Mesoeucrocodylia; Thalattosuchia) during the death-burial interval. – *Palaeobiodiversity and Palaeoenvironments*, 92, pp. 83–98.
- Beardmore, S.R., P.J. Orr, T. Manocchi, H. Furrer, C. Johnson 2012b: Death, decay and disarticulation: a method of modelling the skeletal taphonomy of marine reptiles demonstrated using *Serpianosaurus* (Reptilia; Sauropterygia). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 337–338, pp. 1–13.
- Behrensmeyer, A.K. 1975: The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf Kenya. – *Bulletin of The Museum of Comparative Zoology*, 146, pp. 473–578.
- Behrensmeyer, A.K. 1982: Time resolution in fluvial vertebrate assemblages. – *Paleobiology*, 8/3, pp. 211–227.
- Behrensmeyer, A.K. 1988: Vertebrate Preservation in Fluvial Channels. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 63/1–3, pp. 183–199.
- Bérczi-Makk, A. 1986: Mesozoic formation types of the Great Hungarian Plain. – *Acta Geologica Hungarica*, 29/3–4, pp. 261–282.
- Bérczi-Makk, Á., Gy. Konrád, E. Rálich-Felgenhauer, Á. Török 2004: Tiszai Egység (Tisza Unit). – In: Haas, J. (Ed): Magyarország geológiája. Triász. ELTE Eötvös Kiadó, pp. 303–360.
- Blazejowski, B. 2004: Shark teeth from the Lower Triassic of Spitsbergen and their histology. – *Polish Polar Research*, 25, pp. 153–167.
- Bleahu, M., S. Bordea, S. Panin, M. Ștefănescu, K. Sikić, J. Haas, S. Kovács, Cs. Péror, A. Bérczi-Makk, Gy. Konrád, E. Nagy, E. Rálich-Felgenhauer, Á. Török 1994: Triassic facies types, evolution and paleogeographic relations of the Tisza Megaunit. – *Acta Geologica Hungarica*, 37/3–4, pp. 187–234.
- Botha, J., A. Chinsamy 2000: Growth patterns deduced from the bone histology of the cynodonts *Diademodon* and *Cynognathus*. – *Journal of Vertebrate Paleontology*, 20/4, pp. 705–711.
- Botha, J., A. Chinsamy 2004: Growth and life habits of the Triassic cynodont *Trirachodon*, inferred from bone histology. – *Acta Palaeontologica Polonica*, 49/4, pp. 619–627.
- Botha-Brink, J., R.M.H. Smith 2011: Osteohistology of the Triassic archosauriforms *Prolacerta*, *Proterosuchus*, *Euparkeria* and *Erythrosuchus* from the Karoo Basin of South Africa. – *Journal of Vertebrate Paleontology*, 31/6, pp. 1238–1254.
- Britt, B.B., D.A. Eberth, R.D. Scheetz, B.W. Greenhalgh, K.L. Stadtman 2009: Taphonomy of debris-flow hosted dinosaur bonebeds at Dalton Wells, Utah (Lower Cretaceous, Cedar Mountain Formation, USA). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 280, pp. 1–22.

- Brough, J. 1935: On the structure and relationships of the hybodont sharks. – *Memoirs and Proceedings of the Manchester Literary and Philosophical Society*, 79, pp. 35–50.
- Buffeteaut, E., M.A. Novak 2008: Cyamodontid placodont (Reptilia: Sauropterygia) from the Triassic of Slovenia. – *Palaeontology*, 51, pp. 1301–1306.
- Buffrénil, V. de, A. Caanoville, R. D'Anastasio, D.P. Domning 2010: Evolution of sirenian pachyosteosclerosis, a model-case for the study of bone structure in aquatic tetrapods. – *Journal of Mammalian Evolution*, 17, pp. 101–120.
- Chatterjee, S. 1985: Postosuchus, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. – *Philosophical Transactions of the Royal Society of London B*, 309, pp. 395–460.
- Chhabra, N.L., V.P. Mishra 2002: Middle Triassic fish teeth from the Kalapani Limestone of Malla Johar, Chamoli district (Uttaranchal). – *Journal of the Palaeontological Society of India*, 47, pp. 151–155.
- Csontos, L., A. Vörös 2004: Mesozoic plate tectonic reconstruction of the Carpathian region. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 210, pp. 1–56.
- Cuny, G., G. Ramboer 1991: Nouvelles donnees sur la faune et l'age de Saint Nicolas de Port. – *Revue de Paléobiologie*, 10/1, pp. 69–78.
- Cuny, G., A. Hunt, J.-M. Mazin, R. Rauscher 2000: Teeth of enigmatic neoselachian sharks and an ornithischian dinosaur from the uppermost Triassic of Lons-le-Saunier (Jura, France). – *Paläontologische Zeitschrift*, 74/1–2, pp. 171–185.
- Cuny, G., M. Martin, J.-M. Mazin, R. Rauscher 1998: A new neoselachian shark from the Upper Triassic of Grozon (Jura, France). – *Geological Magazine*, 135/5, pp. 657–668.
- Dalla Vecchia, F.M. 1994: Reptile remains from the Middle–Upper Triassic of Carnic and Julian Alps (Friuli-Venezia Giulia, Northeastern Italy). – *Gortania: Atti del Museo Friulano di Storia Naturale*, 15, pp. 49–66.
- Dalla Vecchia, F.M., G. Carnevale 2011: Ceratodontoid (Dipnoi) calvarial bones from the Triassic of Fucea, Carnic Alps: the first Italian lungfish. – *Italian Journal of Geosciences*, 130/1, pp. 128–135.
- Davis, P.G., D.E.G. Briggs 1998: The impact of decay and disarticulation on the preservation of fossil birds. – *Palaios*, 13, pp. 3–13.
- Delsate, D. 1992: Chondrichthyens mésozoïques du Luxembourg. Note préliminaire. – *Bulletin de la Société des Naturalistes Luxembourgeois*, 93, pp. 181–193.
- Delsate, D., C.J. Duffin, R. Weis 2002: A new microvertebrate fauna from the Middle Hettangian (Early Jurassic) of Fontenoille (Province of Luxembourg, south Belgium). – *Memoirs of the Geological Survey of Belgium*, 48, pp. 1–83.
- Diedrich, C.G. 2011: Fossil Middle Triassic "sea cows" – placodont reptiles as macroalgae feeders along the north-western tethys coastline with pangaea and in the germanic basin. – *Natural Science*, 3, pp. 9–27.
- Dodson, P. 1973: The significance of small bones in paleoecological interpretation. – *University of Wyoming Contributions in Geology*, 12, pp. 15–19.
- Dorka, M. 2001: Shark remains from the Triassic of Schöningen, Lower Saxony, Germany. – *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 221/2, pp. 219–247.
- Doyle, P., M.R. Bennett 1995: Belemnites in biostratigraphy. – *Paleontology*, 38/4, pp. 815–829.
- Duffin, C.J. 1985: Revision of the hybodont selachian genus *Lissodus* Brough (1935). – *Palaeontographica Abt. A*, 188, pp. 105–152.
- Duffin, C.J. 1993: Mesozoic chondrichthyan faunas 1. Middle Norian (Upper Triassic) of Luxembourg. – *Palaeontographica Abt. A*, 229, pp. 15–36.
- Duffin, C.J. 2001: Synopsis of the selachian genus *Lissodus* Brough, 1935. – *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 221, pp. 145–218.
- Feist-Burkhardt, S., A.E. Götz, J. Szulc (coordinators), R. Borkhataria, M. Geluk, J. Haas, J. Hornung, P. Jordan, O. Kempf, J. Michalík, J. Nawrocki, L. Reinhardt, W. Ricken, G.-H. Röhling, T. Ruffer, Á. Török, R. Zühlke 2008: Triassic. – In: McCann, T. (Ed): *The Geology of Central Europe*, Geological Society of London, Vol. 2, pp. 749–821.
- Gauthier, J.A., A.G. Kluge, T. Rowe 1988: Amniote phylogeny and the importance of fossils. – *Cladistics*, 4/2, pp. 105–209.

- Glückman, L.S. 1964: Class Chondrychthyes, subclass Elasmobranchii. – In: Obruchev, D.V. (Ed): Fundamentals of Paleontology. *Izvestija Akademii Nauk SSSR*, 11, pp. 196–237.
- Goodrich, E.S. 1909: Vertebrata Craniata (First fascicle: Cyclostomes and Fishes). – In: Lankester, R. (Ed): A treatise on Zoology. Adam and Charles Black, Part IX, 518 p.
- Gürich, G.J.E. 1884: Über einige Saurier des oberschlesischen Muschelkalkes. – *Zeitschrift der Deutschen Geologischen Gesellschaft*, 36/1, pp. 125–144.
- Haas, J., Cs. Péro 2004: Mesozoic evolution of the Tisza Mega-unit. – *International Journal of Earth Sciences*, 93, pp. 297–313.
- Hill, A. 1979: Disarticulation and scattering of mammal skeletons. – *Paleobiology*, 5/3, pp. 261–274.
- Houssaye, A. 2013: Bone histology of aquatic reptiles: What does it tell us about secondary adaptation to an aquatic life? – *Biological Journal of the Linnean Society*, 108, pp. 3–21.
- Huxley, T.H. 1880: On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. – *Proceedings of the Zoological Society of London*, 43, pp. 649–662.
- Jaekel, O. 1901: Reste eines neuen Placodontiden aus dem unteren Keuper von Veszprém am Plattensee in Ungarn. – *Zeitschrift der Deutschen Geologischen Gesellschaft*, 53, pp. 56–57.
- Jaekel, O. 1902a: Über Placochelys n. g. und ihre Bedeutung für die Stammesgeschichte der Schildkröten. – *Neues Jahrbuch für Mineralogie, Geologie und Palaontologie, Abhandlungen*, 1, pp. 127–144.
- Jaekel, O. 1902b: Wirbeltierreste aus der Trias des Bakonyerwaldes. – In: *Resultate der wissenschaftlichen Erforschung des Balatonsees, Palaontologischer Anhang*. Victor Hornyanszky, 1/1, pp. 4–17.
- Jaekel, O. 1907: Placochelys placodonta aus der Obertrias des Bakony. *Resultate der wissenschaftlichen Erforschung des Balatonsees. – Palaontologischer Anhang*. Victor Hornyanszky, 3/8, pp. 1–91.
- Jurcsák, T. 1987: Triassic reptilian fauna from Bihor, Romania. – In: Currie, P.M., E.H. Koster (Eds): Fourth Symposium on Mesozoic Ecosystems. Short Papers, pp. 125–128.
- Kaufmann, C., M.A. Gutiérrez, M.C. Álvarez, M.E. González, A. Massigoge 2011: Fluvial dispersal potential of guanaco bones (*Lama guanicoe*) under controlled experimental conditions: the influence of age classes to the hydrodynamic behavior. – *Journal of Archaeological Science*, 38, pp. 334–344.
- Krainer, K., S. Lucas, M. Strasser 2011: Vertebrate Fossils from the Northalpine Raibl Beds, western Northern Calcareous Alps, Tyrol (Austria). – *Austrian Journal of Earth Sciences*, 104, pp. 97–106.
- Li, J.L., O. Rieppel 2004: A new nothosaur from Middle Triassic of Guizhou, China. – *Vertebrata Palasiatica*, 42, pp. 1–12.
- Lóczy, L. ifj. 1912: A Villányi és Báni hegység geológiai viszonyai (Die geologische Verhältnisse der Villányer und Bányer Gebirge). – *Földtani Közlöny*, 42, pp. 672–695, pp. 781–807.
- Lóczy, L. ifj. 1915: Monographie der Villányer Callovien–Ammoniten. – *Geologica Hungarica*, 1/3–4, pp. 255–502.
- Lóczy, L. ifj. 1945: Igazgatói jelentés a m. Kir. Földtani Intézet 1943. évi működéséről (Direktionsbericht über die Tätigkeit des Kön. Ung. Geologischen Anstalt im Jahre 1943). – *A Magyar Állami Földtani Intézet Évi Jelentése 1943-ról*, pp. 1–45.
- Lórenthey, I. 1907: Vannak-e juraidőszaki rétegek Budapesten? (Are there any Jurassic beds at Budapest?) – *Földtani Közlöny*, 37, pp. 359–368.
- Meyer, H.v. 1849: Fossile Fische aus dem Muschelkalk von Jena, Querfurt und Esperstädt. – *Palaontographica*, 1, pp. 195–208.
- Meyer, H. von 1863: Die Placodonten, eine Familie von Sauriern der Trias. – *Palaontology*, 11, pp. 175–221.
- Murry, P. A., R.E. Kirby 2002: A new hybodont shark from the Chinle and Bull Canyon formations, Arizona, Utah and New Mexico. Upper Triassic Stratigraphy and Paleontology, – *New Mexico Museum of Natural History and Science Bulletin*, 21, pp. 87–106.

- Mutter, R.J., A.B. Heckert 2006: Re-investigation of enigmatic fish bones known as colobodontid/perleiid toothplates from the Upper Triassic Chinle Group (southwestern U.S.A.). – *New Mexico Museum of Natural History and Science Bulletin*, 37, pp. 530–542.
- Münster, G. 1834: Vorläufige Nachricht über einige neue Reptilien im Muschelkalk von Baiern. – *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 1834, pp. 521–527.
- Nagy, E., I. Nagy 1976: Triasbildungen des Villányi Gebirges. – *Geologica Hungarica Series Geologica*, 17, pp. 113–227.
- Nesbitt, S.J. 2011: The early evolution of archosaurs: relationships and the origin of major clades. – *Bulletin of the American Museum of Natural History*, 352, pp. 1–292.
- Nesbitt, S.J., P.M. Barrett, S. Werning, C.A. Sidor, A.J. Charig 2012: The oldest dinosaur. – *A Middle Triassic dinosauriform from Tanzania*. – *Biology Letters*. <http://dx.doi.org/10.1098/rsbl.2012.0949>
- Nopcsa, F. 1923: Die Familien der Reptilien. – *Fortschritte der Geologie und Paläontologie*, 2, pp. 1–210.
- Owen, R. 1846: Lectures on the comparative anatomy and physiology of the vertebrate animals delivered at the Royal College of Surgeons, England in 1844 and 1846. Part 1. Fishes. – Longman, Brown, Green and Longmans, 308 p.
- Owen, R. 1860: Palaeontology, or a systematic summary of extinct animals and their geological relations. – Adam and Charles Black, 420 p.
- Ósi, A., L. Makádi, M. Rabi, Z. Szentesi, G. Botfalvai, P. Gulyás 2012: The Late Cretaceous continental vertebrate fauna from Iharkút, western Hungary: a review. – In: Godefroit, P. (Ed): *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*. Indiana University Press, pp. 533–568.
- Peyer, B. 1939: Die Triasfauna der Tessiner Kalkalpen. XIV. *Paranotosaurus amsleri* nov. gen. nov. spec. – *Abhandlungen der schweizerischen Paläontologischen Gesellschaft*, 62, pp. 1–87.
- Pinna, G. 1976: *Placochelys zitteli*, *Placochelys stoppanii*, *Placochelyanus malanchinii*: un caso di sinonimia fra i rettili placodonti retici della famiglia Placochelyidae. – *Bollettino della Società Paleontologica Italiana*, 15, pp. 107–110.
- Pinna, G., S. Nosotti 1989: Anatomia, morfologia funzionale e paleoecologia del rettile placodonte *Psephoderma alpinum* Meyer, 1858. – *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 25, pp. 1–50.
- Rálišch-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.
- Ray, S., A. Chinsamy 2004: *Diictodon feliceps* (Therapsida, Dicynodontia): Bone histology, growth and biomechanics. – *Journal of Vertebrate Paleontology*, 24/1, pp. 180–194.
- Ray, S., S. Bandyopadhyay, D. Bhawal 2009: Growth patterns as deduced from bone microstructure of some selected neotherapsids with special emphasis on dicynodonts: Phylogenetic implications. – *Palaeoworld*, 18, pp. 53–66.
- Ray, S., J. Botha, A. Chinsamy 2004: Bone histology and growth patterns of some nonmammalian therapsids. – *Journal of Vertebrate Paleontology*, 24/3, pp. 634–648.
- Renesto, S. 2010: A new specimen of *Nothosaurus* from the Anisian (Middle Triassic) Besano Formation (Grenzbitumenzone) of Italy. – *Rivista Italiana di Paleontologia e Stratigrafia*, 116/2, pp. 145–160.
- Ricqlés, A.J. de, K. Padian, J.R. Horner 2003: On the bone histology of some Triassic pseudosuchian archosaurs and related taxa. – *Annales de Paléontologie*, 89, pp. 67–101.
- Ricqlés, A.J. de, K. Padian, F. Knoll, J.R. Horner 2008: On the origin of high growth rates in archosaurs and their ancient relatives: Complementary histological studies on Triassic archosauriforms and the problem of a "phylogenetic signal" in bone histology. – *Annales de Paléontologie*, 94, pp. 57–76.
- Rieppel, O. 1994: Osteology of *Simosaurus gaillardoti*, and the phylogenetic interrelationships of stem-group Sauropterygia. – *Fieldiana (Geology)*, new series, 28, pp. 1–85.
- Rieppel, O. 1995: The Genus *Placodus*: Systematics, Morphology, Paleobiogeography, and Paleobiology. – *Fieldiana Geology*, new series, 31, pp. 1–44.

- Rieppel, O. 1997: Sauropterygia from the Muschelkalk of Djebel Rehach, southern Tunisia. – *Neues Jahrbuch für Geologie und Palaontologie Monatshefte*, 1997, pp. 517–530.
- Rieppel, O. 2000: Sauropterygia I. Placodontia, Pachypleurosauria, Nothosauroida, Pistosauroida. *Handbuch der Paläoherpetologie*, Teil 12A. – Friedrich Pfeil, 134 p.
- Rieppel, O. 2001a: A new species of Nothosaurus (Reptilia: Sauropterygia) from the Upper Muschelkalk (Lower Ladinian) of southwestern Germany. – *Palaeontographica Abt A*, 263, pp. 137–161.
- Rieppel, O. 2001b: The cranial anatomy of Placochelys placodonta Jaekel, 1902, and a review of the Cyamodontoida (Reptilia, Placodonta). – *Fieldiana (Geology)*, new series, 45, pp. 1–104.
- 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, pp. 33–63.
- Rieppel, O., H. Hagdorn: 1997. Paleobiogeography of Middle Triassic Sauropterygia in Central and Western Europe. – In: Callaway, J.M., E.L. Nicholls (Eds): *Ancient Marine Reptiles*. Academic Press, pp. 121–144.
- Rieppel, O., R. Wild 1996: A revision of the genus Nothosaurus (Reptilia, Sauropterygia) from the Germanic Triassic, with comments on the status of Conchiosaurus clavatus. – *Fieldiana (Geology)*, new series, 34, pp. 1–82.
- Rieppel, O., J.-M. Mazin, E. Tchernov 1999: Sauropterygia from the Middle Triassic of Makhtesh Ramon, Negev, Israel. – *Fieldiana (Geology)*, new series, 40, pp. 1–85.
- Seilacher, A. 1943: Elasmobranchier-Reste aus dem oberen Muschelkalk und dem Keuper Württemburgs. – *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Monatshefte B*, 1943, pp. 256–271.
- Sereno, P.C., A.B. Arcucci 1993: Dinosaurian precursors from the Middle Triassic of Argentina: Lagerpeton chanarensis. – *Journal of Vertebrate Paleontology*, 13, pp. 385–399.
- Soares, M.B. 2003: A taphonomic model for the Mesosauridae assemblage of the Irati Formation (Paraná Basin, Brazil). – *Geologica Acta*, 1, pp. 349–361.
- Stensiö, E.A. 1921: Triassic fishes from Spitzbergen Part I. – *Adolf Holzhausern*, 307 p.
- Sues, H.D. 1987: On the skull of Placodus and the relationships of the Placodontia. – *Journal of Vertebrate Paleontology*, 7, pp. 138–144.
- Török, Á. 1998: A Mecsek–Villányi Egység triász képződményeinek rétegtana (fordítás?). – In: Bérczi I., Á. Jámor (Eds.): *Magyarország geológiai képződményeinek rétegtana*. MOL Rt., MÁFI, Budapest, pp. 253–279.
- Vickers-Rich, P., T.H. Rich, O. Rieppel, A.F. Thulborn, H.A. McClure 1999: A Middle Triassic vertebrate fauna from the Jilh Formation, Saudi Arabia. – *Neues Jahrbuch für Geologie und Palaontologie Abhandlungen*, 213, pp. 201–232.
- Vörös, A. 1972: A Villányi hegység alsó és középső júra képződményeinek üledékföldtani vizsgálata (Lower and Middle Jurassic formations of the Villány Mountains). – *Földtani Közlöny*, 102/1, pp. 12–28.
- Vörös, A. 2009: Tectonically-controlled Late Triassic and Jurassic sedimentary cycles on a peri-Tethyan ridge (Villány, southern Hungary). – *Central European Geology*, 52/2, pp. 125–151.
- Vörös, A. 2010: A villányi mezozoos rétegsor: visszatekintés új nézőpontból. (The Mesozoic sedimentary sequences at Villány). – *Földtani Közlöny*, 140/1, pp. 3–30.
- Vörös, A. 2012: Episodic sedimentation on a peri-Tethyan ridge through the Middle–Late Jurassic transition (Villány Mountains, southern Hungary). – *Facies*, 58, pp. 415–443.
- Wells, N.A. 1989: Making thin sections. – In: Feldmann R.M., R.E. Chapman, J.T. Hannibal (Eds): *Paleotechniques*. University of Tennessee, pp. 120–129.