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New eosauropterygian (Reptilia, Sauropterygia) remains from the Middle Triassic of Villány, Hungary

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“We swim in different oceans,
but land on the same shore.”
(Elizabeth Comstock)

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*Cover page: Artists impression of a *Nothosaurus*. **Credit: Tibor PECSICS**

1. Abstract

Eosauropterygia was a diverse clade of secondary aquatic reptiles, which represented one of the most important vertebrate taxa in the shallow marine communities during the Triassic. However, despite the long history of collection and examination of eosauropterygian remains, previous studies have indicated that the fossil record of this group is affected with a significant incompleteness, making the understanding of their paleobiogeographic relations difficult. Here I describe the new eosauropterygian remains from the Middle Triassic Templomhegy Dolomite Member (Villány - southern Hungary), which were unearthed during the systematic fieldworks of previous years. This material contains isolated bones belonging to *Simosaurus* sp., *Nothosaurus* cf. *mirabilis* and *N.* cf. *marchicus*, while the occurrence of *N. giganteus* is also probable. The faunal composition from Villány is similar to what was described from the western Tethys and within it highly resembles that of the Upper Muschelkalk of Germanic Basin. Along with the widespread taxa, the possible remains of *N. marchicus* proves the hypothesis that this small-sized *Nothosaurus* was present outside of the Germanic Basin too. Besides the isolated elements, a probably associated skeleton of a small-sized eosauropterygian specimen is also known. This locality widens our knowledge on eosauropterygian distribution and provides new information about the previously not well known Middle Triassic vertebrate fauna of the one-time southern Eurasian shelf region.

2. Introduction

2.1. Triassic vertebrates from Hungary

Despite the high amount of Triassic rocks and well documented outcrops, fossils of vertebrates are relatively rare in Hungary from this period. Isolated fish remains were documented from different localities, like from the Bakony Mountains (Jaekel 1902a) and the locality from where the fossils of present work came also provided a rich fish material (Szabó et al. 2019), but exceptional findings of articulated fishes are also known from the Balaton Highland (Ősi et al. 2013).

Fossils of tetrapods from the Mesozoic of Hungary are also mostly rare, isolated finds. The Middle Triassic Felsőörs Limestone Formation provided vertebrae of ichthyosaurs (Ősi et al. 2013). Additional articulated ichthyosaur vertebrae, furthermore a fragment of an eosauropterygian mandible with in situ teeth (under preparation), from Felsőörs are also known from the Middle Triassic Vászoly Formation of Balaton Highland (Ősi et al. 2013). Most recently, an isolated fragmentary eosauropterygian dorsal rib has been found along the main road in debris, between Balatonfüred and Aszófő by Zoltán Batka (A. Ősi, pers. comm.). Maybe the most important Triassic vertebrate finding is the associated *Placochelys placodonta* JAEKEL, 1902b material from Veszprém (Bakony Mountains - probably from the Veszprém Marl Formation), which consists of both cranial and postcranial elements (Jaekel 1901, 1902a, 1902b, 1907; Rieppel 2000). A single *Nothosaurus* MÜNSTER, 1834 vertebra is known from Hetvehely (Lower-Middle Anisian Lapis Limestone Formation) from the Mecsek Mountains (Bodor and Makádi 2016) and isolated nothosaur teeth were also mentioned from this region (Õsi et al. 2013).

Regarding the Villány Hills (southern Hungary), (Lőrenthey 1907) and (Lóczy 1912) briefly mentioned fossils of *Nothosaurus* sp. from a quarry near to the railway station of Villány. Later, Rálisch-Felgenhauer (1981) also reported reptile fossils from an abandoned road cut on Templom Hill. Since then, these remains have been lost, and their detailed description has never done. The above mentioned, bone-bearing beds of Villány represent the Middle Triassic Csukma Dolomite Formation (Vörös 2010; Ősi et al. 2013), the same formation from where the material of the present work was excavated. After the geologist Emilia Pozsgai discovered some teeth, vertebrae and limb elements in the Middle Triassic beds exposed in a construction site on Somssich Hill (Villány), systematic excavations started in 2012 (Ősi et al. 2013). Since then, these re-discovered vertebrate bearing Triassic layers provided thousands of vertebrate fossils – including isolated teeth and bone remains of

different fishes, sauropterygians (placodonts, nothosaurs), vertebrae of *Tanystropheus* VON MEYER, 1852 along with a most probably associated eosauropterygian specimen composed of postcranial elements, and other fragments of undetermined sauropsids (Ősi et al. 2013; Ősi and Botfalvai 2017; Segesdi et al. 2017; Szabó et al. 2019; Gere et al. submitted) - and the construction site in Villány became the second systematically-collected Mesozoic vertebrate site of Hungary.

2.2. Aims and objectives

The aim of this work is to report and describe the new Middle Triassic eosauropterygian aquatic reptile findings unearthed during the fieldworks of previous years from Villány (southern Hungary), and to compare the composition of these faunal elements with the other earlier described Middle Triassic eosauropterygian materials from the surrunding and global paleogeographical regions. The new material provides essential informations on the faunal composition of the site, completing the results of previous studies (see Ősi et al. 2013). The importance of the material presented here is given by the fact that systematically-collected Mesozoic sites are exceptional from Hungary (and also from the Carpathian-Pannonian Region). Moreover, because aquatic and semi-aquatic reptiles played a crucial role in the paleoecosystems of Triassic period (see below), due to their investigations we can get a better insight into the paleoecology and evolution of ancient shallow-marine communities of the Tethyan Realm.

2.3. Triassic eosauropterygians and their paleontological significance

Sauropterygia OWEN, 1860 represents one of the most successful aquatic sauropsid groups from the Mesozoic Era. They were a monophyletic clade of secondary aquatic diapsids (Rieppel 2000; Neenan et al. 2013) with high ecological diversity and numerous adaptations to the life in an aquatic environment (Rieppel 2000, 2002; Klein et al. 2016a).

The two different lineage of Sauropterygia, namely Placodontia COPE, 1871 and Eosauropterygia RIEPPEL, 1994a can be described with radically different body plans, habitats and ecological niches (Rieppel 2000). Besides their diversity, capability to conquer new environments, and the relatively frequent occurrence of their fossils in marine sedimentary rocks, the timing of their emergence makes this group of interest highly significant (Liu et al. 2014; Vermeij and Motani 2018).

Sauropterygians are originated in the late Early Triassic (Benson et al. 2010). They diversified during the faunal recovery after the Permian-Triassic Mass Extinction event which probably triggered the colonization of marine environments by amniotes in this period (Vermeij and Motani 2018). During the recovery interval many lineage of tetrapods emerged and the presence of diverse marine vertebrate communities with large bodied (in certain cases eosauropterygian) top-predators indicates the advanced or complete establishment of the given environment and its ecological networks after the extinction (Liu et al. 2014; Scheyer et al. 2014**)**. Eosauropterygian marine reptiles invented and filled up new trophic niches and become important part of the paleoecosystem, and then they reached their first high diversity peak in the Anisian (Bardet 1994; Benson and Butler 2011; Stubbs and Benton 2016).

Early sauropterygians were most probably near-shore dwellers, (Neenan et al. 2017) and their habitat was confined to the coastal environments, intraplatform basins and shallow epicontinental seas (Rieppel 2000). That is why their evolution and global distribution was strictly connected to the global sea level changes, which led to the flooding of continental territories and the development of new epicontinental basins (Benson and Butler 2011; Kelley et al. 2014). Their distribution can be divided into three main regions: the *western Tethyan province* (epicontinental Germanic Basin, Alpine Triassic with the southern Alps-Transdanubian platform, Mediterranean region, shelf areas of western Tethys); the *western Pacific province* (or *eastern Tethyan province* – southeastern Asia); and the *eastern Pacific province* (western part of North America) (Rieppel and Hagdorn 1997; Rieppel 1999, 2000; Bardet et al. 2014; San et al. 2019). The taxic diversity of Triassic sauropterygians started to decrease following (and probable caused by) the regression phase at the beginning of the Late Triassic (Bardet 1994; Benson and Butler 2011; Kelley et al. 2014). Near-shore dweller stem-group sauropterygians disappeared by the end of the Triassic, while more adopted, well swimmer and more open-water crown-group eosauropterygians survived until the end of the Cretaceous (Rieppel 2000).

2.4. Phylogenetic interrelationships of stem-group Eosauropterygia

All sauropterygians represent the modified diapsid skull type: the euryapsid skull condition, which means the loss of the lower temporal arch in their akinetic skull (Rieppel 2000). Also a common attribute of these reptiles is the unique position of pectoral girdle elements, where all the bones are shifted towards the ventral side of the body (Rieppel 2000). Skeletal paedomorphosis is present and pachyostosis also affects the postcranial skeleton (Rieppel

2000). Traditionally we can differentiate stem-group sauropterygians from the Triassic and crown-group eosauropterygians from the Jurassic and Cretaceous periods (Rieppel 1997, 2000). Phylogeny of Sauropterygia (**Fig.1. A,B**) is still under debate, because many Triassic species from Europe were described based only on cranial material (and sometimes only one specimen is known), and postcranial elements are not identified or isolated bones are not even diagnostic on species level (Rieppel 2000; Klein 2010). However the newer findings from China, frequently containing complete or partial skeletons shed light on some new aspects of the phylogenetic interrelationships of Sauropterygia.

Traditionally, Sauropterygia comprises Placodontia and Eosauropterygia, while the latter contains Pachypleurosauria *sensu* NOPCSA, 1928 and Eusauropterygia *sensu* TSCHANZ, 1989 (Rieppel 1994a, 2000). The two major subclade of Eusauropterygia is Nothosauroidea BAUR, 1889 and Pistosauroidea BAUR, 1887-90. Within Nothosauroidea, Simosauridae HUENE, 1948 is the sister group of Nothosauria BAUR, 1889. Nothosauria contains *Germanosaurus* NOPCSA, 1928 and Nothosauridae BAUR, 1889, while Nothosauridae involves the *Nothosaurus* and *Lariosaurus* CURIONI, 1847 genera. Pistosauroidea contains Cymatosauridae HUENE, 1944 (*Corosaurus* CASE, 1936 and *Cymatosaurus* FRITSCH, 1894 and Pistosauridae BAUR, 1887-90 (*Augustasaurus* SANDER, RIEPPEL AND BUCHER, 1997), *Pistosaurus* MEYER, 1839 and Plesiosauria DE BLAINVILLE, 1835 (see Rieppel 2000:Fig.1.).

However, the phylogenetic analysis of Neenan et al. (2013) led to some different outcomes (**Fig.1. A)**. They proved the monophyly of Eosauropterygia, but the inner relationships are still problematic: they found Pistosauridae to be the sister group of all other eosauropterygians (Cymatosauridae, Pachypleurosauria and Nothosauroidea). Nevertheless, **t**he situation of Pachypleurosauria is also controversial and probably the debate on the phylogenetic relationships of this taxon will continue in the next years, because after the discovery of some exceptionally well preserved skeleton from China with shared nothosaur and pachypleurosaur characters, more and more author questioned the monophyletic condition of this group (and consequently the validity of Eusauropterygia as well) (Holmes et al. 2008). Also some authors suggest, that the 'pachypleurosaurs' from the western side of the Tethyan Realm does not necessarily form a monophyletic group with those were described from the eastern regions (e.g. China) (Cheng et al. 2016). Moreover, histological studies also suggest the paraphyly of Pachypleurosauria (Klein 2010). The analysis of Ma et al. (2015) did not support the Pachypleurosauria clade, but they found a pachypleurosaur-grade within Eosauopterygia. It must be noted, that in the case of small isolated elements, sometimes the authors describe the bones as '*Pachypleurosaurus*', which is logical considering the small size

of the known adult pachypleurosaurs but could be misleading because the juvenile stage of most of the eosauropterygians is not known (Rieppel et al. 1999; Renesto and Dalla Vecchia 2018).

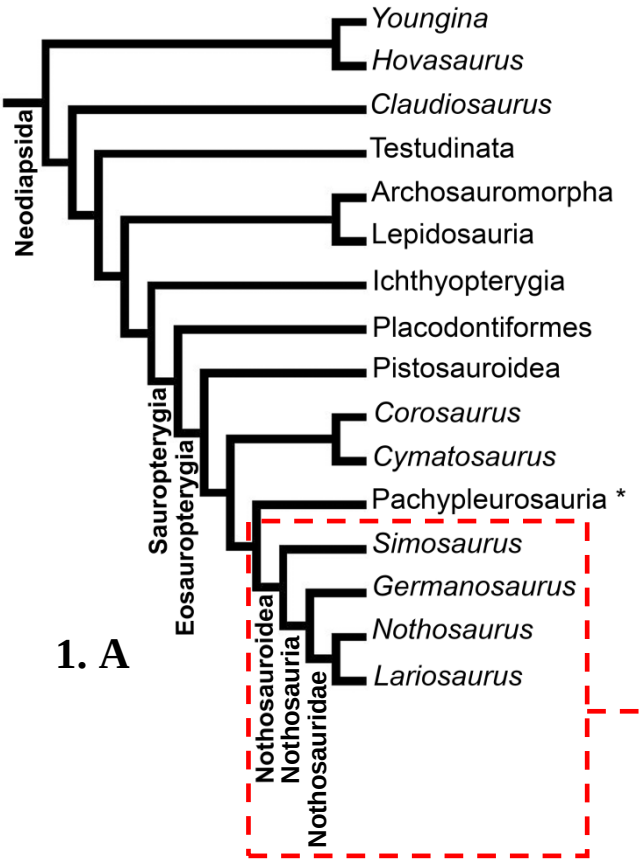
Another change of the past decade is consistent with the interrelationships within Nothosauria. Liu et al. (2014) questioned the monophyletic status of the *Nothosaurus* and *Lariosaurus* genera, which statement was supported by the analysis of Klein et al. (2016b) and Lin et al. (2017). To solve this problem, three species originally described as *Nothosaurus (N. juvenilis* EDINGER, 1921, *N. youngi* LI AND RIEPPEL 2004, and *N. winkelhorsti* KLEIN AND ALBERS 2009 had been placed into the genus *Lariosaurus* (**Fig.1. B**) (Lin et al. 2017). The phylogenetic trees (focusing on Nothosauroidea) of (Liu et al. 2014), Klein et al. (2016b) and Lin et al. (2017) contain a politomy with *Germanosaurus*, *N. zhangi* LIU ET AL., 2014, *N. haasi* RIEPPEL, MAZIN AND TSCHERNOV, 1999 and *N. edingerae* SCHULTZE, 1970 and due to this, the status of Nothosauridae within Nothosauria is not fully resolved, but most probably this is caused by the incomplete material of many poorly known species, like *Germanosaurus* (Rieppel 2000; Klein et al. 2016b) or *N. zhangi* (Liu et al. 2014).

I summarized a hypothetical consensus tree to visualize the phylogenetic relationships of the present work's taxa (**Fig.1. B**). During my work I followed the results of Neenan et al. (2013) for the high systematic level, moreover Liu et al. (2014) and Lin et al. (2017) for Nothosauroidea, completed with Klein et al. (2016b) and (Hinz et al. 2019). All these cited authors agreed with the basal position of Simosauria within Nothosauroidea.

2.5. Paleobiology of stem-group Eosauropterygia

Placodonts (sister group of Eosauropterygia) can be described as mostly durophagous, benthic feeder aquatic reptiles of the shallow-marine realms, they most probably consumed sessile or benthic hard shelled or soft invertebrates, or maybe plant material in case of *Henodus* F. V. HUENE, 1936 (Rieppel 1995, 2000, 2002; Scheyer et al. 2012). In contrast, stem-group eosauropterygians were pelagic feeders, and their potential preys were pelagic soft or hard shelled invertebrates besides other vertebrates including aquatic reptiles and fishes (Rieppel 2000, 2002).

The somewhat elongated neck, short trunk and elongated, laterally compressed tail, moreover the special arrangement of girdle elements indicates the advanced swimming abilities of stem-group eosauropterygians (Storrs 1993; Rieppel 2000; Araújo and Correia 2015).



← Figure 1. A

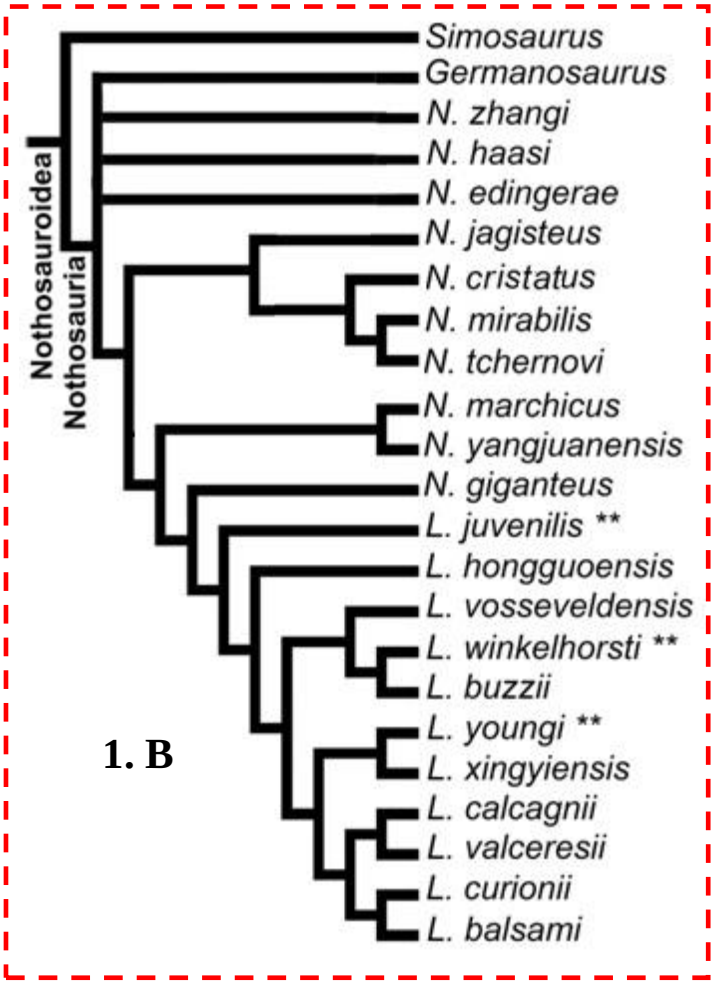
Phylogenetic consensus tree showing the status of Sauropterygia and interrelationships of Eosauropterygia within diapsida, simplified after the work of Neenan et al. (2013).

***** It must be noted, that some author questions the monophyly of Pachypleurosauria [see Holmes et al. (2008); Klein (2010) and Cheng et al. (2016)].

Figure 1. B →

Hypothetical phylogenetic tree showing interrelationships of Nothosauroidea based on the analysis of Lin et al. (2017) and completed with *L. vosseveldensis* KLEIN ET AL., 2016a and with *N. cristatus* HINZ, MATZKE AND PFRETZSCHNER, 2019. ('*N.*' means *Nothosaurus*, while *'L.'* refers to the genus *Lariosaurus*.)

****** Species marked with ' ** ' were originally described as members of the genus *Nothosaurus*, but recent taxonomic works place them into *Lariosaurus* in order to keep the monophyly of the latter [see Liu et al. (2014); Klein et al. (2016b) and Lin et al. (2017)].



Their conservative limb structure was still more similar to those of basal terrestrial diapsids (Caldwell 2002), however the ratios, and flattening of the appendicular elements, general anatomy and muscle attachements of humeri (Storrs 1993; Araujo and Correia 2015), in addition hyperphalangy in some cases (Rieppel 2000), and the presence of pachyostosis and pachyosteoclerosis in their bones (Houssaye 2009) are clearly connected to the adaptation to an aquatic environment. A wide range of different feeding strategies can be separated based on their diverse skull anatomy and tooth morphology (Massare 1987; Rieppel 2000, 2002; Stubbs and Benton 2016).

Pachypleurosaurs (*sensu* Nopcsa 1928) were small sized (about 0.25 m to 1.20 m long), 'lizard-like' eosauropterygians, most probably fed on smaller pelagic soft shelled invertebrates (Rieppel 2002). They showed a relatively plesiomorphic skull structure (Rieppel 2000): only moderately elongated skull with broad and blunt snout, without a rostral constriction; longer preorbital than postorbital region; the orbits are larger than the upper temporal fenestrae. Furthermore pachypleurosaurs had a delicate jaw and in most cases homodont dentition with small, conical and only slightly curved teeth (Rieppel 2000, 2002). Because sometimes their complete skeletons appear in a great number at one locality (e.g. Monte San Giorgio), it was possible to observe the signs of sexual dimorphism (Rieppel 1989; Sander 1989; Lin and Rieppel 1998) and possible viviparity (Sander 1989; Lin and Rieppel 1998**)**. Features connected to sexual dimorphism occurred in the overall size of individuals furthermore in the morphology and ratios of the humeri (Rieppel 1989; Sander 1989; Lin and Rieppel 1998).

The Nothosauroidea subclade (**Fig.1. B)** contains stem-group eosauropterygians in a wide range of size and morpohological variability (Rieppel 2000). In a summary, the members of this taxon are small to large sized (1.5 m to 5-6 m long) animals, characterized by a flat skull with large postorbital region (temporal fenestrae are larger than the orbits) (Rieppel 2000). The strong and robust forelimbs of nothosauroids, in contrast with their proportionally smaller hindlimbs (Rieppel 2000; Klein 2010) clearly indicate their evolutional shift to a forelimb dominated paraxial locomotion (Storrs 1993). The usage of forelimbs for propulsion is suggested by some rare trace fossils as well (Zhang et al. 2014). It is still a question whether nothosauroids were able to do some kind of 'seal-like' terrestrial locomotion (Storrs 1993). Knowing the paedomorphic stage of their bones, large skulls, heavy ribcage and modified limbs with reduced condyles, this type of locomotion could have been very limited, or not even possible (Storrs 1993; Rieppel 2000). Renesto et al. (2003) reported nothosaurid embryos from northern Italy, which remains suggest that viviparity or

ovoviviparity could have been present in this group, and most recently the histological study of Griebeler and Klein (2019) also indicated live-bearing in *Nothosaurus*.

The two known species included in Simosauridae: *Simosaurus gaillardoti* MEYER, 1842 and *Paludidraco multidentatus* (DE MIGUEL CHAVES, ORTEGA AND PÉREZ-GARCIA, 2018a) both represent a special ecology in compared to the other nothosauroids. Despite the high amount of isolated material from different localities, based on the known skulls *Simosaurus* is (to the best of our knowledge) a monospecific genus and *Simosaurus gaillardoti* is the only known valid species (De Miguel Chaves et al. 2018b). The skull of *Simosaurus* and *Paludidraco* is distinctly flattened and blunt, with a broad rostrum which is not constricted (Rieppel 2000; De Miguel Chaves et al. 2018a). Based on its homodont dentition with bulb-like teeth covered with striated enamel, probably *Simosaurus* processed its prey (shelled invertebrates, maybe fish) with crushing before swallowing (Rieppel 2002). In contrast, the more gracile skull and slender jaw, with numerous small teeth forming a comb-like structure of the highly pachyostotic *Paludidraco* suggest that it was a filter feeding animal (De Miguel Chaves et al. 2018a).

Nothosaurids were interpreted as active piscivorous predators, probably fed on small fish and squid (Rieppel 2002). They had narrow, elongated upper temporal fenestrae, extended maxillary toothrow, and in the case of most derived species a narrow elongated rostrum, with large fang-like teeth in the premaxilla and the spoon-shaped symphysis of the mandibles (Rieppel and Wild 1996; Rieppel 2000). Posterior to the symphysis and rostrum, the large fangs were followed by significantly smaller, but still pointed and procumbent teeth (heterodont dentition). Histological studies concluded, that while small-bodied nothosaurs lived in near-shore shallow marine areas (due to their high bone compactness), larger species were capable to inhabit more open water environments (a decrease in their bone mass was detected) (Klein et al. 2016a).

The pistosauroids (*sensu* Baur 1887-90) were medium sized (3-4 meter long) aquatic predators of small to large sized shelled invertebrates and fish (Rieppel 2000, 2002). Their overall bodyplan showed more advanced adaptations (e.g. flipper-like limbs) to the aquatic life than nothosauroids, howewer, they shared many similar features in consequence of the similar piscivorous diet (Rieppel 2002). Pistosauroids had a narrow, elongated dorsoventrally compressed skull with large temporal fenestrae and sagittal crest, constricted rostrum and a heterodont dentition of small and large fang-like procumbent, pointed teeth. Pistosauroidea was the only eosauropterygian group that survived into the Jurassic (Rieppel 2000), and also the one with the largest Triassic geographical distribution (Rieppel 2000;

Bardet et al. 2014). The explanation of the success of this subclade is probably in connection with their advanced pelagic lifestyle and increased metabolic rate (Rieppel 2000; Klein 2010).

2.6. Middle Triassic vertebrates from Bihor Mountains (northwestern Romania)

Due to geological mapping fieldworks of the 1960's in the Bihor Mountains (northwestern Romania, part of the Apuseni Mountains) vertebrate-bearing Triassic limestone beds were reported (Istocescu et al. 1968; Jurcsák 1987; Venczel 1998; Posmosanu 2013). The sauropterygian material discovered in these beds is interesting concerning the present work, because the Bihor Mountains is situated on the same tectonic unit as Villány, and most probably they were located in a similar paleogeographic region, southwards from the Bohemian Massif, during the Triassic (Pozsgai et al. 2017).

The two sites, near the town Alesd (*Élesd*), namely Lugașu de Sus (*Felső-Lugas*) and Pești (*Sólyomkőpestes*) revealed the Pești Shale Member of Lugaş Formation which provided hundreds of vertebrate fossils. These specimens were mainly described by the late paleontologist Tibor Jurcsák (1926-1992) who also led several field trips to collect them (Jurcsák 1973, 1987; Patrulius et al. 1979; Venczel 1998). The Middle Triassic - probably Late Anisian (Jurcsák 1987; Iordan 1993; Posmosanu 2013) - material, consisting of isolated and disarticulated skeletal elements (Posmosanu 2013), is now housed in the Muzeul Ţării Crişurilor (*Körösvidéki Múzeum*) of Oradea (*Nagyvárad*). But unfortunately, the Pești outcrop was destroyed during the 1980's (Posmosanu 2013). On both sites, the (probably Late Anisan) fossiliferous limestone and marl layers are overlain by dolomite beds (believed to be Ladinian in age) (Istocescu et al. 1968; Patrulius et al. 1979; Posmosanu 2013). The age of the bone-bearing sediments was determinded based on invertebrate fossils. For the list of invertebrate taxa see Jurcsák (1978) and Posmosanu (2013). Following the revision of the brachiopod findings ('*Punctospirella fragilis, Coenothyris vulgaris, Aulacothyris geyeri, Aulacothyris* aff. *incurvata'*), the age of Pești Shale is belived to be Upper Anisian (probably Illyrian) (Patrulius et al. 1971; Patrulius et al. 1979; Iordan 1993).

The described Triassic assemblage from the Bihor Mountains contained fossils of invertebrates, fishes, terrestrial, semi-aquatic and aquatic reptiles (Jurcsák 1987; Venczel 1998). Based on the reports of Jurcsák, the Sauropterygians are represented by different placodonts, and also by several eosauropterygians like *Pachypleurosaurus* sp., *Simosaurus* and two *Nothosaurus* species (Jurcsák 1987; Posmosanu 2008). The same taxa were collected

from both fossil sites, howewer, the ratio of the aquatic nothosaur fossils was higher at Peștiș, while remains of *Tanystropheus* sp. were more frequent at Lugașu de Sus (Jurcsák 1987; Posmosanu 2013). Based on the lithologies and fossil contents, briefly Jurcsák (1987) and later Posmosanu (2013) indicated that probably the Peștiș site represents a wave dominated, shallow marine environment, while Lugașu de Sus was probably a shallow lagoon.

Jurcsák reported two species of *Nothosaurus* of different sizes: the middle sized *Nothosaurus mirabilis* MÜNSTER, 1834 and a smaller species, which was described based on a fragmentary skull (*Nr.inv.7653.*) from Peștiș (Jurcsák 1973) as *Nothosaurus* cf. *procerus* SCHROEDER, 1914. In his work Jurcsák (1973) also published pictures and drawings of this skull. Later Jurcsák decided to describe it as a new species: *Nothosaurus transsylvanicus* JURCSÁK, 1976. However, according to Rieppel et al. (1999), the fragmentary skull described by Jurcsák as *N. transsylvanicus* is very similar, maybe identical to *Nothosaurus marchicus* KOKEN, 1893. Moreover, in the revisional work of Rieppel and Wild (1996) *N. procerus* has been assigned as junior synonym of *N. marchicus* and most probably the species described by Jurcsák represents the latter species.

In case of the taxonomic compositon of the Bihor eosauropterygian material we must keep in mind, that the majority of fossils have never been illustrated with good quality pictures (the reports of Jurcsák mainly contains only sketchy drawings) and due to the delayed moving of the housing museum to its new building, most of the remains are not available for study. Some of the determinations are questionable: Jurcsák (1977) published a picture of an isolated dorsal neural arch with elongated neural spine, referred to '*N. mirabilis'*, however the specimen was not fully prepared and the quality of illustration is not good enough to observe every detail, moreover the drawing of 'cf. *Simosaurus sp.*' vertebral centrum from Jurcsák (1978) is not surely represents the remain of a *Simosaurus*. Based on the placodont material, described from Bihor, Pinna (1990) debated the correct classification of the findings, because Jurcsák described species which are normally not present on the same stratigraphic level at localities with well known stratigraphy.

Even though the Middle Triassic vertebrate assemblage (and its stratigraphic position) from Bihor Mountains certainly needs revision (Venczel 1998), its significance is obvious owing to the Triassic location of the region. Because of the lack of further studies and newer results on the exact age of the eosauropterygian material from the Bihor Mountains (E. Posmosanu and M. Venczel, pers. comm.) during my work I accepted the Late Anisan age provided by the previous literature (Patrulius et al. 1979; Iordan 1993).

3. Locality and geological background

3.1. The ’Construction site’ vertebrate locality on the Somssich Hill

The material presented here was excavated at a construction site on Somssich Hill, 200-300 m southwestern from the railway station of Villány, near to the Arany János street (**Fig.2.**). The constructions started here around 2011, and thanks to the earthworks previously unknown Triassic strata had been unearthed (Ősi et al. 2013). The site and the exposed bone-bearing beds are currently available for study (with the permission of the owners).

The southern part of the site is an unfinished basement, and exposes the important bone-bearing layers (dipping to south with 40-50°) of the Templomhegy Dolomite Member (upper part of Csukma Dolomite Formation). In the southwestern part of this hollow, the Mészhegy Sandstone Formation unconformable overlies the Templomhegy Dolomite (**Fig.3.**) (Ősi et al. 2013; Botfalvai et al. 2019).

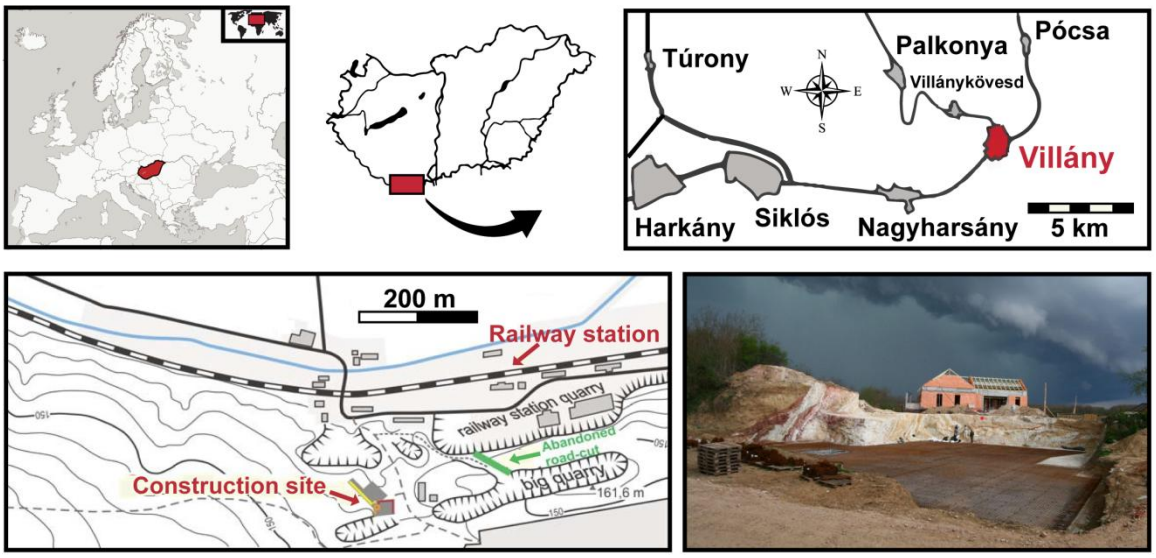


Figure 2. Location and photo of ‘Construction site’ vertebrate locality in Villány, southern Hungary (map modified after Ősi et al. 2013) [photo source: www.magyardinoszaurusz.hu]

3.2. Paleo-position and Triassic sediments of Tisza Megaunit

The Villány Hills is situated on the Tisza Megaunit (**Fig.4.**), which used to be the part of the southern passive margin of the European Plate during the first half of the Mesozoic: it took part in the forming of shelf areas of the northwestern Tethys near to the Germanic Basin (Csontos and Vörös 2004; Haas and Péró 2004). Pozsgai et al. (2017) provided exact informations about the paleo-position of this region and prooved that it was located southwards to the Bohemian Massif during the Triassic (**Fig.5.**).

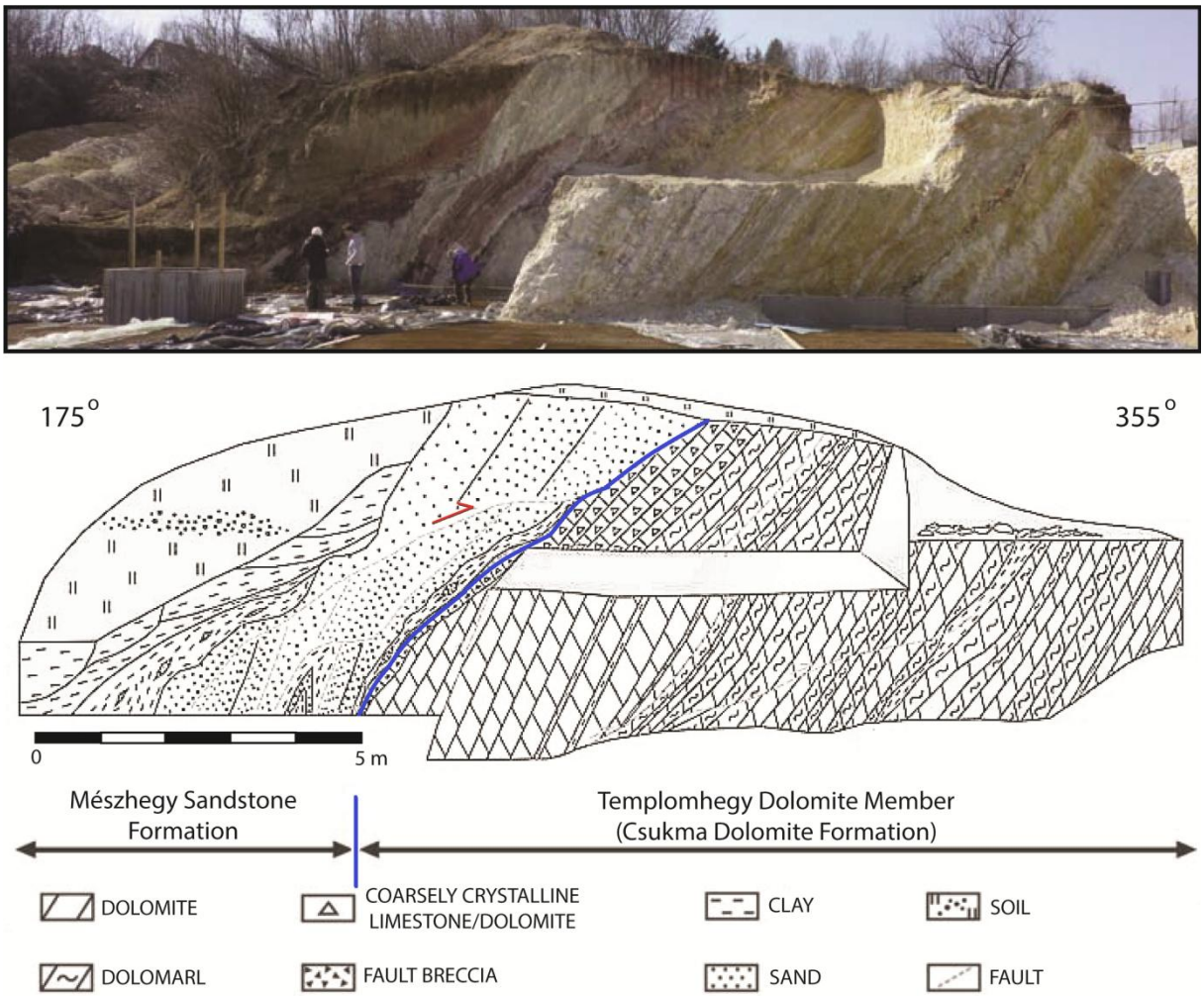


Figure 3. Exposed formations in the southern part of the 'Construction site' vertebrate locality in Villány, southern Hungary (modified after Ősi et al. 2013)

Nowadays, the vast majority of this megaunit is covered by Cenozoic sediments, however it is exposed in the Slavonian Inselbergs (Croatia), Mecsek Mountains and Villány Hills (southern Hungary), in the Apuseni Mountains (northwestern Romania) and near the Eastern and Southern Carpathians (Bleahu et al. 1994; Csontos and Vörös 2004). The parts of the megaunit, namely Mecsek–Szolnok, Villány–Bihor, Békés–Codru Units (Csontos and Vörös 2004) represent different zones of the late passive margin (**Fig.5.**), where the variant paleogeographic positions are reflected in the sediments (Pozsgai et al. 2017; Botfalvai et al. 2019). The terrigeneous income was higher in case of Mecsek–Szolnok Unit, because this zone was in the closest position to the terrestrial areas. In contrast, the more distal Villány-Bihor and Békés-Codru Units show less and less evidence of the terrestrial effects in the sediments composition during the Triassic period (Pozsgai et al. 2017).

The Early and Middle Triassic sediment successions of this area show close generic similarities with the Germanic type sediments (Nagy and Nagy 1976; Török 1997, 1998). During the Early and the beginning of Middle Triassic, terrestial and coastal clastic sedimentation (*Bundsandstein facies*) was typical on the Villány-Bihor Unit, later (at the beginning of Anisian) evaporites formed on the tidal flats and sorrounding sabkha areas under arid climate (*Röt facies*). Following this period (during Anisian-Ladinian) carbonatic sedimentation dominated (*Muschelkalk facies*) and an expansive homoclinal carbonate ramp developed (Török 1997). This ramp on the passive continental margin, with its uniform subsidence rate can be characterized with high production of carbonatic mud and the lack of reef biota (Török 1998). The Late Triassic succession was siliciclastic, with closer affinities to the Carpathian Keuper facies (Bleahu et al. 1994; Feist-Burkhardt et al. 2008).

The formations exposed (**Fig.3.**) at the 'Construction site' vertebrate locality represent the uppermost strata of the Muschelkalk carbonate ramp and a thin clastic Keuper (Bérczi-Makk et al. 2004; Vörös 2009).

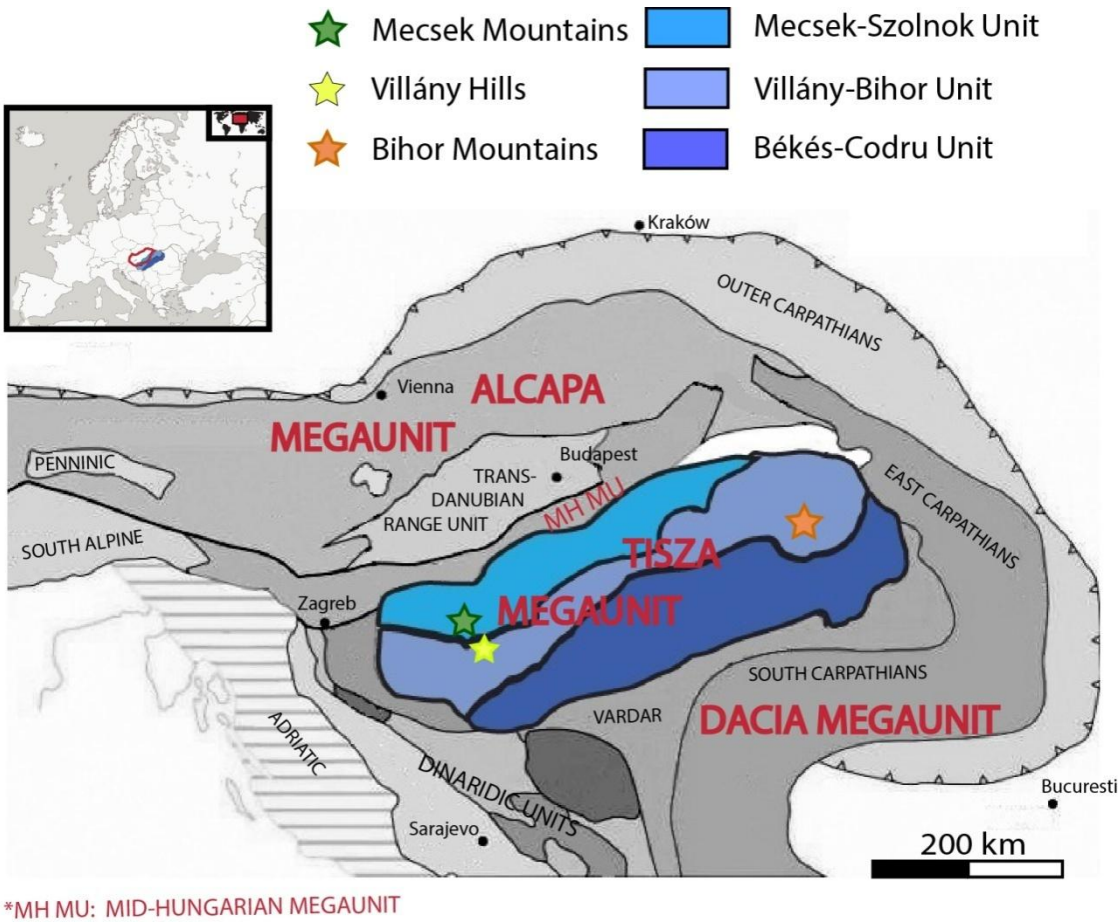


Figure 4. Structure and present-day location of Tisza Megaunit, simplified after Haas et al. (2010)

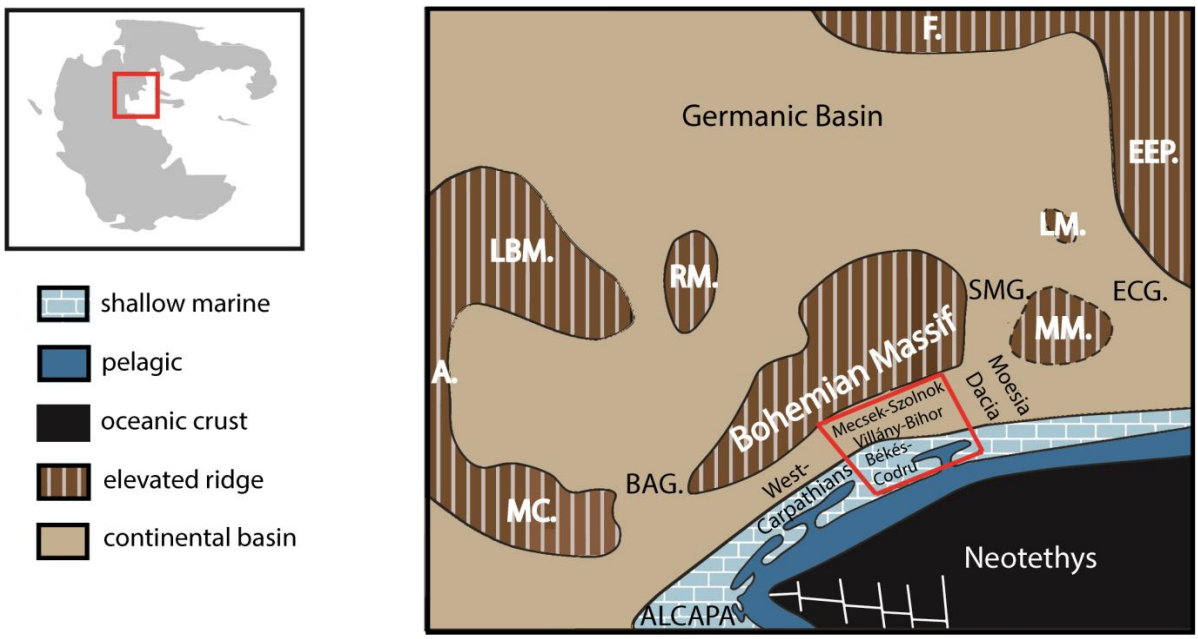


Figure 5. Late (and presumed Middle) Triassic position of Tisza Megaunit (in red square) and the surrounding areas. ALCAPA composite terrane (*Alps* - *Carpathians* - *Pannonian*) involves the parts of Penninic, Austroalpine, Inner and Central Western Carpathian and Pelso composite units (modified after Pozsgai et al. 2017 in which paleotectonic map is based on Szulc 2000; Haas and Péró 2004; Schmid et al. 2008). **LBM.** - *London–Brabant Massif*; **A.** - *Armorican Massif*; **MC.** - *Massif Central*; **RM.** - *Rhenish Massif*; **BAG.** - *Burgundy–Alemannic Gate*; **F.** - *Fennoscandia*; **EEP.** - *East–European Platform*; **LM.** - *Lysogóry Massif*; **SMG.** - *Silesian–Moravian Gate*; **MM.** - *Malopolska Massif;* **ECG.** - *East–Carpathian Gate*

3.3. Stratigraphy and paleoenvironment of the Templomhegy Dolomite Member

On the Muschelkalk carbonate ramp (because of its morphology), eustatic sea-level changes strongly controlled the sedimentation. Therefore three Middle Triassic deepening-shallowing cycles (Early Anisian; Middle-Late Anisian; Ladinian) can be recognized from both the Villány and Mecsek Mountains (Török 2000).

The Zuhánya Limestone Formation (**Fig.6. A**) represents the second cycle. This formation is present in the Mecsek Mountains and Villány Hills as well: based on the foraminifera, crinoid and brachiopod fauna, the age of its fossil-rich lower part, the Bertalanhegy Member (from the Mecsek Mountains) was suggested to be Pelsonian-Lower Illyrian (Nagy 1968; Hagdorn et al. 1997; Bérzci-Makk et al. 2004). The Middle-Upper

Anisian (Upper Pelsonian) age for the Zuhánya Limestone Formation was confirmed with conodont-based stratigraphy (from the Villány Hills), based on samples taken from the Peterd-1 borehole (Bóna 1976; Kovács et al. 2005). Some author suggests, that maybe the upper part of Zuhánya Limestone, namely the Dömörkapu Member (which is poor in fossils) ranged until the Lower Ladinian (Rálisch-Felgenhauer and Török 1993).

Following the Zuhánya Limestone, the gradual shallowing of the Middle Triassic carbonate ramp in the Mecsek Mountains is represented by the Kozár Limestone Formation and Kán Dolomite (Chikán and Konrád 1982): the age of Kozár Limestone, based on crinoids is Upper Illyran, maybe Lower Ladinian (Hagdorn et al. 1997). The heteropic facies of the Kozár Limestone is the Csukma Dolomite Formation in the Villány Hills (Bérzci-Makk et al. 2004). Clay content increases towards the bone-bearing upper part of the Csukma Dolomite that is the Templomhegy Dolomite Member. The depositional environment of this Member was determined as subtidal to peritidal zone on the inner ramp, most probably the sediments were deposited in a shelf lagoon (Rálisch-Felgenhauer and Török 1993; Török 2000; Ősi et al. 2013; Botfalvai et al. 2019). Moreover, the preservation and unreworked condition of the bones also suggest the potential connection with the open marine territories (Ősi et al. 2013; Botfalvai et al. 2019). In this environment, the alternation of sediments was most probably controlled by the sea-level fluctuations, and the recurrent paleosol layers indicate the periodical subaeral exposures (Botfalvai et al. 2019).

The Templomhegy Dolomite Member at the construction site (**Fig.6.**) consists of four lithofacies: *dolomite-*; *dolomarl-*; *sandstone-*; and *reddish calcareous mudstone, claystone* (Botfalvai et al. 2019). The dolomite beds and layers are originated from a shallow, restricted lagoonal environment, while the dolomarl with its higher siliciclast content refers to an intermediate area between the intertidal and subtidal zones. The vertebrate fossils are more common in the marly layers (**Fig.6. B**), especially between the 14th and 24th layers (see Botfalvai et al. 2019). The red calcareous mudstone claystone layers are paleosoil horizons , caused by the subaerial exposure during low sea level phases, however, the origin of sandstone (sandy mudstone) is not fully solved yet (Botfalvai et al. 2019).

Botfalvai et al. (2019) suggest the changes in the depositional environment through the sediment accumulation at the Construction site can be summarized as follows:

- the lowermost strata characterized by dominantly carbonates with low clastic content indicate that this part was deposited when the inner ramp zone was flooded due to sea-level rise and the siliciclastic influx from the land was subordinate;

- the middle part (the richest bone-bearing beds) includes more argillaceuous sediments and paleosol horizons This part was most likely deposited in a period, when the fine terrigenous input significantly increased most probably due to the enhanced humidity and a relative sea-level fall;
- the uppermost part contains dominantly homogeneous dolomite layers, with less siliciclastic content indicating that the carbonate sedimentation became dominant again (Botfalvai et al. 2019).

The fossil content of the Templomhegy Dolomite Member is very poor: besides the bone-bearing section (**Fig.6. B,C,D**), just some rare crinoids, foraminifera, bivalves and brachiopods have been found here (Nagy and Nagy 1976; Rálisch-Felgenhauer and Török 1993; Török 1998; Bérzci-Makk et al. 2004). Since none of these findings are true age diagnostic fossils, the presumed Ladinian age for the bonebeds of Templomhegy Dolomite Member (**Fig.6. A**) is mainly based on its stratigraphic position: it is between the Middle-Upper Anisian (Pelsonian-Lower Illyrian) Zuhánya Limestone and the Carnian Mészhegy Sandstone Formations. The Ladinian age was also suggested previously, based on the described vertebrate material (Ősi et al. 2013).

Following Ladinian tectonic movements, the area became a relatively uplifted terrain resulting in less amount of Late Triassic sediments compared to that of the Mecsek area. The Late Triassic sedimentation was dominantly siliciclastic because of the sea-level fall (Török 1997, 2000; Haas 2001) and sediment influx was increased probably in connection with the Carnian Pluvial Event.

The Templomhegy Dolomite is covered by the siliciclastic (sandstone and claystone) Mészhegy Sandstone Formation, which has been described with different environments by different authors: while Vörös (1972) considered the formation as fluvio-lacustrine, Rálisch-Felgenhauer (1985), Török (1998) and most recently Ősi et al. (2013) and Botfalvai et al. (2019) diagnosed it as shallow marine. The type section of this formation (**Fig.2.**) is an abandoned road cut, close to the 'Construction site' vertebrate locality (Siklóbevágás – 'Road cut' section), where the comform contact of the Templomhegy Dolomite and Mészhegy Sandstone is recognizeable (in the construction site the contact is unconform, tectonic). Based on the palynomorph content of its basal layers, the age of the Mészhegy Sandstone is Carnian (Ősi et al. 2013; Pozsgai et al. 2017).

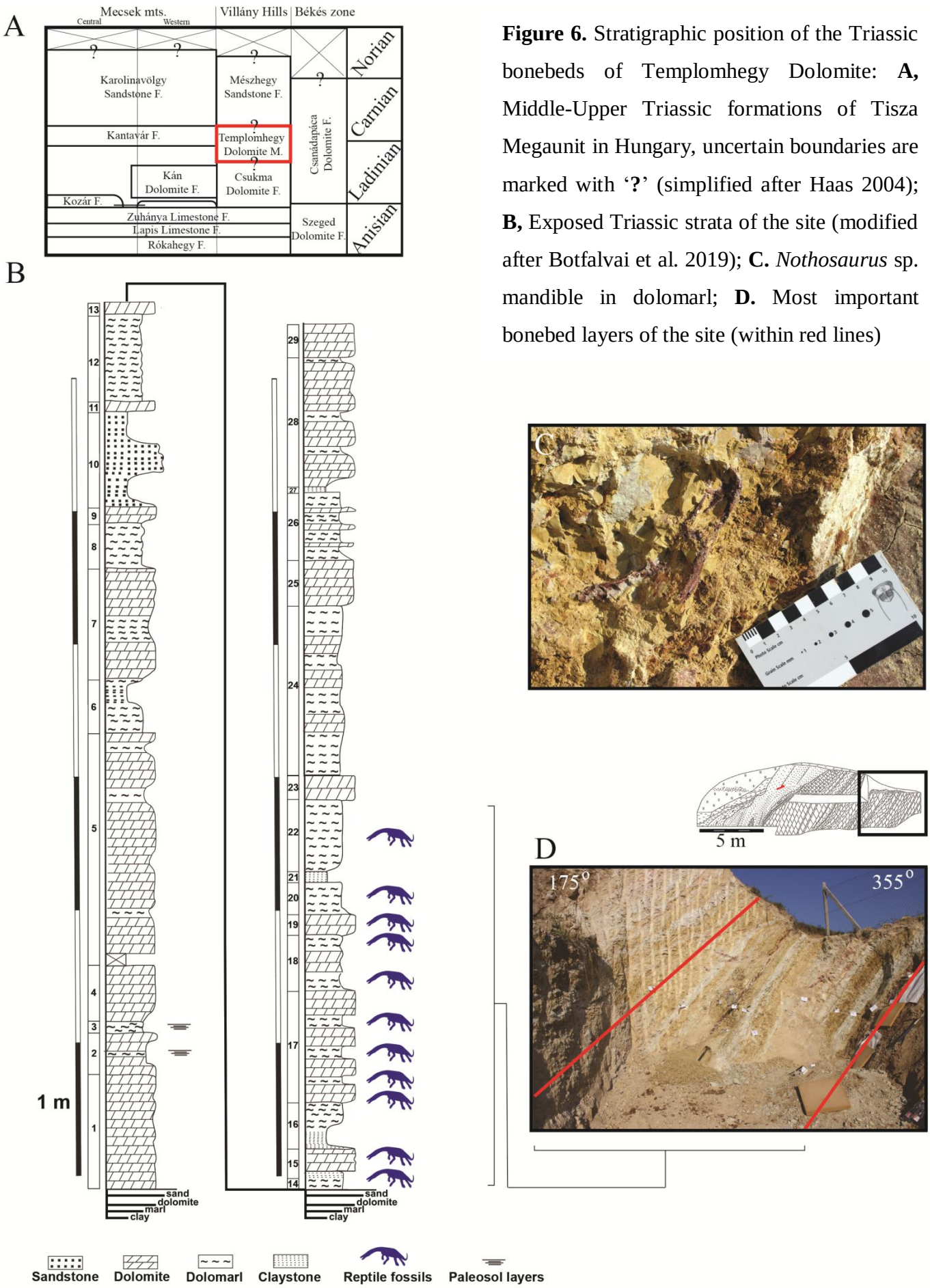


Figure 6. Stratigraphic position of the Triassic bonebeds of Templomhegy Dolomite: **A,** Middle-Upper Triassic formations of Tisza Megaunit in Hungary, uncertain boundaries are marked with '**?**' (simplified after Haas 2004); **B,** Exposed Triassic strata of the site (modified after Botfalvai et al. 2019); **C.** *Nothosaurus* sp. mandible in dolomarl; **D.** Most important bonebed layers of the site (within red lines)

4. Material and methods

The material discussed in the present work contains isolated elements collected in Villány (southern Hungary) from the Middle Triassic Templomhegy Dolomite Member. Besides isolated elements, a most probably associated specimen composed of postcranial elements is also known from the site, which was recorded with bone map on the field. The remains were prepared mechanically and all specimens are housed in the Hungarian Natural History Museum (Vertebrate Collection of the Paleontology and Geology Department). Appendix contains a table of described specimens. Measurements were taken with calipper and tape-measure, photos were edited using Adobe Photoshop CS6. The height of the neural spines was measured from the roof of the neural canal (if the condition of the specimen allowed it).

Anatomical terminology follows the standard names used in previous works written on sauropterygians (e.g. Rieppel 2000) and anatomical directions follows Smith and Dodson (2003).

5. Systematic paleontology

Locality and Horizon: Villány (southern Hungary), construction site on Somssich Hill, Csukma Dolomite Formation (Templomhegy Dolomite Member), Middle Triassic (probably Ladinian) (Ősi et al. 2013; Botfalvai et al. 2019).

Sauropsida HUXLEY, 1864

Sauropterygia OWEN, 1860

Eosauropterygia RIEPPEL, 1994a

Nothosauroidea BAUR, 1889

Nothosauria BAUR, 1889

Nothosauridae BAUR, 1889

Nothosaurus MÜNSTER, 1834

***Nothosaurus* cf. *mirabilis* MÜNSTER, 1834**

(Figure 7.)

Material: dorsal vertebra *PAL 2019.171.1.;* isolated neural arches *PAL 2019.172.1., PAL 2019.175.1.*

Description: PAL 2019.171.1. **(Fig.7. A,B,C)** represents a dorsal vertebra with very high neural spine (overall height is 135 mm). The neural arch is fused with the centrum along the neurocentral suture. The slightly amphicoelous vertebral centrum holds one foramina on both sides, positioned asymmetrically. The height of the neural arch cannot be measured correctly because it is broken and compressed, but it is still distinctly tall (87 mm). The largest width of the transverse processes is 54 mm. They display a slender and elongated morphology, and they are laterally overhanging the centrum. Zygosphene is present, but broken, and the zygantrum is high and narrow with thin bony septum situated medially inside. The ventral side of the transverse processes are almost on the same level as the dorsal side of the vertebral centrum. Pre- and postzygapophyses are not swollen (not pachyostotic). The postzygapophyses are positioned dorsally and their lateral top is clearly higher above of the level of the transverse processes. The articular facets of pre- and postzygapophyses form an angle of 20-25° with the horizontal. The neural canal is narrow, the width of the vertebral

centrum is 27 mm, while the height is 30 mm. There are no infrapre- and infrapostzygapophyses.

PAL 2019.172.1. **(Fig.7. D)** is an isolated dorsal neural arch having a similarly very high neural spine, in a good condition. The anterodorsal region of the neural spine shows a spongy area, moreover the top of the spine holds a saddle-shaped depression, with a smooth inner surface, probably representing an insertion for muscular tendons. The width of transverse processes is 68 mm, however, they cannot be measured exactly because of the torsion of the bone. The height of the neural spine is 99 mm. Vertical striations are present on the lateral surfaces of the latter. Pre- and postzygapophyses are not swollen.

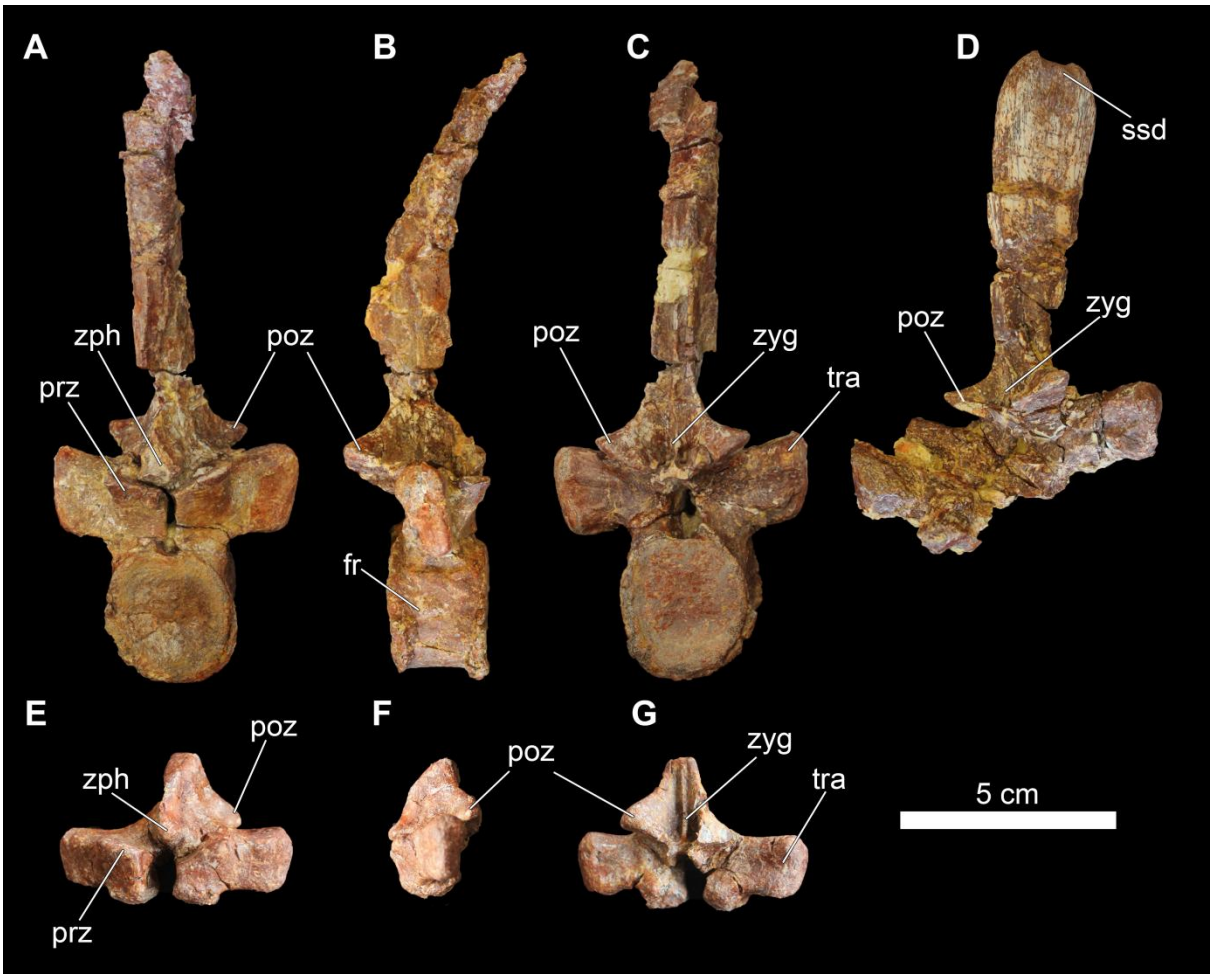


Figure 7. *Nothosaurus* cf. *mirabilis* vertebrae from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A-C**, dorsal vertebra (*PAL 2019.171.1.*) in anterior, right lateral, and posterior view; **D**, isolated dorsal neural arch (*PAL 2019.172.1.*) in posterior view; **E-G**, isolated cervical (?) neural arch (*PAL 2019.175.1.*) in anterior, left lateral, and posterior view. Anatomical abbreviations: *prz*: prezygapophysis, *poz*: postzygapophysis, *zph*: zygosphene, *zyg*: zygantrum, *tra*: transverse process, *ssd*: saddle-shaped depression, *fr*: foramen

PAL 2019.175.1. **(Fig.7. E,F,G)** is an isolated neural arch with a similar morphology like *PAL 2019.172.1.* and *PAL 2019.171.1.*, however this arch displays a lower neural spine which tilts anteriorly. The width of the slender transvese processes is 65 mm, and the heigth of the neural spine is only 27 mm. Pre- and postzygapophyses are not swollen and their articular facets form an angle of 20° with the horizontal. Zygosphene and zygantrum is present, and the latter holds a thin bone septum situated medially inside. The right postzygapophysis is broken, the left is intact, shifted dorsally and its lateral top is situated higher than the dorsal side of transverse processes. The transverse processes ventrally do not reach the level of the neural centrum.

Discussion: The vertebra *PAL 2019.171.1.* and neural arches *PAL 2019.172.1.*, *PAL 2019.175.1.* belong to the genus *Nothosaurus.* They differ from the vertebrae of *Pachypleurosaurus* and *Lariosaurus* because those genera show distinctly lower neural spines and swollen (pachyostotic) pre- and postzygapophyses (Rieppel 2000). The lack of infrapre- and infrapostzygapophyses differentiates them from the vertebrae of *Simosaurus* (Rieppel 1994a). Moreover pistosaurids have narrower zygapophyses, longer transverse processes and the foramens of vertebral centra ('subcentral foramen') are situated symmetrically (Sues 1987; Sander et al. 1997). According to Rieppel and Wild (1996) the isolated nothosaur postcranial material from Europe and the Middle East can be diagnostic in two cases. The very large sized bones may represent the fossils of *N. giganteus*, which species is believed to be the massive top predator of the western Tethyan realm (Rieppel 2000; Liu et al. 2014). Other species-characteristic elements are the dorsal vertebrae with extremely elongated neural spines, which probably belonged to the middle-sized (3-4 m long) *N. mirabilis* (Rieppel and Wild 1996; Rieppel 2000, 2001). The Late Triassic *Bobosaurus forojuliensis* DALLA VECCHIA, 2006 also exhibits highly elongated neural spines, but in case of this species the vertebrae are more complex and exhibit additional infrapre- and infrapostzygapophyses (Dalla Vecchia 2006). *N. tchernovi* HAAS, 1980 and *N. haasi* are also characterized by elongated neural spines. However the postcranial material described as *N. haasi* represents a much smaller size class with more slender vertebrae (Rieppel et al. 1999). The vertebrae with elongated neural spines from Villány also differ from *N. tchernovi*, because in case of this species the transverse processes are positioned more dorsally and they do not take part in the formation of the high neural canal, moreover the postzygapophyses are not situated above the transverse processes (Rieppel et al. 1999). The high neural spines and relative position of postzygapophyses are very similar to the *N. mirabilis* vertebrae illustrated by Rieppel and

Wild (1996), on the other hand, the neural canal is more wider on the illustrated specimen (Rieppel and Wild 1996:Fig.20.). Nonetheless, I suggest that these vertebrae from Villány with very high neural spines most probably belong to *N. mirabilis* or a closely related unknown taxon. *PAL 2019.175.1.* is a similar neural arch, with the same transverse process, zygapophyses, zygosphene and zygantrum morphology as *PAL 2019.171.1.* and *PAL 2019.172.1.* but its neural spine is much lower. Despite this difference, this neural arch probably belonged to the same species but was positioned on a different part of the vertebral column: the cervical vertebrae show lower neural spines in case of *N. mirabilis* too (Rieppel 2001).

Sauropsida HUXLEY, 1864

Sauropterygia OWEN, 1860

Eosauropterygia RIEPPEL, 1994a

Nothosauroidea BAUR, 1889

Nothosauria BAUR, 1889

Nothosauridae BAUR, 1889

Nothosaurus MÜNSTER, 1834

***Nothosaurus* cf. *marchicus* KOKEN, 1893**

(Figure 8.-9.)

Material: two small sized fragmentary skull *PAL 2019.156.1.*, *PAL 2019.181.1*.

Description: PAL 2019.156.1. **(Fig.8.)** is a dorsoventrally flat, small sized partial skull preserved in almost three dimensions and comprises of the posterior region of the braincase and the parietal skull table, the posterior parts of the upper temporal arches and the almost complete basicranium. The total width of the cranium measured across the quadrates is 55 mm, while the thickness is 15 mm measured between the pterygoids and the parietal. The squamosals form the posterior part of the upper temporal arches, and ventrally projecting ridges overhang from their ventral side. The suture of parietal and squamosals are visible by the posterior end of the temporal fenestrae. The unpaired (fused) parietal skull table is posteriorly strongly constricted, it is only 2 mm thick by the narrowest point but does not form a sagittal crest. Due to the incompleteness of the skull, the dimension and exact position of the pineal foramen is unknown, however it is clearly separated from the posterior end of the skull table with a short distance. The anterior opening of the cranioquadrate passage is present posterolaterally to the temporal openings on both sides. The passage is bordered ventrally by the pterygoid and roofed over by the squamosal. The posterior opening of the passage is present on the left side of the skull, while the squamosal is broken on the right side of this region. Ventrally, the basicranium is bordered by the pterygoids, which are posterolaterally diverging to the quadrates. Both quadrates are preserved, but the right one is damaged. They are broad and flat elements, however, effects of compression cannot be excluded. Ventrally the pterygoids are fused with a strong interdigitating suture and ventromedial flanges are present on the backward extending quadrate rami. The right pterygoid is more complete, while the left is laterally broken. The region around the foramen magnum is badly preserved, the ventral (domed) part of supraoccipital is incomplete. The

supraoccipital carries a 1 mm thick sagittal crest. Occipital crest is present dorsally to the supraoccipital, this crest is on average 2 mm high and 1 mm thick. The suture of supraoccipital and parietal is not recognizable due to the poor preservation or the complete ossification of the specimen. The exoccipital and opisthotic cannot be separated, however the jugular and eustachian foramens are visible laterally to the basioccipital. The occipital condyle (5 mm wide horizontally and 4 mm tall vertically) is built of only the basioccipital. Lateroventrally to the condyle, two basioccipital tuberosities are present and the size of them is slightly smaller, but almost reaches the size of the basioccipital (each of them is 4 mm horizontally and 4 mm vertically). The sutures between the exoccipital, supraoccipital, and opisthotic moreover between pterygoid, opisthotic and exoccipital are also not clear.

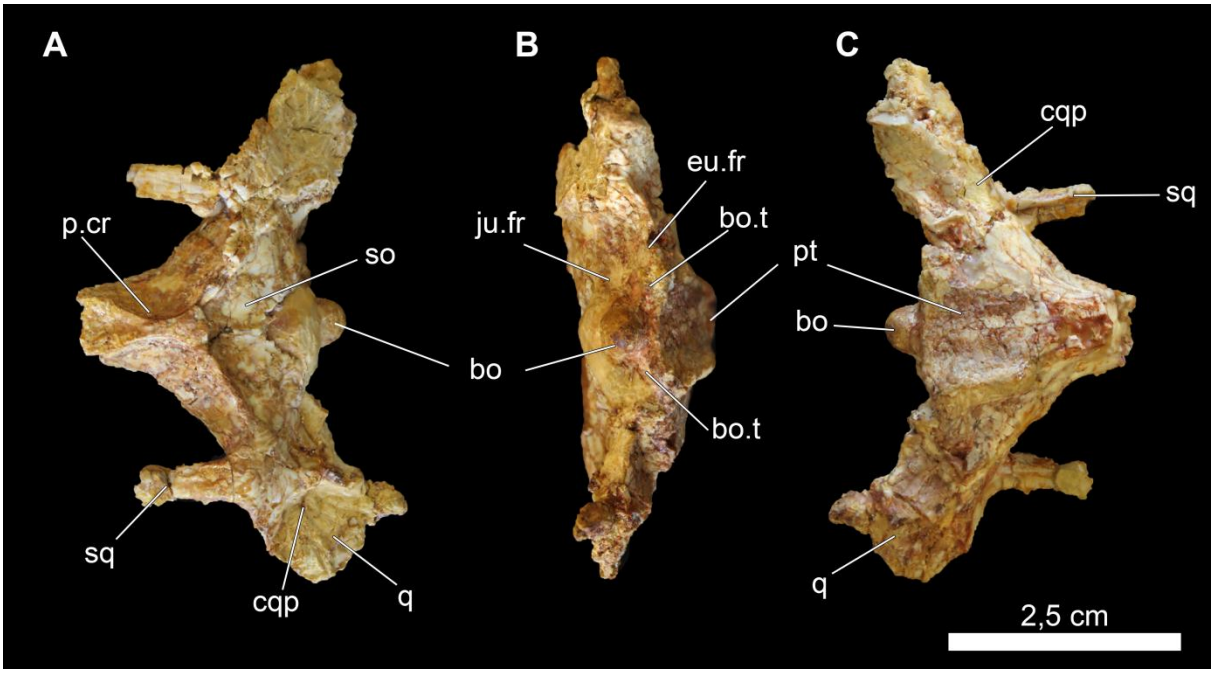


Figure 8. *Nothosaurus* cf. *marchicus* skull fragment (*PAL 2019.156.1.)* from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A**, in dorsal view; **B**, in posterior view; **C**, in ventral view. Anatomical abbreviations: *p.cr*: parietal constriction, *sq*: squamosal, *cqp*: cranioquadrate passage, *q*: quadrate, *bo*: basioccipital, *so*: supraoccipital, *ju.fr*: jugular foramen, *eu.fr*: eustachian foramen, *bo.t*: basioccipital tuber, *pt*: pterygoid

PAL 2019.181.1. **(Fig.9.)** is a fragmentary and dorsoventrally compressed skull, which comprises of a small remained part of the preorbital region, the parts around the right orbit, postorbital region with the left temporal arch, braincase and basicranium. The skull is highly dolomitised anteriorly, especially around the orbits, where the exact boundary between

the bone and enclosing rock is not obvious, consequently the real expansion of the cavity is not known. The largest width of the skull is 86 mm, measured across the compressed quadrates, while the largest length between the most anterior part and the occipital condyle is 120 mm. The width of the skull, by the level of the most anterior points of the temporal fenestrae is 50 mm. The skull is distinctly flat, its thickness is 15 mm measured between the parietal and the pterygoids. The left temporal arch is preserved in better condition: the anteroposterior elongation of the left fenestra is 40 mm, while its largest width is 12 mm. The preserved right nasal is broad, 'leaf-shaped'. Posteriorly to this nasal the connection of frontal and prefrontal is not visible. The frontal starts to widen behind the orbits. The postfrontal contacts the parietal posteriorly, unlike the postorbital which is not extended backwards in medial direction. The suture of parietal and frontal is not visible. Due to the poor preservation of the specimen, the connection of postorbital with the jugal and maxilla, moreover the anterior sutures of squamosals, are not clear. Two small (3 and 4 mm long) pointed teeth with longitudinal striations are preserved in the right, fragmentary maxilla by the level of the orbits. The parietal is fused (unpaired). Foramen parietale is 6 mm long (anteroposteriorly) and 3.5 mm wide, it is separated from the posterior end of the parietal skull table with 10 mm distance. The parietal is strongly constricted behind the parietal foramen (by the narrowest point is only 3 mm wide), but it does not form a sagittal crest. The thickness of occipital crest, present anteriorly to the supraoccipital, is 2 mm, while it is 1 mm high. The openings of cranioquadrate passages are present posterolaterally to the temporal openings on both sides. The passage is bordered by the pterygoid ventrally and roofed over by the squamosal. Ventrally the basicranium is bordered by the pterygoids, which are posterolaterally diverging to the quadrates. They are broad and flat elements, but especially the right quadrate is compressed. Ventrally the pterygoids seem to be fused, however the suture is not visible (probably due to the poor preservation). Ventromedial flanges are present on the backward extending quadrate rami. The suture of supraoccipital and parietal is not recognizable (because of the preservation or the complete ossification). The supraoccipital carries a 1 mm thick sagittal crest. The sutures of the exoccipital, supraoccipital, and opisthotic moreover between the pterygoid, opisthotic and exoccipital are also not clear. The preservation around the occipital condyle and foramen magnum did not allow me to describe the basicranium in detail. The occipital condyle is 6 mm high and 9 mm wide, however the size and position of basioccipital tuberosities also can not be seen.

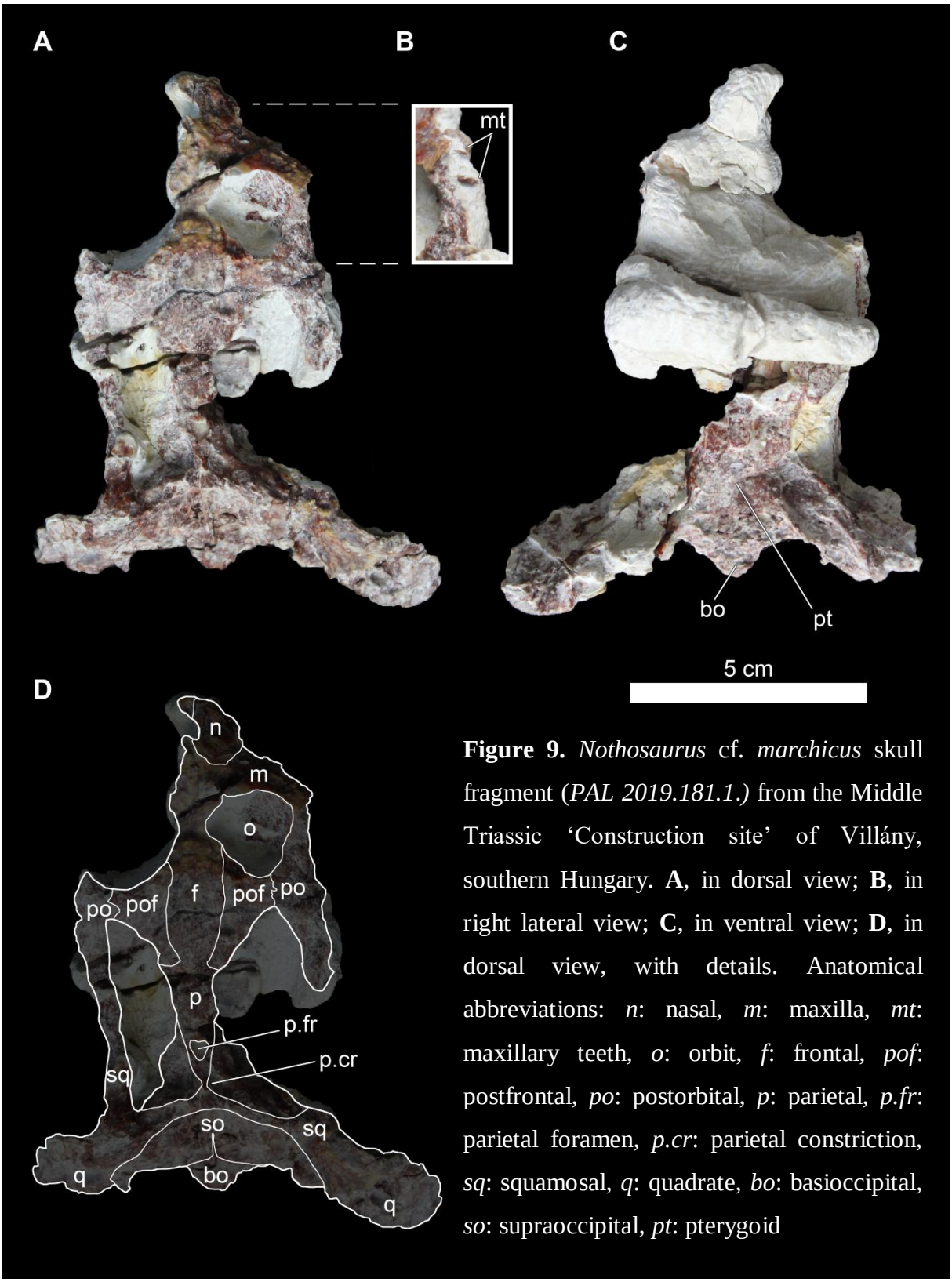


Figure 9. *Nothosaurus* cf. *marchicus* skull fragment (*PAL 2019.181.1.)* from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A**, in dorsal view; **B**, in right lateral view; **C**, in ventral view; **D**, in dorsal view, with details. Anatomical abbreviations: *n*: nasal, *m*: maxilla, *mt*: maxillary teeth, *o*: orbit, *f*: frontal, *pof*: postfrontal, *po*: postorbital, *p*: parietal, *p.fr*: parietal foramen, *p.cr*: parietal constriction, *sq*: squamosal, *q*: quadrate, *bo*: basioccipital, *so*: supraoccipital, *pt*: pterygoid

Discussion: Despite that the skull *PAL 2019.156.1.* is more fragmentary, it is less dolomitised and suffered less torsion, preserved almost in three dimensions. In contrast the other skull (*PAL 2019.181.1.*) shows more features around the orbits, however it is more dolomitised and sligthly compressed. These crania are comparable in size and proportions, and they share the same features on the posterior part of the skull table. However, due to their preservation (or maybe the ossification) some sutures can not be seen clearly. The dorsoventral dimension of the skulls is different from that is typical for *Simosaurus* and pistosaurs, moreover the situation of pterygoids and presence of pterygoid flanges and the occipital crest are characteristics of Nothosauridae and differs from pachypleurosaur skulls (Rieppel 1994b, 2000). Similarly, because the quadrates are almost on the same level as the basioccipital, we can exclude the pistosaurian affinity (Rieppel 2000). The parietal skull table is much broader in *Simosaurus, Germanosaurus* and *Corosaurus*, moreover the latter two genera show paired (not fused) parietals, and especially the pineal foramen of *Corosaurus* is located on the center of the parietals (Storrs 1991). This foramen is also placed on the center of parietals in case of *Cymatosaurus* (Rieppel, 2000).

Unfortunately, the braincase and basicranium morphology is not diagnostic without the anterior region of the skull (Rieppel 2000), thus the anatomy of *PAL 2019.156.1.* is not useful itself for the accurate determination of this skull fragment, because the basicranium and braincase of *Nothosaurus* or *Lariosaurus* genera are very similar (Rieppel 1994b). The ossified braincase and the deeply interdigitating suture of pterygoids suggest that both skulls mentioned here belonged to fully grown animals, but since the ontogenetic stages of many eosauropterygian is unknown, this feature is always a matter of question. Nevertheless it must be noted, that several nothosaurid species are known with a similarly small adult skull size (Rieppel and Wild 1996; Rieppel 2000).

The relative position of parietal foramen (visible on both skull), which is situated somewhat anteriorly than the posterior end of the parietal skull table, moreover the highly constricted parietal - which does not form a sagittal crest - is similar to that of *Nothosaurus jagisteus*, *N. marchicus*, *N. rostellatus* SHANG, 2006, *Lariosaurus xingyiensis* LI, LIU AND RIEPPEL, 2002 and *L. valceresii* TINTORI AND RENESTO, 1990 (Rieppel and Wild 1996; Rieppel 2001; Li et al. 2002; Rieppel et al. 2003; Shang 2006; Tintori and Renesto 2016). This kind of parietal structure is clearly different from that we can expect in case of skulls of middle or larger sized *Nothosaurus* species, such as *N. mirabilis* or *N. giganteus* MÜNSTER, 1834. Another interesting feature of the *PAL 2019.156.1.* skull from Villány, is the large size of basioccipital tuberosities (which are almost as large as the basioccipital). Based on the

available information both *N. marchicus* and *N. jagisteus* can be described with proportionally smaller tubers, however these features are not known in case of every nothosaurid species (Rieppel et al. 2003). The large basioccipital tuberosities are mentioned as an important character of *N. edingerae* (Rieppel and Wild 1994), but this animal had a distinct sagittal crest behind the pineal foramen (a feature, what is missing from the skulls described here). In compared with the more complete skull, the cranium of *N. jagisteus* is different because the postorbital extends backwards medially and meets the parietal posteriorly, and the nasals are slender, elongated elements, moreover the temporal fenestrae are somewhat more elongated (Rieppel 2001). The comparison is difficult, because the rostral region of the skulls from Villány are missing, and the intraspecific variation of *N. jagisteus* is not known, because (as far as I know) only one specimen has been described (Rieppel 2001). *Lariosaurus xingyiensis* also different with its proportionally smaller, triangular-like postfrontals and connected postorbital and parietal (Rieppel et al. 2003, Lin et al. 2017). *N. rostellatus* differs again with its connected postorbital and parietal and the parietal posteriorly seems less constricted (Shang 2006). The parietal-postorbital-postfrontal arrangement of *Lariosaurus valceresii* is similar to the skull (*PAL 2019.181.1.*) from Villány, however the nasals of this species are trapezoidal and on the skull from Villány there is no sign of such a broad prefrontal visible on *L. valceresii* (Tintori and Renesto 1990).

Even though *PAL 2019.156.1.* is more fragmentary and its features are not diagnostic itself on species level, since it is comparable in size, proportions and shows the same (posterior) parietal structure as *PAL 2019.181.1*., following the principle of parsimony I tentatively refer them in the same taxon. The small overall size and posteriorly constricted parietal, moreover the distance between the posteriorly displaced pineal foramen and the posterior margin of parietal skull table are characterstics of *N. marchicus*, which species is also known by its broad and 'leaf-shaped' nasals (Rieppel and Wild 1996; Rieppel 2000). In fact, among the *N. marchicus* specimens, the parietal-postorbital-postfrontal arrengement visible on *PAL 2019.181.1*. is present on the skulls desscribed as *N. procerus* (see Rieppel and Wild 1996:Fig.34.), a species which is known as a synonym of *N. marchicus*. According to Schultze (1970) *N. procerus* and *N. marchicus* were separate species, and one of the main caharacters led to this conclusion was the relation of postfrontal and postorbital with the margin of upper temporal fenestra. In case of *N. procerus*, the participation of postfrontal in the laterally descending flanges of the medial margin of upper temporal feneastra is significant, while the postorbital is not extended medially into the flanges. Following the revison of Rieppel and Wild (1996), *N. procerus* is now believed to be the synonym of *N.*

marchichus, and according to the authors, the characters that differentiated the two species show a continous transition among the *N. marchicus* specimens.

To sum up, despite the poor preservation of these skulls, here I suggest that the Villány skulls most probably belong to *N. marchicus* or a closely related taxon.

Sauropsida HUXLEY, 1864

Sauropterygia OWEN, 1860

Eosauropterygia RIEPPEL, 1994a

Nothosauroidea BAUR, 1889

Nothosauria BAUR, 1889

Nothosauridae BAUR, 1889

Nothosaurus MÜNSTER, 1834

***Nothosaurus* sp.**

(Figure 10.-13.)

Material: a small fragmentary mandible *PAL 2019.153.1.;* a large sized fragmentary right mandibular ramus *PAL 2019.155.1.;* isolated neural arches *PAL 2019.176.1., PAL 2019.177.1.;* a cervical vertebra *Pal 2019.173.1.;* humerus 'Morphotype-1' *PAL 2019.199.1., PAL 2019.200.1., PAL 2019.201.1., PAL 2019.202.1., PAL 2019.203.1., PAL 2019.204.1.;* humerus 'Morphotype-2' *PAL 2019.205.1., PAL 2019.206.1., PAL 2019.207.1., PAL 2019.208.1.;* additional fragmentary humeri *PAL 2019.197.1., PAL 2019.198.1.*

Description: PAL 2019.153.1. **(Fig.10.)** is a fragmentary mandible with preserved in situ teeth. The mandible is exposed only dorsally because it is still situated in the embedding marl (it was too fragmentary to clean it on both sides) and the left side of its symphysis is covered by extraneous bone fragments. The left ramus is almost complete (155 mm long, measured between the anteriormost point of the symphysis and the posterior end of the retroarticular process). Posteriorly the retroarticular process is compressed, but the articular is preserved. The right ramus is broken. The anterior part of the dentaries are fused in a lateromedially slightly wider than anteroposteriorly long spoon-shaped symphysis. The length of the spoon-shaped mandibular symphysis is 14 mm, while the largest width is 18 mm, and the rami are constricted posteriorly to the symphysis. Dorsally the suture of the symphysis is clearly visible and the bone surface is covered with small pits. The symphyseal ratio is 0.77 (length/width=14/18), which refers to a plesiomorphic, relatively blunt mandible and rostrum (Rieppel 2000). The mandibular symphysis is fragmentary, only four large (maximum 11 mm long) procumbent and vertically striated fang-like teeth are preserved. However, based on the preserved teeth, their position and the remained snags of the missing teeth, each ramus originally held five fangs in the symphysis region. The left side of the symphysis holds two preserved teeth, two visible broken piece, and on the right side additional two preserved teeth

and two broken remains are visible. The fifth fang is situated behind the level of the symphysis, and it is very close to the position of the fourth fang (while the other anterior teeth are separated with greater distances). The dentaries hold small pointed teeth (three-four times smaller than the teeth of symphysis) behind the mandibular constriction: the right dentary bears ten small teeth, while only four are preserved on the left side. In the left ramus, the articular, angular, surangular, prearticular, splenial are present, however due to the poor preservation of the specimen, the sutures are not clearly visible. The articular surface is a saddle-shaped and mediolaterally elongated, oval surface (anteroposteriorly 7 mm long, mediolaterally 11 mm wide). Posteriorly there is a small hollow probably indicating the place of chorda tympany foramen. The posteriormost point of the articular surface is 39 mm far from the posteriormost point of the ramus.

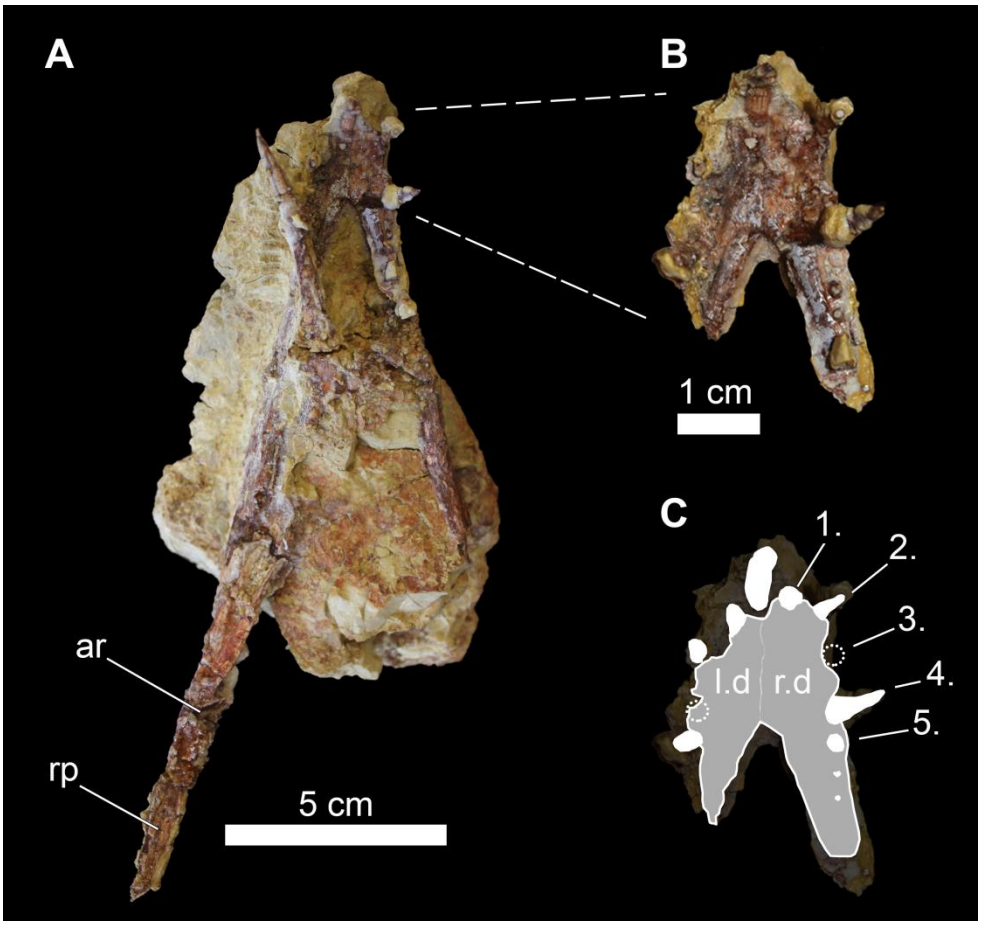


Figure 10. *Nothosaurus* sp. mandible (*PAL 2019.153.1.)* from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A**, in dorsal view; **B**, mandibular symphysis in dorsal view; **C**, mandibular symphysis with details: large symphysis teeth are numbered in the right dentary, missing teeth are drawn with dotted line. Anatomical abbreviations: *ar*: articular, *rp*: retroarticular process, *l.d*: left dentary, *r.d*: right dentary

PAL 2019.155.1. **(Fig.11.)** is a large, 490 mm long, fragmentary rigth mandibular ramus with preserved in situ teeth. The mandible is damaged and because of its poor preservation, the diagnostic features, such as the ratio of its mandibular symphysis, number and position of large anteriorly positioned fangs cannot be noticed. However, the only remained 31 mm long, vertically striated fang-like tooth is clearly the most posteriorly situated one on this ramus because it is immediately followed by the numerous small (between 5-15 mm high) pointed teeth in the dentary. Fifteen small teeth are visible in the dentary, their preservation is very poor, sometimes dolomitised. It is impossible to reconstruct the original morphology of the symphysis region, because anteriorly the bone is crushed and alveoli are not recognizeable. However, the shape of the ramus, and the position of the last fang, which is situated medially close to the level of the dentary, do not suggest a wide lateral expansion for the mandibular symphysis. The ramus is 65 mm high by its middle region, however it was mediolaterally crushed and highly dolomitized. The distance between the last tooth of the symphysis and the posteriormost point of the retroarticular process is 430 mm. The sutures are not clearly recognizeable, but probably the angular reaches the midpoint of the ramus and contacts the splenial. The distance between the posteriormost point of the articular surface and the posteriormost point of the retroarticular process is 68 mm.

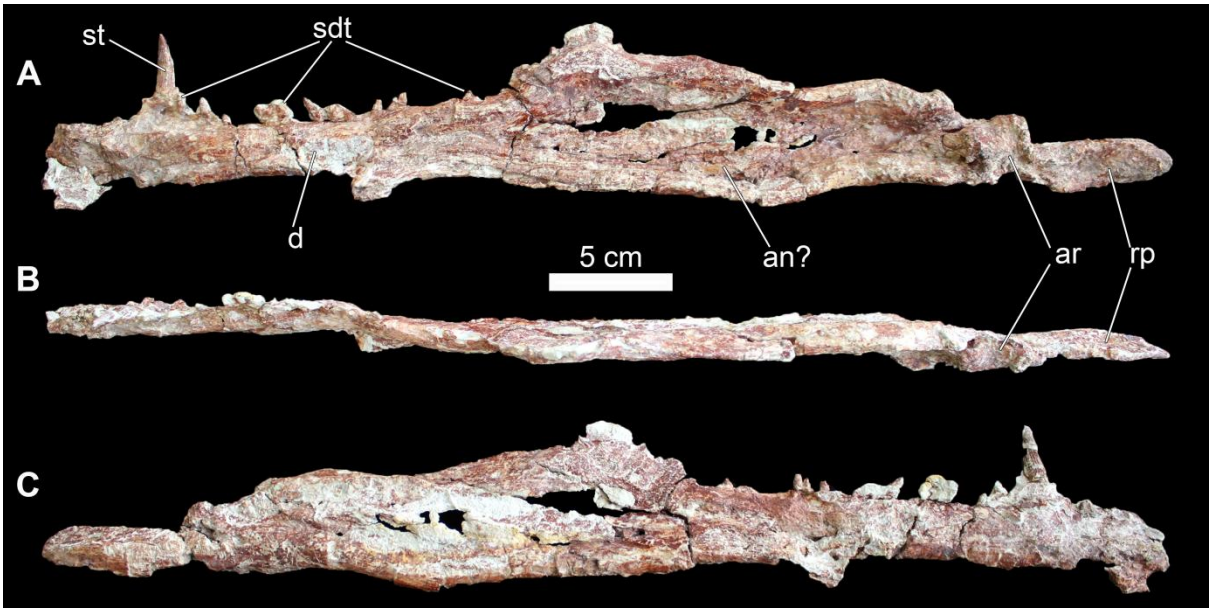


Figure 11. *Nothosaurus* sp. mandibular ramus (*PAL 2019.155.1.)* from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A**, in medial view; **B**, in dorsal view; **C**, in lateral view. Anatomical abbreviations: *ar*: articular, *rp*: retroarticular process, *an:* angular, *st*: symphyseal tooth, *sdt*: series of small dentary teeth, *d*: dentary

PAL 2019.176.1. **(Fig.12. A,B,C)** and *PAL 2019.177.1.* **(Fig.12. D)** are isolated neural arches with similar, moderately elongated neural spines with vertical striations on their lateral surface. Both neural arch represents slender and wide transverse processes (which do not reach the level of the vertebral centrum) and not pachyostotic pre- and postzygapophyses. *PAL 2019.176.1.* has 53 mm tall neural spine and 36 mm transverse process width, while the height of *PAL 2019.177.1.* is 42 mm and the width of the transverse processes is 38 mm. There are no infrapre- and infrapostzygapophyses on them.

Pal 2019.173.1. **(Fig.12. E,F)** is a 52 mm high cervical vertebra with broken transverse processes and a 19 mm tall moderately elongated neural spine. The diameter of the slightly amphicoelous vertebral centrum is 17 mm, striations are not visible on the neural spine. Bicipital cervical ribs are attached to the paraphophysis and diapophysis of the centrum. The zygosphene forms a deep trough posteriorly, the zygantrum is broken and the neurocentral suture is going through the diapophysis. Infrapre- and infrapostzygapophyses are not present.

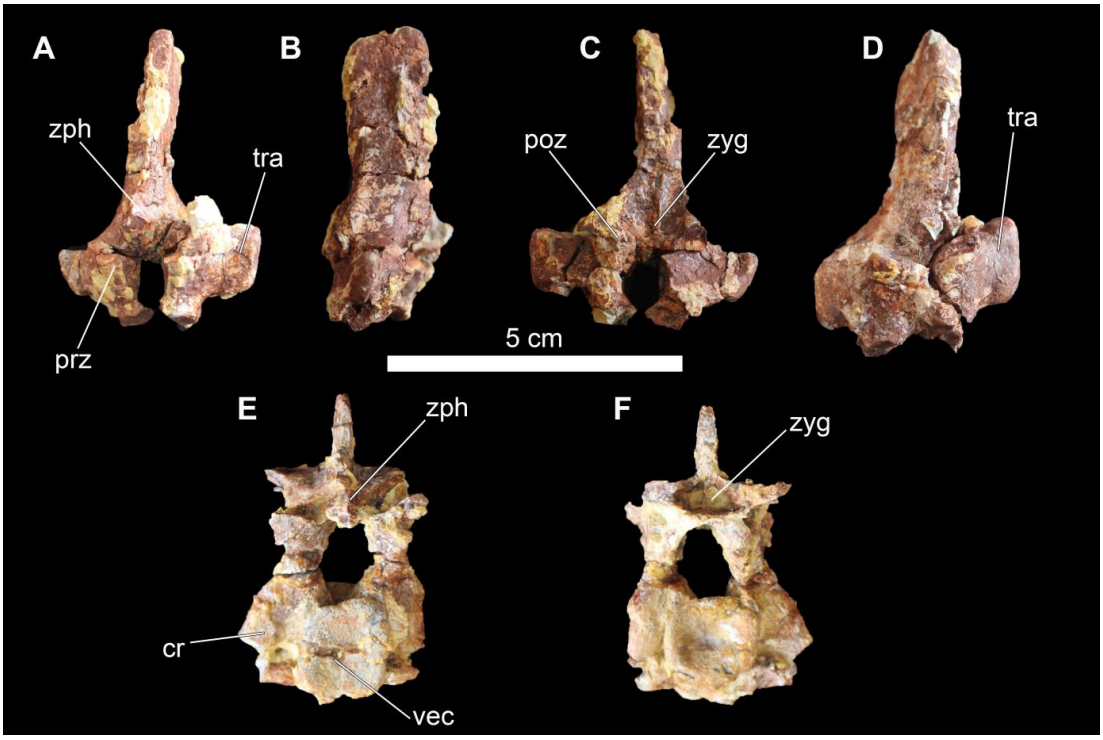


Figure 12. *Nothosaurus* sp. vertebrae from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A-C,** *PAL 2019.176.1.* neural arch in anterior, right lateral, and posterior view; **D,** *PAL 2019.177.1.* in posterior view; **E-F**. *Pal 2019.173.1.* cervical vertebra in anterior and posterior view. Anatomical abbreviations: *prz*: prezygapophysis, *poz*: postzygapophysis, *zph*: zygosphene, *zyg*: zygantrum, *tra*: transverse process, *cr*: cervical rib, *vec:* vertebral centra

The vertebrate material from Villány contains fragmentary and also well preserved humeri **(Fig.13.)**, most probably belonging to indetermined *Nothosaurus* species. The largest humerus (*PAL 2019.198.1.*) is a fragmentary (164 mm long) dorsoventrally chrushed specimen with incomplete proximal and distal portions **(Fig.13. I)**. *PAL 2019.197.1.* is another fragment of a large humerus, representing the 41 mm wide compressed portion of the proximal epiphysis. Besides them, numerous nearly complete smaller humeri have been found, which material can be divided into two morphotypes.

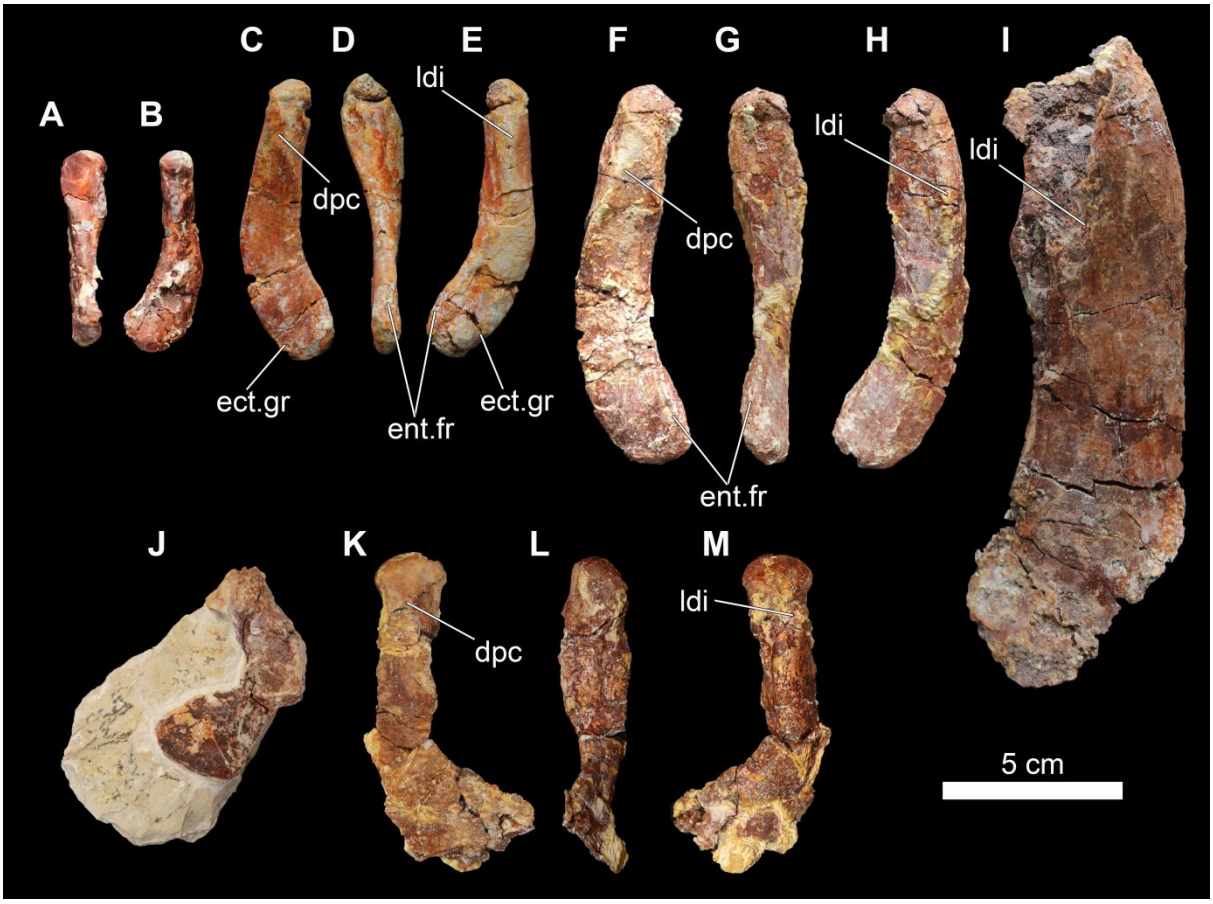


Figure 13. *Nothosaurus* sp. humeri from the Middle Triassic 'Construction site' of Villány, southern Hungary. **['Morphotype-1': A-H; 'Morphotype-2': J-M.] A-B:** *PAL 2019.199.1.* in postaxial and dorsal view; **C-E:** *PAL 2019.201.1.* in ventral, postaxial and dorsal view; **F-H:** *PAL 2019.202.1.* in ventral, postaxial and dorsal view; **I:** *PAL 2019.198.1.* in dorsal view**;** **J:** *PAL 2019.207.1.* in dorsal view; **K-M:** *PAL 2019.206.1.* in ventral, postaxial and dorsal view. Anatomical abbreviations: *dpc*: deltopectoral crest, *ect.gr*: ectepicondylar groove, *ent.fr*: entepicondylar foramen, *ldi*: latissimus dorsi insertion

These humeri are flat on their ventral side, they have a robust proximal and a fan-shaped distal epiphysis with weakly developed epicondyles. The diaphysis is not constricted and the cross section of the midshaft is triangular, indicating a well developed musculus latissimus dorsi insertion (which is a ridge on the dorsal side, proximally). Specimens grouped into 'Morphotype-1' **(Fig.13. A-H)** (*PAL 2019.199.1., PAL 2019.200.1., PAL 2019.201.1., PAL 2019.202.1., PAL 2019.203.1., PAL 2019.204.1.*) are characteristically slender and curved bones, with the angle of flexion on their diaphysis being almost the same on both the pre- and postaxial margins. Distally these humeri are slightly broadened and postaxially they hold an entepicondylar foramen. In case of well preserved specimens a shallow ectepicondylar groove is also visible. They have a bulbous proximal head and their prominent deltopectoral crest (on the ventral side) is slightly protruding in case of larger specimens. Their size ranges between 55-130 mm. Based on its shape *PAL 2019.198.1.* (the largest humerus from the material) is similar to 'Morphoype-1', however the bone is too incomplete to state this clearly.

In contrast, humeri of 'Morphoype-2' **(Fig.13. J-M)** (*PAL 2019.205.1., PAL 2019.206.1., PAL 2019.207.1., PAL 2019.208.1.*) show a more flattened and expanded (shovel-shaped) distal epiphysis. Distally to the bulbous proximal head, the shaft is straight and only after a certain point starts to bend postaxially. Unfortunately the preservation of these specimens is not good enough to detect the presence of entepicondylar foramen or ectepicondylar groove. Their size ranges between 58-90 mm.

Discussion: The most diagnostic region of the nothosaur mandibles is the spoon-shaped mandibular symphysis (Rieppel and Wild 1996), which mirrors the shape and constriction of the rostrum, however other morphological caharacters also can be helpful to separate the *Nothosaurus* remains. In contrast, the mandible of pachypleurosaurs can be described with a more slender appearance, short retroarticular process, without a wide mandibular symphysis (Rieppel 2000; Klein 2009). The mandible of *Simosaurus*, with its bulbous teeth, also lacks the spoon-shaped symphysis structure (Rieppel 1994a). The lower jaw of *Corosaurus* with its distinct coronoid process (Storrs 1991) also different from the *PAL 2019.153.1.* and *PAL 2019.155.1.* specimens. Unfortunately no lower jaw is known for *Cymatosaurus* and *Pistosaurus*, thus detailed comparison with them is not possible (Rieppel 2002). However the skull of *Pistosauruas* and *Augustasaurus* is highly similar, and, as suggested by Rieppel (2002), probably their mandible could have been alike. In case of *Augustasaurus*, heterodonty is present, but the difference between the enlarged anterior (fang-like) and the following teeth behind them is less significant (Rieppel 2002) than what is present on the *PAL 2019.153.1.*

and *PAL 2019.155.1.* mandible specimens (Rieppel 2000, 2002). In general, members of Pistosauridae have fewer and more widely spaced teeth which are more similar in size.

The partial mandible *PAL 2019.153.1.* with its low maximal length/width ratio (L/W: 0.77) suggests a plesiomorphic skull condition (Rieppel 2000). The morphology of the lower jaw material referred to *Lariosaurus* is different from *PAL 2019.153.1.* because this genus can be described with more elongated rostrum region with a less prominent rostral constriction (Rieppel 2000). The ratios of the symphysis, moreover the number and position of the large anterior procumbent fang-like teeth (five large teeth in each dentary, the fifth teeth is behind the level of the symphysis, the fourth and fifth teeth are only separated by a thin bone septum) correspond to the previously described (Ősi et al. 2013:Fig.6.) *Nothosaurus* sp. mandible (*Ver 2013.1.*) from the Villány locality. However, that previously described specimen is much larger and their maximal length/with ratio is 0.86 (Ősi et al. 2013). Among nothosaurs *N. giganteus* (L/W: 1-1.03), *N. marchicus* (L/W: 0.7-1) and *N. zhangi* (L/W: 0.64) was described with similarly low length-to-width ratios (Rieppel and Wild 1996; Rieppel 2000; Liu et al. 2014). Moreover, Rieppel et al. (1999) reported an unspecified Middle Triassic *Nothosaurus* sp. (L/W: 0.54) mandible from Israel with 'unusually low length-to-width ratio' (Rieppel et al. 1999:Fig.45.). In case of this unusaual specimen, both the fourth and fifth teeth are situated behind the level of the symphysis. Unfortunately, the material referred to *N. zhangi* exhibits only the ventral side of the symphysis (Liu et al. 2014), thus further information about the position of the teeth is not available. The average size of the *N. marchicus* mandibles is quiet similar to the *PAL 2019.153.1.* specimen, but in case of *N. marchicus* all of the teeth are separated by the same distance in the symphysis (Rieppel and Wild 1996). The position of the teeth is similar to *N. giganteus* amongst the nothosaurs with plesiomorphic mandible morphology (Rieppel and Wild 1996), however, because the *PAL 2019.153.1.* specimen is too fragmentary and character changes through the ontogenetic stages of nothosaurs are not known, more precize taxonomic identification of *PAL 2019.153.1* is not possible at present. Based on only its anatomy the specimen could represent a juvenile *N. giganteus*, or a species with previously unknown mandible remains, but its affinity to *N. marchicus* is also highly potential.

The large sized (490 mm) fragmentary right mandibular ramus *PAL 2019.155.1.* was definitely longer with several centimeters because the anterior part of the symphysis is broken. The size of the specimen and the presence of highly elongated procumbent teeth in the symphysis suggest its affinity to a larger nothosaur species like *N. giganteus*, *N. zhangi* or maybe *N. mirabilis* (Rieppel and Wild 1996; Rieppel 2000; Liu et al. 2014). The presumed

large size of the animal makes it more similar to a *Nothosaurus* than a *Lariosaurus* species (Rieppel 1998, 2000). The condylobasal skull length of the largest known skull referred to *N. giganteus* is 750 mm, while the largest known full mandible is 610 mm long (Rieppel and Wild 1996). The lower jaw of *N. zhangi* is measured 650 mm (Liu et al. 2014), whereas the largest described *N. mirabilis* skull was 460 mm long (Rieppel 2000) so far as I know. Without the intact characteristic symphysis area, the mandible cannot be described surely neither as *N. mirabilis* nor *N. giganteus* or *N. zhangi*. Its size could fit surely into the known sizes of the two larger species, but because the ontogenteic stages of nothosaurs are not known (Rieppel 2000), I cannot exclude that the mandible belonged to a larger *N. mirabilis* specimen. Moreover, the preserved part of the symphysis area does not suggest a wide lateral expansion, which could refer to *N. giganteus* or *N. zhangi*, in contrast, it is more similar to the elongated mandibular symphysis of *N. mirabilis*, but maybe it is only caused by the mediolateral compression of the specimen.

The isolated neural arches *PAL 2019.176.1.* and *PAL 2019.177.1.*, moreower the cervical vertebra *Pal 2019.173.1.* do not belong to *Pachypleurosaurus* or *Lariosaurus*, because these remains from Villány exhibit higher neural spines and not swollen zygapophyses (Rieppel 2000). The lack of infrapre- and infrapostzygapophyses clearly differentiates them from the vertebrae of *Simosaurus* (Rieppel 1994a). Pistosaurids have more robust neural arches and narrower zygapophyses with shorter neural spines and longer transverse processes (Sues 1987; Sander et al. 1997). Unfortunately, within the genus *Nothosaurus* majority of the postcranial material is not known or can not be linked to a definite species with full certainty (Rieppel et al. 1999; Rieppel 2000). The vertebrae of *N. zhangi*, *N. giganteus* and *N. marchicus* have relatively lower neural spines (Rieppel and Wild 1996, Liu et al. 2014), while *N. haasi*, *N. mirabilis*, *N. tchernovi* and *N. jagisteus* RIEPPEL, 2001 can be described with more elongated neural spines (Rieppel and Wild 1996; Rieppel et al. 1999; Rieppel 2001). In case of *N. mirabilis* and *N. jagisteus*, the postzygapophyses are positioned more dorsally than what is present on these isolated neural arches from Villány (Rieppel and Wild 1996; Rieppel 2001). The dorsal neural arches of *N. haasi* are highly similar to the Villány specimens with their similar size, oval neural canal, slender neural spines. However it must be noted that the postcranial material referred to *N. haasi* is isolated, and the link between this isolated material and the holotype skull of the species is only based on parsimony (Rieppel et al. 1999). The isolated neural arches differ from those of *N. tchernovi*, because this species have more robust transverse processes and more elongated neural canal (Rieppel et al. 1999). Because these remains are fragmentary and have been

unearthed isolated, moreover because similar neural spines in the literature have been assigned to certain species mostly tentatively, here I refer them only to *Nothosaurus* sp.

The isolated humeri with their flat ventral side, robust angulated proximal and sligthly fan-shaped distal epiphyses, weekly developed epicondyles, and triangular cross section (well developed musculus latissimus dorsi insertion) indicates their *Nothosaurus* origin (Bickelmann and Sander 2008; Klein 2010). In contrast, the humeri of placodonts are much more simple, robust elements (Klein 2010). The humerus of *Simosaurus* is also different with its wider fan-shaped distal epiphysis and strongly constricted diaphysis (Rieppel 1994a; Klein and Griebeler 2016). The humeri referred to *Cymatosaurus* (Rieppel 1994a) also differ from the above mentioned elements from Villány with their broad and more complex distal epiphysis, constricted midshaft (Rieppel 1994a). The humeri of *Pistosaurus* are generally straighter, the distal end is more expanded and the whole bone is characteristically flattened (Sues 1987). Despite the close phylogenetic connection of the *Nothosaurus* and *Lariosaurus* genera, the humeri of the two taxa are quiet different. In case of *Lariosaurus*, the deltopectoral crest is less developed, moreower the midshaft is not constricted and the bone gradually widens distally (Rieppel 2000; Lin et al. 2017). Based on these differences I exclude the *Lariosaurus* origin of the above mentioned humeri and I describe them as *Nothosaurus* sp.

The two different morphotypes presented here could belong to different nothosaurs, however they could be representatives of the different sex from the same species. Previously Bickelmann and Sander (2008) described *Nothosaurus* humerus morphotypes from the Germanic Basin. The ‘Morphotye II’ described by Bickelmann and Sander (2008) shows several similarities (overall shape, morphology of the distal end, location of foramina) with the ‘Morphotype-1’ presented here, whereas their ‘Morphotye III’ also resembles in its curvature and strong proximal end the ‘Morphotype-2’ from Villány. Bickelmann and Sander concluded that their ‘Morphotye II’ probably belongs to *N. marchicus*, and maybe their ‘Morphotye III’ could represents the sexual dimorphic variant of the same species. Despite that exact information is not known about the real intraspecific variations of nothosaurs, the similarities between the humeri from Villány and the presumed *N. marchicus* humeri from the Germanic Basin is remarkable.

Sauropsida HUXLEY, 1864

Sauropterygia OWEN, 1860

Eosauropterygia RIEPPEL, 1994a

Nothosauroidea BAUR, 1889

Nothosauria BAUR, 1889

Nothosauridae BAUR, 1889

Nothosauridae indet.

(Figure 14.-15.)

Material: mandibular ramus fragments *Pal 2019.151.1.*, *Pal 2019 152.1.*; two isolated ilia *PAL 2019.157.1.*, *PAL 2019.158.1.*

Description: Pal 2019.152.1. **(Fig.14. A,B,C,D)** is a 84 mm long, posterior fragment of a left mandibular ramus. The retroarticular process distally, and the articular laterally are broken. Surangular, prearticular and angular are present, and possibly the chorda tympany foramen is visible posteriorly to the articular. The splenial and dentary are both missing. The articular surface is roundish in a dorsal view, it is 22 mm long and 24 mm wide. Medially, the posterior part of the adductor fossa is visible, the angular is situated below the mandibular joint.

Pal 2019.151.1. **(Fig.14. E,F,G,H)** is a 116 mm long fragmentary right mandibular ramus. The retroarticular process is intact, but the articular surface is slightly broken. However, the shape of the latter is saddle-like and its appearance suggest a mediolaterally wider (18 mm) than anteroposteriorly long (13 mm) articular surface. The surangular and prearticular are present but the dentary is broken. The surangular defines laterally the ramus. The angular is also damaged and incomplete, but probably it was situated under the mandibular joint. The distance between the posteriormost point of the retroarticular process and the posteriormost point of articular surface is 30 mm.

Two isolated ilia **(Fig.15.)** have been found, *PAL 2019.157.1.* is a 41 mm long, while *PAL 2019.158.1.* is a larger, more fragmentary 59 mm long ilium. They are constricted in the middle, between the dorsal process and the ventrally expanded deeply concave acetabulum. Medially the bone surface is strongly striated.

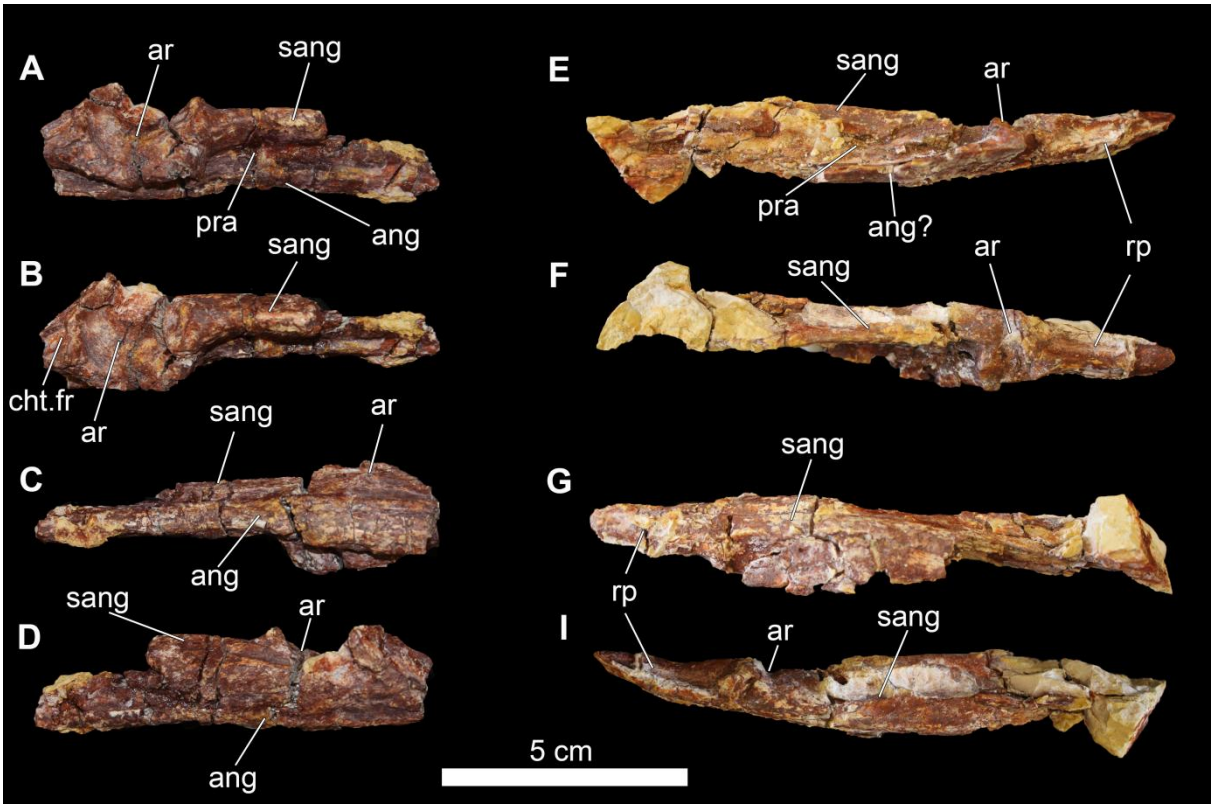


Figure 14. Nothosauridae mandible fragments from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A-D:** *Pal 2019.152.1*. in medial, dorsal, ventral and left lateral view; **E-I:** *Pal 2019.151.1*. in medial, dorsal, ventral and right lateral view. Anatomical abbreviations: *rp*: retroarticular process, *ar*: articular, *sang*: surangular, *pra:prearticular*, *ang*: angular. *cht.fr*: chorda tympany foramen

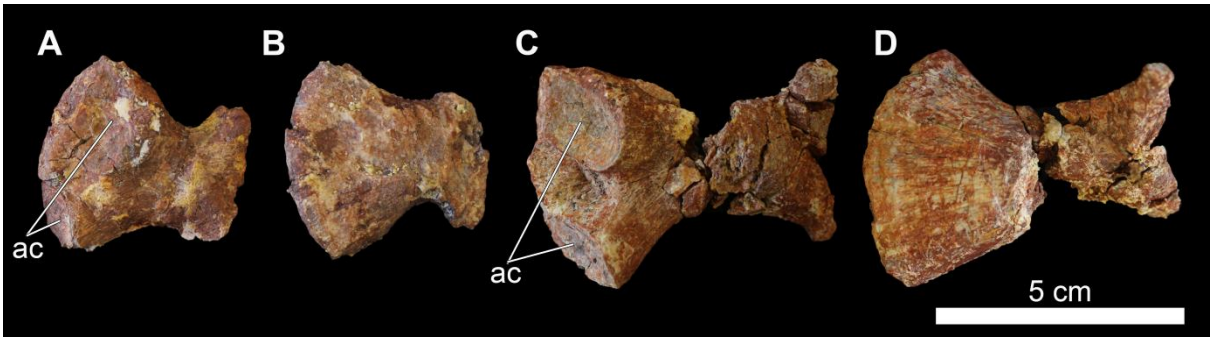


Figure 15. Nothosauridae ilia from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A-B:** *PAL 2019.157.1*. in lateral and medial view*;* **C-D:** *PAL 2019.158.1*. in lateral and medial view. Anatomical abbreviations: *ac*: acetabulum

Discussion: The posterior mandible fragments referred here to Nothosauridae are not diagnostic without the mandibular symphysis (Rieppel and Wild 1996). However, they are straight and slender, which clearly differs from the mandible of *Simosaurus* (Rieppel 1994a). The distinct retroarticular process is not present in the more slender mandibles of pachypleurosaurs (Rieppel 2002). Unfortunately, a comparable three dimensionally preserved *Cymatosaurus* mandible is not known (Rieppel 2000, 2002), however both fragments described here differ from the mandible of *Corosaurus,* because the glenoid on the *Pal 2019.152.1*. specimen is proportiopnally larger than those of the latter genus and the more complete *Pal 2019.151.1*. lacks the distinct coronoid process, which is characteristic for *Corosaurus* (Storrs 1991). The mandible of *Augustasaurus* (and the hypothetical reconstruction of the unknown jaw morphology of *Pistosaurus* based on *Augustasaurus* by Rieppel 2002) is a more curved and dorsoventrally more elevated structure. The laterally projecting shelf of the surangular, and the broadened angular with distinct slender, long retroarticular process suggest their affinity to Nothosauridae (Rieppel 2000, 2002). The mandible fragments described here have different shaped (roundish and more oval) glenoids. The taxonomic importance of these features is not known, nevertheless the mandible fragment *Pal 2019.152.1*. is very similar to those what Rieppel (1994a) tentatively described as *N. mirabilis* (Rieppel 1994a:Fig.12.).

The isolated ilia from Villány differ from the remains belonging to Placodontia, because the dorsal process of those is more expanded, moreover the acetabular portion is squarer. In addition, the anterior and posterior margins of the known placodont ilia are asymmetric (Rieppel 1995, 2000). The ilia of pachypleurosaurs are characterized by a much more reduced dorsal portion (Sues and Carroll 1985; Rieppel 2000). Comparable well preserved ilium of *Cymatosaurus* and *Pistosaurus* are not known (Rieppel 2000), however the ilium of *Corosaurus* (Storrs 1991) is clearly different with its more expanded dorsal portion and asymmetric anterior and posterior margins. The ilia referred to *Simosaurus* (Rieppel 1994a) with their more complex, subdivided acetabulum and prominent sacral rib insertions also differ from the specimens described here. These remains most similar to the ilia believed to be the remains of *Nothosaurus* sp. (Rieppel 2000), however I suggest to describe them as Nothosauridae indet., because the postcranial elements of *Nothosaurus* and *Lariosaurus* are highly similar, and the fragmentary condition of this ilia does not allow me to determine them clearly on genus level.

Sauropsida HUXLEY, 1864

Sauropterygia OWEN, 1860

Eosauropterygia RIEPPEL, 1994a

Nothosauroidea BAUR, 1889

Simosauria RIEPPEL, 2000

Simosauridae HUENE, 1948

Simosaurus MEYER, 1842

***Simosaurus* sp.**

(Figure 16.-18.)

Material: a posterior part of a left mandibular ramus *PAL 2019.154.1.*; two vertebral centra *PAL 2019.182.1.*, *PAL 2019.183.1.*; three isolated dorsal neural arch *Ver 2013.5.*, *PAL 2019.178.1.*, *PAL 2019.179.1.*; one sacral vertebra *PAL 2019.180.1.*; a partial left humerus *PAL 2019.194.1.*; two femora *PAL 2019.195.1.*, *PAL 2019.196.1.*

Description: PAL 2019.154.1. **(Fig. 16.)** is a 120 mm long fragmentary and mediolaterally slightly compressed, posterodorsally curved left mandibular ramus. The articular, angular, prearticular and surangular are present, but the splenial, dentary and probably the coronoid bone are missing. The retroarticular process is short and stout, its posteroventral edge is curved, while dorsally straight.

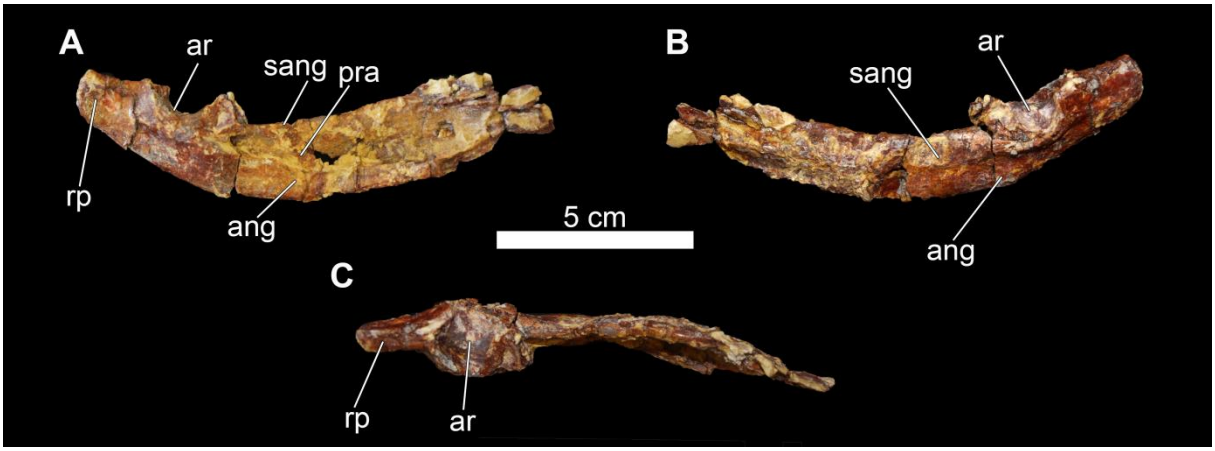


Figure 16. *Simosaurus* sp. mandible fragment (*PAL 2019.154.1.*) from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A**, in medial view; **B**, in lateral view; **C**, in dorsal view. Anatomical abbreviations: *rp*: retroarticular process, *ar*: articular, *sang*: surangular, *pra:*prearticular, *ang*: angular

Due to the bad preservation of the specimen, the presence of the chorda tympany foramen is uncertain. The posterior part of the bone is almost complete, but medially and laterally the edges of the articular are slightly broken. The articular surface is dorsally opened and saddle-shaped. The measureable width of the articular surface is 18 mm, while it is anteroposteriorly 31 mm long. The distance between the posteriormost point of the retroarticular process and the posteriormost point of the articular is 15 mm. On the lateral side of the retroarticular process there is a distinct hollow with a foramen. The presence of coronoid is uncertain due to the breakage, however there is no sign of such a distinct coronoid process. Laterally the surangular covers the ramus, ventrally the angular borders the bone. The adductor fossa is visible medially, with the prearticular being inside. On the medial side, ventrally to the prearticular the angular forms a prominent ridge and the surangular borders the prearticular dorsally.

Isolated dorsal neural arches **(Fig.17. A-D)** (*Ver 2013.5.*, *PAL 2019.178.1.*, *PAL 2019.179.1.*) with moderately high, dorsoventrally grooved neural spines and massive transverse processes are referred here to *Simosaurus*. Besides the pre- and postzygapophyses, additional infrapre- and infrapostzygapophyses can be observed on them. The height of the neural spines is between 44 mm and 66 mm, while the width of transverse processes ranges from 50 mm to 66 mm. The prezygapophyses are wedge-like, the neural canal is high and rectangular in cross section. The top of the neural spine tilts into cranial direction, thin zygosphene and zygantrum are present, however they are mostly fragmentary. *Ver 2013.5.* is a nicely preserved large isolated dorsal neural arch with a 66 mm tall neural spine and with the 66 mm largest width of the transverse processes. This specimen was previously described as *Nothosaurus* sp. (Ősi et al. 2013), however its overall shape, and the presence of infrapre- and cruciform infrapostzygapophyses suggests the simosaurian origin. *PAL 2019.180.1.* **(Fig.17. E,F)** is a sacral vertebra with 26 mm tall naural arch and 38 mm wide transverse processes. The infrapre- and infrapostzygapophyses are reduced in compared to the dorsal vertebrae. The neural arch is fused with the amphicoelus centrum along the neurocentral suture. The additional isolated amphicoelus vertebral centra **(Fig.17. G-J)** clearly show a butterfly/cruciform-shape on the articular platform for the neural arches characteristic for *Simosaurus* (Rieppel 1994a). This dorsal surface of the centra is divided by an anteroposteriorly passing groove. From a dorsal view, the facet of the centra is compressed antero- and posterolaterally and four triangular hollows are present medially to these compressed areas. *PAL 2019.182.1.* is a flat (6 mm tall with 10 mm width) isolated vertebral

centrum, while *PAL 2019.183.1.* is a larger and cylindrical (33 mm tall and 40 mm wide) amphicoelous dorsal centrum.

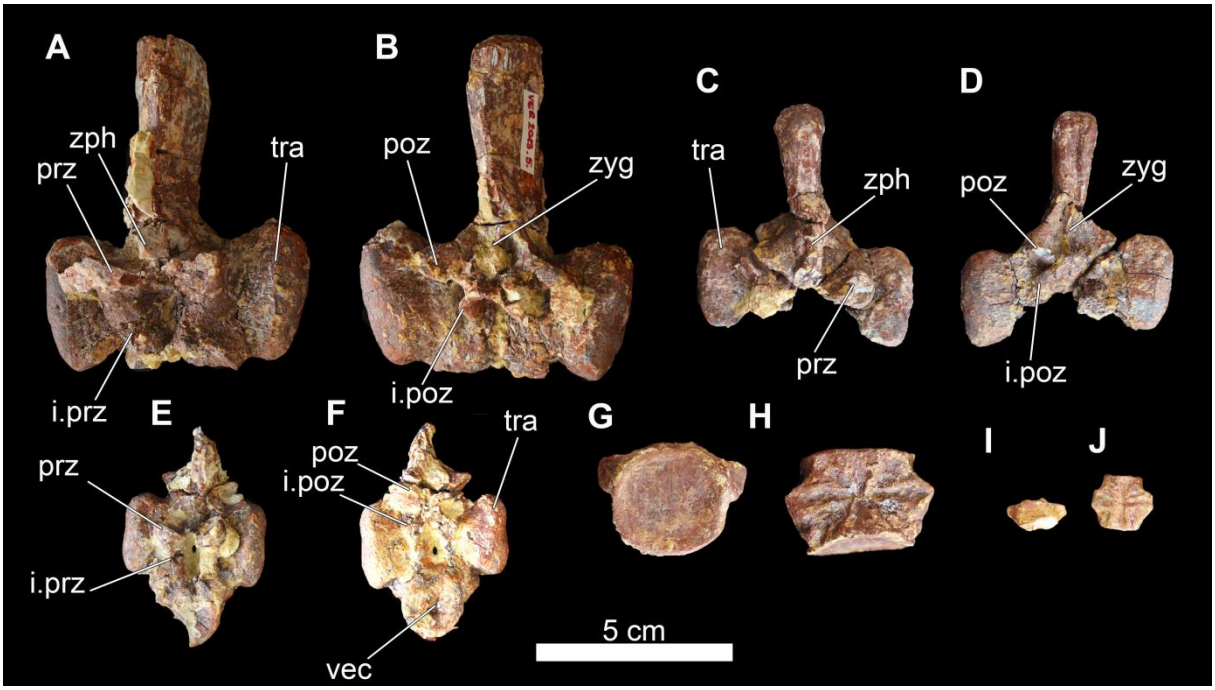


Figure 17. *Simosaurus* sp. vertebrae from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A-B,** *Ver 2013.5.* isolated dorsal neural arch in anterior, and posterior view; **C-D,** *PAL 2019.179.1.* isolated dorsal neural arch in anterior, and posterior view; **E-F**. *PAL 2019.180.1.* sacral vertebra in anteror, and posterior view; **G-H**, *PAL 2019.183.1.* isolated vertebral centra in anterior, and dorsal view; **I-J**, *PAL 2019.182.1.* isolated vertebral centra in anterior, and dorsal view. Anatomical abbreviations: *prz*: prezygapophysis, *poz*: postzygapophysis, *i.prz*: infraprezygapophysis, *i.poz*: infrapostzygapophysis, *zph*: zygosphene, *zyg*: zygantrum, *tra*: transverse process, *vec:* vertebral centra

PAL 2019.194.1. **(Fig.18. A,B)** is a fragmentary 178 mm long left humerus with a broken distal epiphysis. The ventral side of the bone is flattened, the diaphysis is constricted and strongly curved, the postaxial margin is concave, while the preaxial margin holds a distinct protrusion where the bone surface is rough, indicating the strong deltopectoral crest. Distally to this protrusion the preaxial margin is distinctly straighter. The cross section of the diaphysis is oval, dorsoventrally flattened. The proximal head is rounded in cross section and holds a ventropreaxially flat area. The proximal top of the bone is slightly concave.

The material contains two isolated femora **(Fig.18. C-E)**: *PAL 2019.195.1.* is a complete 107 mm long right(?) femur in a good condition, while *PAL 2019.196.1.* is a

complete, but dorsoventrally compressed 106 mm long left(?) femur. These femora are slender, slightly sigmoidal bones with strong constriction of the middle part of the diaphysis, which is circular in cross section. The proximal head is somewhat more expanded than the fan-shaped distal one. On the ventral side of proximal epiphysis the internal trochanter is prominent, the intertrochanteric fossa is shallow. The cross section of proximal head is close to triangular due to the strong internal trochanter, while the distal epiphysis is more flattened and oval in cross section. The proximal and distal surfaces of both epiphyses are convex. The fan-shaped distal epiphysis is twisted in compared to the proximal head and there is a shallow intercondylar fossa faced posterodorsally, separating the reduced articular condyles of tibia and fibula.

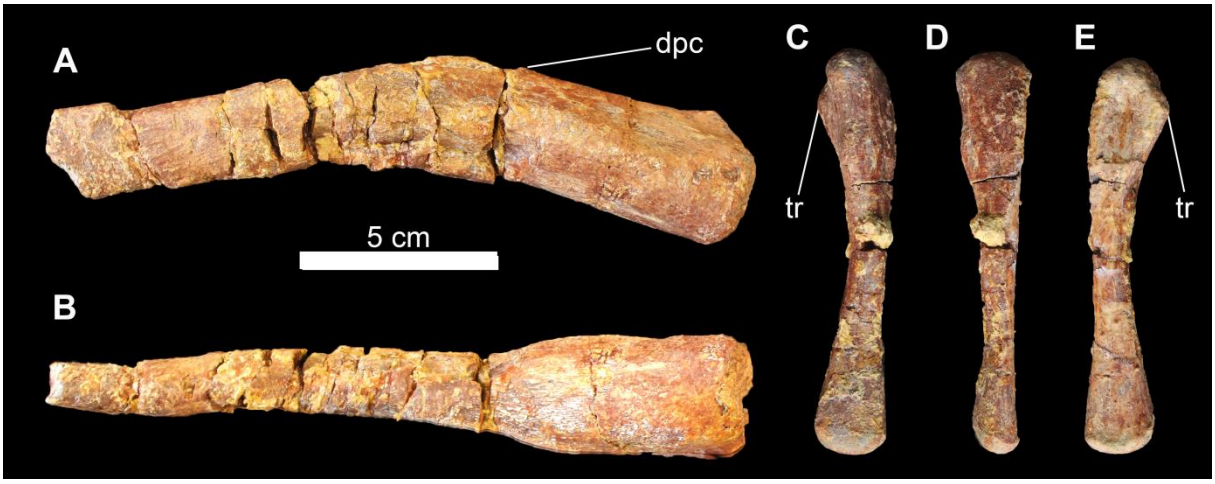


Figure 18. *Simosaurus* sp. limb bones from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A-B,** *PAL 2019.194.1.* humerus in dorsal, and postaxial view (proximal head is on the right); **C-E,** *PAL 2019.195.1.* femur (proximal head is on the top); Anatomical abbreviations: *dpc*: deltopectoral crest , *tr*: internal trochanter

Discussion: Besides the skull elements, some postcranial remains (femora, humeri) of *Simosaurus* can be separated based on associated skeletons (Hagdorn and Rieppel 1999) from bones of other eosauropterygians (Rieppel 1994a, 2000; Dalla Vecchia 2008). The lack of distinct coronoid process on the posterior mandible fragment *PAL 2019.154.1.* differentiate it from the mandible of placodonts and also from *Corosaurus* (Storrs 1991; Rieppel 1995, 2000). The stout retroarticular process of the mandible fragment and its posterodorsal curvature also clearly different than those of pistosauroids, pachypleurosaurs and nothosaurids (Rieppel 2000, 2002).

Among sauropterygians, the presence of infrapre- and cruciform infrapostzygapophyses are specific for *Simosaurus* (Rieppel 1994a) and also *Bobosaurus forojuliensis*, however the vertebrae of the latter show extremely elongated neural spines (Dalla Vecchia 2006). The sister taxon of *Simosaurus* is *Paludidraco*, which genus has highly pachyostotic vertebrae, appendicular elements and a more slender, thinner mandible, which characters differ in the elements of the Villány material (De Miguel Chaves et al. 2018a). The vertebral centra referred here to *Simosaurus* with their concave antero- and posterolateral dorsal articular surfaces differ from the vertebral centra of other eosauropterygians (Rieppel 1994a, 2000).

The *PAL 2019.194.1*. humerus with its constricted, dorsoventrally slightly flattened, distinct diaphysis is unlike the wider humerus of placodonts (Rieppel 1995) and other eosauropterygians, such as *Pistosaurus* (Sues 1987), *Corosaurus* (Storrs 1991), and nothosaurids (Rieppel 2000). The humeri of Pachypleurosauria (Klein 2010, 2012) and the humeri tentatively referred to *Cymatosaurus* also differ from the Villány specimen with their proportionally shorter diaphysis and the more overhanging deltopectoral crest (Rieppel 1994a).

The isolated femora assigned here to *Simosaurus* sp. with their strongly constricted middle part of the diaphysis and fan-shaped distal epiphysis are not like the robust femora of placodonts (Rieppel 1995). They are also different from the much wider femora of *Pistosaurus* (Krahl et al. 2013), and also differ from *Corosaurus* which genus has a stronger, overhanging internal trochanter and less fan-shaped distal epiphysis (Storrs 1991). The latter region on the femur is also more rod-like in case of nothosaurids (Rieppel 1994a; Krahl et al. 2013) and pachypleurosaurids (Sander 1989). The femora described here are most similar to the *Simosaurus* remains presented by Rieppel (1994a).

Within the genus, *Simosaurus gaillardoti* is the only known valid species, however this was concluded based on only cranial material (De Miguel Chaves et al. 2018b). Here I refer these remains to as *Simosaurus* sp. until the description of further cranial material, moreover because the intraspecific variation of the *S. gaillardoti* postcranial material is not known yet.

Sauropsida HUXLEY, 1864

Sauropterygia OWEN, 1860

Eosauropterygia RIEPPEL, 1994a

Nothosauroidea BAUR, 1889

Nothosauroidea indet.

(Figure 19.)

Material: isolated coracoids *PAL 2019.166.1., PAL 2019.167.1., PAL 2019.168.1., PAL 2019.169.1.*

Description: Among girdle elements, four coracoids (*PAL 2019.166.1., PAL 2019.167.1., PAL 2019.168.1., PAL 2019.169.1.)* represent the waisted morphology, typical for Nothosauroidea **(Fig.19.)**. Their mediolateral expansion changes between 106-126 mm. They are flat elements with anteriorly and posteriorly deeply concave margins. They are expanded medially and laterally, moreover their lateral margin forms the medial side of the coracoid foramen. The coracoids presented here both damaged on their lateral side, thus the position of this foramen is visible but its exact expansion and angle are not clear.

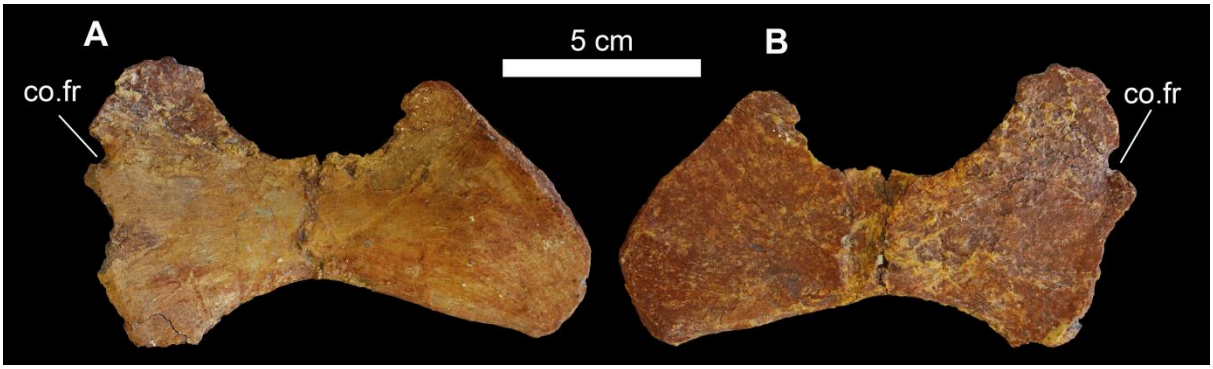


Figure 19. Right nothosauroid coracoid *(PAL 2019.166.1.)* from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A**, in lateral view; **B**, in medial view. Anatomical abbreviations: *co.fr:* coracoid foramen

Discussion: The coracoids presented here, clearly dffer from the coracoids of Placodontia, because those are round and flat elements, with small coracoid foramen (Rieppel 1995, 2000). In case of Pachypleurosauria, the coracoid is not as constricted, and the anterior and posterior margins are less concave than what is seen on the specimens from Villány. Moreover the coracoid foramen is also less prominent, if present (Sander 1989; Klein 2012).

The known coracoids of *Pistosaurus* are flat and plate-like bones (Sues 1987), while *Corosaurus* has a rectangular coracoid which lacks a constriction in the middle part. In case of the genera belonging to Nothosauroidea, the morphology of coracoids is highly similar (Rieppel 1994a, 2000; Rieppel et al. 2003), thus further separation is not possible on genus level.

Sauropsida HUXLEY, 1864

Sauropterygia OWEN, 1860

Eosauropterygia RIEPPEL, 1994a

Eosauropterygia indet.

(Figure 20.-21.)

Material: a skull fragment (temporal arch) *PAL 2019.170.1.*; isolated scapulae *PAL 2019.162.1., PAL 2019.163.1., PAL 2019.164.1., PAL 2019.165.1.;* isolated ischia *PAL 2019.159.1., PAL 2019.160.1., PAL 2019.161.1*.

Description: PAL 2019.170.1. is a skull fragment **(Fig.20.)** possibly representing the right temporal arch, parts of the postorbital region, and the projections of squamosal around the cranio-quadrate passage. The fragment is 109 mm long anteroposteriorly and the width of the squamosal in the arch is between 9-10 mm. The temporal arch is triangular in cross section. The possible cranioquadrate passage is 9 mm wide. Anteromedially the squamosal shows a 36 mm long groove, which probably represents the suture of the postorbital.

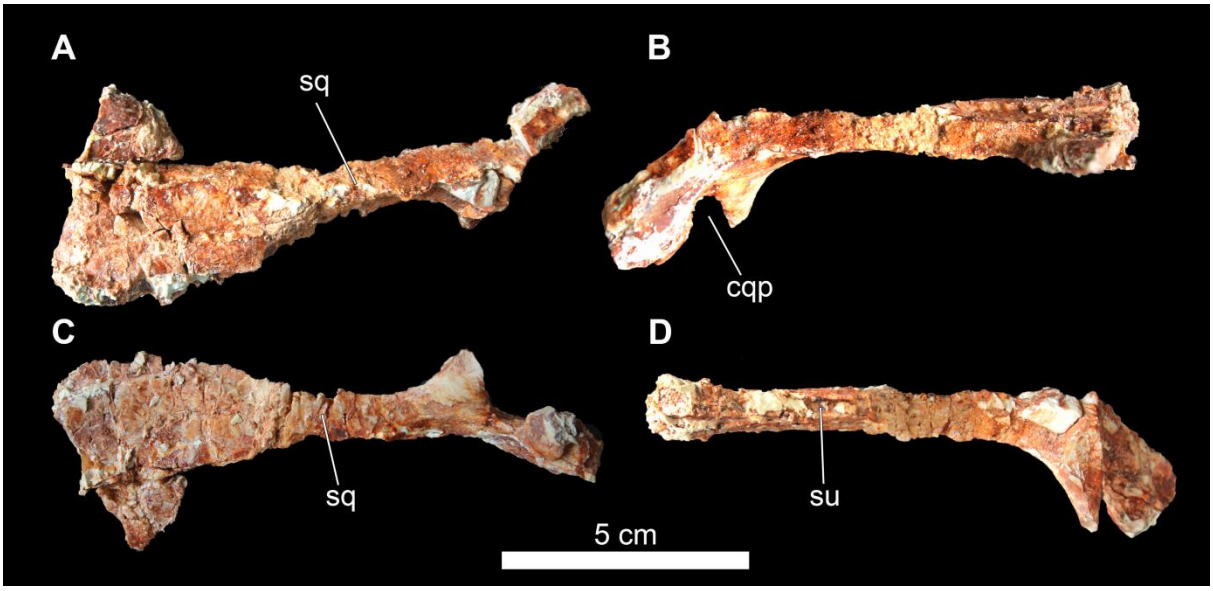


Figure 20. Eosauropterygia indet. skull fragment *(PAL 2019.170.1.)* from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A**, in dorsal view; **B**, in lateral; **C**, in ventral; **D**, in medial view. Anatomical abbreviations: *sq:* squamosal, *cqp:* cranioquadrate passage , *su:* suture

The isolated scapulae (*PAL 2019.162.1., PAL 2019.163.1., PAL 2019.164.1., PAL 2019.165.1.)* display the typical eosauropterygian scapular morphology **(Fig.21. A,B)**. Because of their slender structure they are mostly fragmentary: the wide ventrally expanded (26-36 mm long) glenoidal part is separated by a distinct neck from a narrow posterodorsally oriented (30-46 mm long) reduced scapular blade. If intact, the blade tapers to a constricted but blunt tip. The projection of coracoid foramen is not recognizeable on the specimens from Villány.

The isolated ischia (*PAL 2019.159.1., PAL 2019.160.1., PAL 2019.161.1.*) are also fragmentary elements **(Fig.21. C,D)**. Their size (measured between the constricted dorsal and the expanded ventral parts) ranges between 71-80 mm. The bones are flat elements, the anterior and posterior margins are distinctly concave and the bone surface is striated. Given their fragmentary preservation, the symmetry or asymmetry of the margins is questionable.

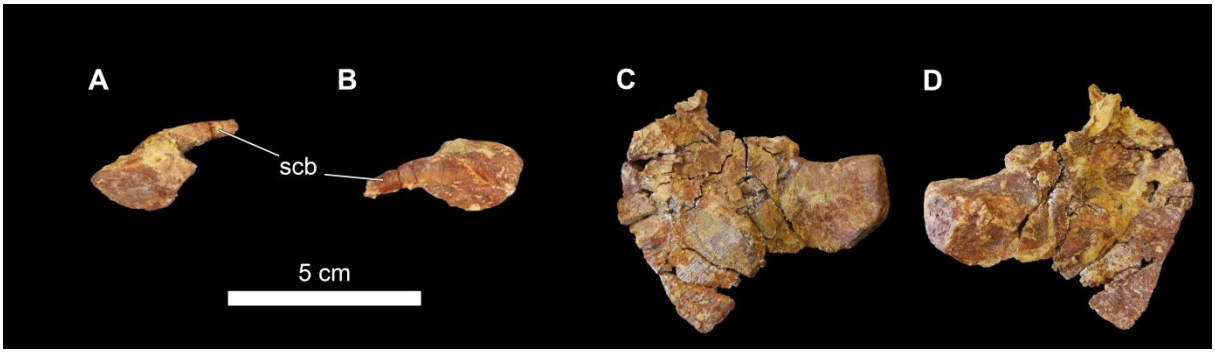


Figure 21. Eosauropterygia indet. girdle elements from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A-B**, *PAL 2019.164.1.* scapula in medial, and lateral view; **C-D**, *PAL 2019.161.1*. ischium. Anatomical abbreviation: *scb*: scapular blade

Discussion: The skull fragment *PAL 2019.170.1.* is clearly slender enough to close out its placodontian origin, moreover *Pistosaurus*, *Simosaurus* and *Germanosaurus* also exhibit a wider temporal arch structure (Sues 1987; Rieppel 2000, 2002; De Miguel Chaves et al. 2018b). The possible size and elongation of the temporal fenestra differ from that of pachypleurosaurs, and most similar to the skull structure of Nothosauria, and also *Corosaurus* and *Cymatosaurus* (Rieppel 2000, 2002). The position of cranioquadrate passage is similar to that of nothosaurids, but the horizontal expansion of the bone in the postorbital area seems different from the nothosaurid skulls, however there is a chance that this region suffered significant torsion.

In case of scapulae, due to their highly fragmentary preservation and the similar morphology of eosauropterygian scapulae I refer them only as Eosauropterygia indet.. In contrast, these girdle elements of placodontians are more simple, plate-like bones (Rieppel 1995, 2000; Scheyer 2010).

Because of the fragmentary preservation of the isolated ischia described here, and the generally homologous ischium morphology of eosauropterygians (Sues and Carrol 1985; Sander 1989; Rieppel 1994a, 2000; Lin et al. 2017) further classification is not possible, so I refer them only as Eosauropterygia indet. thus the flat, rounded plat-like ischia of placodonts are clearly different (Rieppel 1995; 2000).

Sauropsida HUXLEY, 1864

Sauropterygia OWEN, 1860

Sauropterygia indet.

(Figure 22.-23.)

Material: a fragmentary humerus *PAL 2019.217.1.;* isolated femora *PAL 2019.209.1., PAL 2019.210.1., PAL 2019.211.1., PAL 2019.212.1., PAL 2019.213.1.;* unidentified limb bones *PAL 2019.214.1., PAL 2019.215.1., PAL 2019.216.1*.

Description: PAL 2019.217.1. **(Fig.22.)** is an incomplete (109 mm long) left humerus which is broken both on its proximal and distal parts. The ventral side of the bone is flat while dorsally it is domed and due to the prominent latissimus dorsi insertion, the diaphysis is triangular in cross section. The shaft is constricted and clearly separated from the epiphyses. From a dorsal view both the pre- and postaxial margins show similar curvature. The thickest region of the bone is close to the midshaft. On the proximal part of the postaxial side two posterodorsally oriented canal can be separated. Distally the bone is expanded, fan shaped with a capitellum oriented medially. Entepicondylar foramen is not visible but a clear depression is situated on the postaxially faced area of the dorsal side. The distal epiphysis is broken, however its silhouette suggests a proximally shifted entepicondyle.

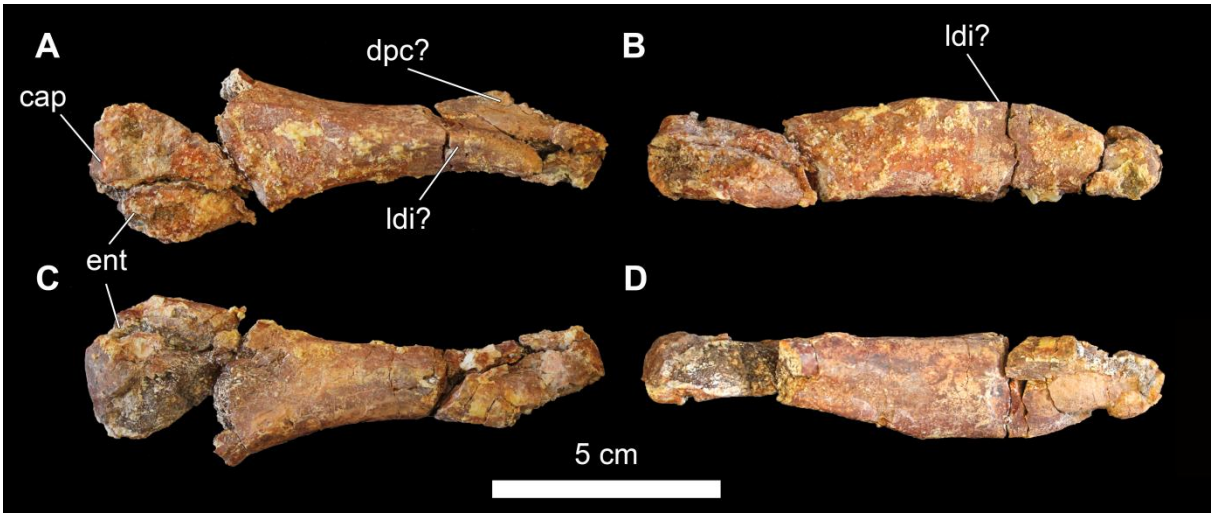


Figure 22. Sauropterygia indet. left humerus *(PAL 2019.217.1.)* from the Middle Triassic 'Construction site' of Villány, southern Hungary (proximal head is on the right). **A**, in dorsal view; **B**, in postaxial; **C**, in ventral; **D**, in preaxial view. Anatomical abbreviations: *dpc*: deltopectoral crest, *cap:* capitellum, *ent*: entepicondyle, *ldi*: latissimus dorsi insertion

The vertebrate material from Villány contains isolated sauropterygian femora **(Fig. 23. A-D)** with a long and slender, constricted diaphysis which is circular or oval in cross section. On the proximal epiphysis the internal trochanter is slightly prominent. Both the proximal and distal ends of the bone are convex: the distal epiphysis is globular with a distinct deep intercondylar fossa. The length of the whole specimens belong to this category ranges between 109-188 mm, however, the largest femur from Villány (*PAL 2019.209.1.)* is only fragmentary and it is 200 mm long.

Other isolated limb bones from Villány (*PAL 2019.214.1.*, *PAL 2019.215.1.*, *PAL 2019.216.1.*) have slightly concave proximal and slightly convex distal ends **(Fig. 23. E-H)**. The shaft region is long and slender and a low ridge is present on the (probable) proximal head. On the distal epiphysis, a shallow depression is present. The distal epiphysis is expanded, but not twisted and its largest width is parallel to the proximal heads expansion. The length of the whole bones ranges between 122 and 127 mm.

Figure 23. Sauropterygia indet. limb bones from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A-D**, femur (*PAL 2019.213.1.)* in ventral, postaxial, dorsal, and preaxial view; **E-H**, unidentified limb bone (*PAL 2019.215.1.)*. Anatomical abbreviations: *tr*: internal trochanter, *icd.f*: intercondylar fossa

Discussion: PAL 2019.217.1. is discussed in recent work because it exhibits characters that are present in some eosauropterygian groups, however the bone is too fragmentary and given that, further histological investigation could only proove its taxonomic position (Klein 2010). The morphology of the bone is much more plesiomorphic than the humeri of nothosaurs, its complex appearance is more similar to those of terrestrial sauropsids. The fan-shaped expanded distal epyphysis makes it quiet similar to the 'pachypleurosaur' morphotype

described by Klein (2010), which morphology could refer to both pachypleurosaur or basal pistosaur origin, nevertheless the diaphysis of *PAL 2019.217.1.* is triangular in cross section, which is more similar to the humerus of nothosaurs (Bickelmann and Sander 2008; Klein 2010). Some larger placodonts also have similar fan-shaped distal epiphysis, but these are more robust and simple bones with more concave postaxial margin (Rieppel 1994a). Until further remains or histological investigation I suggest to identify this specimen as Sauropterygia indet.

The isolated femora described here show simple characters typical to this group (e.g. reduced condyles, the proximal epiphysis is triangular in cross section). Unfortunately, they are not diagnostic enough for closer taxonomic discussion. These remains are different than those of *Placodus* (Rieppel 1994a), because the femora of this genus can be described with much more prominent internal trochanter, moreover the femora attributed to *Simosaurus* also differ in their ratios and their expanded distal epiphyses (Rieppel 1994a). The appearance of these elements from Villány is highly similar to the morphology of the femora of eosauropterygians (Klein 2010), however some newly described Cyamodontoidea NOPCSA, 1923 also had similar femora (see Wang et al. 2019:Fig.7.). Despite this uncertainty I suggest that the largest femora from Villány more probably belonged to larger Eosauropterygians. which cannot be determined in detail.

The other mentioned unidentified limb bones are somewhat similar to the herein described sauropterygian femora: they are elongated bones with a diaphysis which is circular in cross section, they hold a low ridge on the larger ending of the shaft (maybe the internal trochanter?). On the other ending of the bone, a shallow depression could represent an intercondylar fossa. Despite these similarities, these bones also resemble the morphology of eosauropterygian metacarpals (see Rieppel 1994a:Fig.32.), however because they are isolated elements with just a few anatomical characteristics, here I refer them only as Sauropterygia indet.

6. Taphonomical observations and a probable partial eosauropterygian skeleton

Vast majority of the skeletal elements from the ’Construction site’ are isolated, although local concentrations of disarticulated bones were observed too. Many elements with preserved slender spines, or in situ teeth suggest that most of the bones did not suffer significant abrasion before they were buried in the sediment (Ősi et al. 2013; Botfalvai et al. 2019).

Since the bone-bearing layers are tectonized and sometimes slightly folded, moreover because they are dipping to south (with 40-50°), the surface and boundary of the layers was not always traceable, making the bone-mapping impossible in many times. In one case (during the fieldwork in 2016), when the bone concentration on a detectable level was exceptional (in the 16th layer, see **Fig.6. B**), bone map was drawn about a 4 m^2 area (**Fig.24.**). In case of this part, the bone-bearing marl covered a thin layer of a reddish calcareous mudstone, claystone. A significant (northern) part of this area (**Fig.25.**) was fixed and transported in one slab (*PAL 2019.174.1.*) to the Hungarian Natural History Museum. On the mapped surface (**Fig.24.**), completely disarticulated elements from different specimens and multiple taxa have been uncovered. Appendix contains a table of described specimens. Besides the many poorly preserved or not closely diagnostic bone fragment (**Fig.24.: n.o.: 1,3,5,6,7,8,10,12,13,16,17,18,19,20,22)**, a cervical vertebra of *Tanystropheus* sp. (Ősi and Botfalvai 2017) (**Fig.24.: *T*.cv)** and the previously mentioned *N.* cf. *marchicus* skull fragment (*PAL 2019.156.1.* - **Fig.24.: *N*.sf**) have been found.

The northern section of this mapped area with the slab *PAL 2019.174.1.* is the densest in bones in a similar small size. Besides unicipital dorsal and sacral ribs and vertebral centra, a coracoid, a limb element (probably radius), two incomplete ischium and other bone fragments are situated here.

Close to this bone concentration, an additional fragmentary long bone (probably femur) (*PAL 2019.184.1.* - **Fig.24.: n.o: 11**) and fragmentary girdle elements (*PAL 2019.185.1.* - **Fig.24.: n.o: 21,** in two piece) were found. The morphology of vertebral centra and coracoid suggests they eosauropterygian affinity, and there is a chance that the similarly small sized fragmentary femur and girdle element fragments belong to this bone concentration. However, in the proximity of these elements an isolated ischium (*PAL 2019.187.1.* - **Fig.24.: n.o: 4**) was found which clearly represents a larger size class of eosauropterygians. Moreover, it is also noteworthy, that the *N.* cf. *marchicus* skull fragment

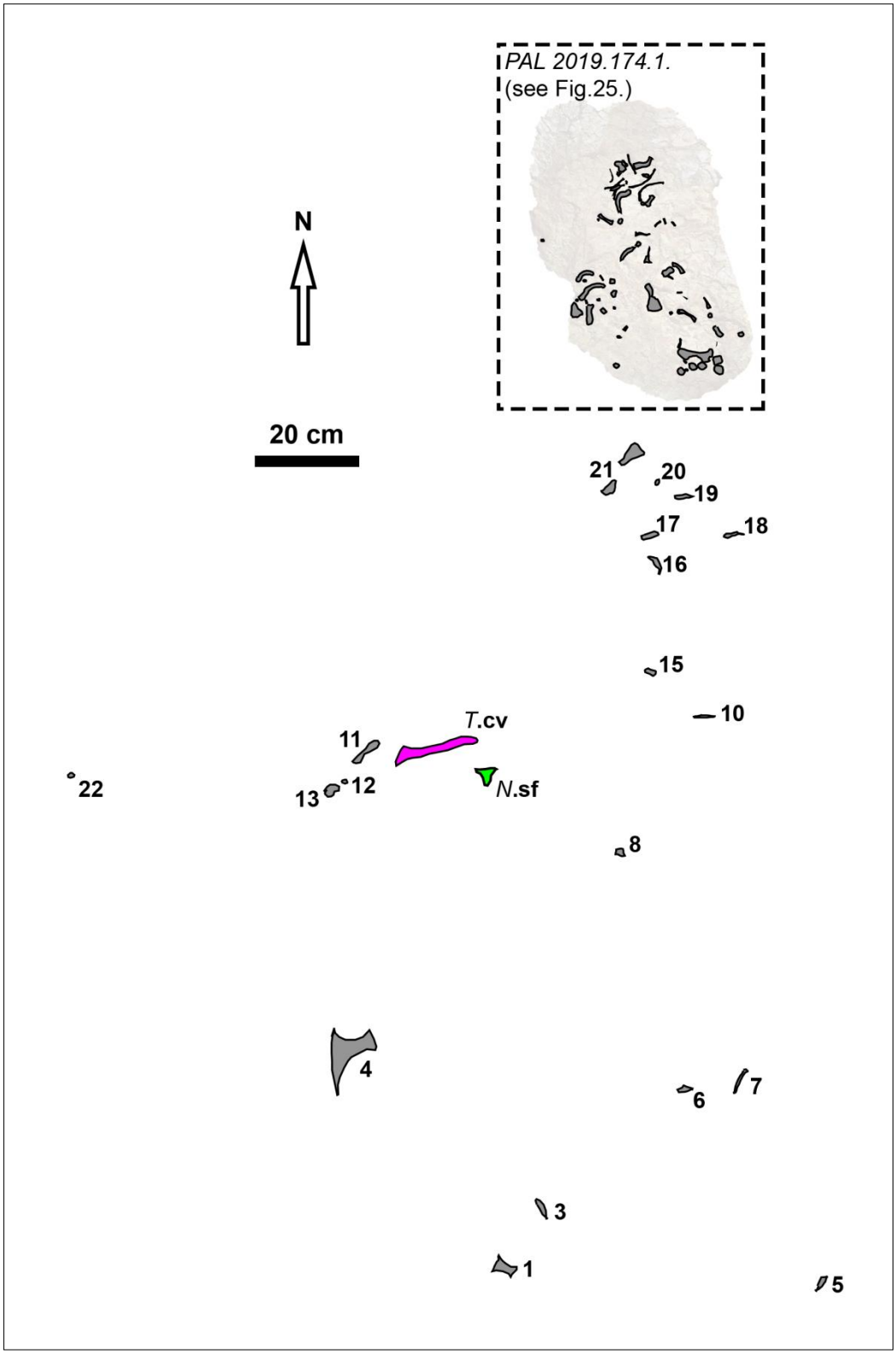


Figure 24. Mapped area of bone-bearing marl with dense bone concentration from the Middle Triassic 'Construction site' of Villány, southern Hungary. The densest bone concentration (see **Fig.25**.) is situated within dotted lines. Appendix contains a table of described specimens. Abbreviations: *T*.cv: *Tanystropheus* sp. cervical vertebra, *N*.sf: *N.* cf. *marchicus* skull fragment (*PAL 2019.156.1.)*

(*PAL 2019.156.1.* - **Fig.24.: *N*.sf**) was in the proximity of this bone-concentration, and since it represents a small-sized specimen, maybe the numerous postcranial elements belonged to this cranium and this area shows an associated skeleton mixed with some additional isolated bones from other specimens and species.

In compared with the previously described *N. marchicus* skeletons (Klein et al. 2015) the dimensions of this associated postcranial material could fit into the size of *N. marchicus*, however, due to the fragmentary preservation of the findings and the clear signs of mixing with other specimens, it is still a matter of question.

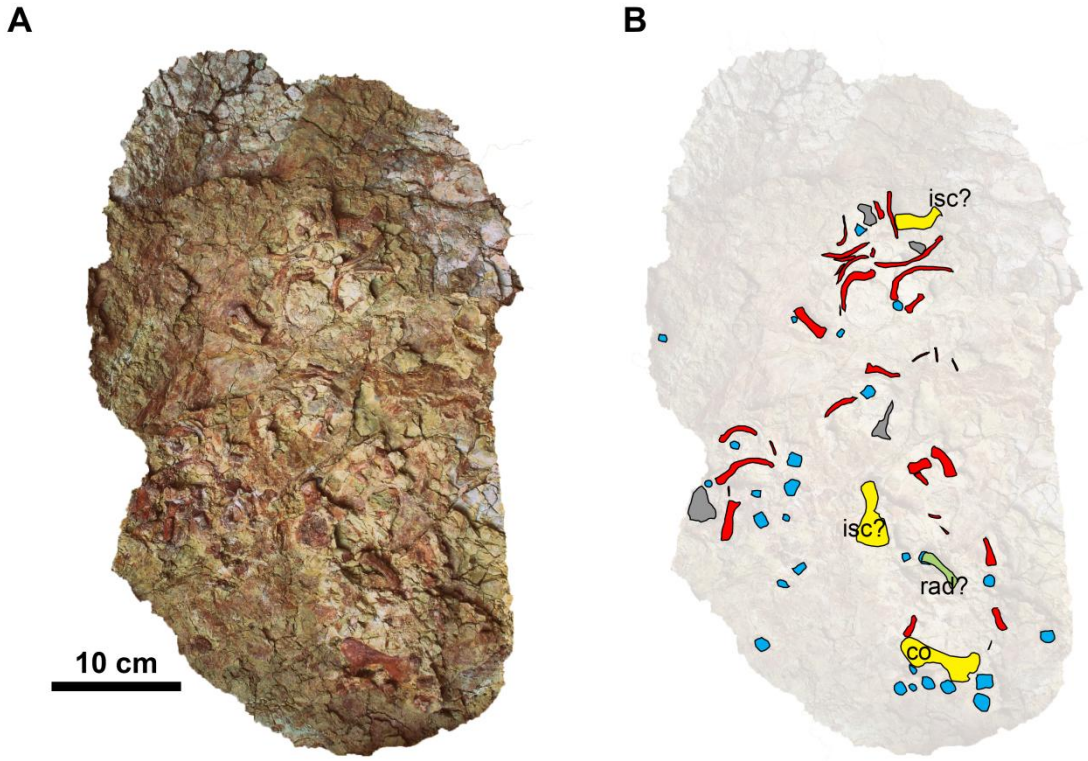


Figure 25. Slab (*PAL 2019.174.1.*) with probable associated eosauropterygian elements from the Middle Triassic 'Construction site' of Villány, southern Hungary. **A,** overall picture; **B,** technical drawing. Abbreviations: co: coracoid, isc: ischium, rad: radius. Colors: ***grey***: unidentified bone fragment, **blue**: vertebral centra, **yellow**: girdle element, **red**: rib, **green**: limb element

Except for the only one associated material of *PAL 2019.174.1.*, all other bones are isolated which suggest rather allochthonous than parautochtonous nature for the discovered assemblage. However, the well preservation of many fragile skeletal parts and the overall lack of abrasion probably indicate that most of the material represent animals living not far from the depositional area (subtidal to peritidal zone of the inner ramp environment),

and their disarticulated remains were buried only after a short period of transportation. Considering these, the vertebrate material from the ‘Construction site’ represents an attritional assemblage, which accumulated through a longer period of time as the results of natural mortality.

The dominant sedimentation on the carbonatic ramp of the Villány area - with high production of carbonatic mud without reef biota (Török 1998) - during the Middle Triassic was similar to the Muschelkalk facies of the Germanic Basin, where the articulated specimens are also very rare (Rieppel 2000; Klein et al. 2015).

7. Discussion

7.1. Faunal composition and ecological connections

Despite that the vertebrate material from Villány contains hundreds of sauropsid fossils, most of them is not preserved well enough for a low-level taxonomic investigation. Effects of diagenesis, dolomitization (Botfalvai et al. 2019) and compression may have caused several alteration on many specimens. Another fact, that makes the determination difficult and sometimes questionable, is that phylogeny of Eosauropterygia is solely based on the well preserved skulls, since remains of Triassic aquatic reptiles are mostly isolated finds from most of the localities of the Germanic Basin and other Middle Triassic areas such as the localities of Gondwana shelf (Rieppel et al. 1999). Moreover the postcranial material for some species, which were otherwise described using skull elements (e.g. *Cymatosaurus* species) is not known (Rieppel 2000). Due to the adaptation to an aquatic environment, significant part of the sauropterygian skeleton shows paedomorphic conditions, reduced condyles, relatively simple, homologous morphology, which can be very similar among only distantly related forms.

Based on the fossils discussed in the present work and previous publications (see Ősi et al. 2013), the vertebrate material from Villány contains at least four different eosauropterygian taxa. The presence of *Simosaurus* sp. is suggested by several characteristic (Rieppel 1994a) elements, such as a mandible fragment, vertebrae and specific limb bones. The vertebrae with highly elongated neural spines most probably belong to *Nothosaurus mirabilis* or a closely related taxon. Besides this species, additional cranial and postcranial matarial (humeri) suggest the presence of *Nothosaurus marchicus* in the material. The small *Nothosaurus* mandible (*PAL 2019.153.1.*) is comparable to the previously described – but significantly larger – *Nothosaurus* sp. mandible from Villány which is highly similar to *N. giganteus* (Ősi et al. 2013). It cannot be excluded, that the mandible described here belonged to a juvenile specimen of an otherwise large bodied *Nothosaurus* species, but it has several common features with the small-sized *N. marchicus* as well. Besides the remains of *Simosaurus* and *Nothosaurus* spp. another fragmentary humerus suggests that an additional eosauropterygian taxon might have inhabited this area.

Because the large *N. giganteus* and the small-sized *N. marchicus* share some anatomical features and their remains can be found together on many different localities, previuos authors discussed whether the latter species could represent a juvenile *N. giganteus*. Both species can be described with a relatively short and broad premaxillary rostrum, a

mandibular symphysis with low length-to-width ratio and the same number of enlarged fangs in the dentary, moreover vertebrae with low neural spines (Rieppel and Wild 1996; Rieppel 2000). Despite these similarities, the known *N. marchicus* crania – based on their well ossified sutures – are believed to be remains of adult specimens (Rieppel and Wild 1996).

The presence of several different sized eosauropterygian taxa from the same region and distinct time interval is not without precedent, in fact a diverse system of trophic specialization is known from many localities of the shallow marine areas of Tethys and surrounding basins (Rieppel 2000, 2002; Liu et al. 2014). The partitioning of habitats with different adult sizes for the sympatric predators is known from the Germanic Basin, and also occurred on the northern Gondwana shelf (Rieppel et al. 1999). Similarly, the Alpine region, moreover the Middle Triassic localities of the Eastern Tethyan province show correspondingly complex ecological pattern, with the spatial and temporal overlapping of different sized eosauropterygian marine reptiles (Rieppel 2000; Liu et al. 2014).

The presumed prey size will depend on the relative size of the animals, and we can expect that adults of large-bodied predators consumed larger prey with higher chance, than vice versa (however large predators could consume small prey too) (Rieppel 2002). Not just their adult sizes, but the general skull and dentition morphology also differed in these coexisting aquatic reptiles. The enigmatic (3-4 m long) *Simosaurus* was widespread together with *Nothosaurus* species (Rieppel 1994a, 2000). However given its blunt skull shape with the several bulbous teeth (in contrast with the 'pincer jaw' of nothosaurs) and stout retroarticular process on its mandible, previous studies reconstructed it as a generalist predator, most probably fed on pelagic (hard or soft shelled) invertebrates and fishes (Rieppel 1994a, 2002; Kelley 2012). According to the dietary classification of Kelley (2012), what was based on measurements and observations on the morphology of skulls and jaws, the medium-sized (3-4 m long) *N. mirabilis* with its elongated longirostrine skull shape was most probably highly specialised for capturing fish. In contrast, the larger body size (5-6 m length) and less elongated jaw with shorter mandibular symphysis of *N. giganteus* suggests its role as a generalist apex/top predator of the shallow marine areas (Rieppel 2000; Kelley 2012). The small bodied *Nothosaurus* species (like the 1-2 m long *N. marchicus*) may have been the predators of small invertebrates and fishes (Rieppel 2000, 2002; Kelley 2012).

Naturally, neither skull shape nor the morphology of the teeth proove with full confidence the real feeding behaviour of a given animal, however, based on the observations of recent animals, a certain level of the outlined trophic relationship is highly probable (Rieppel 2002; Kelley 2012).

7.2. Paleobiogeographical implications

The eosauropterygian fauna described here resembles that of the Bihor Mountains (*Simosaurus, N. mirabilis, N. marchicus*) described by (Jurcsák 1987). Similarly, the presence of *N. giganteus* would not be surprising in Villány, because this species was reported from several localities from the Western Tethyan realm (Rieppel and Wild 1996; Rieppel et al. 1999). Materials related to *Nothosaurus mirabilis* are also widespread in the Germanic Basin, the species was reported from the Bihor Mountains (Jurcsák 1987), its remains are mentioned from the Southern Alps, and some problematic remain may belong to this species from the northern Gondwana shelf (Rieppel and Wild 1996; Rieppel 2000). Most recently (Reolid et al. 2014) mentioned vertebrae with highly elongated neural spines – possibly belonging to the '*mirabilis* clade' – from the South Iberian Paleomargin (Reolid et al. 2014). *Simosaurus* was also a widespread genus, its remains are known from different localities of the Germanic Basin, northern Gondwana shelf and also the Alpine territories (Rieppel and Hagdorn 1997; Rieppel 2000; Dalla Vecchia 2008). Well documented and described fossils related to *N. marchicus* were previously reported only from the Germanic Basin and probably from the Bihor Mountains (Jurcsák 1987; Rieppel and Wild 1996; Rieppel et al. 1999; Rieppel 2000). A fragmentary *Nothosaurus* skeleton was mentioned (without illustrations) from the S-charl Formation (eastern Alpine), by Furrer et al. (1992). According to Rieppel (1998) based on the proportions of its skull, this specimen could represent *N. marchicus*, however, without further description or illustration this remains questionable. The material described herein supports the hypothesis (Jurcsak 1973; Rieppel 1998; Rieppel et al. 1999) that the small-sized *N. marchicus*, was more widespread, and was present outside of the Germanic Basin, on the southern Eurasian shelf.

The coexistence of the small-sized *Nothosaurus marchicus* with *N. mirabilis* and *N. giganteus* was reported from the Upper Muschelkalk (Upper Anisian - Lower Ladinian) of the Germanic Basin, from the localities of Bayreuth and Bad Sulza (Rieppel and Wild 1996). During the Middle-Late Triassic, the Villány area (**Fig.5.**) was located on the southern Eurasian shelf, in the proximity of the Germanic Basin, which was periodically connected to the Tethyan realm through marine straits, like the East-Carpathian Gate, Silesian-Moravian Gate and Burgundy-Alemannic Gate (**Fig.5.**) (Rieppel and Hagdorn 1997; Pozsgai et al. 2017). Given this paleogeographic position, the occurence of both regionally (Western Tethys) widespread and local (Germanic Basin related) eosauropterygian species would not be surprising, because eosauropterygians were adapted to the aquatic environment, as active

swimmers (Storrs 1993; Rieppel 2000), thus they could use the above mentioned gateways during faunal exchanges (Rieppel and Hagdorn 1997). In addition, it was also suggested by Klein et al. (2016a) that small-sized *Nothosaurus* species were bounded to the shallow marine areas. The possible presence of *N. marchicus* in the localities of Bihor Mountains (Jurcsák 1973; Rieppel et al. 1999), moreover the material from Villány suggests, that this species could spread along the homoclinal carbonate ramp of the Tisza Megaunit, and its shallow marine, lagoonal environments (Török 1998; Posmosanu 2013; Botfalvai et al. 2019) which provided proper habitat for both the small near-shore dweller and also for the more pelagic larger eosauropterygians.

Despite that the exact age of the bone-bearing layers in Villány is not known, based on its stratigraphic position, the Csukma Dolomite Formation is most probably Ladinian (Nagy and Nagy 1976; Ősi et al. 2013; Botfalvai et al. 2019). Fossils of *Simosaurus* are known from the Anisian-Ladinian boundary until the Early Carnian (Rieppel et al. 1999; Dalla Vecchia 2008). Both *Nothosaurus mirabilis* and *N. giganteus* existed from the Late Anisian until the end of Ladinian (Rieppel and Wild 1996). In contrast, the range of *N. marchicus* lasts from the Early Anisian until the Early Ladinian (Rieppel and Wild 1996). Even though aquatic reptiles are not always useful for the accurate determination of the age of sediments, this faunal composition described here does not oppose significantly the Ladinian theory, which was suggested previously by Ősi et al. (2013) based on fewer known vertebrate taxa. However, without age diagnostic fossils from the bone-bearing layers, or other succesful investigation to determine the exact age of the formation, I cannot close out completely the chance, that the material presented here came from the Uppermost Anisian.

Rieppel (1999) indicated with the examination of phylogenetic connections of Triassic sauropterygians, that the fossil record of this group may represent an incompleteness of almost 50%, which limits the correct clarification of their paleobiogeographic relations. Systematic collecting of vertebrate fossils started around the 19th century both from the Triassic outcrops of Germany, the Netherlands, northern Italy and other Alpine countries. Therefore, the Triassic sauropterygian fauna of the Germanic Basin and Alpine Triassic is one best known and most diverse (Rieppel 1999, 2000). In contrast, the fewer discovered material and less described faunal elements from the southern Eurasian shelf possibly represent a collecting bias, caused by historical reasons and the different geological structure (e.g. majority of the Tisza Megaunit is covered by Cenozoic sediments) rather than a significant difference in the habitats and diversity of secondary aquatic reptiles.

As it was suggested by Rieppel (1999), the definition of traditional provinces of the stem-group sauroptergyian distribution may have been strongly affected by collecting and preservational bias, accordingly following the discovery of new localities (like in Villány), the Triassic sauropterygian paleobiogeography needs further re-thinking.

8. Conclusions

The aquatic reptile material presented here provides new important informations about the Middle Triassic fauna of a previously not well documented region of the Eurasian shelf. The assemblage, collected from the bone-yielding marl and dolomarl beds of the Middle Triassic Templomhegy Dolomite Member in the last seven years, contains several cranial and postcranial elements of different eosauropterygian taxa.

The occurrence of *Nothosaurus mirabilis* is supported by vertebrae with highly elongated neural spines. Based on postcranial elements, and small-sized fragmentary skulls *Nothosaurus marchicus* is also present in the material. *Simosaurus* also has been pointed out in the fauna. In addition, on the basis of the previously described *Nothosaurus* sp. mandible (Ősi et al. 2013) and the small *Nothosaurus* mandible discussed in the present work, the occurrence of *N. giganteus* is also possible. Additional fragmentary humerus may represent another previously not reported sauropterygian taxon.

The composition and structure of the fauna from Villány resemble the previously described materials from the Western Tethys. Possibly caused by the Triassic position of this region, besides the otherwise widespread taxa (e.g. *Simosaurus, N. giganteus, N. mirabilis*), some finding support previous theories that *Nothosaurus marchicus* - which species was previously believed to be typically Germanic Basin related – also inhabited the Middle-Triassic shallow marine areas of the southern Eurasian shelf.

In case of these aquatic reptile species, habitat partitioning is suggested based on the different presumed sizes of the adult individuals, moreower the diverse skull and dentition morphology also indicates trophic specialisation.

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10. Appendix

List of herein discussed vertebrate remains from the Middle Triassic Templomhegy Dolomite Member (Villány, Hungary):

Collection number	Taxon	Description
PAL 2019.171.1.	*Nothosaurus* cf. *mirabilis*	dorsal vertebra (fragmentary)
PAL 2019.172.1.	*Nothosaurus* cf. *mirabilis*	isolated neural arch (fragmentary)
PAL 2019.175.1.	*Nothosaurus* cf. *mirabilis*	isolated neural arch (fragmentary)
PAL 2019.156.1.	*Nothosaurus* cf. *marchicus*	skull (fragmentary)
PAL 2019.181.1.	*Nothosaurus* cf. *marchicus*	skull (fragmentary)
PAL 2019.153.1.	*Nothosaurus* sp.	mandible (fragmentary)
PAL 2019.155.1.	*Nothosaurus* sp.	mandibular ramus (fragmentary)
PAL 2019.173.1.	*Nothosaurus* sp.	cervical vertebra (fragmentary)
PAL 2019.176.1.	*Nothosaurus* sp.	isolated neural arch (fragmentary)
PAL 2019.177.1	*Nothosaurus* sp.	isolated neural arch (fragmentary)
PAL 2019.197.1.	*Nothosaurus* sp.	humerus (fragmentary)
PAL 2019.198.1.	*Nothosaurus* sp.	humerus (fragmentary)
PAL 2019.199.1.	*Nothosaurus* sp.	humerus ‘Morphotype-1’
PAL 2019.200.1.	*Nothosaurus* sp.	humerus ‘Morphotype-1’
PAL 2019.201.1.	*Nothosaurus* sp.	humerus ‘Morphotype-1’
PAL 2019.202.1.	*Nothosaurus* sp.	humerus ‘Morphotype-1’
PAL 2019.203.1.	*Nothosaurus* sp.	humerus ‘Morphotype-1’ (fragmentary)
PAL 2019.204.1.	*Nothosaurus* sp.	humerus ‘Morphotype-1’ (fragmentary)
PAL 2019.205.1.	*Nothosaurus* sp.	humerus ‘Morphotype-2’ (fragmentary)
PAL 2019.206.1.	*Nothosaurus* sp.	humerus ‘Morphotype-2’ (fragmentary)
PAL 2019.207.1.	*Nothosaurus* sp.	humerus ‘Morphotype-2’ (fragmentary)
PAL 2019.208.1.	*Nothosaurus* sp.	humerus ‘Morphotype-2’
PAL 2019.151.1.	Nothosauridae indet.	mandibular ramus (fragmentary)
PAL 2019.152.1.	Nothosauridae indet.	mandibular ramus (fragmentary)
PAL 2019.157.1.	Nothosauridae indet.	ilium
PAL 2019.158.1.	Nothosauridae indet.	ilium (fragmentary)
PAL 2019.154.1.	*Simosaurus* sp.	mandibular ramus (fragmentary)
PAL 2019.182.1.	*Simosaurus* sp.	isolated vertebral centra
PAL 2019.183.1.	*Simosaurus* sp.	isolated vertebral centra
Ver 2013.5.	*Simosaurus* sp.	isolated neural arch (fragmentary)
PAL 2019.178.1.	*Simosaurus* sp.	isolated neural arch (fragmentary)
PAL 2019.179.1.	*Simosaurus* sp.	isolated neural arch (fragmentary)
PAL 2019.180.1.	*Simosaurus* sp.	sacral vertebra (fragmentary)
PAL 2019.194.1.	*Simosaurus* sp.	humerus (fragmentary)
PAL 2019.195.1.	*Simosaurus* sp.	femur
PAL 2019.196.1.	*Simosaurus* sp.	femur

PAL 2019.166.1.	Nothosauroidea indet.	coracoid (fragmentary)
PAL 2019.167.1.	Nothosauroidea indet.	coracoid (fragmentary)
PAL 2019.168.1.	Nothosauroidea indet.	coracoid (fragmentary)
PAL 2019.169.1.	Nothosauroidea indet.	coracoid (fragmentary)
PAL 2019.159.1.	Eosauropterygia indet.	ischium (fragmentary)
PAL 2019.160.1.	Eosauropterygia indet.	ischium (fragmentary)
PAL 2019.161.1.	Eosauropterygia indet.	ischium (fragmentary)
PAL 2019.170.1.	Eosauropterygia indet.	skull fragment (temporal arch)
PAL 2019.162.1.	Eosauropterygia indet.	scapula (fragmentary)
PAL 2019.163.1.	Eosauropterygia indet.	scapula (fragmentary)
PAL 2019.164.1.	Eosauropterygia indet.	scapula (fragmentary)
PAL 2019.165.1.	Eosauropterygia indet.	scapula (fragmentary)
PAL 2019.217.1.	Sauropterygia indet.	humerus (fragmentary)
PAL 2019.209.1.	Sauropterygia indet.	femur (fragmentary)
PAL 2019.210.1.	Sauropterygia indet.	femur (fragmentary)
PAL 2019.211.1.	Sauropterygia indet.	femur (fragmentary)
PAL 2019.212.1.	Sauropterygia indet.	femur (fragmentary)
PAL 2019.213.1.	Sauropterygia indet.	femur
PAL 2019.214.1.	Sauropterygia indet.	unidentified limb bone (fragmentary)
PAL 2019.215.1.	Sauropterygia indet.	unidentified limb bone
PAL 2019.216.1.	Sauropterygia indet.	unidentified limb bone
PAL 2019.174.1.	Eosauropterygia indet.	associated skeleton - **mapped**
PAL 2019.184.1.	Sauropterygia indet.	femur (fragmentary) - **mapped** (n.o: 11)
PAL 2019.185.1.	Eosauropterygia indet.	girdle elements? (fragmentary) - **mapped** (n.o: 21)
PAL 2019.186.1.	Eosauropterygia indet.	vertebral centra - **mapped** (n.o: 15)
PAL 2019.187.1.	Eosauropterygia indet.	ischium (fragmentary) - **mapped** (n.o: 4)
PAL 2019.188.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 3)
PAL 2019.189.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 1)
PAL 2019.190.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 8)
PAL 2019.191.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 18)
PAL 2019.192.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 16)
PAL 2019.193.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 6)
PAL 2019.218.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 17)
PAL 2019.219.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 22)
PAL 2019.220.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 20)
PAL 2019.221.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 19)
PAL 2019.222.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 5)
PAL 2019.223.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 10)
PAL 2019.224.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 13)
PAL 2019.225.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 12)
PAL 2019.226.1.	Sauropsida indet.	bone fragment - **mapped** (n.o: 7)

11. References

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