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First record of a Triassic terrestrial tetrapode from marine sediments in Croatia: Age, morphology and histology of the epipodial bone

by

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Zusammenfassung

Der erste Nachweis eines triassischen Tetrapoden in Kroatien besteht aus zwei Knochenfagmenten, die in einem marinen Sediment abgelagert, und von einem Fossiliensammler in der Nähe von Muć – am S–Abhang des Berges Svilaja – gefunden worden sind. Diese konnten einem Vertreter der Placodontier zugeschrieben werden. Wegen der unbekannten Herkunft des Fossilmateriales wurde eine petrographische Analyse des umgebenden Gesteins erstellt, die gezeigt hat, dass es sich um ein marines Sediment mit vorwiegend karbonatischer Sedimentation handelt, das jedoch mit Material aus einem explosiv- vulkanischen Eruption gemischt ist. Dieses Sediment ist dann im tieferen Anis (M–Trias) tektonisch gehoben worden.

Die morphologische Analyse des Knochenmaterials hat gezeigt, dass es sich um zwei Bruchstücke der Diaphyse des selben schlanken und geraden Knochenelementes mit einem anterolateralen Grat, also um einen epipodialen Knochen eines Tetrapoden handelt. Dieser war, wie eine histologische Analyse gezeigt hat, mehr ans Landleben angepaßt. Die Verschiedenheit der angetroffenen Merkmale zeigt die begrenzte Verwendbarkeit der Knochenhistologie bei taxonomischen Fragestellungen.

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Abstract

The first fossil record of a Triassic tetrapod in Croatia – consisting of two bone fragments embedded in marine sediments and previously ascribed to the Placodontians – was found by a local fossil collector near Muć on the southern slopes of Mt. Svilaja (Dinarides, N Dalmatia). Owing to the unknown origin of the fossil material, a petrographic analysis of the rock matrix was made showing that the material derived from an explosive volcanic event and was mixed with dominantly carbonate sedimentation in a marine environment, by tectonic movements brought into a shallow sea environment during the Middle Triassic i.e. Lower Anisian.

Morphological analysis of the fossil remains shows that the bone fragments (distal end and part of the shaft) belong to the same slender, subcircular, straight bone with the anterolateral crest but without the medial groove, i.e. to the epipodial bone of a terrestrial tetrapod. Quadrupedal and more terrestrial than aquatic habit of an adult animal was also confirmed by histological analysis. At the same time, some registered characteristics of recent crocodilians, mammals, and birds point at the relatively lower value of the histology of limb bones in taxonomic determination.

Key words: Middle Triassic, tetrapod, epipodial bone, morphology, histology, Muć, Mt. Svilaja, Dalmatia, Croatia

1. Introduction

Until now very few skeletal fragments of Mesozoic reptiles have been found in Croatia; all of them originate from the Cretaceous of the Adriatic coast and islands (references in: KOZARIĆ et al. 1996). The only exception are osseous specimens from Muć (southern slopes of Mt. Svilaja in Dalmatia) found by a local fossil collector in marine sediments of unknown origin, and preliminary determined as a placodontian limb bone (PAUNOVIĆ 1990). Therefore, in this paper the results of morphological and

histological analyses are presented with the aim to establish the taxonomy of the bone remains. Their geological age and origin is now confirmed by petrographical analysis of the rock-matrix and by determination of the associated ammonoid shell.

2. Material and methods

The studied material consits of two rock fragments (about 30 cm in diameter), each of them containing one bone fragment. In association with one of them was an ammonoid shell. The geological origin of both rock fragments is unknown (Fig. 1).

Therefore, owing to the unknown origin of the fossil material, three approaches were used to study the material: the first involved micropaleontological, chemical and petrographical analyses of the matrix, the second study of the morphology of the ammonoid shell, and the third the examination of the morphology and histology of both preserved bone fragments.

The thin sections of both rock fragments were made and analysed with the aid of a polarised microscope. The bone fragments were extracted from the matrix and thin sections for histological analyses were prepared. The first two approaches have been made with the aim to establish the geological age of the bone remains, and the third for their systematic description.

Histological analysis of two osseous fragments was performed by means of thin-sections about 100 μm thickness, which were made from compacta of diaphyseal part of the bone. They were studied and photographed in normal transmitted light and with crossed nicols.

The bones and thin-sections of the rock samples are in the collection of the Institute of Quaternary Palaeontology and Geology (Inv.number.: ZPGK-Muc-1, ZPGK-MUC-2) while the thin-sections of the bone fragments are in the private collection of the second author.

3. Paleontological and petrographical analyses of rock samples

In thin-sections of both rock fragments microfossils were not found (Z. BAJRAKTAREVIĆ, personal communication). Morphology and measurement of the whole ammonoid shell as well as of the median section was studied. The diameter of the strongly deteriorated and recrystalised shell is about 6 cm. The shell is relatively involute with more or less slender outer wall. Curvature section is strongly oval, the scultpure of the wall deteriorated. The damaged outer lobe line probably consists of few equally large lobes with unbroken margin (2 saddles and 2 semicircular lobes, the outer lobe seems to be very broad). Due to the features of the lobes, this fossil belongs to the primitive ceratitid species of Lower-Middle Triassic (Scythian-Anisian) age (L. KRYSTYN, personal communication).

Petrographical analysis of the rock thin-section shows two different parts separated by enlarged concentration of autigenic pyrite crystals. In the first part, recrystalised and dolomitised base dominates with scattered pyrite. There are no relics of primary texture. The second part is composed of mixed pyroclastic sediment components (Fig. 2A). These consist of various amounts of carbonate

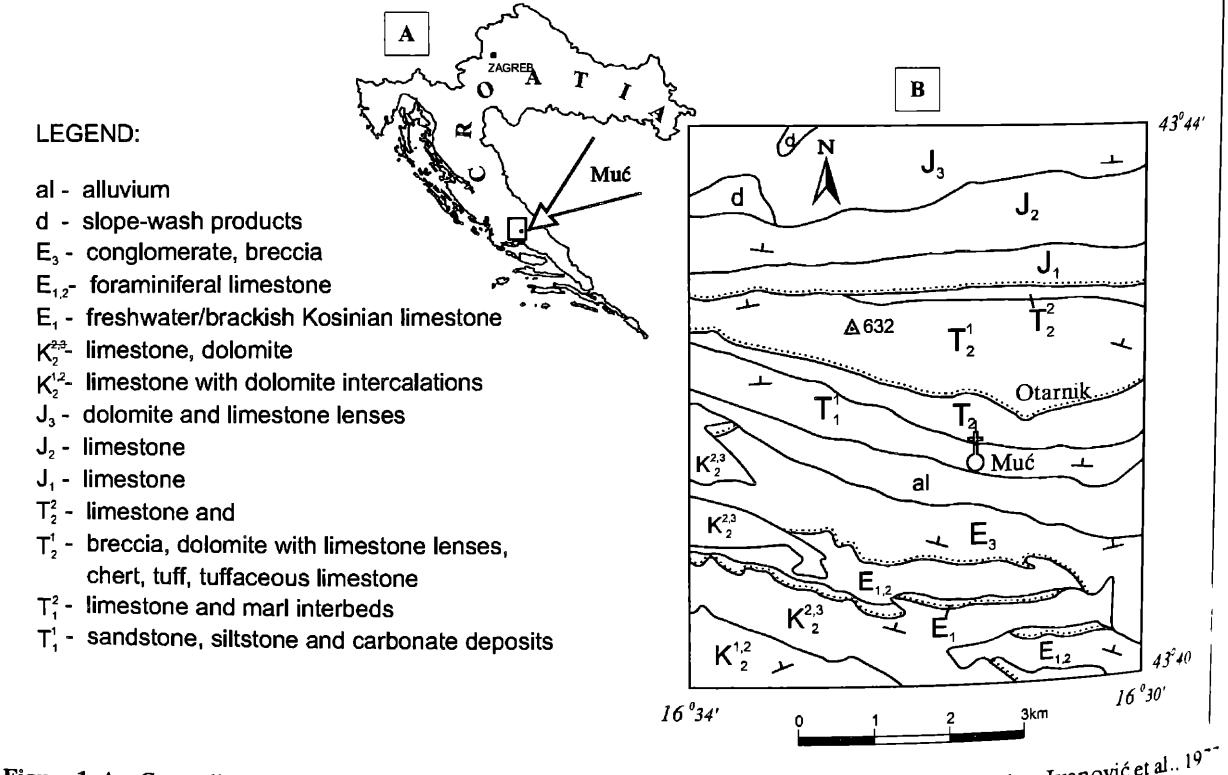

Figure 1: **A** – Generalised geographical map of Croatia. **B** – Geological map of the region of Muć (based on Ivanović et al., 1978, simplified).

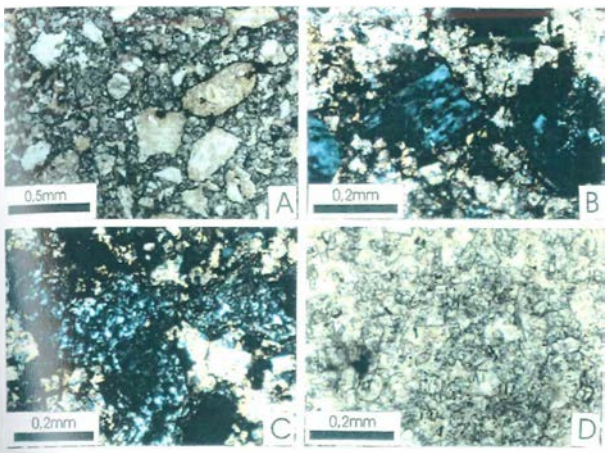

Figure 2: **A** – Devitrified and altered volcanic glass. **B** – Crystaloclast of feldspar. **C** – Chert (microcrystalised quartz). **D** – Rhonboedar crystals of dolomite.

(calcite and dolomite) grains, crystaloclasts of feldspar (Fig. 2B), quartz and chert (Fig. 2C), devitrified and altered volcanic glass. Secondary minerals of microcrystalised quartz and fibrous calcedon are seldom found within devitrified and altered volcanic glass. A larger part of the thin-section is dolomitised with well-developed rhomboedar crystals of dolomite (Fig. 2D) that replace calcite and the volcanogenic matrix.

Therefore the matrix is dolomitised tuffitic limestone, i.e. result of synchronous sedimentation of carbonate and volcanic material. Namely, material from an explosive volcanic event was mixed with dominantly carbonate sedimentation in the existing marine environment, and previously formed rock was by tectonic movements brought into a shallow sea environment with conditions suitable for later diagenetic dolomitisation.

Such conditions, considering the previous investigations of the area (ŠĆAVNIČAR et al. 1984), are characteristic for the Middle Triassic: submarine effusions of basaltic lava and eruptions of volcanogenic material throughout the Middle Triassic were interstratified with marine sediments. Given the above mentioned characteristics, the investigated rock fragments can be compared only with two lithologic units of the Anisian age, that also contain mixed tuffitic rocks (ŠĆAVNIČAR et al. 1984):

1. The "Older volcanic and volcanoclastic rocks" characterized by nodular limestone which contain limestone, sporadically dolomite, altered volcanic glass, pyroclasts of feldspar and quartz, fibres of chalcedon and clusters of autigenic pyrite, as well as sporadically casts of ammonites), and
2. The "Lower carbonate beds" comprises the layers of recrystalised and dolomitised limestone lacking primary texture. Rarely, small nests of chalcedon can be observed. The limestone and dolomites are often tuffaceous and contain pyroclasts of feldspar and quartz.

4. Morphology of the bone specimens

Two bone fragments are distal parts of one straight, rather slender bone (Fig. 3, Table 1). The partially broken distal articulation has a smooth somewhat helical surface, and thus the posterior part projected down below the anterior portion. The shaft is subcircular in section. Anterolateral there is a thin longitudinal crest. The medial groove – characteristic for an adaptation for bipedalism – is missing. On the surface, there is concretionary coating. Bone is still strongly birefringent indicating that the original apatite crystallites are still there, and that only the organic material is lost. Traces of longer transport are not visible.

Fragment	Length	max. Width	min. Width
distal part	71,8 mm	32,23 mm	30,68 mm
shaft	50,92 mm	19,47 mm	25,08 mm

Table 1: Measurements of the bone fragments.

Figure 3: Anterolateral view of the epipodial bone from Muć. **A.** Distal part. **B.** Shaft

After ROMER (1956) the main characteristics of reptile epipodial bones are subcircular shaft in section, and somewhat transverserely and moderately thickened distal end. So, regarding morphology, the Mud-specimens are fragments of one epipodial bone which shows mixture of the features characteristic for the archosauromorphs rather than lepidosauromorphs, and therapsids, but at the same time also for placodonts confined to the shallow, coastal waters with limbs only moderately specialised as paddles (BONAPARTE 1984; CARROLL 1988; COLBERT 1970; GALTON 1977, 1986; HUENE 1926; KREBS 1963a, 1963b, 1973; ROMER 1956). Yet, the most significant morphological resemblance is found to be with quadrupedal *Rauisuchus tiradentes* HUENE from the Anisian Santa Maria–Formation of South Brazil. Krebs (1973) described features of the tibia as follows: „The tibia is 215 mm long, stouter than the fibula, widened at the distal end. At the posteromedial upper part of the tibia one embankment is reaching the proximal end. The shaft is rounded, with a obtuse crest on the anterolateral side of the tibia. The crest grows stronger at the distal part of the bone." Nevertheless, due to the lack of the proximal surface and smaller aberancy in morphology of the distal part as well as in dimension, the Mud-specimen can only be described as epipodial bone of a terrestrial tetrapod.

Microscopically, the structure of superficial part of the bone is not fully preserved. The bone wall thickness is about 1/5 of the cross sectional diameter of the diaphysis. This compact bone surrounds a large medullar cavity devoid of trabeculae which are visible only on the small area. Transitional zone between compacta and trabecular part of the bone wall is absent. The superficial part of compacta, in place where it is preserved, has stratified arrangement and is slightly vascularized with longitudinally arranged vascular canals (Fig. 4A). In this part of the bone, two very conspicuous growth marks are visible. In deeper parts of compacta, a well-developed reticular network of vascular canals occurs. The canals are arranged in rows parallel to the surface of the diaphysis. The fibrolamellar bone deposition around vascular canals forms primary osteons, which are mainly in longitudinal direction. An avascular woven bone matrix is embedded between the rows of primary osteons (Fig. 4B).

In the middle part of compacta, woven bone tissue is interrupted with a few light circumferential bands. Under crossed nicols these bands are dark and they are interpreted as lines of arrested growth. In the deeper part of compacta parallel arrangement of vascular canals disappeared and a resorptive areas are clearly visible (Fig. 4C, D).

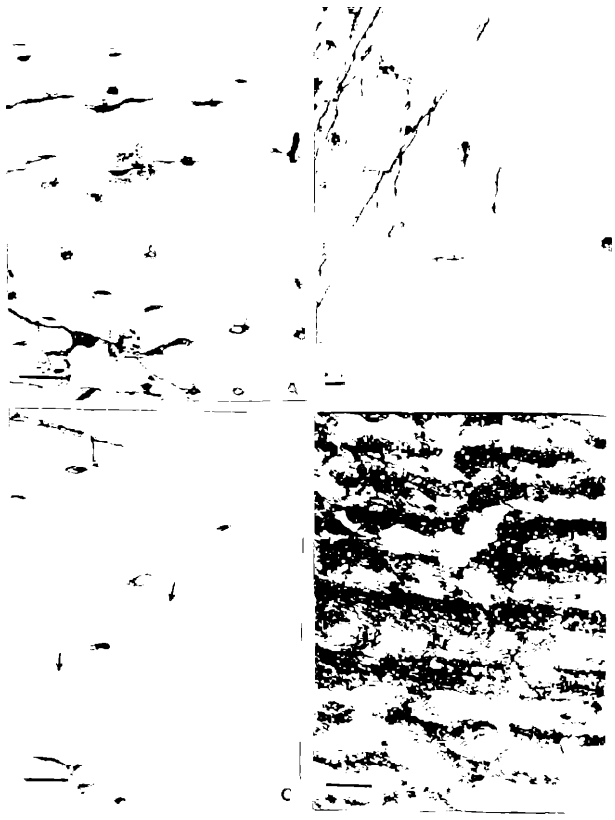

Figure 4: Mid – diaphyseal transverse section of reptilian bone. **A.** Stratified outer region of compacta, and fibro – lamellar inner region. Ordinary light. **B.** Central fibro – lamellar region of bone. Rows of primary osteons are embedded in woven bone. Ordinary light. **C.** Central fibro – lamellar region of bone. Lines of arrested growth (arrow). Ordinary light. **D.** A similar region as C. Cross – polarised light. Scale bar = 100 μm

5. Histology

Comparison of the results of histological analysis shows a similarity with the bone structure of the saurischians *Syntarsus* (Upper Triassic) and *Troodon* (Upper Cretaceous), as well as of the Upper Jurassic ornitischian *Dryosaurus* (CHINSAMY 1990, 1995; VARRICHIO 1993). The cross-section of the bone fragment from Mud was correlated with the results of the researches directed to the comparative analyses of the bone microstructure of both recent and extinct reptiles (ENLOW 1969; CHINSAMY 1993; RICQLES 1975, 1983, 1989; SMITH 1960; CASTANET & RICQLES 1986-1987; CASTANET et al. 1988; BUFFRENIL & MAZIN 1990, 1992;), and on the basis of the bone microstructure it was possible to determine approximative individual age and growth rate of the animal (NOPSCA 1933; CHINSAMY 1990,1993; VARRICHIO 1993; CASTANET et al. 1988; ESTEBAN et al. 1996).

The described bone structure shows a well developed cortical part and very large medullar cavity, and the scarce trabecular bone tissue only on small area in the inner surface of the bone. Such features are characteristic for long bones of mammals and birds, as well as for predominantly terrestrial reptiles and amphibians (WALL 1983; ESTEBAN et al. 1996), while in tetrapods adapted to aquatic environment they are absent or poorly developed (BUFFRENIL et al. 1990a; BUFFRENIL & MAZIN 1990). Also, a progressive endosteal transitional zone between outer cortex and inner cancalleous bone, otherwise characteristic for aquatic animals (BUFFRENIL et al. 1990b; BUFFRENIL & MAZIN 1990), is absent indicating a terrestrial pattern. The superficial part of the compacta of the studied bone consists of circumferentially arranged and poorly

vascularized bone tissue. This type of bone deposition is typical for the final ontogenetic stage, and in recent animals (e.g. crocodiles) similar tissues are often deposited after sexual maturity is reached and associated with a slowdown in growth (BUFFRENIL 1980; HUTTON 1986; RICQLES 1980). In deeper parts of investigated compacta, primary bone was deposited as highly vascularized fibro-lamellar tissue. Such tissue was among extant vertebrates, i.e. mammals and birds, associated with more or less rapid, continuous deposition of bone (REID 1984; RICQLES 1980), and was also found in some recent reptiles as well as in dinosaurs and plesiosaurs (BENNET 1993; PADIAN et al. 1995; RICQLES 1975: RICQLES et al. 1992; VARRICHIO 1993).

In the investigated bone, the lines of arrested growth are found in the middle part of compacta indicating interruption in bone deposition probably caused by some physiological stress or by short changes in environmental conditions, coinciding with observations in some fossil (CHINSAMY 1990, 1995; VARRICHIO 1993) and recent reptiles and amphibians (ENLOW 1969, ESTEBAN et al. 1996).

6. Conclusion

Two bone fragments deriving from limestone rock fragments of Muć (Mt. Svilaja, Dalmatia), are after the morphological and histological analysis identified and described as one epipodial bone of an adult terrestrial tetrapod. Therefore the preliminary assignment to the Placodontians (PAUNOVIĆ 1990) must be abandoned.

Because the geological allocation of the investigated bone remains is now confirmed by the nature of the rock matrix, and because their age is estimated to be Middle Triassic i.e. Lower Anisian, they must be derived from one of the lithologic units – designed as "Lower carbonate beds" or "Older volcanic or volcanoclastic rocks" – which extend on the southern slopes of Mt. Svilaja (Dinarides, Dalmatia) in a stretch of about 18 km. Thus the described epipodial bone represents the first record of a Triassic terrestrial tetrapod in Croatia.

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