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First Record of Fossil Fish (Enchodontoidei, Actinopterygii) in the Struganik Quarry in Western Serbia

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Key words: *Enhodontoidei, Enchodus, Upper Cretaceous, Struganik Limestone, western Serbia.*

Abstract. This paper presents the first Upper Cretaceous remains of fish in Serbia, discovered near the village of Struganik. This is also the first described find of Mesozoic fish in Serbia. A stone slab with visible contours of an almost complete fish, with a total body length of about 20 cm, was excavated from the Struganik quarry. Most bones are preserved as imprints. The number of vertebrae, the shape and position of the cranial bones, the type of teeth, and the position of the first dorsal fin all indicate that the studied specimen belongs to the genus *Enchodus* known from several Upper Cretaceous localities in the Tethys domain.

Кључне речи: *Enhodontoidei, Enchodus, горња креда, струганички кречњаци, западна Србија.*

Апстракт. У овом раду су приказани први горњокредни остаци риба из Србије, откривени на профилу који се налази у селу Струганик. Из струганичког каменолома ископана је камена плоча са видљивим контурама скоро комплетног тела рибе, укупне дужине око 20 cm. Већи део скелета сачуван је у виду отиска. Број пршљенова, облик и положај кранијалних костију, као и положај првог дорзалног пераја указују на то да проучавани примерак припада роду *Enchodus*, који је до сада познат из области Тетиса са неколико локалитета горњокредне старости.

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Introduction

The quarry near the village Struganik in western Serbia (Figs. 1, 3a) represents a key location to study the depositional evolution and paleogeography of the distal Adriatic continental margin towards the end of Cretaceous times. This paper presents the first record of the Upper Cretaceous fossil fish discovered in the Upper Santonian-Lower Campanian thin-bedded marly limestones outcropping in the Struganik quarry. The taxonomic identification enabled meaningful new inferences regarding the paleoenvironmental conditions on the distal Adriatic margin at the Santonian-Campanian transition.

Geological setting

The Cretaceous sedimentation across the entire distal continental margin of Adria was associated with the continuous shortening and overall transgression, which was driven by the subduction of the Adriatic plate beneath the overriding European plate (i.e., the Sava subduction system, Schmid et al., 2020). Following the latest Jurassic obduction of

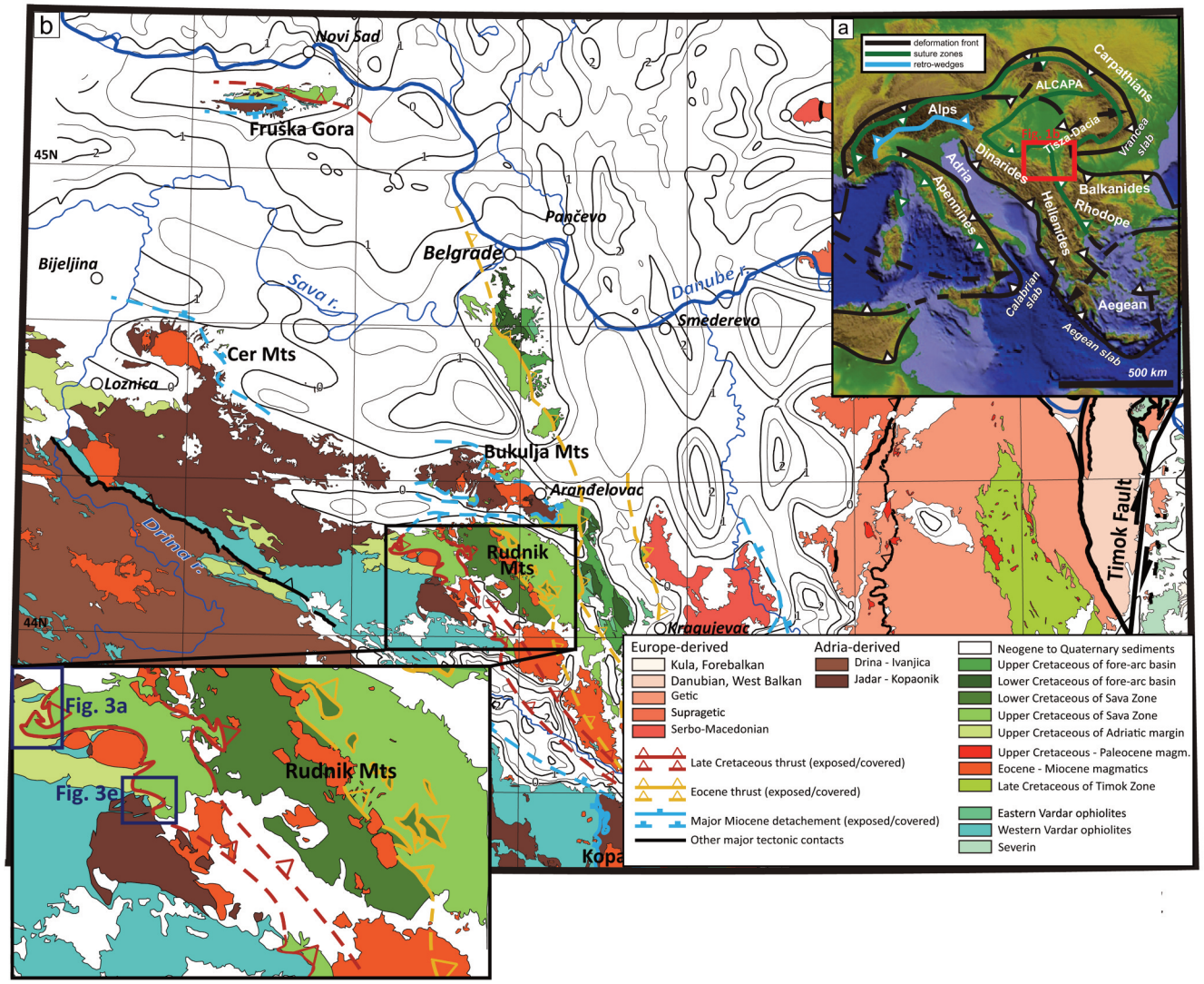

Fig. 1. a) *Topographic map of Central Mediterranean orogens, displaying suture zones, orogenic fronts, and retro-wedges (modified after Krstekanić et al., 2020). The red rectangle marks the position of Figure 1b;* ***b)*** *Geological map of the connection between the Dinarides, South Carpathians, and Pannonian Basin, with the zoom-in view of the broader study area delimited by the black rectangle (modified after Stojadinovic et al., 2022). Blue rectangles in the zoom-in indicate the location of local geological maps in Figure 3.*

ophiolites over the distal Adriatic margin (the Western Vardar Ophiolites Unit of Schmid et al., 2020, Fig. 1b), the new cycle of deposition started with the Albian–Cenomanian transgressive coarse clastics that are gradually deepening into clastic-carbonatic shelf deposits (Figs. 2, 3).

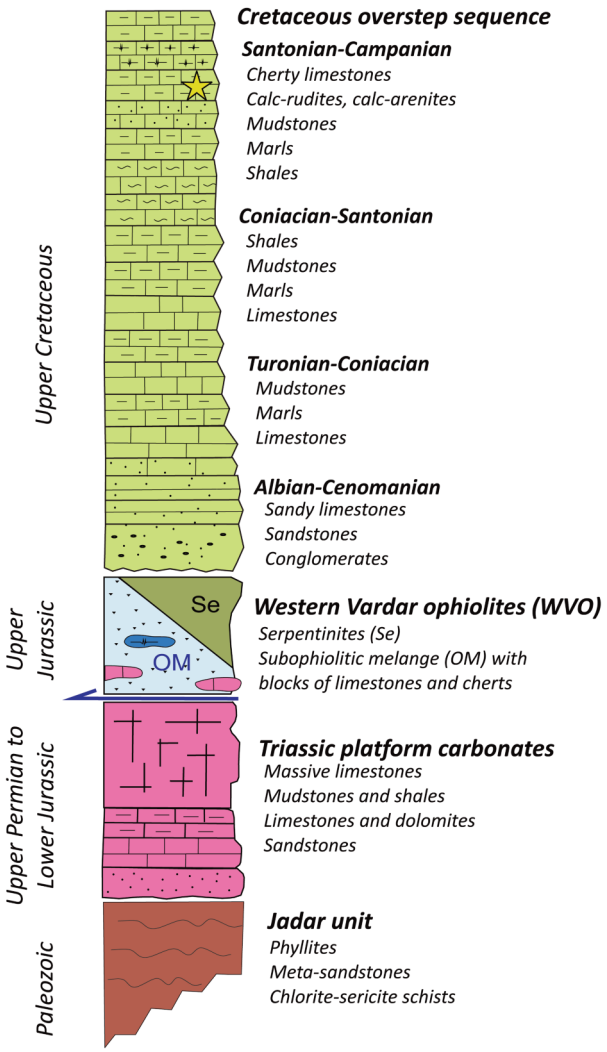

Fig. 2. *General lithostratigraphic column of Mesozoic sedimentation along the distal Adriatic margin (Filipović et al., 1976; Djerić & Gerzina, 2014; Bragina et al., 2020). The yellow star marks the approximate stratigraphic position of the analyzed specimen.*

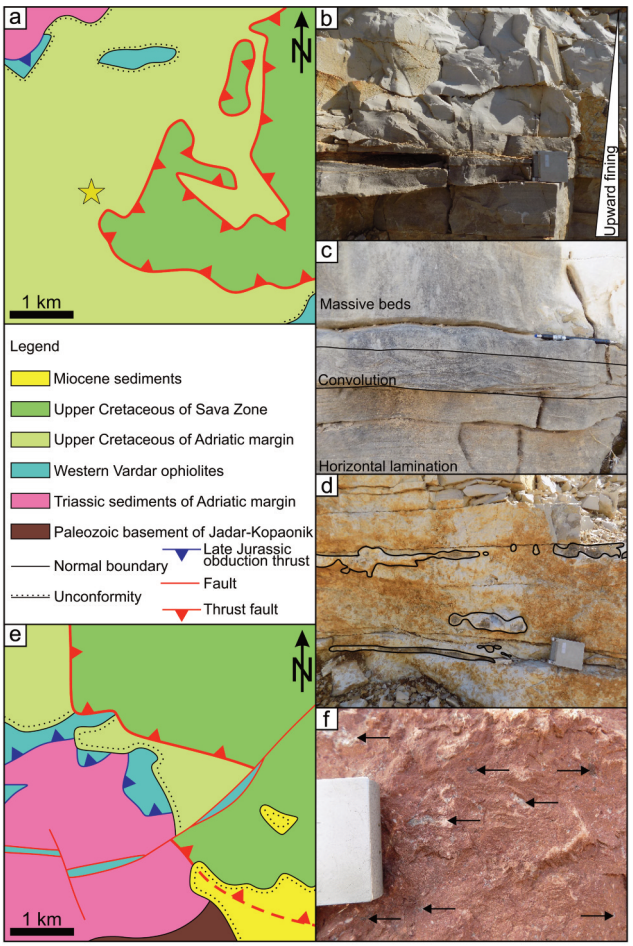

Fig. 3. a) *Local geological map of the Struganik area where the Upper Cretaceous Sava trench turbidites are thrust on top of the Santonian-Campanian carbonates of the Adriatic margin. The yellow star marks the position of the outcrop with the analyzed specimen;* ***b)*** *Upward fining in the Santonian-Campanian calc-arenites and limestones;* ***c)*** *Turbiditic sedimentary textures in the Santonian-Campanian calc-arenites;* ***d)*** *Santonian-Campanian limestones with chert nodules (outlined in black);* ***e)*** *Local geological map of the Rajac area where the Upper Cretaceous Sava trench turbidites are thrust on top of the Albian-Cenomanian Western Vardar ophiolites overstep sequence;* ***f)*** *Basal deposits of the Cretaceous sedimentation over the Adriatic margin represented by the Albian-Cenomanian sandy limestones with centimeter-scale fragments of serpentinized peridotites, indicated by arrows.*

The onset of the Cretaceous overstep sequence is marked by conglomerates, sandstones, and sandy limestones with fragments of serpentinized peridotites (Figs. 3e, f). The continued subsidence led to the deposition of the distal shelf to proximal slope carbonates and clastics during the Turonian–Santonian (see Djerić & Gerzina, 2014), followed by distal slope sedimentation during the Santonian–Campanian (i.e., the Struganik facies, Figs 2, 3a-d; Bragina et al., 2020).

Material

The specimen was collected in 2020 by Predrag Petrović in the Struganik quarry. The material com-

prises one slab with a fossil fish and is deposited in the Paleontological collection of the Stone Museum in Paštrić village.

Systematic paleontology

TELEOSTEI Müller, 1846
Order AULOPIFORMES Rosen, 1973
Family ENCHODONTIDAE Woodward, 1901
ENCHODUS Agassiz, 1835

***Enchodus* sp.**
(Figs. 4-6)

Diagnosis. The studied specimen represents one almost wholly preserved skeleton. The fish skeleton has a total length of 20 cm, with a head length of about one-fourth of the entire body length. The vertebrate column contains 32 vertebrae and 17 abdominal vertebrae but is not wholly preserved and probably contains more vertebrae.

Fig. 4. *Slab with an imprint of an almost complete fish Enchodus sp. Scale bar 1 cm.*

The skull includes well-preserved bones of the jaws and partly preserved bones of the neurocranium, while bones of the opercular series are entirely missing. All skull bones are preserved as imprints.

The first dorsal fin is partly preserved, and it starts between the 6th and 7th vertebrae and includes 7 or more rays. The caudal, anal, and pectoral fins are not preserved.

Neurocranium. Only the frontal bone is preserved. It is a large, slender bone representing about 80% of the skull roof. The lateral margin of this bone is excavated above the orbit and forms a spine shape near the suture with the autosphenotic. The posterior border of the frontal is not visible, and contiguous bones such as the pterotic, parietals, and supraoccipital are missing. The sensory canal and tubercular surface of the bone are not noticeable. The orbit is large and oval.

Jaws. The contour of the premaxilla is partly visible. Posteriorly, the pedicel of the premaxilla is not preserved. The anterior margin close to the palatine is slightly denticulate. The premaxilla wears one strong tooth, which may represent the terminal tooth of the dermopalatine (dpal). The ectopterygoid is a long, thin bone that gradually spreads posteriorly and bears 7 or more canine-like teeth. There is no apparent connection visible with the palatine, posteriorly, there is a crack where contact with the hyomandibula and quadrate would be expected. The dentary is long, as is characteristic of all enchodontids. Anteriorly, it bears two teeth comparable in size and shape, and postero-medially is only one much larger tooth. The remainder of the oral margin bears 5 or more equally sized teeth. The posterior oral margin is without teeth. Partly can observe angulo-articular, ventrally is clear visible contact with the dentary, like V-shape. Eight branchial rays are noticeable under the angulo-articular.

Remarks. The described specimen was assigned to the genus *Enchodus* sp. (Aulopiformes) based on the presence of fangs on the dermopalatine and an ectopterygoid with a minimum of seven teeth. The head makes up approximately one-fourth of the total length of the specimen, of which the large mouth opening stands out. The size of these jaws positions *Enchodus* in the middle of the food chain (Fielitz, 2004). It is considered that it probably fed on cephalopods (Grandstaff & Paris, 1990), but it was also the prey of larger predators, such as other teleosts or plesiosaurs (Cavin, 1999). The spindly shape of the body and the

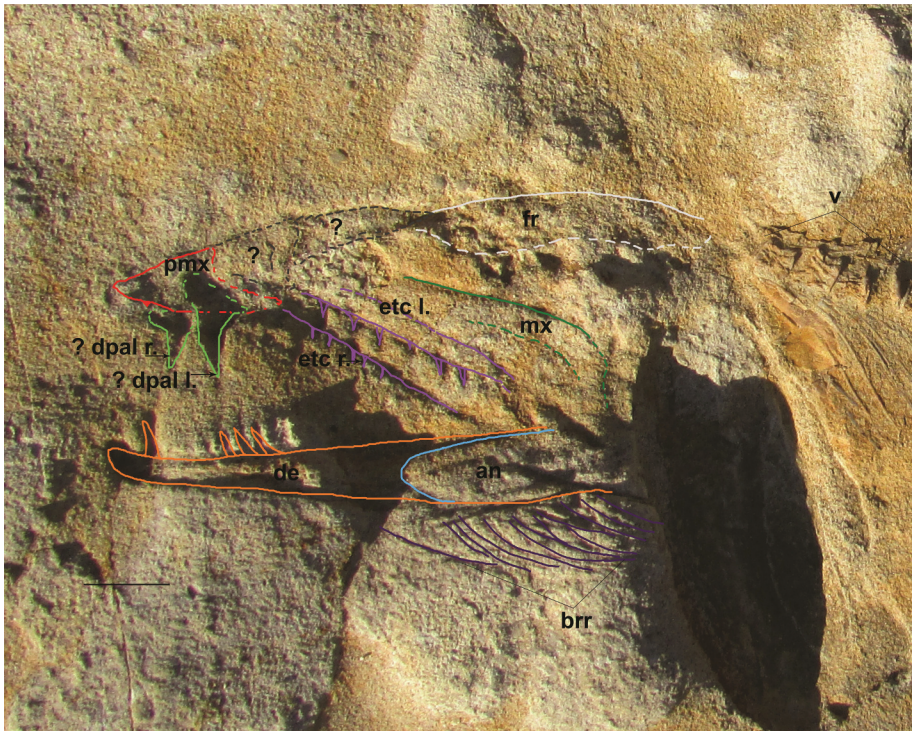

Fig. 5. *Enchodus sp. Skull with line drawing highlighting certain bones. Abbreviations: an-angular, brr-branchiostegal rays, de-dentary, fr-frontal, mx-maxilla, pmx-premaxilla, etc.-ectopterygoid, dpal-dermopalatine, v-vertebrae. . Scale bar 1 cm.*

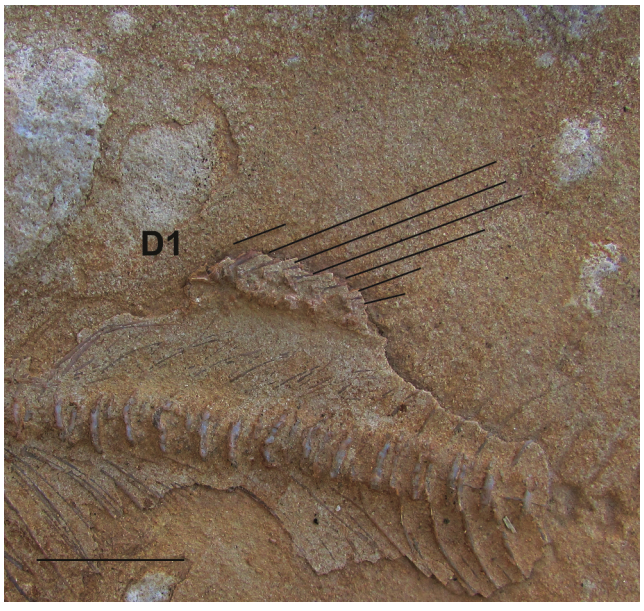

Fig. 6. *Enchodus sp. Dorsal fin with line drawing. Scale bar 1 cm.*

position of the dorsal fin indicates an active swimmer. The poor preservation of the remains did not permit identification beyond the genus level.

Discussion

The Enchodontidae is a family of extinct marine teleosts characterized by an elongate fusiform body and a narrow elongate maxilla (Nelson, 2006). They belong to the Aulopiformes, the so-called lizardfishes, which include fifteen recent and nine extinct families (Silva & Gallo, 2007). These marine fishes are distributed from estuaries to the abyssal, occupying both benthic and pelagic habitats (Baldwin & Johnson, 1996; Nelson, 2006). The first fossil remains of Enchodontidae occur from the early Cretaceous. The most numerous are those from the late Cretaceous. According to Cavin et al. (2012), representatives of the genus, Enchodus were fast swimmers, middle-sized pelagic fishes, and significant ichthyophagous predators during the Late Cretaceous. They appeared to become extinct at the Cretaceous–Palaeogene boundary. The isolated finds of teeth from the Eocene, mentioned by some authors (Silva & Gallo, 2011; Rana et al., 2005), are unreliable and may represent reworked material.

The paleogeographic distribution of the genus *Enchodus* is related primarily to the Tethys (today's Mediterranean region), the Western Interior Sea, and the eastern coast of present-day North America (Fielitz, 2004; Cavin et al., 2012; Holloway et al., 2017). Most species of this genus inhabited epicontinental seas, and their evolution during the Late Cretaceous resulted in a greater distribution of *Enchodus* species (Díaz-Cruz et al., 2020; Gouiric-Cavalli et al., 2016).

Compared to the Hungarian Santonian fauna (Szabó & Ősi, 2017) or the younger, Maastrichtian faunas of Romania (Trif & Codrea, 2022), which presents typical continental faunal elements of the

European Late Cretaceous archipelago, the Struganik fish fauna of similar geological age indicates marine environment. A rich fish fauna of the marine environment of the Senonian age is known from Croatia (area of the central Dalmatian inland; Radovčić et al., 1983). The Upper Cretaceous, marine fish fossil associations with representatives of the genus Enchodus, have been described worldwide (e.g., Greece, Italy, Israel, Syria, Lebanon, Morocco, Egypt, Libya, India, Brazil, Mexico, North America) (Cavin et al., 2012; Holloway et al., 2017), but it should be emphasized that the most of the *Enchodus* occurrences are based on fragmentary remains, especially isolated teeth (Cavin et al., 2012). Although some species show a large area of distribution, which agrees with the data that they are fast-swimmer pelagic fishes, most species are restricted to epicontinental seas. They do not cross oceanic basins (Gouiric-Cavalli et al., 2016). The occurrence of several *Enchodus* species in western Tethys and central Tethys can be considered a result of a vicariant event (Cavin et al., 2012).

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Резиме

Први налаз фосилне рибе (Enchodontoidei, Actinopterygii) у каменолому Струганика у западној Србији

У овом раду је приказан први налаз фосилне рибе из горњокредних кречњака локалитета Струганик (западна Србија, сл. 1, 3а). Детерминација ове рибе је дала важне податке о палеоеколошким условима на дисталној адријској маргини на прелазу сантон- кампан.

На целој дисталној континенталној маргини Адрије, током креде седиментација је била повезана са континуираним скраћивањем и свеукупном трансгресијом, која је била изазвана субдукцијом адријске плоче испод европске плоче (тј., Сава субдукциони систем, Schmid et al., 2020). Фације Струганика (сл. 3а) чине танкослојевити лапоровити кречњаци, калк-рудити и калк-аренити који показују фину ламинацију и фино уситњавање (сл. 3б) и конволуцију (сл. 3ц), као и кречњаци. са нодулама рожнаца (сл. 3д). Током кредно- палеогене колизије између Адрије и Европе, горњокредни турбидити рова Сава зоне (тј. Љишка формација; Stojadinović et al., 2022) били су навучени преко кредног седиментног покрова адријске маргине (сл. 1б, 3а, е).

Описани примерак је детерминисан као *Enchodus* sp. (Aulopiformes) на основу присуства израслина у виду зуба- дермопалатинума и најмање седам зуба на ектоптеригоидној кости. Глава чини отприлике једну четвртину укупне дужине тела, од чега се истиче велики отвор уста. Величина ових чељусти поставља *Enchodus* у средину ланца исхране (Fielitz, 2004). Сматра се да се вероватно хранио главоношцима (Grandstaff & Paris, 1990), али је био и плен већих риба (Cavin, 1999). Вретенаст облик тела и положај првог дорзалног пераја указују на активног пливача. Низак ниво очуваности примерка је условио детерминацио само до нивоа рода. Enchodontidae је изумрла породица морских телеостеа, које карактерише издужено, вретенасто тело и уска издужена максила (Nelson, 2006). Ове морске рибе су распрострањене од естуара до абисала, заузимајући и бентоска и пелагична станишта (Baldwin & Johnson, 1996; Nelson, 2006). Први фосилни остаци Enchodontidae су познати из доње креде. Најбројнији су наласци из горње креде. Палеогеографско распрострањење рода *Enchodus* везано је првенствено за Тетис (данашњи Медитеран) и Западно унутрашње море и источну обалу данашње Северне Америке (Fielitz, 2004; Cavin et al., 2012; Holloway et al., 2017). У поређењу са Мађарском сантонском

фауном (Szabó & Ősi, 2017), или млађом маастрихтском фауном Румуније (Trif & Codrea, 2022) која представља типичне елементе континенталне фауне европског архипелага горње креде, фауна риба из Струганика сличне старости јасно указује на морско окружење. Асоцијације фосилних морских риба горње креде са представницима рода *Enchodus* описане су широм света (Cavin et al., 2012; Holloway et al., 2017). Иако неке врсте показују велико подручје распрострањења, што је у складу са подацима да су пелагичне рибе које брзо пливају, већина врста је ограничена на епиконтинентална мора.

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