

Novel findings of Late Cenomanian-Turonian Pachyophiid snakes, fishes and plants in the SE Bosnia-Herzegovina

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Abstract. New fossils from the Late Cenomanian-Turonian locality in the Bileća area are reported. The fossils include a diverse assemblage of snake-like reptile remains, fishes and plants. While fossil snakes have already been found in this area, the remains of fish and plants are reported for the first time. Based on the state of fossil preservation, the following were identified: the snake *Pachyophis* (Simoliophiidae), the pycnodont fish *Coelodus* sp., and plant remains of the flowering plants groups *Magnoliidae* ex. *Liliana*, *Arecaceae* (palm trees), and *Cycadopsida*.

Апстракт. У овом раду су приказани нови горњоценоманско-туронски фосилни налази пронађени на локалитету у подручју Билеће. Фосилни остаци представљају разнолику асоцијацију остатака рептила сличних змијама, риба и биљака. Док су фосилне змије већ пронађене на овим просторима, по први пут се наводе остаци риба и биљака. На основу стања очуваности фосила идентификовани су: остаци змија рода *Pachyophis* (Simoliophiidae), пикнодонтне рибе рода *Coelodus* и биљни остаци група цветница *Magnoliidae* ex. *Liliana*, *Arecaceae* (палме) и *Cycadopsida*.

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Introduction

In the northern part of Herzegovina, particularly in the Bileća area (Fig. 1), there are a large number of quarries excavating limestone known as the Bileća Stone. In the last decade, the popularity of this limestone and its use has increased, thus, the number of accidental finds of fossil remains has also increased. According to the data obtained during geological mapping in the areas of Bileća and Trebinje, NATEVIĆ & PETROVIĆ (1970) considered the Bileća limestones as Turonian, while HRVATOVIĆ (2006) states that bituminous limestones with snake-like reptile remains (*Pachyophis*) from the Bileća area are Late Cenomanian in age. These dense well-bedded limestones are known to have produced four pachyostotic snake specimen thus far. Fossil remains of two

pachyostotic snakes (non-pathological increases in bone thickness) (HOUSSAYE, 2013) from the early Late Cretaceous (Turonian, Cenomanian) of the Bileća area have been known for 100 years (SLIŠKOVIĆ, 1970). These two specimens, *Pachyophis woodwardi* NOPCSA (1923) and *Mesophis nopcsai* BOLKAY (1925) come from the same locality of Selišta, north of Bileća. The holotype of *Pachyophis woodwardi* (NHMW 1912-I8) is in the collections of the Naturhistorische Museum Vienna, while *Mesophis nopcsai* is in the (Zemaljski muzej) National Museum of Bosnia and Herzegovina in Sarajevo as part of a permanent exhibition. The fourth specimen of a pachyostotic snake was found at the quarry referred to as Dubovac, three kilometers northwest of Bileća, during 2016 and is housed in the Natural History Museum in Belgrade (NHMBEO MV 280; DJURIĆ et al., 2017).

In this work, we describe several new pachyostotic snake fossils from the Bileća area, together with the associated fish and plant fossils.

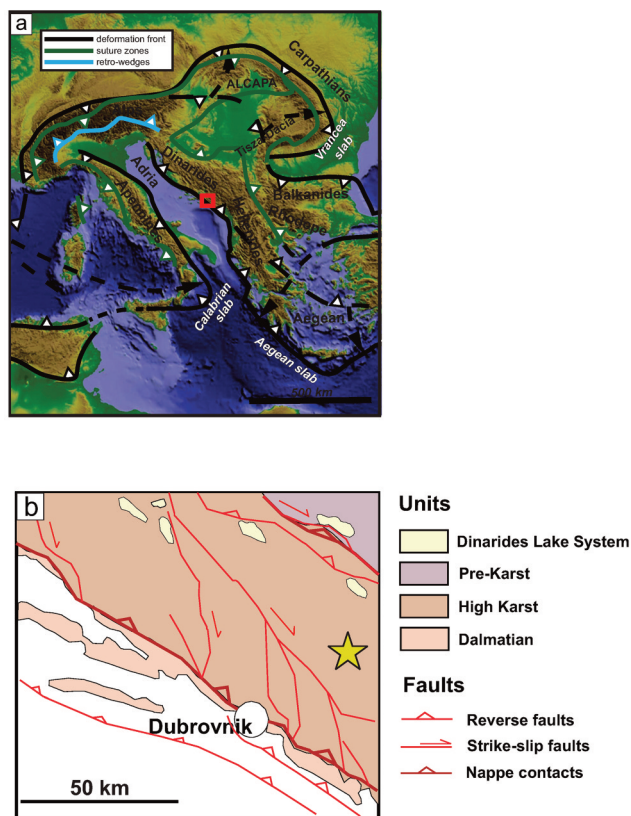


Fig. 1. **a.** Topographic map of Central Mediterranean orogens, displaying suture zones, orogenic fronts, and retro-wedges (modified after KRSTEKANIĆ et al., 2020). The red rectangle marks the position of figure 1b; **b.** Tectonic map of the contact area between the External Dinarides' High Karst and Dalmatian Units in the SE Bosnia-Herzegovina (modified after VAN UNEN et al., 2019). The yellow star marks the location of the Bileća area.

Geological setting

The Rogošina quarry (42°51'34"N 18°24'50"E) is located in the SE Bosnia-Herzegovina, three kilometers south of the town of Bileća. Tectonically, this entire region comprises parts of the External Dinarides' High-Karst Unit, which was formed during the Cretaceous to Paleogene due to convergence between Adria- and Europe-derived continental units (Figs 1a, b; DIMITRIJEVIĆ, 1997; SCHMID et al., 2020). The stratigraphic record within the High-Karst Unit yields evidence for long geological evolution ranging from Late Triassic through Miocene times (NATEVIĆ & PETROVIĆ, 1970). Mesozoic sedimentation took place in a carbonate platform environment, predominantly characterized by shallow-water marine conditions (VLAHOVIĆ et al., 2005; DJAKOVIĆ et al., 2021). The most prominent stratigraphic members are represented by massive and stratified limestones and dolomites (Fig. 2). The analyzed fossil remains were discovered within the thin-bedded limestones, stratigraphically defined as lower Turonian in age (Fig. 2; NATEVIĆ & PETROVIĆ, 1970). The Mesozoic carbonates were highly tectonized following Eocene-Oligocene thrusting in the external parts

of the Dinarides (van UNEN et al., 2019). The subsequent Miocene extension in the External Dinarides was associated with the formation of a group of intermontane basins (i.e. the Dinarides Lake System; MANDIĆ et al., 2011). The extension was followed by renewed shortening, which started during the late Miocene and remains presently active (van UNEN et al., 2019).

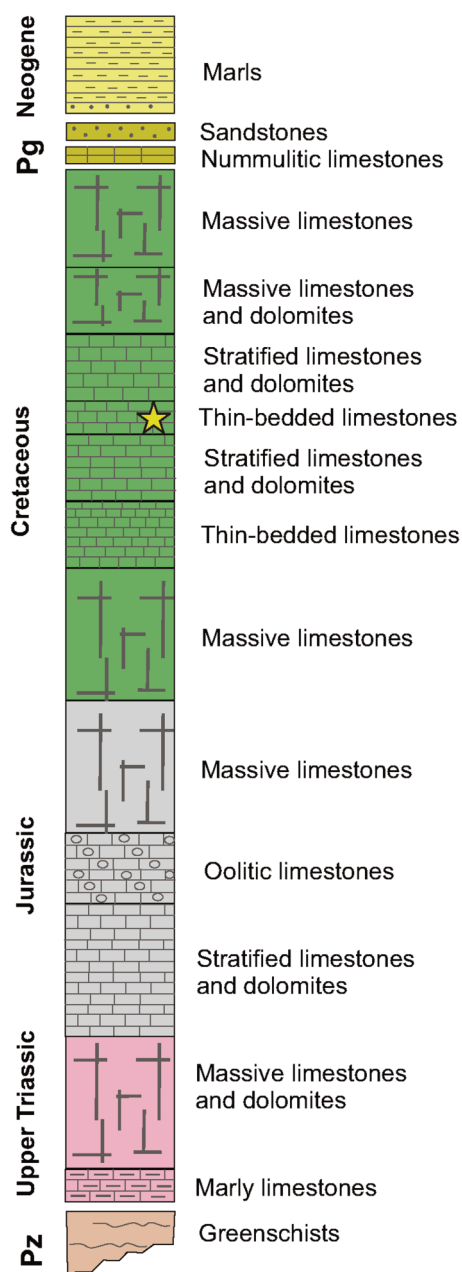


Fig. 2. General lithostratigraphic column of the High Karst Unit (simplified after NATEVIĆ & PETROVIĆ, 1970). The yellow star marks the approximate stratigraphic position of the analyzed samples. Abbreviations: Pz - Paleozoic, Pg - Paleogene.

The surrounding area of Bileća (Fig. 1) is made of Cretaceous sediments which belong to the deposits of the Adriatic Carbonate Platform of the peri-Mediterranean realm. The overall paleogeographic conditions of the northeastern part of the Adriatic Carbonate Platform during the Late Cretaceous were controlled by synsedimentary tectonics, eustatic sea level changes, and increases in the amount of carbonate production (VLAHOVIĆ et al., 2005). Such conditions led to local emergences of the platform and shallow-water depositional environments (VLAHOVIĆ et al., 2005). The Late Cretaceous sedimentary succession near Bileća consists mainly of limestones and dolomites which were deformed into large-scale open folds, locally truncated by thrusts during the Cenozoic uplift of the Dinarides.

No detailed stratigraphic analysis of the site has been performed, whereas its stratigraphic position according to the Basic Geological Map of Yugoslavia is considered to be within lower Turonian sediments (NATEVIĆ & PETROVIĆ, 1970). The mapped lower Turonian lithostratigraphic unit is composed of thin-bedded limestones with interbedded dolomites and is positioned above Cenomanian dolomites and below sediments in which the bivalve *Chondrodonta* appears (middle Turonian).

Paleontology

The material upon which this study was based will be deposited in the collections of the Bileća Cultural Center “Jevto Dedijer”, indicated by the numbers: CCJD-R 1-11. It represents the result of several years of data collection from the site. All of the material described herein was found in well-bedded limestones of the Rogošina quarry (Fig. 3).

Snake fossils

The remains of snakes brought from the Rogošina site are preserved on 6 individual plates showing different degrees of preservation. Three plates represent the part and counterpart of the same specimen (Fig. 4). Most of the vertebrae were damaged when the plates were broken. Skull remains have not been



Fig. 3. The Rogošina quarry.

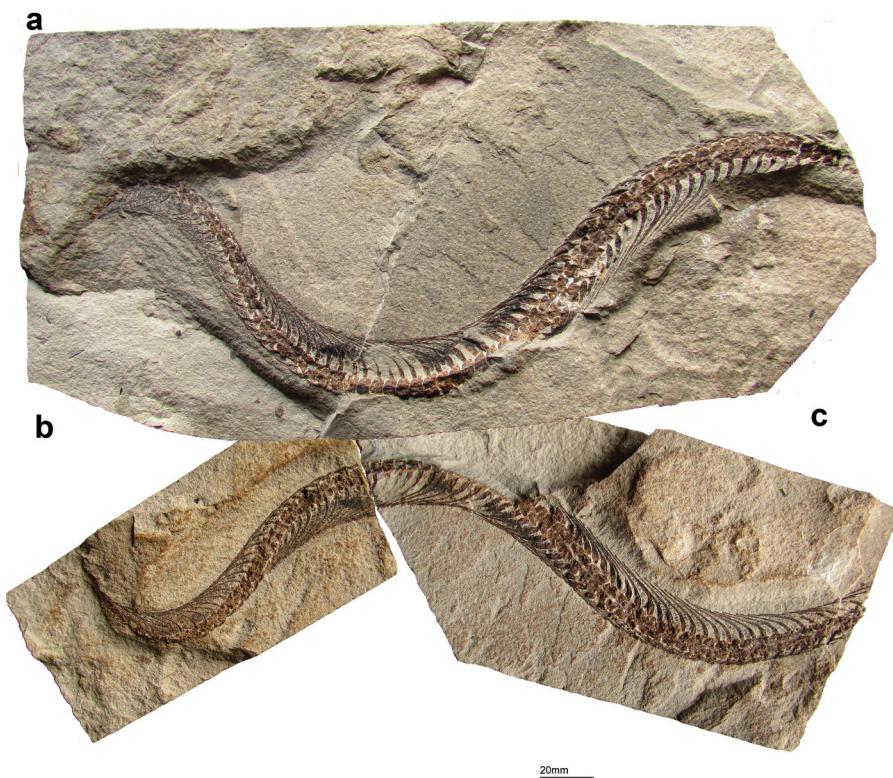


Fig. 4. “Hind-limbed” snake remains *Pachyophis* sp.; part (a) and counterpart (b, c) of the same specimen (a-CCJD-R 1, b-CCJD-R 2, c-CCJD-R 3).

found on any of the specimens, nor are there traces of hind-limb or pelvic elements known from other pachyophiids (e.g., CALDWELL & LEE, 1997). Specimens consist exclusively of the remains of vertebrae and ribs. Morphologically, pachyostosis of the vertebrae and ribs is visible, but to a lesser degree than the specimen from 2016 (ĐURIĆ et al., 2017). The longest specimen (Fig. 4a) probably corresponds to the middle and part of the posterior trunk of the body, about 28 cm long with 73 visible vertebrae. The vertebrae from 33 to 48 positions of the preserved column are exposed on the ventral side and are relatively well preserved. The second and third plates are the counterparts of this specimen (Fig. 4b, c).

Ribs are visible along the entire length of the specimen with pachyostotic proximal parts. The most swollen ribs are from the 14th to 40th vertebrae. The balance of the specimen’s vertebral remains is disturbed and mechanically polished (Fig. 5). The shape of the vertebrae and pachyostosis indicate that the specimens belong to the snake *Pachyophis*, but later analyses will show the exact affiliation.

Fish fossils

Fossil remains of fish were found on two sedimentary plates. One plate was cut and polished during cutting in the quarry so that the teeth were damaged (Fig. 6a). Two rows of ellipsoidal to rectangular teeth can be identified as molariform teeth, probably from the prearticular bone. On the second plate, there is a partially preserved remnant of a vomer on which four rows of teeth can be seen. The teeth of the central row are ellipsoidal to rectangular. On both sides (left and right) there is a row of oval teeth. The fourth row of ellipsoidal teeth was exposed only on the left side of



Fig. 5. *Pachyophis* sp. fragments of vertebral column; (a-CCJD-R 4, b-CCJD-R 5, c-CCJD-R 6).

the vomer. According to the appearance and arrangement of the teeth on the vomer, it can be assumed that this specimen belongs to the genus *Coelodus* (Fig. 6b). These remains certainly belong to pycnodont fish, although the generic identification based only on isolated teeth is not reliable (KRIVET, 2005). According to POIATO-ARIZA, (2003) identification only based on dental remains can be considered parataxonomy.

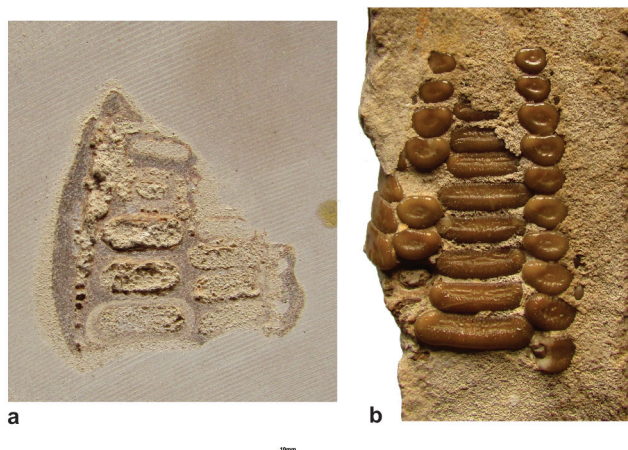


Fig. 6. Isolated dentition of pycnodont fishes: **a.** fragment of praearticulare dentition an indetermnated pycnodont, CCJD-R 8; **b.** vomerine dentition of *Coelodus* sp. CCJD-R 7.

Plants

Three specimens of fossilized plants were found at the site. Specimens represent imprints and compressions of individual parts of plants.

The first specimen represents an imprint-compression of a twig on which sympodial branching can be clearly seen (Fig. 7). This type of branching indicates that the fossilized parts most likely belong to one of the numerous species of phanerophyte flowering plants (*Angiospermae*). Remains of leaves, leaf scars, leaf stalks, or buds are not visible. The absence of leaves can be affected by long transport of the specimen to the depositional environment, mechanical damage due to which the branch dried up, or even seasonal leaf loss which would indicate seasonal changes. On the basis of this solitary specimen nothing more can be said except that it belongs to *Magnoliidae* (flowering plants) excluding *Liliana* (monocots).



Fig. 7. *Magnoliidae* exc. *Liliana*, ramunculus, imprint-compression of twig (sympodial branching), CCJD-R 9.

The second specimen is represented by imprints-compressions of two parts (positive and negative) of the same plant organ, which overlaps in its lower, i.e., the upper end (Fig. 8a). The specimen is characterized by regular, straight, and parallel margins (Fig. 8a, b) and shows two structures similar to “plant shoots” that separate to the left and right of the base (Fig. 8b). The “plant shoots” are

short, unusually small in relation to the size of the main axis, and an alternating position about it. Microscopy confirmed that these structures are an integral part of the plant and that they are not independent parts on top of and beneath the fossilized specimen. If we connect the positive and the negative (Fig. 8a), it can be seen that these “plant shoots” are isolated, i.e., that there are no similar structures above or below them. There is also no indication that there is a node from which these “shoots” would erupt. They do not look like branches or buds and it is quite possible that they are simply mechanical damage. Both, positive and negative compressions are characterized by an extremely thick layer of carbonized organic matter, which indicates that it is either a woody organ or an organ with a lot of mechanical tissue and a thick layer of cuticle. In practice, there are not many plant fossils



Fig. 8. ?*Arecaceae* vel *Cycadopsida*, petiolus, imprint-compression of leaf stalk; **a.** approximate appearance and length of the entire fossil remains CCJD-R 10-11 (red rectangle - the overlapping of positives and negatives); **b.** detail with “shoots” CCJD-R 11.

that could easily be compared to this specimen. For now, this imprint most closely resembles a part of petiole (leaf stalk) or midrib of *Arecaceae* (palm trees) or *Cycadopsida* (cycads and bennettites).

Discussion

Snakes from the Bileća location (Bosnia and Herzegovina) have been well known for more than a century. On the contrary, remains of fish and plants were found in this area for the first time. Unfortunately, all these findings were collected accidentally during the excavation of the building stone. For this reason, we cannot claim that all the remains have the same stratigraphic origin.

According to BARDET et al. (2008) “hind-limbed” marine snakes were characteristic for the margin of the Mediterranean Tethys (from south-western Europe, Adriatic, to Middle-East and North Africa). *Pachyrhachis*, *Haasiophis* and *Eupodophis* are unquestionable hind-limbed snakes from the southeast margin of Tethys (Middle-East). Other snake fossils *Simoliophis*, *Mesophis*, and *Pachiophis*, for which no limb has been preserved or discovered, are known from the northern Tethyan margin (Bosnia-Herzegovina, Portugal, and France). All known hind-limbed snakes belong to the Simoliophiidae and were found exclusively in areas of former tropical expanded carbonate platforms during the Cenomanian–Turonian. They are characterized by pachystosis of the vertebrae and ribs, a laterally compressed body, and a small head. During the middle Cretaceous, the Adriatic Carbonate Platform was one of the largest carbonate platforms of the peri-Mediterranean region (VLAHOVIĆ et al., 2005) that facilitated the evolution and radiation of marine snakes. It is assumed that they were probably slow ambush predators living in and around the margins of reef mounds on a shallow-water carbonate platform (BUFFRÉNIL & RAGE, 1993; SCANLON et al., 1999; CALDWELL & ALBINO, 2001).

Unlike the snake fossil remains, which are so far known only from the Bileća area (SLIŠKOVIĆ, 1970; DJURIĆ et al., 2017), a diverse fossil fish fauna in the Adriatic Cretaceous are found in many localities (e.g., RADOVIĆ et al., 1983; PALCI et al., 2008; JURKOVŠEK

et al., 2016). At approximately the same age, in the nearest locality Komen in Slovenia (PALCI et al., 2008; CAVIN et al., 2000), an abundant fish fauna was described with common Pycnodont remains. Most pycnodont remains indicate shallow marine water on the upper slope of the shelf zone (KRIWET 2001a), although brackish, and freshwater pycnodonts are also known (POYATO-ARIZA, 2005). According to NURSALL (1996), the fin shape and structure indicate that these fish inhabit areas of reefs or lagoons. Molariform teeth indicate a durophagous diet (NURSALL, 1996; POYATO-ARIZA, 2003; KRIWET & SCHMITZ, 2005), but not exclusively so according to POYATO-ARIZA (2005).

Based on two specimens of fossil plants, not much can be said about the vegetation that inhabited the explored areas during the Cretaceous. However, these data are valuable for two reasons: the first is the confirmation that during the late Cenomanian-Turonian this area was inhabited by flowering plants *Magnoliidae* (Angiospermae) which appear in the Cenomanian in greater numbers. The second reason is the fact that this is one of the rare, if not the first published findings of the Cretaceous macroflora from Bosnia and Herzegovina (HRVATOVIĆ, H. 2006; SOKLIĆ, 2019).

The latest fossil finds of the pachyophiids and pycnodonts at the Bileća site certainly indicate a shallow water environment. However, the increasingly frequent finds of these fossils, as well as the first finds of the remains of flowering plants, require more attention to and data collections at this site.

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Резиме

Нови налази горњоценоманско-туронских пахиофидних змија, риба и биљака у југоисточној Босни и Херцеговини

У северном делу Херцеговине, посебно на подручју Билеће (Сл. 1), постоји велики број каменолома који ископавају кречњак познат као Билећки камен. Према подацима добијеним током геолошког картирања подручја Билеће и Требиња, NATEVIĆ & PETROVIĆ (1970) сматрају билећке кречњаке туронским, док HRVATOVIĆ (2006) наводи да су битуминозни кречњаци са остацима змијоликог гмизавца (*Pachyophis*) из Билеће касноценоманске старости. Прва два пронађена примерка *Pachyophis woodwardi* NORCSA (1923) и *Mesophis norcsai* ВОЛКАУ (1925) потичу са локалитета Селишта, северно од Билеће. Холотип *Pachyophis woodwardi* (NHMW 1912-I8) и други примерак чувају се у збирци Природњачког музеја у Бечу, док се *Mesophis norcsai* налази у Земаљском музеју Босне и Херцеговине у Сарајеву у оквиру сталне поставке. Четврти примерак пахиостотичне змије пронађен је у каменолому Дубовац, три километра северозападно од Билеће и налази се у Природњачком музеју у Београду (NHMBEO MV 280; DJURIĆ et al., 2017). У овом раду описујемо нове налазе пахиостотичних змија, риба и биљака који потичу из каменолома Рогошина око 3 km јужно од Билеће.

Седиментација мезозоица овог подручја одвијала се у окружењу карбонатне платформе, коју претежно карактеришу плитководни морски услови (VLANOVIĆ et al., 2005; DJAKOVIĆ et al., 2021). Најистакнутије стратиграфске чланове представљају масивни и слојевити кречњаци и доломити (сл. 2). Анализирани фосилни остаци откривени су унутар танкослојевитих кречњака.

Змије са локалитета Билећа (Босна и Херцеговина) познате су већ читав век, међутим, остаци риба и биљака први пут су пронађени на овом подручју. Нажалост, сви ови налази су случајно прикупљени приликом ископавања грађевинског камена, због чега не можемо да

тврдимо да сви остаци имају исто стратиграфско порекло. Према BARDET et al. (2008), морске змије са „задњим екстремитетима” су биле карактеристичне за обод медитеранског Тетиса (од југозападне Европе, Јадрана, до Блиског истока и северне Африке). *Pachyrhachis*, *Haasiophis* и *Eupodophis* су недвосмислено змије са задњим екстремитетима са југоисточне маргине Тетиса (Блиски исток). Остале пахиостотичне змије *Simoliophis*, *Mesophis*, и *Pachioophis*, код којих нема доказа о постојању задњих екстремитета, познате су са северног обода Тетиса (Босна и Херцеговина, Португал и Француска). Све ове пахиостотичне змије припадају фамилији Simoliophiidae и пронађене су искључиво у областима некадашњих тропских проширених карбонатних платформи током ценоманско-туронског периода. Карактерише их пахиостоза (непатолошко увећање коштане масе, HOUSSAYE, 2013) пршљенова и ребара, бочно спљоштено тело и мала глава. Током средње креде, Јадранска карбонатна платформа је била једна од највећих карбонатних платформи перимедитеранског региона (VLANOVIĆ et al., 2005) која је омогућила еволуцију и диверзификацију морских змија. Претпоставља се да су то вероватно били спори грабљивци који су живели на и око ивица морских гребена у плиткој води (BUFFRÉNIL & RAGE, 1993; SCANLON et al., 1999; CALDWELL & ALVINO, 2001). За разлику од фосилних остатака змија, који су до сада познати само са подручја Билеће (SLIŠKOVIĆ, 1970; DJURIĆ et al., 2017), разноврсна фосилна фауна риба из креде пронађена је на многим локалитетима јадранског приобаља (RADOVIĆ, TIŠLJAR & JELASKA, 1983; PALCI et al., 2008; JURKOVŠEK et al., 2016). На најближем локалитету, Комен, у Словенији, који је приближно исте старости (PALCI et al., 2008; CAVIN et al., 2000), описана је богата фауна риба са учесталим остацима пикнодонтних риба. Већина остатака ових риба указује на плитку морску средину на горњој падини континенталног прага (KRIWET 2001a), иако су познати фосилни налази и из бракичних и слатководних седимената (POYATO-ARIZA, 2005). Према NURSALL (1996), облик и структура пераја указују на то да ове рибе насељавају подручја гребена или

лагуна, док молариформни зуби указују на дуурофагни начин исхране (NURSALL, 1996; ROYATO-ARIZA, 2003; KRIWET & SCHMITZ, 2005). Међутим, ROYATO-ARIZA (2005) сматра да је код ових риба исхрана била разноврснија и да дуурофагија није била искључива.

На основу два примерка фосилних биљака не може се много рећи о вегетацији која је насељавала истражена подручја током креде. Међутим, ови подаци су драгоцени из два разлога: први је потврда да су током касног ценоманатурона ово подручје насељавале цветнице *Magnoliidae* (Angiospermae) које се у ценоману

јављају у већем броју. Други разлог је чињеница да се ради о једном од ретких, ако не и о првим објављеним налазима кредне макрофлоре из Босне и Херцеговине (HRVATOVIĆ, H. 2006; SOKLIĆ, 2019). Најновији фосилни налази пахиофида и пикнодонта на локалитету Билећа свакако указују на плитководну средину. Међутим, све чешћи налази ових фосила, као и први налази остатака цветница, захтевају већу пажњу и прикупљање података са овог локалитета.

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