A new evidence for pachyostotic snake from Turonian of Bosnia-Herzegovina

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Abstract. Records of Cretaceous marine snakes from Bosnia and Herzegovina have been known for nearly a hundred years. This paper presents a new finding of a pachyostotic snake from the local quarry Dubovac, three kilometers northwest of Bileća. The specimen consists of 29 vertebrae, seven of which are detached from the slab. The two best preserved vertebrae are almost square-shaped resembling Simoliophis rochebrunei but neural arches are much more swollen. Vertebrae and ribs are extremely pachyostotic as in Pachyophis woodwardi. Since there are no three-dimensional vertebrae of this species preserved from Bosnia and Herzegovina, precise identification was limited to a certain extent.

Key words: Turonian, Bileća, hind-limbed snake, pachyostosis, Pachyophis.

Introduction

Cretaceous marine snakes represent a significant link in the interpretation of the phylogeny of Squamata and they are important for the understanding of snake origins (Zaher & Rieppel, 1999, 2002; Lee & Scanlon, 2002; Caldwell et al., 2015). Until today several taxa of pachyostotic snakes have been collected and all of them come from Cenomanian coastal regions of the Mediterranean Tethys (Rage & Escuille, 2003). Among these finds are fossils with preserved hind limbs (Eupodophis, Haasiophis and Pachyrhachis), as well as others in which the existence of hind limbs cannot be confirmed (Mesophis, Pachyophis and Simoliophis). Around one hundred years ago, the fossil remains of two pachyostotic (non-pathological increase in bone thickness (Houssaye, 2013) snakes were found in the Cenomanian sediments of Bosnia and Herzegovina (Stišković, 1970). Both species, Pachyophis woodwardi (Nopcsa, 1923) and Mesophis nopcsai (Bol-Kay, 1925) come from the same locality of Selišta, north of Bileća. The holotype of Pachyophis woodwardi (NHMW 1912-I8) is housed in the Naturhistorisches Museum Vienna (NHMW) while for Mesophis nopcsai there is no clear evidence whether it was preserved or lost (Lee et al., 1999; Rage & Escuille, 2003; Bardet et al., 2008; Houssaye, 2010).

The specimen presented in this paper undoubtedly belongs to the ancient marine squamate (Pachyophiidae) with the unsolved phylogenetic position. There is
no consensus on whether Pachyophiidae present the sister group to all other snakes (Caldwell & Lee, 1997; Lee & Caldwell, 1998), or they belong to advanced macrostomatan snakes, which is of no relevance to the origins of snakes (Zaher, 1998; Zaher & Rieppel, 1999). This report will briefly describe the main morphological features of the specimen.

The locality and depositional environment

In the beginning of 2017, the authors of this paper received a piece of a thin limestone slab with fossil remains. The specimen was found in a local quarry Dubovac (Fig. 1c), three kilometers northwest of Bileća (Bosnia and Herzegovina). 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 of the amount of carbonate material 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 analysis of the site was performed, while its stratigraphic position according to the Basic Geological Map of Yugoslavia is 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 occur appear (middle Turonian). The specimen is situated in the Natural History Museum in Belgrade (NHMBEO MV 280).

Description

The specimen is represented by a string of 29 vertebrae associated with the corresponding ribs (Fig. 2). The majority of vertebrae are complete and embedded in the sediment with the exception of the last two represented only by their imprints on the slab.

The first three vertebrae that are exposed in dorsal view are heavily damaged. Most of the following vertebrae are exposed with their lateral side on the slab. The last seven vertebrae in the string (two of which are best preserved) are detached from the slab and their lateral and ventral surface can be observed. In dorsal view (Fig. 3b) the vertebrae are slightly wider
than long and somewhat “butterfly-shaped” (Lee et al., 1999). The prezygapophyses are oval in shape and do not markedly project laterally like in *Simoliophis* (Rage et al., 2016). Prezygapophyseal processes are lacking. The neural arches are distinctly swollen and their posterior border is strongly concave (Fig. 3b). The dorsal margin of the neural spine is swollen, elongated and almost triangular in shape. Its anterior border is somewhat inclined posteriorly. The exposed zygosphenal roof has concave edge.

In lateral view (Fig. 3a) the vertebrae are visibly higher than long. The neural spine is twice as long then high and slightly overhanging posteriorly. The interzygapophyseal ridge is thick and extremely swollen. The paradiapophysis are almost rectangular and inclined anteroventrally to posterodorsally. In ventral view the centrum appears plate-like, wider than long. The hemal keel is absent. Mid region of the ventral surface of centrum is occupied by a shallow groove with small unequal triangular extensions on anterior and posterior side. In posterior view (Fig. 3c) the neural arches are convex. The centrum is thick and surrounding condyle. The neural canal is ogival in shape. Its size is approximately equal to condyle.

Ribs are associated with corresponding vertebrae, but are not visibly articulated to them because they are covered with sediment. They are well exposed along the entire left side of the vertebral column. Proximal ends of the ribs are so swollen that the intercostal space is practically absent. Their thickness increases moderately throughout this vertebral segment, while the distal tip remains very slender. The vertebrae and ribs are strongly pachyostotic. Their size and level of pachyostosis increase gradually from anterior to posterior region of the specimen.

**Discussion**

The specimen consists of 29 articulated vertebrae with adjoining ribs. Although the sediment was broken in a few fragments, it has been determined that all
belong to one individual as shown in Fig. 2. Pachyostosis is well developed on all vertebrae and ribs and gradually increases anteroposteriorly. Since pachyostosis is the most prominent in the middle-trunk region (LEE et al., 1999), we can propose that this preserved segment belongs to anterior trunk and/or middle trunk part of the snake. The entire column is mostly exposed laterally and dorsally. Several of the last vertebrae display the highest degree of pachyostosis and the greatest similarity with the described holotype of Pachyophis (LEE et al., 1999). The last seven preserved vertebrae are completely isolated from the sediment with visible ventral surface. The general shape of the vertebrae is almost rectangular as in Simoliophis (RAGE et al., 2016). Centrum is slightly concave and shows clear absence of the hemal keel. The plate-like centrum, absence of hemal keel, shallow groove on ventral surface of centrum is common with Simoliophis. The prezygapophyses do not markedly project laterally and the interzygapophyseal constriction is little expressed as in Simoliophis (RAGE et al., 2016). The neural arches are much more swollen than in Simoliophis and their posterior border is strongly concave in dorsal view. The latter is much more similar to Pachyophis (LEE et al., 1999). The neural spines rise from the zygosphene and attain their highest point at the posterior end as in Pachyophis woodwardi (LEE et al., 1999; HOSSAYE, 2010). Unlike Simoliophis the neural spine is very low, twice as long as high and extends over the condyle. The paradiapophysis almost rectangular inclined anteroventrally to posterodorsally. In Simoliophis they are rather vertically (RAGE et al., 2016). The vertebrae are extremely swollen. The neural arches display the higher degree of pachyostosis than centrum, while the centrum is more pachyostotic than arches as in the case of Simoliophis.

The ribs are extremely swollen, circular in cross section and abruptly curved proximally, continuing more straight and tapering to distal ends. It suggests that this snake was laterally compressed, and therefore, probably was living in a marine environment (LEE et al., 1999). This conclusion is supported by a previously mentioned shallow-water depositional environment of the Adriatic Carbonate Platform where the specimen was found.

Conclusions

Opinion of the authors is that the studied specimen is most similar to Pachyophis woodwardi primarily because of the conspicuous pachyostosis of neural arches, their strongly concave posterior border and considerably low neural spine. Pachyrhachis and Eupodophis do not show that strong pachyostosis (RAGE & ESCUILLIE, 2003; HOSSAYE, 2010). Regarding the similarities with Simoliophis, the plate-like centrum, shallow groove on ventral surface of the centrum and the absence of hemal keel, they couldn’t prevail in comparison with the observed characters that determine Pachyophis woodwardi. Since there are no three-dimensional vertebrae of this species preserved from Bosnia and Herzegovina, precise identification was limited to a certain extent.

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References

BARDET, N., HOSSAYE, A., RAGE, J.-C. & PEREDA SUBERBIOLA, X. 2008. The Cenomanian-Turonian (Late Cretaceous) radiation of marine squamates (Reptilia): the role of the Mediterranean Tethys. Bulletin de la Société Géologique de France, 179: 605–622.

BOLKAY, S.J. 1925. Mesophis nopcsai n.g. n.sp. ein neues, schlagenähnliches Reptil aus der unteren Kreide (Neocom) von Bilek-Selišta (Ost-Hercegovina). Glasnik zemaljskog Muzeja u Bosni i Hercegovini, 37: 125–135.

CALDWELL, M.W. & LEE, M.S.Y. 1997. A snake with legs from the marine Cretaceous of the Middle East. Nature, 386: 705–709.

CALDWELL, M.W., NYDAM, R.L., PALCI, A. & APESTEGUÍA, S. 2015. The oldest known snakes from the Middle Jurassic – Lower Cretaceous provide insights on snake evolution. Nature Communications, 6: 1–11.

HOSSAYE, A. 2010. Rediscovery and description of the second specimen of the hind-limbed snake Pachyophis woodwardi Nopcsa, 1923 (Squamata, Ophidia) from the Cenomanian of Bosnia Herzegovina. Journal of Vertebrate Paleontology, 30 (1): 276–279.

HOSSAYE, A. 2013. Palaeoecological and morphofunctional interpretation of bone mass increase: an example in Late Cretaceous shallow marine squamates. Biological Reviews, 88: 117–139.

LEE, M.S.Y. & CALDWELL, M.W. 1998. Anatomy and relationships of Pachyrhachis problematicus, a primitive snake with hindlimbs. Philosophical Transactions of the Royal Society London, B, 353: 1521–1552.

LEE, M.S.Y., CALDWELL, M.W. & SCANLON, J.D. 1999. A second primitive marine snake: Pachyophis woodwardi from the Cretaceous of Bosnia-Herzegovina. Journal of Zoology, 248: 509–520.

LEE, M.S.Y. & SCANLON, J. D. 2002. Snake phylogeny based on osteology, soft anatomy and ecology. Biological Review, 77: 333–401.
Natević, LJ. & Petrović, V. 1970. Osnovna geološka karta SFRJ 1:100,000. List Trebinje [Basic Geological Map of Former Yugoslavia 1:100,000. Sheet Trebinje – in Serbian]. Savezni geološki zavod, Beograd.

Nopcsai, F. 1923. Eidosaurus und Pachyophis: zweineue Neocom-Reptilien. Palaeontographica, 65: 96–154.

Rage, J-C. & Escullie, F. 2003. The Cenomanian: stage of hindlimbed snakes. Carnets de Géologie/Notebooks on Geology, 2003/01: 1–11.

Rage, J-C., Vullo, R. & Neraudeau, D. 2016. The mid-Cretaceous snake Simoliophis rochebrunei Sauvage, 1880 (Squamata: Ophidia) from its type area (Charentes, southwestern France): Redescription, distribution, and palaeoecology. Cretaceous Research, 58: 234–253.

Slišković, T. 1970. Die stratigraphische Lage der Schichtenmit Pachyophiidae aus Seliste bei Bileca (Ostherzegowina). Bulletin scientifique, Conseil des Académies des Sciences et des Arts de la RSF de Yougoslavie, 15: 389–390.

Vlahović, I., Tislar, J., Velić, I. & Matićec, D. 2005: Evolution of the Adriatic Carbonate Platform: Palaeogeography, main events and depositional dynamics. Evolution of the Adriatic Carbonate Platform: Palaeogeography, main events and depositional dynamics. Palaeogeography, Palaeoclimatology, Palaeoecology, 220: 333–360.

Zaher, H. 1998. The phylogenetic position of Pachyrhachis within snakes (Squamata, Lepidosauria). Journal of Vertebrate Paleontology, 18 (1): 1–3.

Zaher, H. & Rieppel, O. 2002. On the phylogenetic relationships of the Cretaceous snakes with legs, with special reference to Pachyrhachis problematicus (Squamata, Serpentes). Journal of Vertebrate paleontology, 22: 104–109.

Резиме

Нови налаз пахиостотске змије из турона Босне и Херцеговине

Морске змије из кроте представљају значајну карику за тумачење филогеније Squamata као и по-река змија. До данас је познато више таксона пахиостотичких змија са “задњим ногама”. Код не-ких су задњи екстремитети видљиви у фосилним остацима (Eupodophis, Haasiaephis, and Pachyrha- chis), док код других нема доказ њиховог постоја-ња (Mesophis, Pachyophis, and Simoliophis). Пре ско-ро сто година у седиментима ценомана у околини Биљење (Босна и Херцеговина) пронађене су две змије из ове групе, Pachyophis woodwordyi и Mesophi- phis nopcsai (Slisković, 1970). У овом раду описан је нови налаз пахиостотичне змије пронађене у локалном камерном Дубовац, три километра сев-ерозападно од Биљење.

Примерак чини низ од 29 пршљенова са ребри- ма у кречњачком седименту. Према Houssaye (2013) пахиостоза (непатолошко повећање волуме- на косту из које добијају облик) је веома изражена на пршљеновима и ребрима и расте од предњег ка задњем делу сачуваног дела тела. Како је пахиостоза најизраженија средином трупног региона (Lee et al., 1999) можемо закључити да сачувани примерак представља предњи до средњи део трупа змије. Последњих седам пршљенова је изоловано из седимента, од којих су два најбоље очувана. Ови пршљенови уједно показују и навећи степен пахиостозе и имају облик налик лептиру, као код холотипа Pachyophis woodwardyi (Lee et al., 1999). Презигапофизе су овалне и нису превише истурене бочно. Презигапофизни наставци не по- стоје. Неурали луци показују већи степен пахио- стозе од Simoliophis, а њихова постерниорна ивица је изразито конкавна као код Pachyophis woodwar- di. Неурали гребен је такође пахиостотичан и бочно гледано прелази дужину кондиле. Такође се на овим пршљеновима може уочити да са вен- тралне стране центрум изгледа заврањено, кроз средину са плитким жљебом који се неједнако левкасто шири ка предњем и задњем крају и има скоро правоугаони облик као и Simoliophis (Rage et al., 2016). Ребра су изложена, у проксималном делу изразито пахиостотична, а међуребарни про- стор скоро да не постоји, као што је то случај код Pachyophis woodwardyi (Lee et al., 1999). У прокси- малајном делу нагло се савијају вентрално, што зми- ји даје бочно сљоштен изглед, типичан за станов- нике морских станишта.

Прочувани примерак показује највише слично- сти са Pachyophis woodwardyi, нарочито у погледу изражене пахиостозе неуралних лука, њихове конкавне задње ивице, као и изразито ниско- го и вео- ма отеченог неуралног гребена. Насупрот овом од- сутство хемалног гребена на вентралној страни цен- трума, заврањен и скоро четвртаст облик веома су слични као код Simoliophis rochebrunei (Rage et al., 2016). Такође, постојање веома плитког канала кроз средину центрума са неједнаким левкастим проши- рењима на оба краја пршљена, овај примерак пове- зује са Simoliophis rochebrunei. Без обзира на све сличности са Simoliophis rochebrunei аутори су ми- шљења да је ова пахиостотична змија најсличнија Pachyophis woodwardyi. Међутим, узимајући у обзир да до сада нису познати изоловани пршљенови ове врсте из Босне и Херцеговине, прецизна идентифи- кација је била делимично ограничена.
