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A MIDDLE MIOCENE BALEEN WHALE FROM BELE VODE IN BELGRADE, SERBIA

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Abstract: There was a fauna of baleen whales (Cetacea: Mysticeti) in the Central Paratethys, a Miocene water body which covered the area of present-day Central Europe. Most of the fossil baleen whales from the Central Paratethys have been found in strata assigned to the regional Badenian age and comprise endemic forms, known only from this region. Here a new description is provided for a fragmentary skeleton of a whale found in Belgrade, Serbia, and its age context and biological aspects are discussed. This specimen, consisting of a fragmentary horizontal ramus of the mandible and eight caudal vertebrae, is tentatively identified as ?*Parietobalaena* sp., a globally known Miocene taxon, with related forms having been recorded earlier from the Eastern Paratethys. An early Sarmatian age (i.e., about 12.7-12.4 Ma) is proposed for the specimen. Based on epiphyseal fusion of caudal vertebrae, the specimen's age is identified as a subadult, with a body length of around 2.5 m and an estimated adult body length around 3-3.5 m, which is extremely small for baleen whales. This find represents one of the latest records of baleen whales in the Central Paratethys and one of the latest published records of *Parietobalaena*-like taxa in the world.

INTRODUCTION

The Central Paratethys, a Miocene water body that covered the area of modern Central Europe, hosted a fauna of baleen whales (Mysticeti). At least two mysticete species have been described from this region: *Mesocetus agrami* Van Beneden, 1884 from Croatia, and *Mesocetus hungaricus* Kadić, 1904 from Hungary. In addition, *Pinocetus polonicus* Czyzewska & Ryziewicz, 1976 has been described from the neighboring Fore-Carpathian Basin. None of these species is known outside of this area. Moreover, a few findings of fragmentary specimens have been reported across the region (Stepanović 1938; Paunović 1993; Sabol & Holec 2002, and references therein; Stefanović 2010). Most of these reported specimens have been assigned to the Badenian regional age, Middle Miocene (16.3-12.8 Mya, as by Hohenegger et al., 2014). Notable exceptions are the holotype of *Mesocetus agrami* and the specimen from Serbia which is discussed below: both were originally assigned to a later time interval, the Sarmatian regional age (Stepanović 1938; Stefanović 2010 and references therein).

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Cetacean remains were discovered in autumn 1935 in Bele Vode, now a western sub-neighborhood of Žarkovo, in the southwestern part of Belgrade (Fig. 1), during commercial limestone exploitation in a local quarry (approximate geographic coordinates 44°45' N, 20°25' E). They were originally discovered by the workers of the quarry, at the rock profile in the vicinity of the Bele Vode wellhead. The workers informed Branko Stepanović, at that time working as a geologist from the Water Supply service of the City of Belgrade, about their find. In his subsequent paper, published in Serbian in the *Annales géologiques de la péninsule Balkanique*, Stepanović (1938) described two mandibular fragments and one vertebral centrum of a fossil cetacean. However, Stepanović (1938) also noted that the workers had initially discovered an even larger number of bones (namely, vertebrae), but he was unable to find them at the time the article was written. Luckily, a total of eight caudal vertebrae were eventually rediscovered, and donated to the Natural History Museum in Belgrade, where they are kept today. According to the curators of the museum, Sanja Alaburić and Zoran Marković, the caudal vertebrae, as indicated on the field labels, represent a part of the same find reported by Stepanović. Here

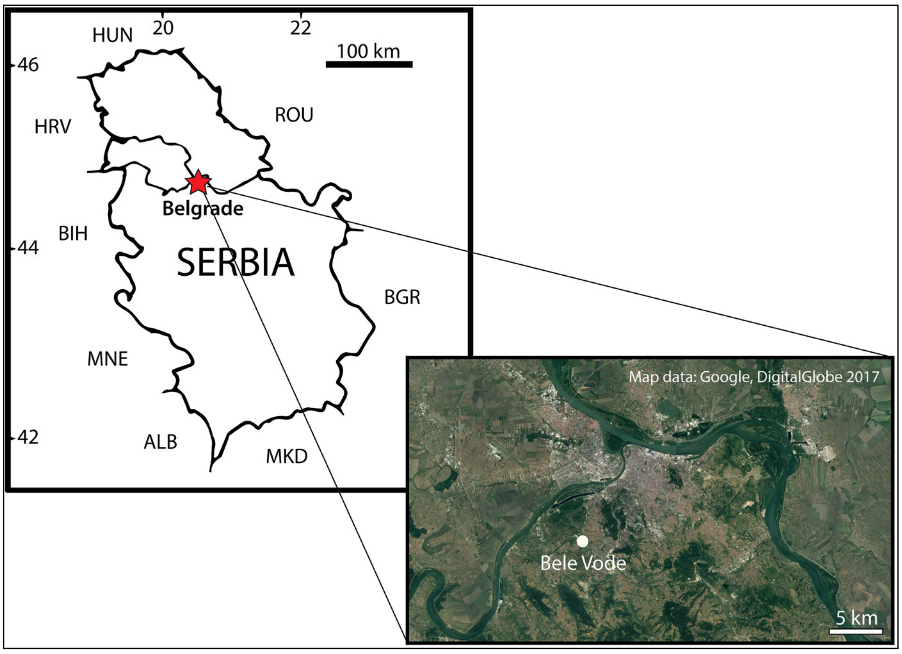

Fig. 1 - A simplified geographic position of Belgrade and the Bele Vode site with a satellite view.

we provide a description of these remains and discuss their age, context and biological aspects. Meanwhile, the whereabouts of the fragments originally described by Stepanović are currently unknown (we were not able to locate them in any of the known collections, and we consider them as temporarily lost), and we re-examined them based on the published descriptions, measurements and photographs.

GEOLOGICAL SETTING

The Sarmatian (*sensu stricto*) sediments of the upper Middle Miocene of the Central Paratethys are known to be widespread in Belgrade and its vicinities. These are shallow-water marine sediments, which either lie conformably over Badenian (Middle Miocene) strata (reef deposits etc.), or more often lie unconformably over Mesozoic rocks (Stevanović 1977; Anđelković et al. 1991; Knežević et al. 2012). In terms of lithology, there are two main Sarmatian units: an older unit of siliciclastic sediments, mostly developed in the northeastern part of the city (neighborhoods Mirijevo, Lešće, Vinča, Ritopek etc.), and the younger unit of marls, sandy limestones and organogenic limestones, developed farther to the south (neighborhoods Žarkovo, Čukarica, Rakovica, Sremčica, Barajevo etc.) (Schwarzhans et al. 2015). As proposed by Papp (1958), four main molluscan zones are identified in the Sarmatian deposits: the *Mohrensternia* Zone (also known as the *Rissoa-Hydrobia* beds, ca. 12.7-12.4 Mya), the Lower and Upper *Ervilia* Zones (ca. 12.4-12.1 and 12.1-11.9 Mya, respectively), and the *Sarmatimactra* Zone (also known as the *Mactra* beds, ca. 11.9-11.6 Mya) (Stevanović 1977, 1982; time spans after Harzhauser & Piller 2004). The Sarmatian strata are thus included in the Serravallian stage. When defined as a twofold stage, the Sarmatian of the Central Paratethys consists of the Lower Sarmatian (the *Mohrensternia* and the Lower *Ervilia* Zones) and the Upper Sarmatian (the Upper *Ervilia* and *Sarmatimactra* Zones) (Harzhauser & Piller 2004).

The Upper Miocene Pannonian (*sensu stricto*) sediments constitute more than 70 % of all Miocene sediments in Belgrade, exhibiting a total thickness of more than 50 m (Rundić et al. 2011). These are lacustrine sediments of Lake Pannon, which contain a peculiar mollusk fauna, showing rapid evolutionary radiations and endemism (Müller et al. 1999). On the basis of this mollusk fauna, Stevanović (1985) divided the Pannonian *s.s.* stage into two substages – the Lower Pannonian (Slavonian) and the Upper Pannonian (Serbian). Due to the frequent presence of bivalve genus *Congeria*, the Lower Pannonian sediments are also known as the "lower *Congeria* beds" (Stevanović 1982; Lubenescu 2016). In Belgrade and its vicinity, Pannonian sediments are represented by two main facies, shallow-water sands and limestones and deep-water marls/marly clays (Stevanović 1977). At the southern parts

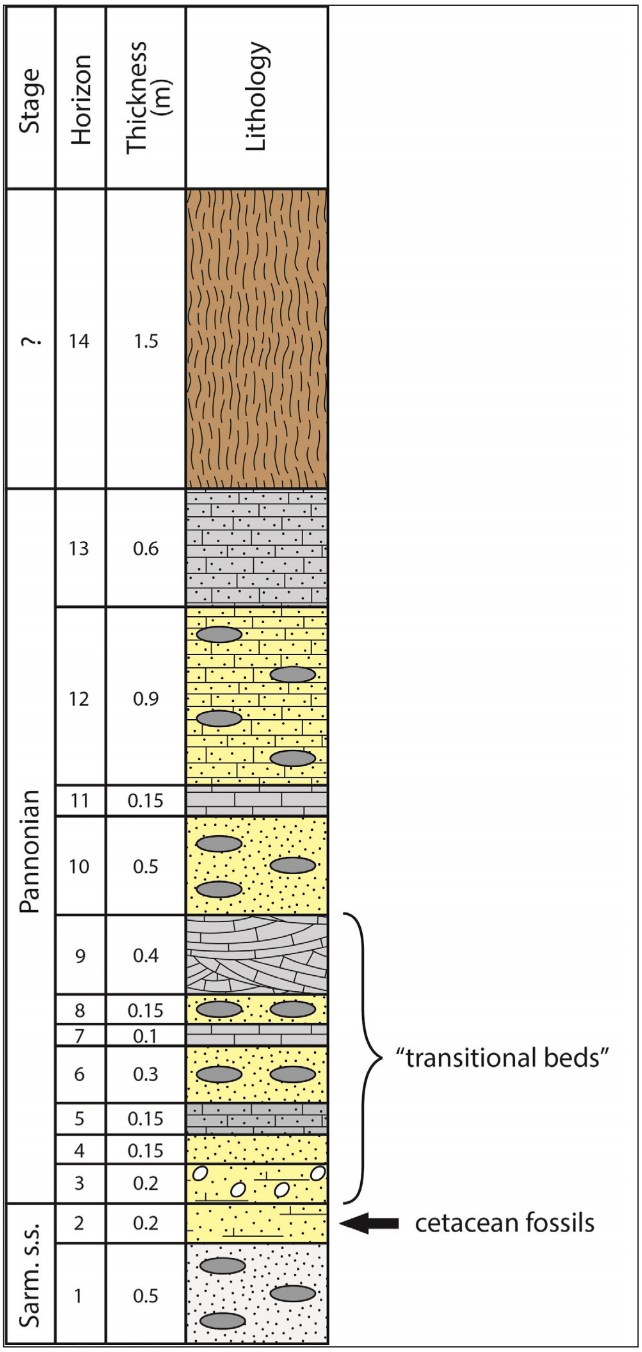

Fig. 2 - Stratigraphic sequence from the Bele Vode quarry, drawn after Stepanović (1938); detailed descriptions for each horizon are provided in the text. The black arrow marks the horizon with cetacean fossils, grey ovals mark marl/clay lenses. The designation "transitional beds" marks horizons with mixed Sarmatian and Pannonian invertebrate fauna. Sarm. s.s. = Sarmatian sensu stricto.

of the city (including Bele Vode) the Pannonian strata are said to lie conformably above the upper Sarmatian limestone-marl unit (Stevanović 1977; Knežević et al. 2012).

Although the profiles from the former quarry at Bele Vode have been destroyed and are no longer available for direct study, Stepanović (1938) provided a very detailed stratigraphic framework. He described a stratigraphic succession starting from the "deepest profile in the quarry". The sequence was 5.8 m thick, and subdivided into 14 horizons (Fig. 2). The descriptions of each horizon, top to bottom, with the fossil taxa given as originally identified, are as follows:

14) surface loam (1.5 m);

13) grey, firm, fine-grained limestone with rare imprints of *Limnocardium* sp. (0.6 m);

12) yellowish, firm, fine-grained limestone with lenses of marly clay (0.9 m);

11) greyish firm limestone (0.15 m);

10) yellow fine marly sand, with lenses of firm marl and crumbly specimens of *Melanopsis cf. nešići* Brus. (0.5 m);

9) firm greyish sandy limestone with cross-bedding, containing imprints of *Cardium* sp., *Limnocardium* sp., *Mactra podolica* Eichw., smaller *Congeria* sp. forms, *Trochus* cf. *affinis* Eichw., *Trochus* cf. *pictus* Eichw., *Hydrobia frauenfeldi* Schw., *Melania* sp., *Cerithium pictum* Bast. and *Cyclostoma*? sp. (0.4 m);

8) yellowish marly sand with dark clay lenses, containing numerous specimens of *Cardium protractum* Eichw., rare *Cerithium rubiginosum* Eichw. specimens, bryozoans, fish skeletons and coprolites (0.15 m);

7) greyish firm limestone (0.1 m);

6) described only as "similar to Layer 8" (0.3 m);

5) grey sandy limestone, in some places containing numerous imprints of *Cardium obsoletum* Eichw, *Tapes gregaria* Partsch., very large specimens of *Melanopsis impressa cf. bonellii* Sism., *Cerithium pictum* Bast. and *Cerithium disjunctum* Sow (0.15 m);

4) yellowish marly sand, containing friable fossils of *Melanopsis* sp. and indeterminable gastropod remains (0.15 m);

3) yellowish carbonate sand/sandstone with limestone pebbles (of supposed Cretaceous origin), in some places "teeming" with fossil imprints of *Cardium obsoletum* Eichw., *Cardium protractum* Eichw., *Tapes gregaria* Partsch., *Melanopsis impressa cf. bonellii* Sism., *Cerithium pictum* Bast., *Cerithium disjunctum* Sow., *Bulla* sp. and *Cyclostoma*? sp. (0.2 m);

2) yellowish friable carbonate sandstone or sandstone with dark lenses of marly clay, containing *Cardium protractum* Eichw., rare *Cerithium* imprints and fish remains (0.2 m);

1) whitish, firm fine-grained sandstone, with leaf impressions and mollusks – *Cardium obsoletum* Eichw., *Cerithium pictum* Bast., *Trochus* sp. etc. (0.5 m);

According to Stepanović (1938), the cetacean remains originated from a profile located about 50 m south of the Bele Vode wellhead. The exact place of the wellhead cannot be determined today. Although the majority of strata from the different profiles in the quarry could be correlated very well, the profile that yielded the cetacean remains displayed a somewhat simpler stratigraphy. Namely, instead of Horizons 7 – 3, there was only one corresponding layer of fine yellow sand, about 0.6 m thick (as estimated from Stepanović, 1938: fig. 1). In

Fig. 3 - Fragments published by Stepanović (1938) - two mandibular fragments in lateral (top row) and lingual (middle row) projections, and damaged vertebra (bottom row). Scale bar 5 cm.

terms of the lithology, profiles were characterized as conformable sequences of fine-grained sandstones, sandy limestones, and very fine-grained yellow sands, in some places with interstratified clay lenses containing cardiids and fish remains (Stepanović 1938*)*. This predominantly siliciclastic and carbonate character points to a shallow-water environment (Boggs 2014), throughout the sequence. Carbonates were probably deposited in littoral lacustrine settings, while the presence of clays and marls may indicate a deposition in a sublittoral zone (Vrsaljko 1999). Based on mollusk assemblages, Horizons 13 – 10 were originally assigned to the "lower *Congeria* beds" from the "lower Pontian". The usage of the term "lower Pontian" instead of lower Pannonian reflects an obsolete terminology (see Spajić 1975: 195). Horizons 9 – 3 were originally described as "transitional" due to the presence of a mixed Sarmatian-Pannonian malacofauna (see also Pavlović 1900). The lowermost Horizons 2 – 1 were assigned to the "lower Sarmatian". The cetacean fossils were discovered in Horizon 2.

As noted by Stepanović (1938), the mollusks from Horizons 1 and 2 indeed indicate a Sarmatian age. The gastropod *Cerithium pictum* Bast. is found in the *Mohrensternia* and Lower/Upper *Ervillia* Zones, mostly in sandy facies (Papp 1954; Tămaș et al. 2013; Ganić et al. 2010; Poljak et al. 2016). The bivalve *Cardium obsoletum* Eichw. is found in the sandy facies of the Badenian and Sarmatian of the Central Paratethys (Papp 1954; Vrsaljko 1999). Moreover, Studencka (2015) suggests this species to be typical of upper Badenian and lower Sarmatian strata. It is also one of the most frequent Sarmatian species found on the territory of Belgrade (Stevanović 1977; Knežević & Šumar 1993). Significantly, the bivalve *Cardium protractum* Eichw. was found in Horizon 2, the same layer which yielded the cetacean remains. This species is known from the terminal Upper Badenian limestone in Budapest (Kojumdgieva 1969), and from the Vienna basin, where it is found exclusively in the *Mohrensternia* Zone of the Lower Sarmatian (Papp 1954; Papp et al. 1974).

The majority of mollusks from the "transitional" horizons were also Sarmatian. *Cerithium rubiginosum* Eichw. is usually found in sandy facies of the *Mohrensternia* and *Ervillia* Zones (Papp 1954; Piller & Harzhauser 2005; Poljak et al. 2016). *Cerithium disjunctum* Sow. is found both in the *Ervillia* and *Sarmatimactra* Zones in the Vienna basin (Papp 1954). *Hydrobia frauenfeldi* is known from sandy facies, throughout the Sarmatian (Papp 1954). The bivalve *Mactra podolica* is regarded as a typical species of the Sarmatian, and it is very frequent in Serbia (Mitrović & Pavlović 1980: 285). In the Vienna basin, *Tapes gregaria* Partsch. is typical of the *Ervillia* Zone, and it is very common in the territory of Belgrade (Stevanović 1977). The presence of freshwater mollusks (*Melanopsis*, *Limnocardium* and *Congeria*) within the "transitional beds" at Bele Vode indicates a change from marine conditions of the Sarmatian Sea, to lacustrine conditions of Lake Pannon (Piller & Harzhauser 2005). Anđelković et al. (1991) correlated transitional beds in Belgrade with the marine regression at the beginning of the

Pannonian which was caused by the uplift of the Carpathians (ter Borgh et al. 2013). This phase was characterized by a progradation of fluvial facies, which resulted in the reworking of older Sarmatian strata and redeposition of Sarmatian fossils. We believe that this scenario is applicable to the situation observed at Bele Vode. This is supported by the presence of *M. impressa*, which lived in agitated, fluvial-deltaic coastal environments (Harzhauser & Kowalke 2002), and by siliciclastic sediments indicating fluvial activity (Boggs 2014). Further up the sequence at Bele Vode, Horizons 10 – 13 show only the Pannonian taxa.

Based on our reassessment, we conclude that the interpretation of the stratigraphic sequence at Bele Vode provided by Stepanović (1938) was essentially correct. Beneath the level of surface soil (Horizon 14) are the Lower Pannonian Horizons 13 – 3, which represent shallow-water lacustrine sediments of considerable thickness (3.6 m). The lower part of this sequence (Horizons 9 – 3) contains a mixed Sarmatian-Pannonian fauna, and probably documents a fluvial-influenced reworking of the older strata. Finally, Horizons 2 – 1 do not show the presence of lacustrine Pannonian taxa, and were probably deposited in a marginal marine setting during the Sarmatian (*sensu stricto*). Moreover, the associated mollusk fauna suggests that the cetacean fossils probably come from the lower part of the Sarmatian, 12.7-12.4 Ma.

Materials and methods

The fossil material studied in this paper is stored at the Natural History Museum in Belgrade (NHMBEO). This previously unpublished material includes eight caudal vertebrae (NHMBEO 111349/4, NHMBEO 111349/3, NHMBEO 111349/5, NHMBEO 111349/6, NHMBEO 111349/2, NHMBEO 111349/7, NHMBEO 111349/8, NHMBEO 111349/1), and a small fragment of the caudal vertebral epiphysis (NHMBEO 111349/9). Hereinafter, only an abridged version (the last four numbers) of the official complete inventory number (NHMBEO 111…/.) is given for each specimen. We also reassessed two lost fragments of a mandibular ramus and one damaged vertebral centrum, based on their illustrated original descriptions (Stepanović 1938). The measurements of the caudal vertebrae follow Gol'din et al. (2014) and were taken using a digital caliper (with a precision of 0.01 mm). All measurements are reported in Tables 1 and 2.

The institutional abbreviations are: Georgian National Museum, Tbilisi, Georgia (GNM), Natural History Museum in Belgrade, Serbia (NHMBEO). National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev, Ukraine (NHNM-P), University of California Museum of Paleontology, Berkeley, California, USA (UCMP).

Systematic paleontology

Cetacea Brisson, 1762
Mysticeti Flower, 1864
Cetotherioidea sensu Gol'din & Steeman 2015

?*Parietobalaena* Kellogg, 1924
?*Parietobalaena* sp.
Cetotherium sp. Stepanović, 1938

Referred specimens: Two fragments of a mandible (Fragments 1 and 2), a lumbar vertebra, eight caudal vertebrae (NHMBEO 111349/4, NHMBEO 111349/3, NHMBEO 111349/5, NHMBEO 111349/6, NHMBEO 111349/2, NHMBEO 111349/7, NHMBEO 111349/8, NHMBEO 111349/1), and a fragment of a caudal vertebral epiphysis (NHMBEO 111349/9).

Locality and age: Bele Vode, Belgrade, Serbia (approximate geographical coordinates 44°45' N, 20°25' E). Early Sarmatian (Serravallian), Middle Miocene, 12.7-12.4 Ma.

Specimen	Fragment length	Corpus height	Corpus thickness
Fragment 1	300	60	45
Fragment 2	210	65	45

Tab.1 - Measurements (in mm) of the mandibular fragments from Bele Vode, as reported by Stepanović (1938).

Description

The cetacean remains originally described by Stepanović (1938) consist of two edentulous mandibular fragments and one damaged vertebral centrum. Measurements of these are given in Table 1. The longer mandibular fragment represents a median portion of the left mandibular ramus, anterior to the coronoid process, which displays a roughly straight outline of the ventral border, and a dorsal rim which curves upwards at the proximal end, forming the anterior margin of the coronoid process. According to Stepanović (1938), the fragment shows a flat medial and a convex lateral surface, which can indeed be confirmed on the basis of the available photographs (Stepanović 1938: fig. 1). An open alveolar groove forming a distinct single canal is seen along the dorsomedial surface of the bone. Several anteriorly oriented foramina are present near the dorsal rim of the specimen, on both the medial and the lateral surfaces: these are known as gingival and mental foramina, respectively (Marx et al. 2016). The latter ones (or even all of them) are possibly formed by dorsal branches of the inferior alveolar artery and/or nerve (Peredo et al. 2017). Also, there are deep vascular grooves extending from each of the foramina towards the anterior end of the mandibular segment. These fo-

Fig. 4 - Caudal vertebrae in cranial projections – specimens in the top row, left to right: 349/4, 349/3, 349/5 and 349/6; specimens in the bottom row, left to right: 349/2, 349/7, 349/8 and 349/1. Scale bar 5 cm.

ramina are known to be connected with mandibular canals (Bouetel & Muizon 2006; Peredo et al. 2017). The condition described above is identical to that observed in small whales of the family Cetotheriidae, such as *Piscobalaena nana* (Bouetel & Muizon 2006) and *Cetotherium riabinini* (Gol'din et al. 2014), all of which have a distinct alveolar groove, close to a mandibular canal. Also, the strictly anterior orientation of vascular grooves resembles the living pygmy right whale *Caperea marginata* (Peredo et al. 2017). The shorter mandibular fragment appears to be very similar to the former one in terms of morphology, showing a straight profile, flat medial and convex lateral surfaces, and numerous dorsolateral and dorsomedial foramina. The fragment is also part of the left ramus, as demonstrated by the orientation of the foramina, as well as by the direction of the corresponding vascular grooves. However, there are also some slight differences. Compared to the proximal fragment, there is no curvature in the dorsal border, and the fragment seemingly shows an even more pronounced flatness of the medial surface. According to Stepanović 1938, this indicates that the second fragment represents a more distal portion of the horizontal ramus, a statement with which we agree. Stepanović (1938) even contended that the fragments probably belonged to different individuals, based on the fact that the distal segment is slightly (0.5 cm) dorsoventrally higher than the proximal segment (See Tab. 1). However, proxi-

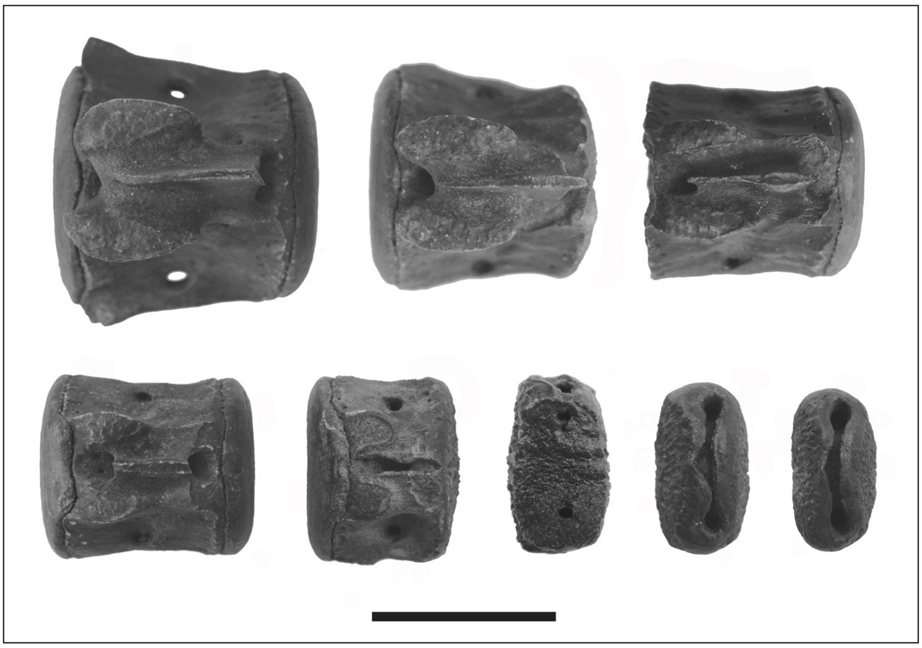

Fig. 5 - Caudal vertebrae in dorsal projections – specimens in the top row, left to right: 349/4, 349/3 and 349/5; specimens in the bottom row, left to right: 349/6, 349/2, 349/7, 349/8 and 349/1. Scale bar 5 cm.

Fig. 6 - Caudal vertebrae in right lateral projections – specimens in the top row, right to left: 349/4, 349/3, 349/5 and 349/6; specimens in the bottom row, right to left: 349/2, 349/7, 349/8 and 349/1. Scale bar 5 cm.

modistally increasing mandible height reaching its maximum in a middle part, although rare for baleen whales, is a very distinct trait observed in a few other Middle Miocene taxa related to *Parietobalaena*, such as *P. palmeri* (Kellogg 1968), *P. campiniana* (Bisconti et al. 2013) and *Otradnocetus virodovi* (Mchedlidze 1984), but differing from Cetotheriidae s.s. (see below).

Another fragment illustrated by Stepanović (1938) is an incomplete lumbar vertebra, of which only the centrum has been preserved, with damaged surface. The centrum is dumbbell-shaped and anteroposteriorly elongated, approximately twice as long as wide. The base of the transverse process, as preserved, is anteroposteriorly short. The base of the broken neural spine is exposed; no signs of pachyostosis or pachyosteosclerosis of vertebral processes or centrum itself are observable.

The caudal vertebrae (Figs 4, 5 and 6) are generally in a good state of preservation, showing no macroscopically observable traces of erosion or re-deposition. They include median and posterior caudal elements, and given their uniform appearance and preservation state, as well as absence of repeating elements, they come likely from a single individual. Moreover, measurements (Tab. 2) indicate that the vertebrae probably represent a consecutive series. The overall shape of the centra changes with decreasing size. In dorsal view (Fig. 5), the first four centra are shaped as elongated, flattened cones with slightly broader anterior sides, which narrow gradually from the anterior to posterior vertebrae, while the fifth centrum (349/2) becomes evidently shorter, thus losing its conical shape. Where epiphyses are preserved, centra 2-5 (349/3, 349/5, 349/6 and 349/2) show convex outlines in lateral views (Fig. 6); these specimens likely represent ball vertebrae, which are positioned between the penducular and fluke regions, and function as a main locus of the bending motion in the tail (Marx et al. 2016).

Tab. 2 - Measurements (in mm) of the vertebrae from Bele Vode. Specimens with both epiphyses present are marked with *. Comparative measurements for centrum lengths and total length of caudal vertebrae series of *Cetotherium riabinini* and *Parietobalaena palmeri* are also given.

Specimen	Tentative position	Centrum length	Centrum width (cranial)	Centrum width (caudal)	Centrum height (cranial)	Centrum height (caudal)	Total height	Centrum length (comparison)	
								Cetotherium riabinini NMNH-P 1668/1 (Gol'din et al., 2014), skeleton length 2.97 m	*Parietobalaena palmeri* USNM 16667 (Kellogg, 1968), skeleton length < 4.5 m
349/4*	CA7	56.25	53.08	49.77	51.96	51.92	76.72	60	83
349/3	CA8	48	50.51	44.97	52.06	52.58	69.08	55	78
349/5	CA9	45.53	43.08	42.44	51.33	50.1	59.96	55	68
349/6*	CA10	45.3	42.16	40.05	49.46	46.82	54.46	48	51
349/2	CA11	32.76	41.03	39.95	44.82	42.26	46.74	39	34+
349/7	CA12	22.09	37.34	36.96	-	-	-	29	29
349/8	CA13	19.21	32.84	30.78	30.92	29.85	32.48	24	22
349/1	CA14	18.07	28.19	26.82	27.53	26.19	27.82	24	19
Total length		287.21						334	384+

In dorsal view, the three posteriormost centra, the smallest ones (349/7, 349/8 and 349/1), are divided into anterior and posterior halves by deep transverse grooves. These anteroposteriorly short and dorsoventrally compressed vertebrae likely represent elements of the fluke (Buchholtz 2001). Also, the four anterior vertebrae bear neural arches with spines and short metapophyses, whereas the fifth one has only a rudiment with a shallow neural canal. The fluke vertebrae do not have any processes or traces of a neural canal.

The anteriormost vertebra has transversely small transverse processes, with pointed anterolateral margins. The next vertebra has only reduced processes appearing as transverse ridges. All the other vertebrae lack transverse processes. In all the vertebrae, transverse processes or lateral portions of the corpora (where the processes are absent) are perforated by a pair of bilateral, vertical foramina for the transmission of vertebral arteries (Marx et al. 2016).

Epiphyseal fusion was still in progress in all the caudal vertebrae. The anteriormost five vertebrae (349/4, 349/3, 349/5, 349/6, and 349/2) show incomplete fusion, where one or both vertebral epiphyses are attached to centra, but with very distinct, open suture lines. The posteriormost vertebrae show no traces of epiphyseal fusion whatsoever. A small fragment of an unfused caudal epiphysis (349/9) did not belong to any of the preserved centra. Where ossified, neural arches and spinal canals are very small; also, metapophyses and spinal processes are not fused to the corresponding centra.

Therefore, the whale from Bele Vode is a small whale which is distinct among Neogene toothless baleen whales in the straight (rather than dorsoventrally curved from the lateral view) horizontal ramus of the mandible, which is proximodistally heightening anterior to the coronoid process; elongated lumbar vertebrae and all the preserved vertebrae without signs of pachyosteosclerosis; and the extremely small size of preserved bones.

Discussion

Bone anatomy and ontogeny

The caudal vertebrae are very similar to the consecutive series of caudal vertebrae of *Cetotherium riabinini* (Gol'din et al. 2014), from CA7 to CA14 (Tab. 2). This is a rare and good example of a rather complete vertebral anatomy of the smallest baleen whales and, therefore, we also identify the caudal vertebrae from Belgrade as CA7-CA14. Notably, this vertebral anatomy is characterized by a relatively small overall number of caudal vertebrae, in total 17-20 (see also Gol'din et al. 2014). Among extant mysticetes, this low count of vertebrae is shared only by the minke whale *Balaenoptera acutorostrata* and the pygmy right whale *Caperea marginata* (Omura 1971; Buchholtz 2011). However, *Caperea* significantly differs from other cetaceans, including cetotheres, in its vertebral anatomy: in particular, it has only 8 or 9 (rather than 10 or 11, as in *Balaenoptera acutorostrata* or *Cetotherium riabinini*) pre-fluke caudal vertebrae (Buchholtz 2011), whereas vertebrae of the whale from Belgrade, as preserved, seem to share a small *Balaenoptera-Cetotherium* pattern. A striking feature of the whale from Belgrade is its extremely small size. The mandible height is similar to that of *Cetotherium riabinini*, whereas the caudal vertebrae are smaller in all dimensions, including centrum width and height.

The degree of fusion of caudal vertebral epiphyses indicates a non-neonate juvenile or a subadult individual. Kato (1988) found a similar degree of caudal epiphyseal fusion in female minke whales of about 9 m long, with 0 or 1 ovulation scars on the ovary, and in males 9 m long that approximately correspond to the age of 5 to 10 years (Kato 1987). However, unlike in the minke whale or other mysticetes [e.g., *Balaenoptera physalus* (Ohsumi et al. 1958) or *Cetotherium riabinini* (Gol'din et al. 2014)], the posteriormost (fluke) vertebrae in the whale from Belgrade have unfused epiphyses. Thus, the epiphyseal fusion started from the pre-fluke vertebrae, showing an ossification sequence different from the most of cetaceans (Galatius & Kinze 2003). Kato (1988) reported such a state from a single female of the minke whale with traces of a single ovulation. Therefore, we conclude that the whale from Belgrade was a subadult, possibly near the age of sexual maturity. Meanwhile, it is impossible to speculate on how special or typical this ossification sequence is, based on a single specimen.

Comparison and taxonomy

Historically, baleen whales from the Central Paratethys have been identified as members of the family Cetotheriidae (Czyzewska & Ryziewicz 1976). Indeed, this was the dominating group among baleen whales in the neighboring sea, the Eastern Paratethys, during the latest Middle and Late Miocene (Gol'din & Startsev 2017). However, the family Cetotheriidae has been a "wastebasket taxon" for many Neogene baleen whales until recently (Bouetel & Muizon 2006), and some of the earlier reported specimens need revision now. Many Miocene records of baleen whales of the Central Paratethys were referred to as members of genus *Mesocetus*, including *Mesocetus agrami* (Van Beneden 1884) and *Mesocetus hungaricus* (Kadić 1904), or somewhat related forms. However, the genus *Mesocetus* also historically served as a "wastebasket taxon" for very different whales, mostly from Europe, and at some point, it was even regarded as a *nomen dubium* because of controversial nature of type materials (Steeman 2010). In recent times the type species of the genus *Mesocetus* (*i.e.*, *Mesocetus longirostris* Van Beneden, 1880, from Belgium) was identified as a member of the newly established family Tranatocetidae (Gol'din & Steeman 2015), leaving Paratethyan "*Mesocetus*" materials without any specific taxonomical references.

Meanwhile, some finds from the Central Paratethys were specifically identified as Cetotheriidae *s.s.* For example, Stefanović (2010) reported a specimen from Štrbci in Bosnia having a bulla of a typical cetotheriid shape, which he identified as *Cetotherium* aff. *rathkei*. Moreover, the apparently non-cetotheriid *Pinocetus polonicus* (Steeman 2007; Marx & Fordyce 2015) was recovered as closely related to Cetotheriidae, in some recent phylogenies (Gol'din & Steeman 2015; Gol'din & Startsev 2017). Also, two whales from the Eastern Paratethys, *Otradnocetus virodovi* (Mchedlidze 1984) and ?Cetotheriidae indet. VSEGEI 2401 (Riabinin 1934), were identified as related to *Parietobalaena* sp. (Gol'din & Startsev 2017) and, thus, represent stem taxa of Cetotheroidea.

The baleen whale specimen from Belgrade clearly differs from all the Badenian and Sarmatian records identified as *Mesocetus*. First, it is extremely small, far smaller than all the records reported before, and this size difference cannot be explained only by ontogenetic factors because its tentatively estimated subadult age (see above) suggests a body length at least as long as 80% of adult body size, as compared with modern *Balaenoptera acutorostrata* or *Caperea marginata* (Kato 1988; Kemper & Leppard 1999). The mandibular dimensions are identical to the holotype of *Parietobalaena campiniana* (Bisconti et al. 2013) and similar to those of *Cetotherium riabinini* (Gol'din et al. 2014). The caudal vertebrae are even slightly smaller than in *C. riabinini* in width and height, as well as in length: their combined length is 14% shorter than in *C. riabinini* (Tab. 1). Meanwhile, the total skeleton length of *C. riabinini* is only 2.97 m (Gol'din et al. 2014) which is among the smallest Neogene baleen whales (Bouetel & Muizon 2006; Lambert et al. 2010). It means that total body length of the whale from Belgrade was about only 2.5 m. Therefore, the adult body size, if compared with growth parameters of living whales (Kato 1987; Kemper & Leppard 1999; Sumich et al. 2013), did not exceed 3-3.5 m. It further differs from *M. hungaricus* in peculiar apomorphic mandibular anatomy with the ramus distally heightening toward its median part. Meanwhile, the whale from Bele Vode also differs from *C. riabinini* and other cetotheriids for which vertebrae are known, including a cetotheriid whale from Štrbci (Stefanović 2010), in the primitive state of the elongated lumbar vertebrae (ca. 70 mm vs 56 mm in *C. riabinini*) combined with the small width (ca. 40 mm) and height (the primitive state of mysticete anatomical pattern, as stated by Buchholtz 2001). This lumbar elongation is even more developed than in *M. agrami* and *M. hungaricus*. It is similar in proportions to *Parietobalaena palmeri* (Kellogg 1968) from which it differs in its smaller size even in comparison with a juvenile specimen (Tab. 2).

The whale from Bele Vode has a straight, proximodistally heightening horizontal ramus of the mandible, a rare trait shared only by *Parietobalaena* and *Otradnocetus*. This state differs as from whales of the subfamily Cetotheriinae, in which it proximodistally lowers (Gol'din et al. 2014), as from some other cetotheriids, including *Piscobalaena nana* (Bouetel & Muizon 2006) and Herpetocetinae (Boessenecker 2011), in which the ramus, if it heightens, is also dorsoventrally S-curved (Fig. 7). In addition, it lacks pachyostosis of the lumbar vertebrae, unlike *Otradnocetus* or any Paratethyan cetothere. Also, it has an extremely small body size, like *Parietobalaena* or *Cetotherium*. Therefore, based on these traits, although highly fragmentary, we tentatively identify the Belgrade specimen as ?*Parietobalaena* sp. It is the first record of a *Parietobalaena*-like whale from the Central Paratethys. Moreover,

Fig. 7 - Schematic comparison of shape of the horizontal ramus of Cetotheroidea, lateral view, top to bottom: *Otradnocetus virodovi* GNM CO-2, *Cetotherium riabinini* NMNH-P 1668/1 and Herpetocetinae indet. UCMP 119999. Scale bars are 10 cm each.

Parietobalaena is the sole non-endemic mysticete taxon recorded in the Paratethyan region, which is distinct for its isolated fauna (Gol'din & Startsev 2017).

Notably, there is at least one *Parietobalaena* taxon, i.e. *Parietobalaena yamaokai* (Otsuka & Ota 2008; Tsai 2017), which is considerably larger in body size: a physically immature specimen was estimated to be 5-8 m long, and definitive body length could be even greater (Tsai 2017). This is evidence for the size disparity within this group of Middle Miocene mysticetes.

The specimen from the Serravallian of Bele Vode is one of the latest representatives of *Parietobalaena* and related taxa in the world. However, there is at least one whale, *Heterocetus affinis* (or *Parietobalaena affinis*) from Diest Fm. of Belgium which is dated as late as Tortonian (Steeman 2010); therefore, the ?*Parietobalaena* sp. specimen from Bele Vode can be accurately placed within the chronostratigraphic range of *Parietobalaena* and related taxa.

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