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A new elephantoid dental specimen from the Miocene of Kruševac Basin in Central Serbia

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Abstract. Elephantoid cheek teeth from the late Early and Middle Miocene of Europe frequently display mixtures of bunodont and zygodont features, making their taxonomical attributions difficult and subjective. Today, these teeth with "intermediate" morphologies are attributed either to the mammutid species *Zygolophodon turicensis*, or to the gomphothere genus *Gomphotherium* - as a variation of *G. angustidens* or as a separate species *G. subtapiroideum*. This paper presents one such specimen, a fragmented lower third molar which originated from Miocene sandstones within the Kruševac Basin (possibly from the village of Bela Voda) in Central Serbia. We described the fossil and examined its metric properties in comparative context. Furthermore, we applied the semiquantitative method of Wang et al. (2016) in order to reduce subjectivity in our assessment of the degree of specimen's zygodonty. Our results suggested that the specimen resembles *Z. turicensis* more closely than either *G. angustidens* and *G. subtapiroideum*, both in terms of the metrics and the degree of zygodonty. However, we were not able to make a firm taxonomical attribution, due to the fact that the specimen represents an isolated and incomplete fossil.

Key words: bunodont, zygodont, elephantoid, *Gomphotherium*, *Zygolophodon*, Miocene, Kruševac Basin, Serbia.

Апстракт. Зуби елефантоида из касног-раног и средњег миоцена Европе често показују мешавине бунодонтних и зигодонтних карактеристика, што отежава и субјективизује њихову таксономску атрибуцију. Овакви зуби са "интермедијарним" морфолошким карактеристикама данас се сврставају или у оквире мамутидске врсте *Zygolophodon turicensis*, или међу припаднике гомфотеридског рода *Gomphotherium* - као варијација врсте *G. angustidens* или као засебна врста *G. subtapiroideum*. У овом раду је представљен један такав примерак фрагментираног доњег трећег кутњака, који потиче из миоценских пешчара у оквиру крушевачког басена (могуће из села Бела Вода) у централној Србији. Описали смо фосилни примерак и испитали његове метричке особине у компаративном контексту. Такође, применили смо полуквантитативни метод Wang et al. (2016) како би смањили субјективност приликом процене степена зигодонције. Наши резултати сугеришу да примерак више подсећа на врсту *Z. turicensis* него на врсте *G. angustidens* и *G. subtapiroideum,* како у погледу метричких карактеристика, тако и у погледу степена зигодонције. Међутим, нисмо успели да успоставимо сигурнију таксономску атрибуцију, због чињенице да примерак представља изоловани и некомплетан фосил.

Кључне речи: бунодонт, зигодонт, елефантоид, *Gomphotherium, Zygolophodon*, миоцен, крушевачки басен, Србија.

Introduction

Throughout the most of the Miocene epoch, proboscideans were well represented in Europe by deinotheres and diverse forms of "mastodonts" (mammutids, gomphotheres, amebelodonts, and choerolophodonts) (Göhlich, 1999, 2010). Among the members of superfamily Elephantoidea Gray, 1821, there is a major morphological distinction based on the form of cheek dentition, which are differentiated between the so-called bunodont and zygodont patterns. The patterns are typified by the gomphothere

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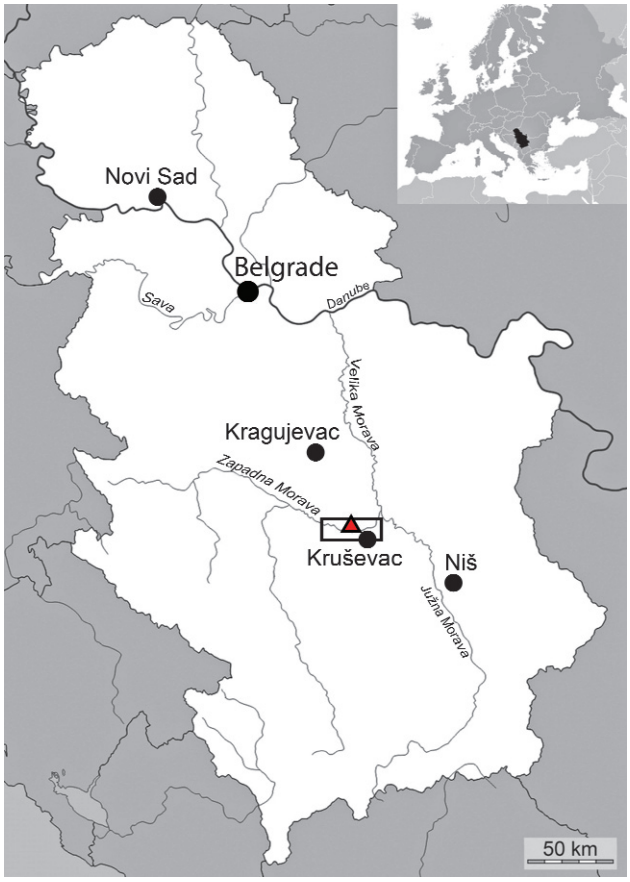

Fig. 1. Map of Serbia showing position of the Kruševac Basin (black rectangle), and Bela Voda site (red triangle).

Gomphotherium and the mammutid *Zygolophodon*, which were among the earliest proboscideans to arrive in Europe at the end of MN3 (early Orleanian; MEIN, 1999), with the record of the deinothere *Prodeinotherium bavaricum* from Lesvos island (Greece) as early as MN3b (KOUFOS et al., 2003). However, dental specimens from the late Early and Middle Miocene of Europe frequently show mixtures of bunodont and zygodont features, making their taxonomical attributions rather difficult and subjective (TOBIEN, 1972; MAZO, 1996). Among the multitude of elephantoid specimens recorded in the Neogene of Serbia (PAVLOVIĆ, 1981, 1998), only a small number of specimens show these "intermediate" morphologies. In this paper, we describe and examine a fragmented elephantoid molar with intermediate morphology, discovered recently in Central Serbia. In order to minimize the subjectivity in our assessment of the specimen's zygodonty, we applied a new, semiquantitative method suggested by WANG et al. (2016). The specimen originated from the Kruševac Basin, a semi-isolated Neo-Alpine tectonic depression (graben), mostly filled with thick Early and Middle Miocene lacustrine clastics (KNEŽEVIĆ, 1997; MAROVIĆ et al., 2007). These sediments have been known for the abundance of proboscidean fossils (PETKOVIĆ, 1926; PAVLOVIĆ et al., 1977; MARKOVIĆ et al., 2004). Unfortunately, the specimen reported herein represents an accidental find by a local, so the exact geographical location and the stratigraphic provenance of the fossil remains unknown. However, there is a distinct possibility that the specimen originated from the lacustrine sediments in Bela Voda village near Kruševac (Fig. 1), recently dated to MN5-6 (MARKOVIĆ, 2008).

Materials and methods

The material consists of an isolated and fragmented left lower third molar crown (m3 sin.), NMKVRS.P5. The specimen is curated at the National Museum Kraljevo (abbreviated NMKVRS), Serbia. The odontological terminology in this paper follows TASSY (1996), TOBIEN (1996), and WANG et al. (2016) (Fig. 2), and the measurements were taken after GÖHLICH (1998). The specimen's degree of zygodonty was assessed using the method proposed by WANG et al. (2016). For metric comparisons, we applied an adjusted z-score analysis, which allows the comparison of

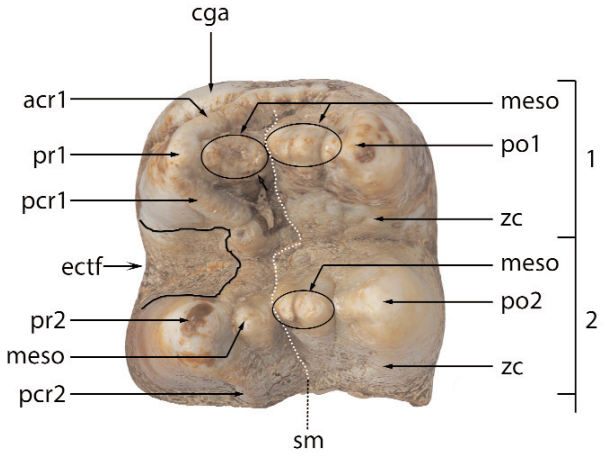

Fig. 2. Dental nomenclature: **acr1)** anterior crescentoid (i.e. central conule) of the first lophid; **cga)** anterior cingulum; **ectf)** ectoflexid (its 'U'-shaped form marked with line); meso – mesoconelets; **pcr1, pcr2**) posterior pretrite crescentoids of the first and second lophids; **po1, po2)** posttrite main cusps of the first and second lophids (metaconid and entoconid, respectively); **pr1, pr2)** pretrite main cusps of the first and second lophids (protoconid and hypoconid, respectively); **sm)** median sulcus; **zc)** zygodont (vestibular) crests. Numbers on the right mark the first and second lophids, separated by the transverse (interlophid) valley.

unbalanced samples, often limitative for the fossil record, using the Student's t inverse distribution (SCOLAN et al., 2012; ZANOLLI, 2013). In addition, we used a method based on the likelihood ratio test to determine whether the measurements for NMKVRS.P5 were more representative of one of two elephantoid

samples (species) within a given pair (VAN BUUREN, 2004; NOWACZEWSKA et al., 2013). The following taxa and localities were used for comparative analysis – *Z. turicensis*: Malartic (France, MN7), Wartenberg (Germany, MN8), Bitola (FYR Macedonia, Miocene) (TASSY, 1977; GÖHLICH, 1998; GAREVSKI et al., 2012); *G. angustidens*: Feldmoching (Germany, Miocene), Achldort (Germany, MN7), Simorre (France, MN7), En Péjouan (France, MN7) (GÖHLICH, 1998; TASSY, 1974; TASSY, 2014); *G. subtapiroideum*: Massenhausen (Germany, MN8/9), Sandelzhausen (Germany, MN5) (GÖHLICH, 1998, 2010). Abbreviations: MN – Mammalian Neogene; sin. – sinistra (left); p – mandibular premolar; m – mandibular molar.

Description

The fossil is a mesial portion of m3 sin. crown, preserving the first two lophids, and missing the root (Fig. 3). The occlusal morphology can be studied in detail, since the crown shows no macroscopically observable wear. The lophids are somewhat antero-posteriorly compressed and separated by a deep and wide transverse (interlophid) valley, not obstructed by conules. The antero-posterior compression is most evident on the labial side when viewed laterally (Fig. 3F), with strait (not convex) pretrite walls. The lophids were probably positioned slightly obliquely relative to the long axis of the crown (i.e., posterolabially-anteriolingually), indicating a mandibular molar; this is especially evident in the second lophid, where the pretrite main cusp (hypoconid) is displaced slightly posteriorly, relative to the corresponding posttrite main cusp (entoconid). The anterior cingulum is strongly developed, mostly restricted to the pretrite part. The pretrite and posttrite parts of the both lophids are separated by a clear median sulcus. The first pretrite half-lophid consists of a large main cusp (protoconid) and a smaller mesoconelet, weakly subdivided into three or four aligned conelets (unclear due to the damaged tips), running from the tip of the protoconid to the median sulcus. The first posttrite is made up by a large main cusp (metaconid), and a much smaller mesoconelet, and is also weakly subdivided into four aligned, blunt individual conelets, of which the largest and highest one is the second from metaconid. The second pretrite includes a large hypoconid and only a singular mesoconelet, which is large, but evidently smaller then hypoconid. In the second posttrite, there is a large entoconid, and a mesoconelet, strongly subdivided into two aligned conelets (a large one next to the entoconid, and a much smaller one near the median sulcus). In anterior/posterior views (Fig. 3C-D), the posttrite parts of the both lophids are broader and higher then the pretrite half-lophids; also, the labial walls are inclined (dorso-medially to ventro-laterally), while the lingual walls are vertical. In the

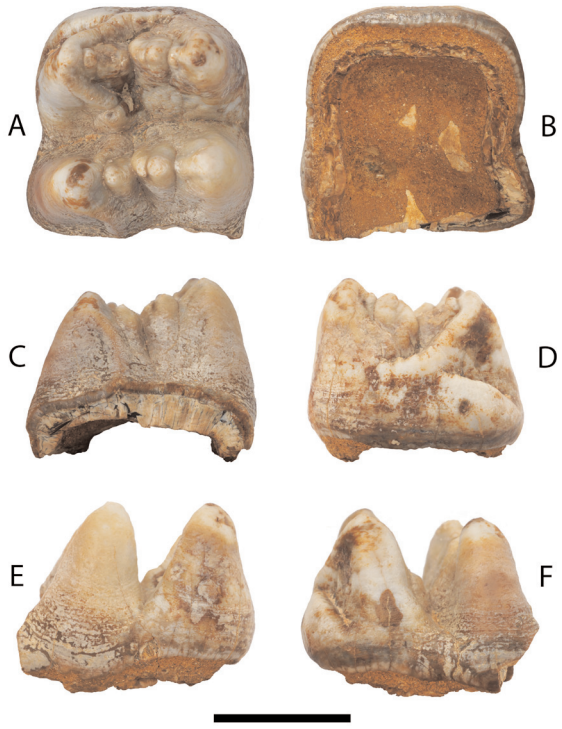

Fig. 3. The lower left m3 fragment from the Kruševac Basin (possibly Bela Voda site) NMKVRS.P5: **A)** occlusal view; **B)** inferior view; **C)** distal view; **D)** mesial view; **E)** lingual view; **F)** labial view; scale bar = 5 cm.

first pretrite, both the anterior and posterior central conules form inflated crests (i.e. crescentoid). The anterior crescentoid runs from the tip of the protoconid, down to the posttrite, where it merges with the anterior cingulum; its mesial end is subdivided into smaller individual conules. The posterior crescentoid is noticeably serrated, and labialy deliniated by a clear sulcus; it extends from the tip of the protoconid down to another small conule in the interlophid (with a damaged tip). In the second pretrite, the posterior central conule forms a gracile (less inflated) but sharp crest, which continually extends from the tip of the hypoconid to the posterior interlophid; the anterior central conule fails to reach the tip of hypoconid, and rather extends from the interlophid to the boundary of the pretrite main cusp and pretrite mesoconelet. The conules are not massive enough to block the interlophid valley. In occlusal view (Fig. 3A), the ectoflexid (labial notch of the interlophid) is clearly ′U′-shaped. Zygodont crests are present on the anterior and posterior surfaces of the posttrites (more noticeable on the second posttrite), but they are very weakly developed.

Remarks

The existence of “intermediate” elephantoid dental specimens had been a long-standing problem in

mastodont systematics and taxonomy (MAZO & VAN DER MADE, 2012). As noted by MAZO (1996), taxonomical identification of these specimens carries an implied subjectivity that does not facilitate taxonomy or systematization. Recently, WANG et al. (2016) attempted to standardize assessments of zygodonty in proboscidean dentition by introducing a four-level scale, where a higher number indicates a higher degree of zygodonty. In their scale, level 0 denotes fully bunodont forms (e.g. *G. angustidens*), level 1 marks the forms with "intermediate" bunodont-zygodont morphologies (e.g. *G. subtapiroideum*), while levels 3 and 4 designate well developed zygodonty (as seen in *Zygolophodon* and *Mammut*, respectively). Tested against the scale of WANG et al. (2016), the molar from Kruševac Basin falls between levels 1 and 2; the results are given in Table 1, and briefly discussed bellow.

Pretrite main cusps: In an unworn, typical zygodont tooth, the tip of the pretrite main cusp is sharp, located close to the median axis; in contrast, typical bunodonts (e.g. *G. angustidens*) show blunt pretrite main cusps, located farther from the median axis (WANG et al., 2016). In the fragmented NMKVRS.P5 molar, the protoconid and hypoconid evidently display sharp tips. However, the pretrite main cusps do not seem to be positioned medially.

Pretrite mesoconelets: In a typical bunodont tooth, the pretrite mesoconelet is relatively small, and non-subdivided. In zygodonts, this element is represented by a thin sharp crest that runs from the tip of the pretrite main cusp to the median sulcus; however, the pretrite mesoconelet may also be represented by a very small, nearly absent conelet. In intermediate forms (e.g. *G. subtapiroideum*), the pretrite mesoconelet may be subdivided into several small aligned conelets running from the tip of the pretrite main cusp to the median sulcus (WANG et al., 2016).

Pretrite central conules: In a typical zygodont tooth, these elements consist of strong, sharp enamel crests, extending from the tip of the pretrite main cusp to the anterior and posterior interloph(id)s, respectively (WANG et al., 2016). According to TOBIEN (1973, 1996), these crests give a certain selenodont 'crescentoid' habitus to the pretrite parts, reminiscent of the anterior and posterior arms of selenodont/bunoselenodont molar of an artiodactyl. In contrast, bunodonts usually show singular or duplicated conule(s), although some taxa (*Cuvieronius, Notiomastodon, Stegomastodon*) show extra accessory conules present in interloph(id)s (also non-crestlike). In an intermediate form, these elements are subdivided into three to four individual conules, clearly separated in unworn specimens; in

Table 1. Assessment of zygodonty in NMKVRS.P5, following WANG et al. (2016).

Morphological element	State	Notes
Pretrite main cusp	Sharp	The tips are not manifestly close to the median axis.
Pretrite mesoconelet	Moderately crest-like (1^{st}); non-crest-like (2^{nd})	The 1^{st} mesoconelet bears very shallow sulci, which tend to subdivide this structure into several (2?) small, aligned conelets; unfortunately, the damage of the tip obscures a full assessment of this parameter. In the 2^{nd} pretrite, there is only a singular (non-subdivided) mesoconelet.
Posttrite main cusp	Highly crest-like	Represented by a thick crest. The anterior central conule of the 2^{nd} pretrite does not reach the tip of the hypoconid.
Pretrite central conules	Moderately crest-like	The metaconid shows a slight anteroposterior compression (it is subdivided, however); the entoconid also shows a slight anteroposterior compression (and tends to be subdivided).
Posttrite mesoconelet	Moderately crest-like	The 1^{st} mesoconelet is weakly subdivided into several aligned conelets; the 2^{nd} is subdivided into 2 conelets; however, individual conelets in both posttrite half-lophids are thick, blunt, and do not form sharp crests. Posttrite main cusps and mesoconelets are clearly separated by a distinct sulcus.
Vestibular crests	Weak	Present, but exceptionally weak.
Posttrite central conules	Absent	–
Interlophids	Wide anteroposteriorly	This feature is also evident in the 'U'-shaped first ectoflexid.

some lower molars, the anterior central conule does not extend from the tip of the pretrite main cusp but rather from the boundary of the pretrite mesoconelet and pretrite main cusp (Wang et al., 2016). In the NMKVRS.P5 m3 fragment, pretrite central conules clearly form crest-like structures. However, as in *G. subtapiroideum*, the anterior central conule of the second pretrite does not reach the tip of the hypoconid.

Posttrite main cusps and mesoconelets: A typical bunodont shows bulky and pear-shaped posttrite half-loph(id)s, where a shallow sulcus separates a blunt main cusp from a non-subdivided mesoconelet; there is no anteroposterior compression of the posttrite whatsoever. In a typical zygodont, the posttrite main cusps and mesoconelets are poorly separated, strongly anteroposteriorly compressed and transversely extended, forming a sharp crest; the mesoconelets are usually subdivided into three or more aligned conelets. In taxa with intermediate morphology, the posttrite half-loph(id)s show a slight anteroposterior compression, resulting in an oval ring ?gure if wear is present; the mesoconelet is subdivided into two aligned conelets, and the main cusp also tends to be subdivided (Wang et al., 2016; Wang et al., 2017). As seen in occlusal projection (Fig. 3A), NMKVRS.P5 specimen is similar to *G. subtapiroideum* in this regard, showing a slight anteroposterior compression of posttrite half-lophids; although subdivided into aligned conelets, posttrite mesoconelets are bunodont, so they do not form particularly sharp crests. As in a typical bunodont tooth, posttrite main cusps and mesoconelets are clearly separated by deep sulci.

Vestibular crests: These enamel structures are synonymous with zygodont crests of Tobien (1996); they run from the tip of the outermost conule of the posttrite main cusp, along the anterior or posterior walls of posttrite half-lophid, and end in the interlophid valleys (Wang et al., 2016). Vestibular crests are typical for zygodont, and absent or weakly developed in bunodont cheek teeth (Tobien, 1975; 1996). In the specimen from Kruševac Basin, these crests are indeed present (more so on the second posttrite), but extremely weak; moreover, they are weaker than those seen in *G. subtapiroideum* (e.g. Göhlich, 2010, Figs. 7d-e, g-i, 8e).

Posttrite central conules: These features are also known as posttrite enamel pillars (Tobien, 1975). In bunodonts, these elements vary significantly with taxonomy; however, if they are present, they do not assume crest-like habitus. In mammutids, posttrite central conules are represented by very thin crests, which are seldom present in *Zygolophodon*, and more frequent in *Mammut* (Wang et al., 2016). In NMKVRS.P5, posttrite central conules (of any form) are absent altogether.

Interlophids: In contrast to a typical bunodont tooth, which shows anteroposteriorly narrow interloph(id) valleys blocked by relatively large central conules, a typical zygodont tooth is characterized by anteroposteriorly wide and open interloph(id)s (Wang et al., 2016). The valley-blocking central conules, typical for bunodont teeth, are reduced or almost completely lacking in zygodonts (Göhlich, 1999). According to Tobien (1996), the pretrite conules in *Zygolophodon* can be more or less developed, in some cases almost blocking the open interloph(id) valley. In the specimen from the Kruševac Basin, the conules are not massive enough to block the interophid, so the molar clearly displays the state seen in mammutids and intermediate forms, such as *G. subtapiroideum*. Furthermore, the ectoflexid is ′U′-shaped (Fig. 3A), like those seen in *G. subtapiroideum*, and unlike the ′V′-shaped ectoflexid of the lower molars of *G. angustidens*, which reflect a compressed interlophid (Wang et al., 2017).

An oblique arrangement of lophids (posterolabially-anterolingually, relative to the median axis of the crown) represents another taxonomically important feature of the mammutid lower molar crowns. Although the lower molars of *Zygolophodon* do not show as strongly oblique lophids as those seen in more derived forms such as *Mammut* (Osborn, 1936), Tobien (1996) claims that this rather distinctive mammutid character can be used for differentiation between the molars of early *Zygolophodon* and *Gomphotherium*. Unfortunately, the relative positions of lophids in NMKVRS.P5 can not be assessed with certainty, since the specimen only preserves the mesial portion of the crown; nevertheless, an oblique arrangement is evident in its slightly posteriorly displaced hypoconid. Furthermore, this oblique position in NMKVRS.P5 seems less pronounced then in many m3 specimens classified as *Zygolophodon turicensis* (e.g. Schlesinger, 1917, Pl. 22, Fig. 3; Tobien, 1975, Figs. 9-10; Garevski et al., 2012, Fig. 1 c-d), and more akin to the state observed in *G. subtapiroideum* from Sandelzhausen (e.g. Göhlich, 2010, Figs. 7d-e, g-i, 8e).

Finally, the inclination of the labial and lingual walls in NMKVRS.P5 follows the pattern observed both in zygodont and majority of bunodont lower molars (lingual walls are vertical, labial walls are inclined; see Tobien, 1973, 1975); this feature further confirms that the specimen indeed represents fragment of a lower molar, but it is not taxonomically informative in this context.

Metric analysis

The results of our metric analysis are given in Tables 2 and 3. As seen in Table 2, the width of the first lophid (W1) is closest to the mean values for *Zygolophodon turicensis*. However, there are no statistically significant differences (outside the estimated 95% limit of variation) with the other two samples (i.e. *Gomphotherium angustidens* and *G. subtapiroideum*). The adjusted z-score value for the width of the second lophid (W2)

Table 2. Measurements of NMKVRS.P5 m3 sin. compared to three samples. The 95% limit of variation expressed for each comparative group lies between –1 and +1, with the mean at 0. Abbreviations: **W1** = width of the first lophid, **W2** = width of the talonid; **SD** = standard deviation; **n** = number of specimens per sample: **z** = adjusted z-score value.

Measurement	**NMKVRS.P5**	***Zygolophodon turicensis* mean (SD/n)**	***Gomphotherium angustidens* mean (SD/n)**	***Gomphotherium subtapiroideum* mean (SD/n)**
W1	**77.4**	74.85 (3.03/4)	63.4 (9.34/5)	64.61 (8.42/9)
		z = 0.24	z = 0.49	z = 0.62
W2	**83**	80 (6.55/5)	66.55 (8.5/10)	70.83 (6.25/12)
		z = 0.15	z = 0.82	z = 0.85

Table 3. Results of the likelihood ratio analysis calculated for the metric traits of NMKVRS.P5 m3 sin., showing to which of two species this tooth is more likely to belong (the values of the likelihood ratios are given in parentheses). Abbreviations: **W1** = width of the first lophid, **W2** = width of the talonid.

Measurement	**NMKVRS.P5 as *Z. turicensis* or *G. angustidens***	**NMKVRS.P5 as *Z. turicensis* or *G. subtapiroideum***	**NMKVRS.P5 as *G. subtapiroideum* or *G. angustidens***
W1	*Z. turicensis* (6.65)	*Z. turicensis* (6.18)	*G. subtapiroideum* (1.08)
W2	*Z. turicensis* (7.60)	*Z. turicensis* (5.72)	*G. subtapiroideum* (1.33)

also shows no significant differences with any of the three species, but again, the value is closest to the *Z. turicensis* mean. As shown on Table 3, the calculated probability (LR) indicates that, for W1 and W2, NMKVRS.P5 more likely represents a *Z. turicensis* m3 than those from *G. angustidens* and *G. subtapiroideum*. Furthermore, the specimen more likely belongs to *G. subtapiroideum* than to *G. angustidens*.

The height of the specimen (H), as measured at the second posttrite, is 63 mm. As a quantitative measure of hypsodonty, the hypsodonty index (HI) was defined by JANIS (1988) as the height of the unworn third molar crown divided by the occlusal width of the same tooth (i.e. HI = Hm3/Wm3); the calculated HI equals to 1.32, which puts NMKVRS.P5 specimen into the category of low-crowned (brachydont) molars (HI<1.5; see PFRETZSCHNER, 1992). Following TOBIEN (1973), we also calculated the index in which the height of the second lophid is expressed as a percentage of its width (H*100/W); this gives the result 75.9, also demonstrating a brachyodont state.

Discussion

As it is known, the members of the family Gomphotheriidae HAY, 1922 (e.g. *Gomphotherium angustidens*) are characterized by their bunodont intermediate and third molars, consisting of blunt cone-like elements (pretrites and posttrites) arranged in several transverse ridges (loph(id)s), separated by narrow transverse valleys which are blocked by massive conules (TOBIEN, 1973; GÖHLICH, 1999). In contrast, Mammutidae HAY, 1922, or the "true mastodonts" (e.g. *Zygolophodon turicensis*), are distinguished by their zygodont cheek teeth, where pretrite and posttrite elements form yoke-like, sharp transverse crests, separated by deep and open transverse valleys (TOBIEN, 1975, 1996). Like lophodont dentition of deinotheres, zygodont dentition functioned in vertical shearing (probably an adaptation to folivory), as opposed to crushing-shearing mastication in the bunolophodont gomphotheres (TOBIEN, 1996; VAN DER MADE, 2010; ZHANG et al., 2017). The zygodont pattern is easily recognizable in European mammutids dated from MN7 onwards; however, during the earlier, MN3b/4-6 (early Orleanian – late Astaracian) interval, there was a significant morphological overlap between cheek dentition of *Gomphotherium* and *Zygolophodon*, which show mixtures of zygodont and bunodont features (MAZO, 1996; MAZO & VAN DER MADE, 2012). As noted by MAZO & VAN DER MADE (2012), it is surprising that zygodont morphology is not fully developed in Europe in MN4-6, considering

the presence of the well developed zygodont morphology in the genus *Eozygodon* from the basal Early Miocene of Africa (Aquitanian).

These "intermediate" dental specimens have proven to be extremely hard to classify as one genus/family or another. In general, there are three major views regarding this problem. According to some (e.g. LEHMANN, 1950; TOBIEN, 1972, 1973, 1975, 1996; MAZO, 1985, 1996), the intermediate dental specimens are best understood as variants within the polymorph *G. angustidens* species. This view was first introduced by SCHLESINGER (1917) when he described fossils from the Lower Miocene lignites of Vordersdorf near Eibiswald (Styria, Austria) as *Mastodon* (*Bunolophodon*) *angustidens* forma *subtapiroidea*, in order to distinguish them from a typical form of the species, *M.* (*B.*) *angustidens* forma *typica* (i.e. *G. angustidens*). He remarked that molars of this "subtapiroid form" look very similar to those of *Z. turicensis*. Particularly interesting in this context is the mandible from Paracuellos 5 (MN6; Spain) which displays fully zygodont p4 and m1, and bunodont m2 (MAZO, 1985). As noted by MAZO (1996), the occurrence of both zygodont and bunodont teeth in the jaw fragment of the same individual demonstrates that many isolated zygodont specimens from the early Astaracian of Europe could in fact represent remains of a highly plastic *G. angustidens*. Therefore, this peculiar case shows that attributions of isolated elephantoid dental specimens are particularly susceptible to errors, and unreliable. The alternative view (e.g. GÖHLICH, 1998, 2010) holds that (at least some) intermediate dental specimens do in fact represent a distinct species within the genus *Gomphotherium*. OSBORN (1936) was first to consider Schlesinger's "forma *subtapiroidea*" to be a valid species (within his genus *Serridentinus* OSBORN 1923). GAZIRY (1994) regarded molar specimens from the Upper Freshwater Molasse (southern Germany) as representatives of a valid taxon *Bunolophodon subtapiroides* (i.e. *G. subtapiroides*, since *Bunolophodon* VACEK 1877 became mostly synonymized with *Gomphotherium*; see TASSY, 1985; SHOSHANI & TASSY, 1996). GÖHLICH (1998, 2010) used the name *G. subtapiroideum* for the intermediate dental specimens from Sandelzhausen (MN5) and Massenhausen (MN8), both located in the southern part of Germany. The species is accepted as a valid taxon by WANG et al. (2016), who included *G. subtapiroideum* into their 'derived *Gomphotherium* group' (which, interestingly, appears to correspond to Osborn's *Serridentinus*). According to the interpretation by TASSY (1985), most intermediate specimens actually represent a "robust" form of *Zygolophodon turicensis*, which he differentiates from a "slender" morphotype of the species. In his division of *Gomphotherium* based on evolutionary grade, TASSY (1985) did recognize the subspecies *G. angustidens subtapiroideum* as a part of his "*G. angustidens* group", but he allocated most of the early intermediate specimens from Europe into his robust *Z. turicensis* morphotype. Indeed, dental morphology within Mammutidae is known to be highly variable (DUANGKRAYOM et al., 2017).

As our morphological analysis has shown (Tab. 1), NMKVRS.P5 does not fit easily in the range of variation of *G. subtapiroideum*, nor *G. angustidens*. In fact, the specimen falls somewhere on the morphological spectrum between *G. subtapiroideum* and mammutids, slightly closer to the latter group. The specific combination of *G. subtapiroideum*-like features (e.g. non-crest-like second pretrite mesoconelet, absence of posttrite central conules) and zygodont features (e.g. highly crest-like pretrite central conules, presence of vestibular crests) contribute to the specimen's distinctive "intermediate" form. The oblique arrangement of the lophids does not seem as pronounced as in mammutid m3s, but this can not be asserted with certainty due to the fragmentary nature of the specimen. Our metric analysis (Tabs. 2, 3) has shown that NMKVRS.P5 specimen has a particularly wide crown, closer to *Z. turicensis* than to *Gomphotherium*; this is especially evident in the width of the second lophid (W2), which is larger than the largest m3 specimens attributed to *G. subtapiroideum* (see GÖHLICH, 2010, Tab. 3). This is in agreement with TOBIEN's (1975, 1996) claim that mammutid m3s tend to show wider crowns than those of gomphotheres; *G. subtapiroideum* m3s are known to be smaller than the large sized specimens of *Z. turicensis* (GÖHLICH, 2010), and the size difference is even greater between *G. angustidens* and *Z. turicensis* (TASSY, 1977; TOBIEN, 1975). Like the majority of proboscideans, the specimen from the Kruševac Basin displays brachydonty. Evolutionary trends towards hypsodonty (or "subhypsodonty" *sensu* OSBORN, 1936: 393) in proboscideans (as in other herbivorous mammals) are linked with a transition from browsing to a more abrasive diet such as grazing (JANIS & FORTELIUS, 1988; SHOSHANI, 1998; DAMUTH & JANIS, 2011). A full-scale change to high-crowned (hypsodont) cheek teeth is found in elephants (GÖHLICH, 1999). However, some bunodont elephantoids show a tendency towards subhypsodonty (e.g. *Platybelodon*, *Gnathabelodon, Choerolophodon*), but they never reach the degree of hypsodonty which is already known already from the earliest elephants; in zygodont mammutids there is no clear tendency to subhypsodonty (TOBIEN, 1975). Importantly, hypsodonty of many mastodont molars depends upon tooth size, and there is actually an allometric relation between these two variables; this means that molars of large size tend to be relatively hypsodont, while smaller molars appear to be relatively brachyodont (TOBIEN, 1972, 1973, 1975). However, despite the large size (i.e. width), NMKVRS.P5 does not show particularly high crown.

In terms of chronology, the fragmented m3 from Kruševac Basin is (most probably) Miocene-aged. It is known that the Basin sedimentary fill contains Early

and Middle Miocene lacustrine clastics – most notably sandstones (KNEŽEVIĆ, 1997). The fossil clearly originated from a sandstone bed, which is evidenced by the yellow coarse sandstone matrix preserved on the underside of the crown (Fig. 3B). If the specimen was indeed discovered at Bela Voda locality (14 km north-west from Kruševac), then it is possible that it came from the sandstones which were recently dated to an MN5-6 interval (based on the presence of characteristic rodent taxa – *Cricetodon meini, Democricetodon mutilus* and *Miodyromys aegercii*; see MARKOVIĆ, 2008). This dating of NMKVRS.P5 is even more likely considering that the majority of other intermediate elephantoid specimens in Europe come from this interval.

Other intermediate proboscid specimens were reported from Serbia in the past (e.g. PETRONIJEVIĆ 1952, 1967). However, most of those "subtapiroid" teeth were published more than fifty years ago, and would certainly benefit from future revisions. This is exemplified by the paired m3s from Sibnica (Levač, Central Serbia), which were originally attributed to "*Mastodon* (*Bunodont*) *angustidens* Cuv. forma *subtapiroidea*" by PETRONIJEVIĆ (1967); in the recent analysis by STEFANOVIĆ et al. (2016), the specimens were reclassified as molars of *G. angustidens*.

Conclusions

Although we can not fully reject the possibility that NMKVRS.P5 represents *Gomphotherium*, we are more inclined to classify the specimen as an early, robust form of *Zygolophodon turicensis*. This is supported both by the results of our morphological and metric analyses. However, due to the fact that the specimen represents only an isolated fragment of a single elephantoid tooth, it is not possible to make a firm taxonomical attribution.

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Резиме

Нови примерак зуба елефантоида из миоцена крушевачког басена у централној Србији

Међу члановима надфамилије Elephantoidea GRAY, 1821 постоје изразите разлике у морфолошким карактеристикама бочних зуба, при чему се издвајају две основне структуре – тзв. бунодонтна и зигодонтна. Типични представници ових двеју денталних форми су родови *Gomphoterium* (бунодонт) и *Zygolophodon* (зигодонт), чији представници (врсте *G. angustidens* и *Z. turicensis*) спадају међу најраније сурлаше у Европи (MN3b/4; MEIN, 1999). Иако ови родови припадају различитим фамилијама и у начелу имају врло дистинктивне денталне морфологије, зуби из каснијег дела раног и средњег миоцена Европе често показују комбинације бунодонтних и зигодонтних карактеристика, што умногоме отежава њихову таксономску атрибуцију. Један такав „интермедијарни“ примерак је описан и анализиран у овом раду.

Испитивани фрагмент доњег трећег кутњака сурлаша (NMKVRS.P5) потиче из крушевачког басена, полуизоловане тектонске депресије испуњене језерским кластитима доњег и средњег миоцена (KNEŽEVIĆ, 1997; MAROVIĆ et al., 2007). Ови седименти су већ дуго познати по налазима фосилних сурлаша (PETKOVIĆ, 1926; PAVLOVIĆ et al., 1977; MARKOVIĆ et al., 2004). Нажалост, примерак из крушевачког басена представља случајни налаз од стране аматера, па тачна географска локација и стратиграфска припадност остају непознате. Ипак, налаз највероватније потиче из седимената села Бела Вода код Крушевца, који према новијим подацима припадају зони MN5-6 (MARKOVIĆ, 2008).

Како би се утврдила таксономска припадност фосила, приступило се примени више метода – степен зигодонције је оцењен применом метода који су предложили WANG et al. (2016), а анализа метричких података у компаративном контексту је спроведена применом тзв. прилагођене „z“ скор анализе (SCOLAN et al., 2012; ZANOLLI, 2013) и метода заснованог на тесту односа вероватноћа (VAN BURREN, 2004; NOWACZEWSKA et al., 2013). Зигодонција примерка из крушевачког басена оцењена је као прелазна између првог (карактеристичног за врсту *G. subtapiroideum*) и другог (*Z. turicensis*) степена, нешто ближе другом степену (Табела 1). Метричка анализа (Табеле 2 и 3) показала је да су ширине оба лофида (W1 и W2) ближе средњим вредностима за врсту *Z. turicensis* него средњим вредностима за врсте *G. angustidens* и *G. subtapiroideum*; међутим, треба нагласити да не постоје статистички значајне разлике (за ниво поверења од 95%). На основу резултата анализе не можемо у потпуности одбацити могућност да NMKVRS.P5 припада роду *Gomphoterium,* али смо ипак склони да примерак класификујемо као рану, робустну форму врсте *Z. turicensis.* С обзиром на чињеницу да налаз представља изоловани фрагмент само једног зуба, није могуће поузданије утврдити таксономску припадност.

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