Rhinocerotidae from the early middle Miocene locality Gračanica (Bugojno Basin, Bosnia-Herzegovina)

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Abstract

The early middle Miocene (European Land Mammal Zone MN5) locality Gračanica (Bugojno Basin, Bosnia-Herzegovina) has yielded numerous well-preserved dental remains of four Rhinocerotidae species: *Brachypotherium brachypus*, *Lartetotherium sansaniense*, *Plesiaceratherium balkanicum* sp. nov. and *Hispanotherium* cf. *matritense*. This rhinocerotid assemblage is typical of the Orleanian European Land Mammal Age and indicates a mesic woodland with diverse habitats from swampy forest to drier and more open environment.

Keywords *Brachypotherium* · *Lartetotherium* · *Plesiaceratherium balkanicum* sp. nov. · *Hispanotherium* · Early middle Miocene · Southeastern Europe · Bosnia-Herzegovina

Introduction

Among perissodactyls, rhinocerotids are major components of Miocene faunas in Eurasia (Heissig 1999; Antoine 2002). They were successful large to mega herbivores living in a wide array of habitats, ranging from savannahs to swamps and forests (e.g. Cerdeño and Nieto 1995; Becker et al. 2009). Here, we report dental remains referable to Rhinocerotidae and originating from the early middle Miocene coal mine of Gračanica (Bugojno Basin, Bosnia-Herzegovina). This mine, situated near the Village Gračanica about 10 km SSE from the centre of Bugojno, was initially exploited in 1939 and rhinocerotid

specimens, as other vertebrate remains, were regularly found in the lower part of the recorded section represented by coal and coaly clays (Mandic et al. 2016; Mandic et al. in prep. a, this issue). Several other groups of mammals from the same locality are described by different contributors of this special issue (Suoidea by van der Made (in prep., this issue); Ruminantia by Aiglstorfer and Mayda (in press, this issue); Carnivora by Bastl et al. (in press, this issue); Castoridae by Stefen (in press, this issue); Rodentia by Wessels et al. (in press, this issue); Proboscidea by Göhlich (in prep., this issue); Equidae by Göhlich and NN (in prep., this issue); Chalicotheriidae by Coombs and Göhlich (in press, this issue).

Likewise, the geological features of the region and the stratigraphical record of the locality are studied by Mandic et al. (in prep. a, this issue). So far, the regional mollusc stratigraphy implied an age range from 15.4 to 15.0 Ma for the Gračanica succession (Harzhauser et al. in press, this issue), which correlates with the Langhian (early middle Miocene) and with the European Land Mammal Zone MN5 (Hilgen et al. 2012). The ongoing magnetostratigraphic analyses currently indicates to a slightly younger dating somewhere in the age range between 15.2 and 14.0 Ma (pers. comm. O. Mandic). For the final integrative biostratigraphic and magnetostratigraphic dating of the Gračanica section see Mandic et al. (in prep. b, this issue).

The studied material of Rhinocerotidae allows describing a new species of plesiaceratherE, *Plesiaceratherium balkanicum* sp. nov., beside *Hispanotherium* cf. *matritense* and two other species known in the Miocene of Europe, *Brachypotherium brachypus* and *Lartetotherium sansaniense*. This rhinocerotid

assemblage can furthermore provide new data for their bio-stratigraphic range estimate and for palaeoenvironmental reconstruction of the Gračanica locality.

Materials and methods

The referred specimens from the locality of Gračanica are stored in the collection of the Natural History Museum Vienna, Austria. The fossils are described and identified by means of anatomical descriptions, comparative anatomy, and biometrical measurements. Dental features described correspond basically to cladistic characters used and listed by Antoine (2002). The dental terminology follows Heissig (1969) and Antoine (2002), while measurements were taken according to Guérin (1980). All dimensions are in millimeters.

The stratigraphical framework is based on geological time scales and European Land Mammal Ages (ELMA) for the Neogene (Hilgen et al. 2012). Successions of Mammal Neogene units (MN) were correlated based on biostratigraphic and magnetostratigraphic data (BiochroM'97 1997; Engesser and Mödden 1997; Kempf et al. 1997, 1999; Legendre and Lévêque 1997; Mein 1999; Steininger 1999; Agustí et al. 2001; Hilgen et al. 2012).

Abbreviations
FAD First Appearance Datum. **I/i** upper/lower incisor, **M/m** upper/lower molar, and **P/p** upper/lower premolar. **APD** antero-posterior diameter, **H** height, **L** length, **TD** transverse diameter, and **W** width. **MHNM** Muséum d'histoire naturelle Marseille, France; **NHMW** Natur-historisches Museum Wien, Austria.

Systematic palaeontology

The suprageneric arrangement follows that proposed by Antoine et al. (2010).

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Tribe Rhinocerotini Gray, 1821
Subtribe Teleoceratina Hay, 1902

Genus *Brachypotherium* Roger, 1904

Type species: *Rhinoceros brachypus* Lartet, 1837, by original designation.
Other referred species: According to several authors, a full revision of the Eurasian and African material of *Brachypotherium* is seriously needed (e.g. Guérin 2008; Geraads and Miller 2013). However, from the current knowledge of the genus (e.g. Heissig

1972a, 1999, 2012; Guérin 2000, 2008; Fukuchi and Kawai 2011; Geraads and Miller 2013), we can reasonably assume the following species as belonging to *Brachypotherium*: *Brachypotherium goldfussi* (Kaup 1834) from Europe, late Miocene (MN9–10); *Brachypotherium perimense* (Falconer and Cautley, 1847) from Southern Asia, early to late Miocene; *Brachypotherium heinzelini* Hooijer, 1963 from Africa, Miocene to? Pliocene; *Brachypotherium lewisi* Hooijer and Patterson 1972 from Kenya and Libya (Africa), late Miocene to ?Pliocene; *Brachypotherium snowi* (Fourteau, 1920) from Egypt and Lybia (Africa), early to middle Miocene; *Brachypotherium minor* Geraads and Miller 2013 from Kenya (Africa), early Miocene. The generic attribution of *Brachypotherium fatehjangense* (Pilgrim, 1910), *Brachypotherium pugnator* (Matsumoto 1921) and *Brachypotherium shanwangense* (Wang, 1965) from the Miocene of Asia is doubtful (Antoine, 2002; Lu et al. 2016). Based on a cladistic analysis, Antoine et al. (2003) considered the species *Aprotodon fatehjangense* as included in Teleoceratina but excluded from the genus *Brachypotherium*. Formerly described as *Teleoceras (Brachypotherium) pugnator* by Matsumoto (1921) and as *Chilotherium pugnator* by Okumura et al. (1977), this taxa was tentatively assigned to the genus *Plesiaceratherium* by Wang (1965) and then reassessed to *Brachypotherium* by Fukuchi and Kawai (2011) only on the basis of a few fragmented upper cheek teeth only and using measurements as the key character for identification. Following Lu et al. (2016), *Brachypotherium shanwangensis* is considered as a junior synonym of *Plesiaceratherium gracile*.

Brachypotherium brachypus (Lartet, 1837)
Fig. 1, Table 1

Type material: not designated.
Type locality: Simorre, Gers, France, middle Miocene (MN7–MN8).
Occurrence: late early Miocene to middle Miocene (MN4b–MN8) of Western Europe including Spain, France, Switzerland, Germany and Austria (see Heissig 1999, 2012, Becker 2003).
According to Heissig (1996), Codrea (1996, 2000), Geraads and Spassov (2009), Koufos and Kostopoulos (2013), Zervanová et al. (2013) and this study, the species could be present in the middle and late Miocene of Eastern and Southeastern Europe (Bosnia, Bulgaria, Greece, Poland, Romania, Slovakia). Fortelius (1990) also described remains of *B. brachypus* from Paşalar in Anatolia (Turkey, Asia Minor).
Referred material: right P1 (NHMW 2013/0003/0011); right P4 (NHMW 2013/0004/0007); left M2 (NHMW 2013/0004/0006); right M3 (NHMW 2013/0004/0005); right p3 (NHMW 2013/0003/0004); right p4 (NHMW 2013/0004/0002); right m1 (NHMW 2013/0004/0003); left m1
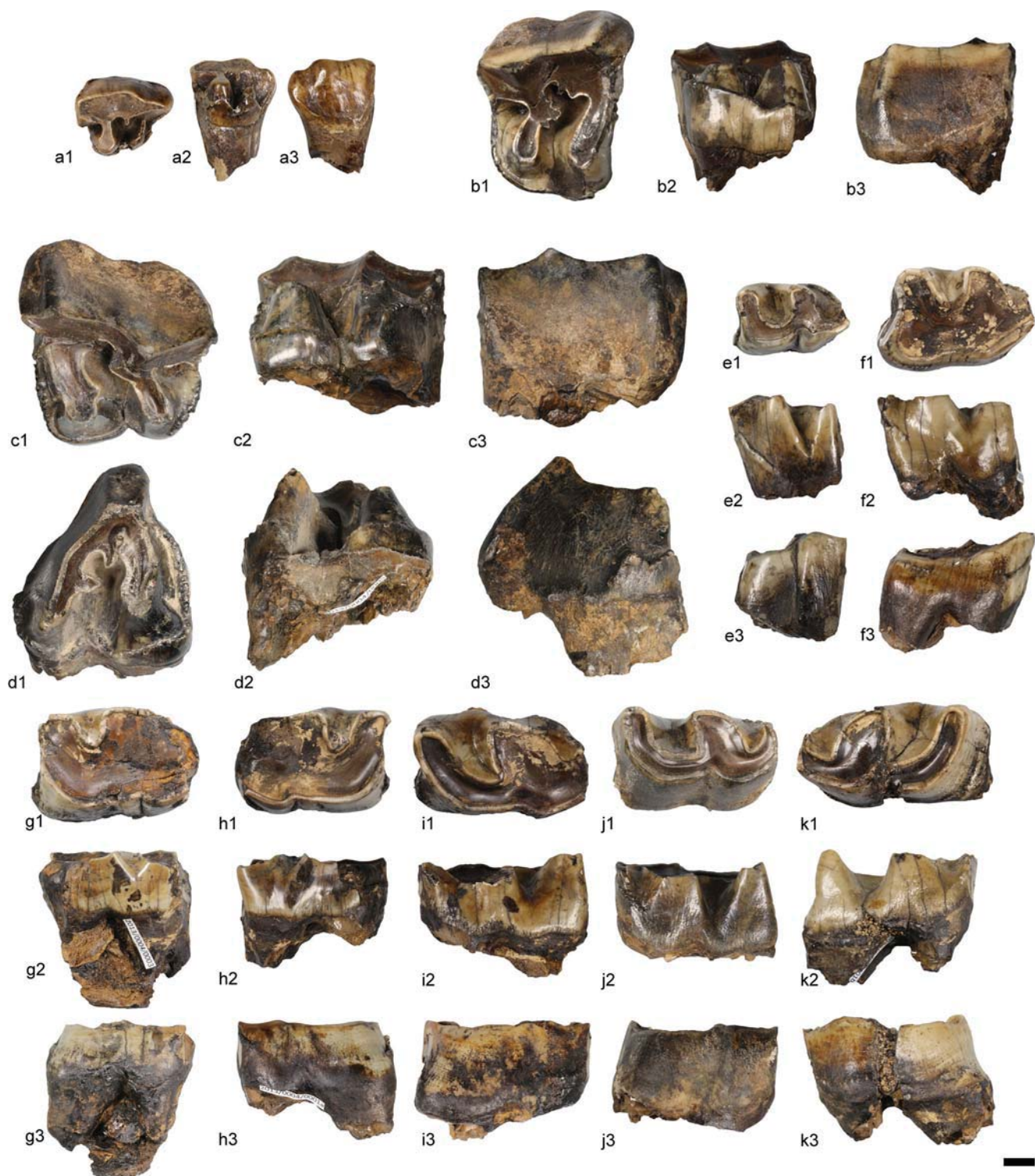
Fig. 1 *Brachypotherium brachypus* from Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina). **a** Right P1 (NHMW 20013/0003/0011) in occlusal (a1), lingual (a2) and labial (a3) views. **b** Right P4 (NHMW 2013/0004/0007) in occlusal (b1), lingual (b2) and labial (b3) views. **c** Left M2 (NHMW 2013/0004/0006) in occlusal (c1), lingual (c2) and labial (c3) views. **d** Right M3 (NHMW 2013/0004/0005) in occlusal (d1), lingual (d2) and labial (d3) views. **e** Right p3 (NHMW 2013/0003/0004) in occlusal (e1), lingual (e2) and labial (e3) views. **f** Right p4 (NHMW 2013/0004/0002) in occlusal (f1), lingual (f2) and labial (f3) views. **g** Right m1 (NHMW 2013/0004/0003) in occlusal (g1), lingual (g2) and labial (g3) views. **h** Left m1 (NHMW 2013/0004/0001a) in occlusal (h1), lingual (h2) and labial (h3) views. **i** Right m2 (NHMW 2013/0004/0004) in occlusal (i1), lingual (i2) and labial (i3) views. **j** Right m2 (NHMW 2013/0004/0009) in occlusal (j1), lingual (j2) and labial (j3) views. **k** left m3 (NHMW 2013/0004/0001b) in occlusal (k1), lingual (k2) and labial (k3) views. Scale bar equals 1 cm

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Table 1 Measurements (in mm) of cheek teeth of *Brachypotherium brachypus*, Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina)

Tooth	Inventory number	L	W
P1	NHMW 2013/0003/0011	26.0	21.1
P4	NHMW 2013/0004/0007	43.7	60.5
M2	NHMW 2013/0004/0006	58.3	63.3
M3	NHMW 2013/0004/0005	51.8	57.7
p3	NHMW 2013/0003/0004	33.8	22.3
p4	NHMW 2013/0004/0002	42.8	32.9
m1	NHMW 2013/0004/0003	46.5	34.9
m1	NHMW 2013/0004/0001a	46.5	33.5
m2	NHMW 2013/0004/0004	53.6	34.7
m2	NHMW 2013/0004/0009	52.2	31.5
m3	NHMW 2013/0004/0001b	55.2	33.3

(NHMW 2013/0004/0001a); right m2's (NHMW 2013/0004/0004, NHMW 2013/0004/0009); left m3 (NHMW 2013/0004/0001b).

Description: Basically the cheek teeth have neither enamel folding nor cement preserved. The enamel is wrinkled and arborescent at the top of the crown. The crowns are low and the roots are joined.

The P1 NHMW 2013/0003/0011 is one-rooted, with a very robust root, and is persistent in adult. It is drop-shaped in occlusal view, with a thin, interrupted and posterolingually oriented protoloph as well as a faint crista and a thick and transverse metaloph. The roughly convex ectoloph does not bear any parastylar groove, paracone fold or labial cingulum. A sharp anterolingual cingulum is present, closing the lingual valley but reduced at the level of the protocone. The P4 NHMW 2013/0004/0007 is rectangular, wider than long and molariform (sensu Heissig 1969) with complete and parallel protoloph and metaloph as well as posterolingually oriented protocone and metacone, lacking any constriction. The labial cingulum is absent, whereas the lingual cingulum is strongly developed and continuous. The crochet is forked and the crista is bifid but they do not form a medifossette. The antecrochet is lacking. The postfossette is narrow and deep, but the median valley is deeper. In occlusal view, the protoloph is straight, the median valley S-shaped, the metaloph V-shaped and the ectoloph roughly straight except for a developed paracone fold.

The upper molars are lacking labial cingulum. The antecrochet and the crochet are present and simple, the crochet being more developed. The protocone is weakly constricted. There is neither medifossette nor cristella or hypocone constriction. Crista is very weak in M2 NHMW 2013/0004/0006, but well developed in M3 NHMW 2013/0004/0005. The lingual cingulum is strong and generally continuous, only reduced at the level of the hypocone of the M2 NHMW 2013/0004/0006. On the latter, the metaloph is long, the postfossette narrow and deep, the

median valley deeper and the ectoloph nearly concave. It bears a sagittal parastyle, a long metastyle, a weakly developed paracone fold, a weak mesostyle but no metacone fold. The protoloph is transverse on the M3 NHMW 2013/0004/0005, the ectoloph and the metaloph are fused into an ectometaloph and it bears a thick spur-shaped posterior cingulum near the lingual side. In occlusal view, the outline is roughly triangular with a narrow posterior side, corresponding to the remnant metaloph.

The lower cheek teeth are low-crowned but the openings of the lingual valleys are high. The labial cingulum is always weakly developed and reduced at the base of the trigonid, except on the m3 where it is roughly continuous. Likewise, the lingual cingulum is reduced, forming a short ridge, stronger on premolars than on molars and located below the opening of the anterior valley. The ectolophid groove is very shallow and vanishing before the neck. Only the p3 NHMW 2013/0003/0004 displays an ectolophid groove slightly more developed in the upper half of the crown. Lingual cusps are never constricted but lingually flattened. The trigonid is rather rounded and right-angled, with a rather short paralophid in occlusal view. The lingual valleys are generally V-shaped in lingual view, the anterior one being narrower and shallower. Only the m3 NHMW 2013/0004/0001b displays a lingual opening of the posterior valley in between V- and U-shaped. Lower premolars have transversely oriented lophids and wide hypolophids compared to trigonids. The p3 NHMW 2013/0003/0004 bears a clear anterior contact facet for p2 and a slight vertical external roughness at the base of the trigonid. On lower molars, the hypolophid is very oblique and there is no lingual groove on the entoconid.

Remarks: Dimensions and typical dental features, such as the presence of an antecrochet and of a constricted protocone on upper molars (Cerdeño 1993; Cerdeño and Nieto 1995; Antoine et al. 2003, 2010), point to a large-sized rhinocerotid. Among them, three species are known in the MN4-MN5 biozones in Europe (Cerdeño and Nieto 1995; Heissig 1999): the teleoceratines *Brachypotherium brachypus* (Lartet, 1837), *Diaceratherium aurelianense* (Nouel, 1866) and *Prosantorhinus douvillei* (Osborn, 1900, including *Gaindatherium (Iberotherium) rexmanueli* Antunes and Ginsburg, 1983, according to Heissig 2017).

Diaceratherium aurelianense differs by slightly smaller dimensions, the absence of crista in upper cheek teeth, the presence of an antecrochet and of a constriction of the protocone in P2–4, a developed external groove and a rounded trigonid in lower cheek teeth as well as the absence of labial cingulum in lower premolars (Antunes and Ginsburg 1983, Boada Saña 2008). *Prosantorhinus douvillei* is of smaller size and differs by distinct roots in cheek teeth, the absence of crista and the presence of antecrochet in P3–4 as well as the strong reduction of lingual cingulum in upper molars (Cerdeño 1996a, Heissig, 2017, Antoine et al. in press).

Following Guérin (1980), Cerdeño (1993), Heissig (1972a, 2012) and Koufos and Kostopoulos (2013), the referred specimens display the characteristics of *Brachypotherium*, such as large dimensions, brachyodont cheek teeth, developed paracone fold, somewhat flattened ectoloph profile and strong lingual cingulum on the upper molars as well as a shallow and smooth ectolophid groove in lower cheek teeth. Moreover, the referred specimens share with *B. brachypus* numerous features such as a continuous lingual cingulum, the presence of a crochet and a crista, and the absence of an antecrochet and of protocone constriction in P3–4, a developed crochet, a constricted protocone and a crista that can be present in upper molars, a visible mesostyle in M2, a triangular M3, and a V-shaped opening of the lingual valleys in p3–4. Though the dental remains are slightly smaller than typical *B. brachypus*, they lie within the range size of the smaller specimens described in literature (e.g. Guérin 1980; Cerdeño 1993; Codrea 2000; Koufos and Kostopoulos 2013). Accordingly, the dimensions and the set of above-mentioned characters permit to assign with confidence the reported specimens to *B. brachypus*.

Subfamily Rhinocerotinae Gray, 1821
Subtribe Rhinocerotina Gray, 1821
Genus *Lartetotherium* Ginsburg, 1974

Type and only species: *Rhinoceros sansaniensis* Lartet in Laurillard, 1848.

Lartetotherium sansaniense (Lartet in Laurillard, 1848)
Fig. 2, Table 2

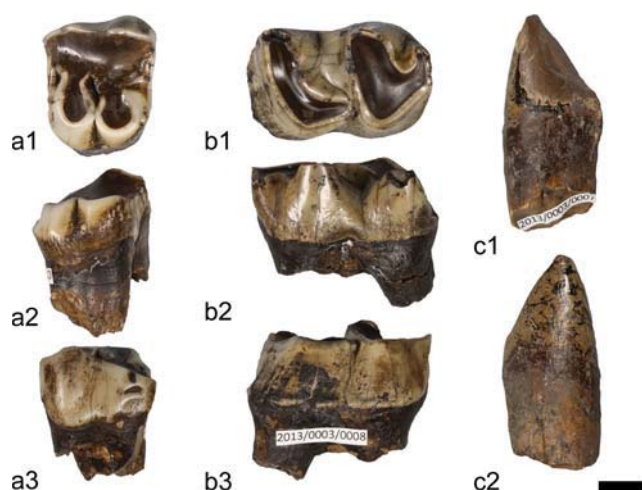**Type material:** Skull and mandible (MNHN Sa 6478).

Fig. 2 *Lartetotherium sansaniense* from Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina). **a** Left P2 (NHMW 2013/0003/0010) in occlusal (a1), lingual (a2) and labial (a3) views. **b** Right m3 (NHMW 2013/0003/0008) in occlusal (b1), lingual (b2) and labial (b3) views. **c** Left i2 (NHMW 2013/0003/0007) in posterior (c1) and anterior (c2) views. Scale bar equals 1 cm

Table 2 Measurements (in mm) of cheek teeth of *Lartetotherium sansaniense*, Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina)

Tooth	Inventory number	L	W
P2	NHMW 2013/0003/0010	25.2	30.1
m3	NHMW 2013/0003/0008	39.3	25.1

Type locality: Sansan, Gers, France, middle Miocene (MN6).
Occurrence: late early Miocene to early late Miocene (MN4b–MN9) of Europe (see Heissig 1999, 2012).
Referred material: Left i2 (NHMW 2013/0003/0007); left P2 (NHMW 2013/0003/0010); right m3 (NHMW 2013/0003/0008).
Description: The i2 NHMW 2013/0003/0007 is tusk-like with a robust and probable straight root. The crown is rather short (APD = 22.6, TD = 15.0, H = 27.3) and of triangular shape, with an acute anterior edge and a rounded posterior border in cross section, and displays an important wear facet in its anterior side.

The cheek teeth are low-crowned and lacking any cement. The P2 NHMW 2013/0003/0010 has joined roots and a worn, rounded and polished crown. There are no enamel foldings. The tooth is molariform with lingual cusps (protocone and hypocone) of equal development that are well separated in the upper part of the crown but in contact at the base. The ectoloph displays a wide paracone fold and a weaker metacone fold. The protoloph and metaloph are transverse, parallel and not constricted. There is no labial and lingual cingulum, but very weak anterolingual roughnesses at the base of the protocone are visible. The postfossette seems rather long.

The m3 NHMW 2013/0003/0008 displays an enamel thinly wrinkled vertically and even squared because of horizontal striae. The labial and lingual cingula are completely lacking, whereas the anterior and posterior ones are strongly reduced. In occlusal view, the lophids are oriented transversely, the paralophid is well developed and the trigonid is angular with an acute dihedron. The openings of the lingual valleys are low, narrow and V-shaped, the posterior one being slightly wider but about of similar depth. The ectolophid groove is developed, vanishing before the neck, and points upward and frontward in labial view. The metaconid and the entoconid are not constricted and bear no lingual groove.

Remarks: From their dimensions, the referred material can be assigned to a small-sized rhinocerotid. From their morphological characters, it differs from Elasmotheriinae by the absence of cement in cheek teeth and of a lingual wall in P2 (Antoine 2002). According to Heissig (1972b), Guérin (1980) and Antoine et al. (2003), the small-sized Rhinocerotinae from the middle Miocene of Europe displaying roughly similar dimensions are restricted to *Prosantorhinus germanicus* (Wang, 1928), *Alicornops simorrense* (Lartet in Laurillard, 1848),

Lartetotherium sansaniense (Lartet in Laurillard, 1848), *Dicerorhinus steinheimensis* (Jäger, 1839) and some *Plesiaceratherium* species. However, the referred material clearly differs from *P. germanicus* and *A. simorrense* by the complete absence of labial and lingual cingula in cheek teeth as well as by a P2 with lingual cusps of equal development and an ectoloph bearing both paracone and metacone folds (Guérin 1980; Cerdeño 1996a; Cerdeño and Sánchez 2000; Antoine et al. 2003). Additionally, *A. simorrense*, like other Aceratheriini, possesses lower cheek teeth with shorter paralophids (Zervanová et al. 2013; Aiglstorfer et al. 2014b). Within genus *Plesiaceratherium*, the species *P. fahlbuschi* (Heissig, 1972b), *P. platyodon* (Mermier, 1895) and *P. balkanicum* sp. nov. have a similar size to the referred specimens (Tables 2 and 3). However, they differ by a P2 bearing a lingual cingulum and lacking a metacone fold, and by a shorter paralophid of lower cheek teeth as well as cingula always present that can be reduced or continuous (Heissig 1972b; Antunes and Ginsburg 1983). Concerning *D. steinheimensis* (Jaeger, 1839), very little data is available in the literature, and although this taxon is regularly cited (e.g. Osborn 1900; Roger 1900; Santafe Llopis 1978; Guérin 1980; Heissig 1984; Pickford 2013), it remains badly known and uncommon in the fossil record. However, according to Guérin (1980), the referred specimens share with *D. steinheimensis* a strongly reduced cingulum, but they differ by slightly larger dimensions, a P2 with a protoloph joined to the ectoloph and a roughly similar depth of the openings of the two lingual valleys of m3.

Compared to *L. sansaniensis*, the specimens are very similar in size and very close in morphology, notably by the triangular section of the i2, the absence of labial and lingual cingula in cheek teeth, the presence of a low lingual bridge joining the protocone to the hypocone in P2 and a m3 with anterior and posterior cingula and revealing a developed external groove vanishing before the neck (Heissig 1972b, 2012; Guérin 1980). To sum up, all the metric and morphological features observed in the available material are consistent with those of the hypodigm of *L. sansaniense* from Sansan (Heissig 2012).

Subfamily Rhinocerotinae Gray, 1821
Aceratheres *sensu lato*
Genus *Plesiaceratherium* Young, 1937

Type species: *Plesiaceratherium gracile* Young, 1937
Other species of the genus: According to Yan and Heissig (1986), Antoine and Becker (2013) and Lu et al. (2016), the genus comprises *Plesiaceratherium platyodon* (Mermier 1895), *Plesiaceratherium aquitanicum* (Répelin 1917), *Plesiaceratherium mirallesi* (Crusafont, Villalta and Truyols 1955), *Plesiaceratherium fahlbuschi* (Heissig 1972b) and *Plesiaceratherium lumiarense* (Antunes and Ginsburg 1983). Moreover, Antoine et al. (2010) indicate the presence of *Plesiaceratherium naricum* (Pilgrim, 1910) in the earliest Miocene of Pakistan.
Emended diagnosis: Modified from Yan and Heissig (1986). Medium-sized to large aceratheriine; limb bones more slender than in other Miocene aceratheriine genera; upper incisor I1 medium-sized (sagittal length of the crown about 30 mm); lingual cingulum always present and continuous on upper premolars, medifossette often present on P2–4 and protocone constriction usually absent on P3 and P4.

Table 3 Measurements (in mm) of cheek teeth of *Plesiaceratherium balkanicum* sp. nov., Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina) and comparison with other *Plesiaceratherium* species [after pers. obs. of the type series (MHNM N94, MHNM N105) for *P. aquitanicum*; Yan and Heissig (1986), tab. 3–4: for *P. gracile*, *P. fahlbuschi*, *P. platyodon* and *P. mirallesi*; Wang (1928: tab. p. 190) for D2 of *P. mirallesi*; Antunes and Ginsburg (1983: tab. p. 92) and Ginsburg and Bulot (1984: p. 354) for *P. lumiarense*]. The measurements are presented as length/width

Tooth	*P. balkanicum* type series	*P. aquitanicum* type series	*P. gracile*	*P. fahlbuschi*	*P. platyodon*	*P. mirallesi*	*P. lumiarense* type series
LP2–4	89	99	110	87	91	102	
D1	20/13						
D2	33/30					31/30	33/33
P1	21/20				20/18	23/20	23/19
P2	29/37	29/36	31/36	24/33	30/35	29/36	29/35
P3	34/43	34/46	34/42	29/39	29/43	35/45	35/44
P4	35/47	36/51	37/43	32/43	34/46	38/49	38/49
M1	34/41	–/–	46/48	32/44	36/43	42/47	45/49
M2	38/45	47/53	48/50	36/47	38/46	46/51	45/50
M3	33–36/37–40	42/49	43/45	41/42	37/42	42/45	38/49
m2	36/24	–/–	40/26	38/24	38/24	46/24	42/29
m3	39/24	–/–	43/27	39/23	40/23	47/25	43/27

Plesiaceratherium balkanicum sp. nov.
Fig. 3, Tables 3–5

Holotype: Complete left premolars row with D1 (NHMW 2013/0003/0006d), P2 (NHMW 2013/0003/0006c), P3 (NHMW 2013/0003/0006b) and P4 (NHMW 2013/0003/0006a) from the same individual.

Paratype: Left M2 (NHMW 2013/0003/0002a) and M3 (NHMW 2013/0003/0002b), and left m2 (NHMW 2013/0003/0001a) and m3 (NHMW 2013/0003/0001b) possibly all from the same individual; right lower i2 (NHMW 2013/0004/0010); right upper D1 and D2 on maxillary fragment (NHMW 2013/0004/0008).

Type locality: Gračanica, Bugojno Basin, Bosnia-Herzegovina, early middle Miocene (MN5).

Derivation of name: From the Balkan region, where the new material belonging to this species was discovered.

Occurrence: Only known in the early middle Miocene (MN5) of the type locality Gračanica.

Referred material: Heavily worn right M1 (NHMW 2013/0003/0009), right M3 (NHMW 2013/0003/0005).
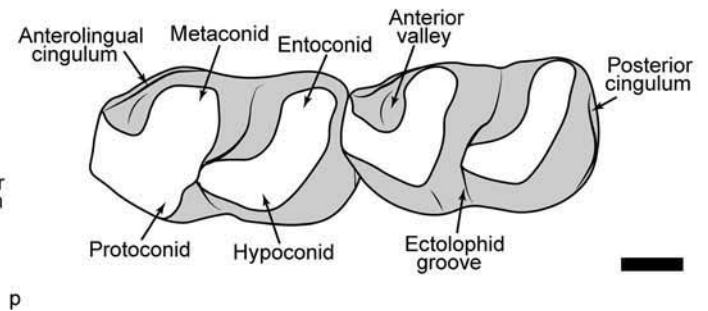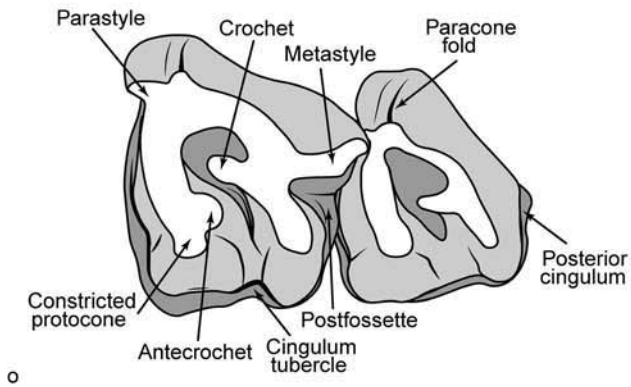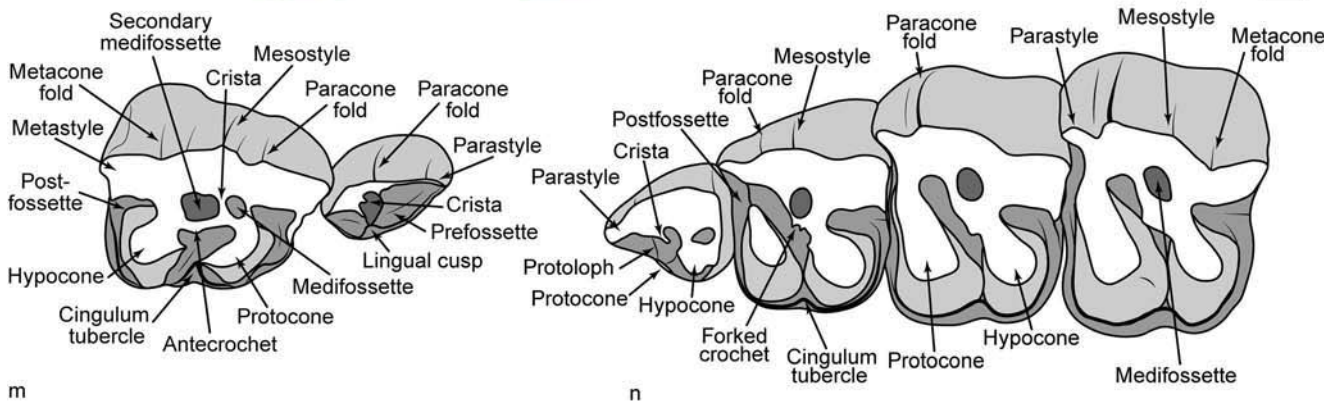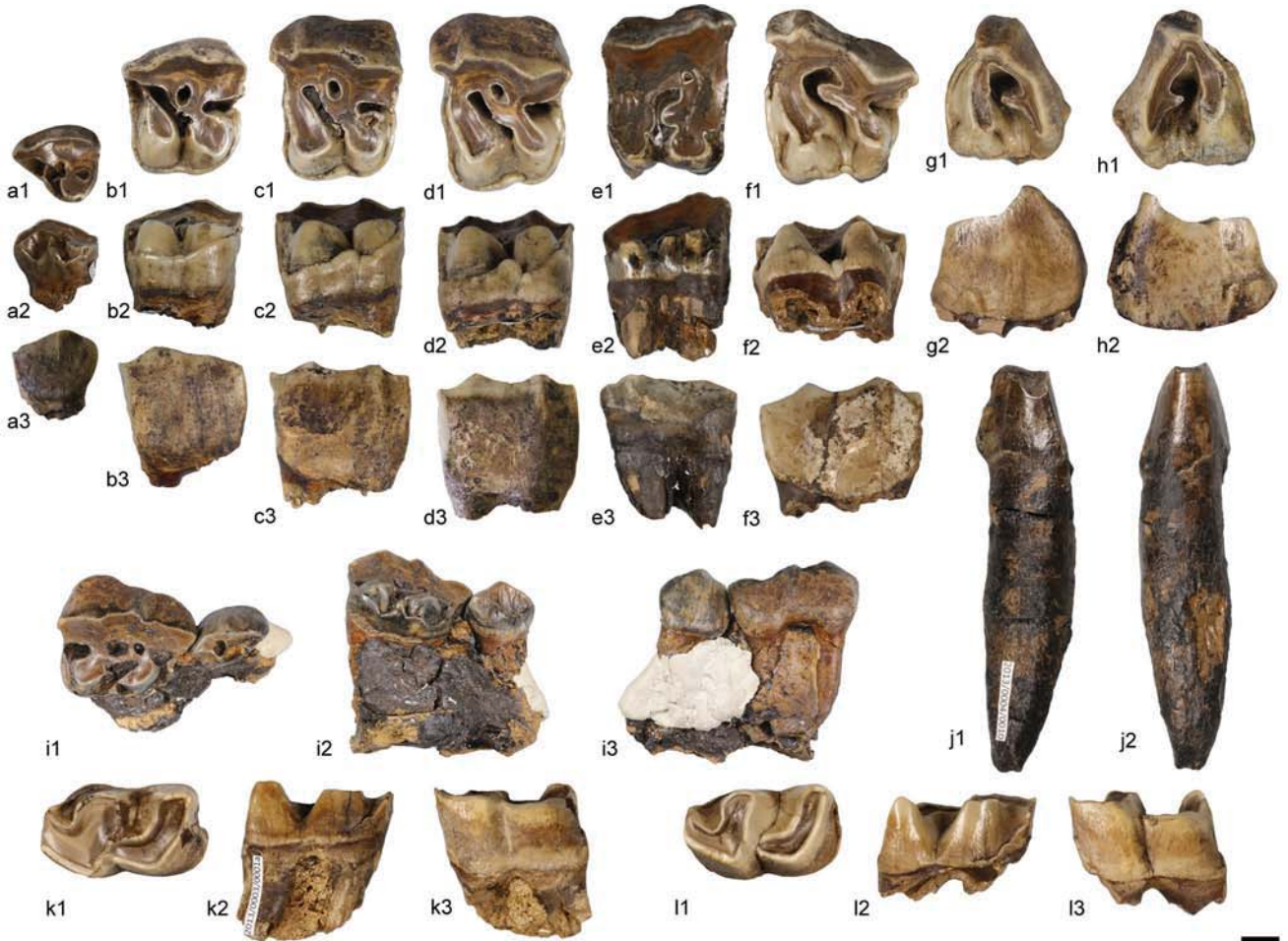
Diagnosis: Small-sized species of the genus characterised by separated protocone and hypocone on upper premolars, as well as the presence of a large and deep medifossette on P2–4. Differs from *P. gracile* by a smaller size, by a reduction of lingual cingulum of upper molars, the absence of incision of the lingual cingulum on upper premolars, the absence of a bridge connecting protocone and hypocone on P2–4, the absence of a mesostyle on P3 and the absence of labial cingulum on lower molars. Differs from *P. aquitanicum* by a smaller size, by the absence of crista on upper molars, by stepped lingual cingulum of upper premolars and by separated protocone and hypocone on P2. Differs from *P. lumiarense* and *P. fahlbuschi* by the junction between crista and crochet on upper premolars forming a medifossette and by the isolated protocone on P2. Further differs from *P. lumiarense* by the presence of a strong lingual cusp (hypocone) on P1. Further differs from *P. fahlbuschi* by the less transversally developed hypocone on P3–4. Differs from *P. platyodon* by the absence of labial cingulum and by the separation of protocone and hypocone on upper premolars, the well-developed crochet on upper molars, as well as the absence of labial cingulum on lower molars. Differs from *P. mirallesi* by a separated protoloph and ectoloph on P2, labial cingulum that is always absent on upper premolars and a triangular M3 in occlusal view.

Description: All teeth except the M1 are not very worn. Cement is present in rather small quantity on upper cheek teeth and possibly on the ectolophid of lower cheek teeth as well. Teeth crown is low. Roots are not preserved on upper teeth.

D1 is very simple and elongated. It is one-rooted, and the root is short. Protocone and hypocone are fused since there is only one small lingual cusp that erects from the lingual cingulum. Metaloph and protoloph are very weak and join lingually, forming a closed medifossette-like structure. There is a small crista between the two lophs. The paracone fold is strong, and the parastyle is weak. Postfossette and prefossette are closed by cingulum and there is no labial cingulum. D2 is much larger than D1 and longer than wide. Lingual cingulum is continuous and waved, with a strong lingual tubercle at the level of the median valley. Protocone and hypocone are strong, separated and posterolingually elongated. There is a crista and antecrochet that are connected and create a medifossette. The crochet is long and joins the medifossette, creating a secondary posterior medifossette. Postfossette is long and deep. Parastyle and metastyle are long. The mesostyle is salient, but paracone and metacone folds are weak. There is also a weak secondary fold between the metacone fold and the mesostyle. Labial cingulum is very faint and discontinuous. Roots are joined lingually but labially separated.

Labial cingulum is absent on upper premolars. Anterolingual cingulum is present on P1. It differs from D1 by its greater width, thicker enamel, stronger root and a much stronger hypocone as well as the presence of a protocone. Labially, the root may divide into two but this part is very incomplete. The hypocone is strong but the protocone is very weak. The crista is present and the protoloph joins the ectoloph but it is very thin and low. There is a small bridge connecting protocone and hypocone. The prefossette is triangular and the postfossette is small. We believe this tooth is a true P1, and not a D1 because it is not very worn compared to the other teeth of the row, whereas it should have been very worn if it was a D1. According to Antoine (2002), P1 can be distinguished from D1 by its stronger size, especially the width, and stronger root, which is consistent with our observations. Paracone fold is present on P3–4 but the metacone fold is only present on P4, though it is very weak. There is also a weak mesostyle on P2 and P4. Crochet is present on P2–4 and it is multiple on P2 but simple on P3–4. Metaloph is not constricted. The lingual cingulum is strong and continuous on P2–4, with a marked tubercle at the opening of the lingual valley, where it is much higher than under protocone and hypocone. It is very high posteriorly and low anteriorly, but well above the neck. The postfossette is long and narrow and it is very deep. Antecrochet is only present on P4, but weak. Protocone and hypocone of P2 are separated. Its metaloph is directed posterolingually and protocone is as strong as the hypocone. Protoloph is present but interrupted and does not join the ectoloph on P2. Medifossette is always present on P2–4, formed by the junction between crista and crochet. Protocone is not constricted on P3–4 though there are superficial grooves on anterior and posterior sides. Protocone and hypocone are separated on P3–4 and metaloph is directed very posterolingually. The hypocone of P3–4 is not very developed transversally, the outline of these teeth is not square. Protoloph is joined to the ectoloph on P3 and there is no pseudometaloph. Metaloph of P4 is continuous.

Secondary medifossette
Metacone fold
Metastyle
Crista
Mesostyle
Paracone fold
Paracone fold
Parastyle
Post-fossette
Crista
Prefossette
Lingual cusp
Hypocone
Medifossette
Cingulum tubercle
Antecrochet
Protocone

m

Paracone fold
Mesostyle
Paracone fold
Parastyle
Mesostyle
Metacone fold
Postfossette
Crista
Parastyle
Protoloph
Protocone
Hypocone
Forked crochet
Cingulum tubercle
Protocone
Hypocone
Medifossette

n

Parastyle
Crochet
Metastyle
Paracone fold
Constricted protocone
Antecrochet
Cingulum tubercle
Postfossette
Posterior cingulum

o

Anterolingual cingulum
Metaconid
Entoconid
Anterior valley
Posterior cingulum
Protoconid
Hypoconid
Ectolophid groove

p

8

◀ **Fig. 3** *Plesiaceratherium balkanicum* sp. nov. from Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina). **a–d** Holotype, left premolars row with D1 (NHMW 2013/0003/0006d) in occlusal (**a1**), lingual (**a2**) and labial (**a3**) views, P2 (NHMW 2013/0003/0006c) in occlusal (**b1**), lingual (**b2**) and labial (**b3**) views, P3 (NHMW 2013/0003/0006b) in occlusal (**c1**), lingual (**c2**) and labial (**c3**) views, P4 (NHMW 2013/0003/0006a) in occlusal (**d1**), lingual (**d2**) and labial (**d3**) views. **e** Right M1 (NHMW 2013/0003/0009) in occlusal (**e1**), lingual (**e2**) and labial (**e3**) views. **f–g** and **k–l** Paratype, left dental series possibly from the same individual with M2 (NHMW 2013/0003/0002a) in occlusal (**f1**), lingual (**f2**) and labial (**f3**) views, M3 (NHMW 2013/0003/0002b) in occlusal (**g1**) and labial (**g2**) views, m2 (NHMW 2013/0003/0001a) in occlusal (**k1**), lingual (**k2**) and labial (**k3**) views, m3 (NHMW 2013/0003/0001b) in occlusal (l1), lingual (l2) and labial (l3) views. **i–j** Paratype, right upper D1 and D2 on maxillary fragment (NHMW 2013/0004/0008) in occlusal (**i1**), lingual (**i2**) and labial (**i3**) views, right lower i2 (NHMW 2013/0004/0010) in posterior (**j1**) and anterior (**j2**) views. **h** Right M3 (NHMW 2013/0003/0005) in occlusal (**h1**) and labial (**h2**) views. **m** Paratype, right upper D1 and D2 (NHMW 2013/0004/0008) in occlusal view. **n** Holotype, left premolars row with D1 (NHMW 2013/0003/0006d), P2 (NHMW 2013/0003/0006c), P3 (NHMW 2013/0003/0006b) and P4 (NHMW 2013/0003/0006a) in occlusal view. **o** Paratype, left M2 (NHMW 2013/0003/0002a) and M3 (NHMW 2013/0003/0002b) in occlusal view. **p** Paratype, left m2 (NHMW 2013/0003/0001a) and m3 (NHMW 2013/0003/0001b) in occlusal view. Scale bar equals 1 cm

The labial cingulum is mostly absent on M1–2, there is only a very weak ridge under the metacone. Antecrochet and crochet are present on upper molars. The base of the antecrochet is lingually extended to the entrance of the median valley in NHMW 2013/0003/0002a and b, separating the lingual valley into two. Crista, cristella and medifossette are always absent. Lingual cingulum is weak and only present in the opening of the lingual valleys of M2 and one M3 (NHMW 2013/0003/0002b). The protocone is constricted. The hypocone is anteriorly constricted on M1–2. Paracone fold is strong and metacone fold is absent. There is a mesostyle on M1 only. Metastyle of M2 is long and its metaloph is short. The posterior part of the ectoloph of M2 is concave. Posterior cingulum of M2 is high but notched under the postfossette. The postfossette is deep and narrow. Metaloph is not constricted on M2 and antecrochet is separated from the hypocone on upper molars. There is a very weak groove under the protocone of M2, with faint cingulum at its base. Ectoloph and metaloph are fused on the M3 and its outline is quadrangular. Protocone is constricted and trefoil-shaped. The protoloph is transverse and there is no posterior groove on the ectometaloph. Posterior cingulum is present.

The right lower i2 NHMW 2013/0004/0010 is the only known anterior teeth (APD = 26.0, TD = 15.0, H > 27.3, L root = 80.0). The root is almost complete but the crown is incomplete. The root is straight, short and oval in cross section. The crown is well differentiated from the root by the presence of an anterior projection. There is no wear facet on the mesial side of the crown, which may be explained by the reduction of contact with upper I1, as in most plesiacratheres (Yan and Heissig 1986). The crown has an almost triangular cross section: the posterior side is flat, with a marked mesial ridge, the mesial side is flattened and the distal side is convex. There is an acute anterior ridge.

The ectolophid groove of m2–3 is developed, but not acute, and does not vanish before the neck. The trigonid is angular and acute. Metaconid and entoconid are not constricted. The hypolophid is oblique and there is no lingual groove on the entoconid. Posterior valley is low, almost at the same level as the neck, and V-shaped. Anterolingual cingulum is well developed, continuous and extends up to the base of metaconid, but there is no cingulum in the posterior valley or under the entoconid. Labial cingulum is completely absent except in the most anterior part.

Remarks: Within the small- to medium-sized rhinocerotids from the early middle Miocene (Table 4), this new material differs from *Alicornops simorrense* by the reduction of labial and lingual cingulum of lower molars, the presence of a medifossette on upper premolars and a longer crochet on upper molars (Ginsburg and Guérin 1979; Cerdeño and Sánchez 2000; Heissig 2012). It also differs from *Lartetotherium sansaniense* by the absence of metacone fold on upper premolars and the presence of strong lingual cingulum, the presence of crista, crochet and medifossette on P2–4 as well as a longer postfossette, the presence of crochet and protocone constriction on upper molars and the presence of anterolingual cingulum on lower molars (Antunes and Ginsburg 1983; Heissig 2012). It differs from *Hoploaceratherium tetradactylum* by a larger and deeper medifossette (when present) on P2–4, a crista that is never duplicated and uninterrupted cingulum on upper premolars, by the absence of labial cingulum on upper premolars, the absence of medifossette on upper molars, the absence of a posterior groove on the ectoloph of M3 and the absence of labial cingulum in the talonid basin of lower molars (Osborn 1900; Heissig 2012). It differs from the genus *Prosantorhinus* [including species *P. douvillei*, *P. germanicus*, *P. laubei*, *P. aurelianensis* and possibly *P. tagicus* according to Heissig (2017)] by unreduced premolars row compared to molars row, the presence of medifossette on upper premolars and an upper M3 with quadrangular outline and developed posterior cingulum (Heissig 2017). Within Elasmotheriinae, it differs from *Hispanotherium beonense* by the presence of a continuous protoloph on P3–4, by an unconstricted hypocone on P4 and the presence of lingual cingulum and of a medifossette on upper premolars (Antoine 1997, 2002). It also differs from *Hispanotherium matritense* by the absence of cement in valleys and fossettes of cheek teeth, less developed enamel foldings, separated protocone and hypocone on upper premolars and less constricted protocone of upper molars (Antunes and Ginsburg 1983; Cerdeño 1992a). Finally, it differs from

Table 4 Measurements (in mm) of cheek teeth of *Hoploaceratherium tetradactylum* and *Lartetotherium sansaniense* based on Heissig (2012: tab. 4, 6, 15, 17), of *Alicornops simorrense* based on Yan and Heissig (1986: tab. 3, 4) and on Heissig (2012: tab. 8) for D1 and of *Prosantorhinus douvillei* based on Sach and Heizmann (2001: tab. 10, 12). The measurements are presented as length/width, those between parentheses are averages based on several specimens

Tooth	*Hoploaceratherium tetradactylum* lectotype	*Hoploaceratherium tetradactylum* minimum dimensions	*Lartetotherium sansaniense*	*Alicornops simorrense*	*Prosantorhinus douvillei*
LP2–4	104	95	90	92	
D1	25/20	21/20	(21/19)	(21/18)	(21/1/7)
P2	31/41	28/35	(25/33)	25/33	(27/34)
P3	34/49 1	30/43	(32/40)	35/38	(33/40)
P4	40/54	36/48	(35/45)	36/42	(38/47)
M1	45/53	38/48	(36/44)	36/45	(48/52)
M2	51/55	43/49	(41/49)	38/45	(52/54)
M3		40/40	(38/45)	39/42	(44/48)
m2		39/26	(40/26)	38/24	(42/26)
m3		39/25	(41/25)	42/23	(44/24)

Dicerorhinus steinheimensis by the absence of metacone fold on upper premolars, the presence of medifossette and crista on P2 and the presence of antecrochet on upper molars (Santafe Llopis 1978).

However, it shares with the genus *Plesiaceratherium* an almost straight i2, the absence of protocone constriction on P3–4, a posterolingually directed metaloph on P2–3 and the presence of continuous lingual cingulum on upper premolars, as well as the absence of crista and medifossette and the presence of a crochet on upper molars. It also shares with most species of the genus the presence of a medifossette on P2–4. Therefore, based on this combination of characters, we refer this new material to the genus *Plesiaceratherium*. It can be distinguished from other species of the genus by the complete absence of labial cingulum on upper premolars. According to Lu et al. (2016), labial cingulum is always present on the upper premolars and is a synapomorphy of this genus, so they included this character in the emended diagnosis. Based on our observations, labial cingulum seems to be also completely lacking in at least some specimens of *P. lumiarense* (including holotype) and *P. platyodon* (e.g. Antunes and Ginsburg 1983: pl. III fig. 11c, pl. IV fig. 4a and pl. V fig. 2a). Therefore, this character may be quite labile and may not be a diagnostic character. However, strong continuous lingual cingulum is always observed in upper premolars of *Plesiaceratherium*. We emended the diagnosis of the genus to reflect this. Furthermore, there also seems to be some mismatches concerning the characters coding for *P. mirallesi* in the data matrix of Lu et al. (2016). Though they did not make direct observation of the material for this taxon, there are many discrepancies compared to the characters directly observed on material from Montréal-du-Gers and illustrated by Antoine (2002). This should explain the position of *P. mirallesi* far away from the other species of the genus retrieved by Lu et al. (2016). Therefore, we still consider the species *P. mirallesi* as belonging to the genus *Plesiaceratherium* indeed. Finally, the new material is clearly differentiated from all known species of the genus by a unique combination of characters among the genus: separated protoloph and ectoloph on P2, separated protocone and hypocone on P2–4, stepped lingual cingulum on P3–4, strong crochet and absence of crista on M2–3 and quadrangular M3 (see Table 5). Based on this, we attribute this material to a new species, *P. balkanicum* sp. nov.

Subfamily Elasmotheriinae Bonaparte, 1845
Tribe Elasmotheriini Bonaparte, 1845
Subtribe Elasmotheriina Bonaparte, 1845
Genus *Hispanotherium* Crusafont and Villalta, 1947

Type species: *Rhinoceros matritense* Lartet in Prado 1864, by original designation.
Other referred species: According to the phylogenetic analysis of Antoine (2003) and Pandolfi (2015), the generic assignation of *Hispanotherium corcolense* Antoine, Alférez and Iñigo, 2002 from Spain (late early Miocene, MN4a), *Hispanotherium beonense* (Antoine, 1997) from France (late early to middle Miocene, MN4b–MN5) and *Hispanotherium grimmi* Heissig, 1974 from Turkey (middle Miocene, MN6–MN8) makes *Hispanotherium sensu lato* paraphyletic.

Hispanotherium cf. *matritense*
Fig. 4, Table 6

Occurrence: Only known in Gračanica (this study).
Referred material: Fragmented left hemi mandible with p2–m3 (NHMW 2013/0003/0003).
Description: The fragmented left mandible with p2–m3 (NHMW 2013/0003/0003) is only partly preserved. It is not

Table 5 Character comparisons of upper cheek teeth in species of the genus *Plesiaceratherium* (after Mermier 1895; Répelin 1917; Wang 1928; Young 1937; Heissig 1972b; Antunes and Ginsburg 1983; Ginsburg and Bulot 1984; Yan and Heissig 1986; Antoine 2002; pers. obs.)

Dental characters	*P. balkanicum* type series	*P. aquitanicum* type series	*P. gracile*	*P. fahlbuschi*	*P. platyodon*	*P. mirallesi*	*P. lumiarense*
P2: protoloph and ectoloph	separated	separated	connected	connected	?	connected	connected
P2–4: protocone and hypocone	separated	connected	connected	separated	connected	separated	mostly separated
P2–4: medifossette	always present	sometimes present	sometimes present	sometimes present	always present	sometimes present	sometimes present
P3–4: lingual cingulum	stepped	not stepped	incised	not stepped	incised	stepped	incised
M2–3: crochet	strong	strong	strong	strong	weak or absent	strong	strong
M2–3: crista	absent	present	present	absent	absent	absent	absent
M3: shape of the outline	quadrangular	triangular	?	quadrangular	triangular	triangular	quadrangular

possible to control the presence or absence of a d1/p1, the m1 is incomplete, the symphysis and the ramus are lacking, whereas the corpus is broken in two parts yielding few morphological features. The corpus is low (H at the level p2/3 = ca. 65.0), the *spatium retromolare* is shorter than the length of the m3, the *corpus* does not seem to display a *sulcus mylohyoideus* and a small *foramen mentale* is located in front of the p2, at the middle of the height of the corpus. The lower premolar series is short when compared to the molar series [(Lp3–4 = 50.7, Lm1–3 = 107.2; Ip/m = 0.496; sensu Antoine (2002)]. The crown is low and the cingula are completely lacking in lower cheek teeth. Cement can be observed either in thin layers on some parts of the crowns or in abundance in the lingual valleys and the ectolophid grooves. Lophids are oriented transversely in premolars and m3 while they are oriented rather obliquely on m2. The paralophid is generally well developed, except on p2, and the lingual valleys are low, the posterior one being significantly deeper than the anterior one in all lower cheek teeth. The ectolophid groove, V-shaped and developed until the neck, points upward and frontward in labial view. In premolars, the lingual opening of the posterior valley is narrow and V-shaped, but wider in molars. On p2, the paralophid is curved without constriction, the paraconid is developed and the posterior valley is lingually open. On molars, the trigonid is angular with a right dihedron in occlusal view. The metaconid and the entoconid are not constricted and bear no lingual groove.

Remarks: This material can be almost unambiguously referred to Elasmotheriinae by the presence of large quantities of cement and an acute trigonid in lower cheek teeth, which are diagnostic characters of this subfamily (Antoine 2002). It differs from Diceratheriini by V-shaped posterior valleys in lower premolars and by the absence of lingual cingulum in lower molars. It is referred to Elasmotheriini by the V-shaped ectolophid groove of lower cheek teeth and the unconstructed paralophid on p2. Within this tribe, four genera are recognised by Antoine (2002, 2003) in the late early to middle Miocene, although three of them are paraphyletic: *Hispanotherium* (*H. beonense*,

H. corcolense and *H. grimmi* included), *Caementodon*, *Procoelodonta* and *Huaqingtherium*.

Deng (2003) considered *Huaqingtherium lintungense*, the only species of the genus after Antoine (2003), as junior synonym of *Hispanotherium matritense*. However, Antoine (2003) pointed out a series of derived characters not shared by the European type material of *H. matritense*, validating *Huaqingtherium lintungense* as a species. Furthermore, the referred specimen NHMW 2013/0003/0003 from Gračanica differs from *H. lintungense* by a V-shaped anterior valley in lower molars and an unconstricted metaconid in lower premolars (Cerdeño 1996b). No lower teeth are known for *Procoelodonta mongoliense*, and they are very poorly known for *P. borissiaki*; therefore, material cannot be compared with these two taxa (Antoine 2003). However, it differs from *P. tekkaya* by an open posterior valley in p2 and the absence of mesial and distal cingulum on lower cheek teeth (Fortelius 1990). It differs from *Caementodon oettingenae* by a lower crown-height of lower cheek teeth and by the absence of anterior cingulum (Heissig 1972a; Antoine 2002: fig. 147A) and from *C. caucasicum* by an ectolophid groove developed until the neck on lower cheek teeth (Antoine 2002) as well as a less oblique hypolophid on m2 (Borissiak 1935: pl. I fig. 3). It is not possible to compare this material with *C. fangxianense* because lower cheek teeth are unknown from this taxon (Antoine 2003). Within genus *Hispanotherium*, the new material differs from *H. grimmi* by a much smaller size, a shorter talonid and the absence of posterior cingulum on m3 (Heissig 1974; pl. 2 fig. 13) as well as an acute trigonid of lower cheek teeth (Antoine et al. 2002: tab. 1). It differs from *H. corcolense* by smaller size, unconstricted metaconid on p3 and cingulum completely absent (Iñigo and Cerdeño 1997). It differs from *H. beonense* by a much smaller size, an unconstricted metaconid on p3–4 and the absence of anterior and posterior cingulum on lower cheek teeth (Antoine 1997). It shares with *H. matritense* a similar size and a very close morphology (presence of cement in large quantity, angular and acute
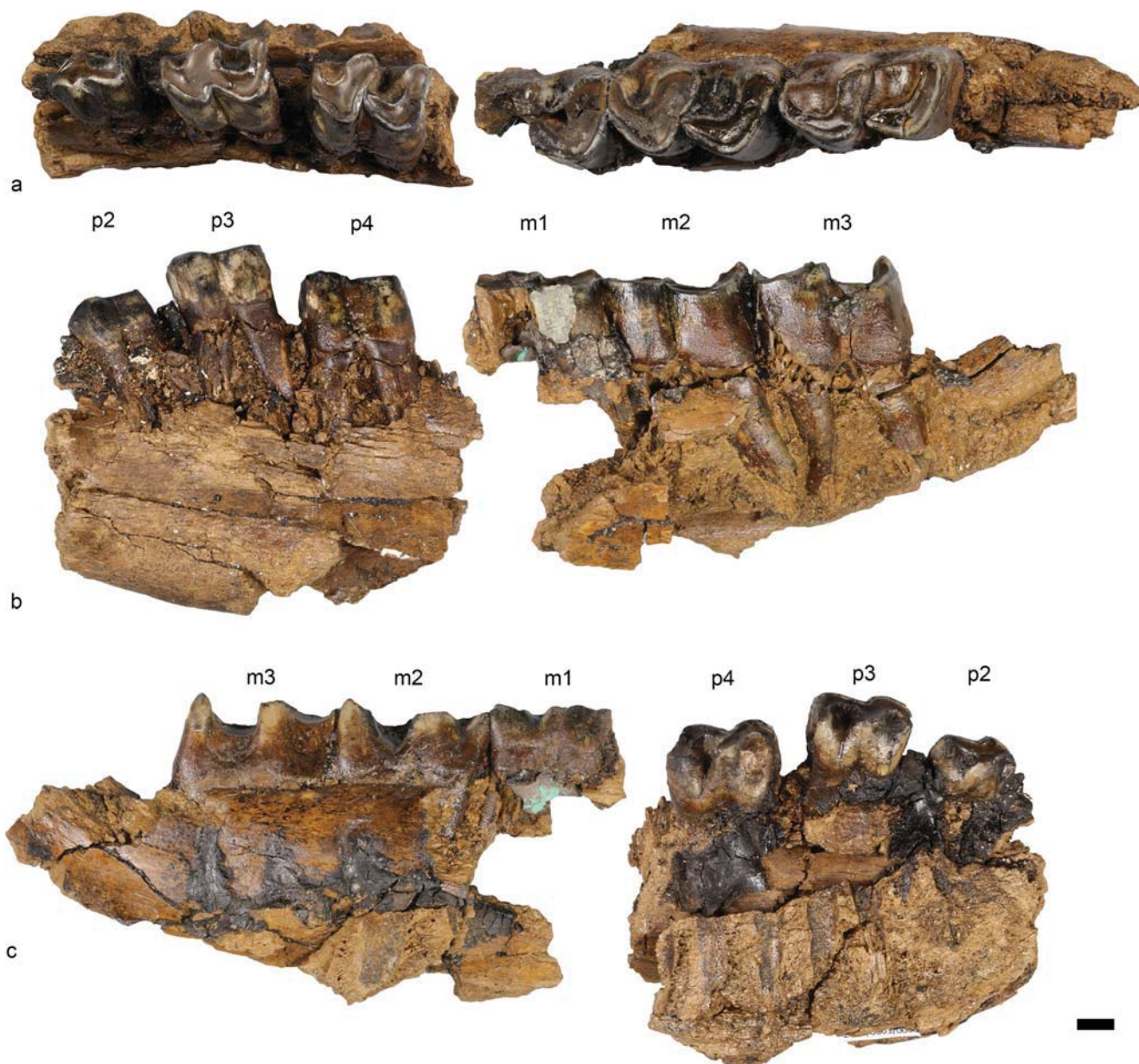
Fig. 4 *Hispanotherium* cf. *matritense* from Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina). Fragmented left hemi mandible with p2–m3 (NHMW 2013/0003/0003) in occlusal (**a**), lingual (**b**) and labial (**c**) views. Scale bar equals 1 cm

Table 6 Measurements (in mm) of cheek teeth of *Hispanotherium* cf. *matritense*, Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina)

Tooth	Inventory number	L	W
p2	NHMW 2013/0003/0003	19.7	13.1
p3	NHMW 2013/0003/0003	23.5	18.0
p4	NHMW 2013/0003/0003	25.8	19.3
m1	NHMW 2013/0003/0003	29.4	23.1
m2	NHMW 2013/0003/0003	36.9	23.8
m3	NHMW 2013/0003/0003	36.7	22.7

trigonid, V-shaped ectolophid groove and reduced premolars series compared to molar series). However, it differs from it by a shorter paralophid in lower molars (Antunes and Ginsburg 1983: pl. XII fig. 3, pl. XIII fig. 1 and pl. 15 fig. 5) though in some other referred specimens, paralophid length is similar (e.g. Cerdeño 1992a: pl. 1 fig. 1). Given the known variability of *H. matritense* (Iñigo and Cerdeño 1997) and that the incomplete material from Gračanica only encompasses poorly diagnostic lower dental material, it can only be tentatively referred to *H.* cf. *matritense*.
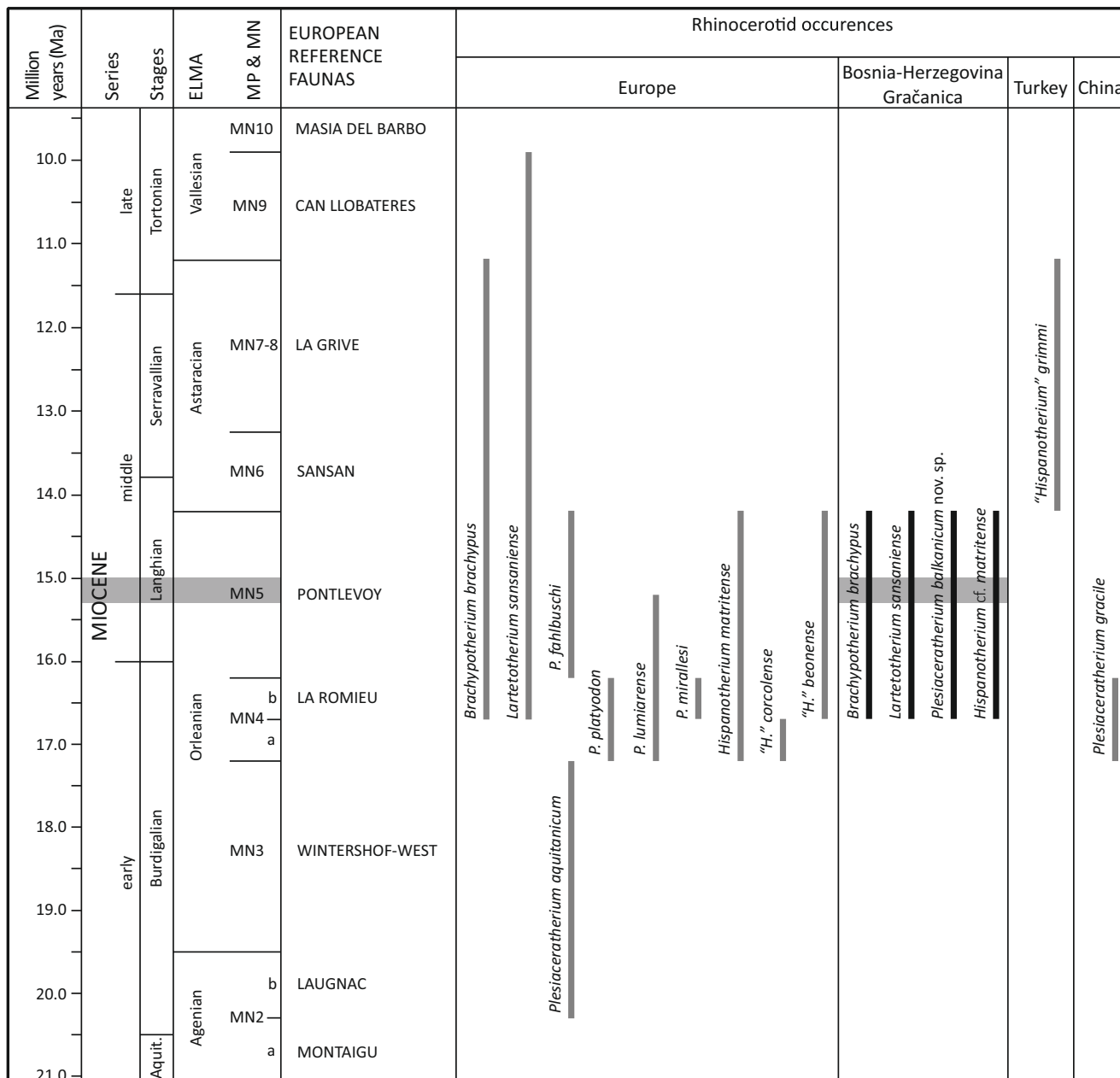
12

Fig. 5 Biostratigraphy of the Rhinocerotidae of Gračanica (early middle Miocene, Bugojno Basin, Bosnia-Herzegovina), according to the European reference faunas (capital). See "Material and methods" section for stratigraphical correlation and calibration. The occurences of the Rhinocerotidae taxa are from Guérin (1980), Yan and Heissig (1986), Heissig (1999, 2012), Antoine et al. (2000), Antoine (2002), Becker et al. (2009), Antoine and Becker (2013) and Lu et al. (2016). Grey area = stratigraphic range of the locality Gračanica (after Harzhauser et al. in press, ths issue)

Stratigraphic, biogeographical and ecological considerations

According to the stratigraphic data of Harzhauser et al. (in press) and Mandic et al. (in prep. a, this issue), an age MN5 is most likely for the locality Gračanica, which is consistent with the observed rhinoceroses association. Indeed, the stratigraphic ranges of *Brachypotherium brachypus* and *Lartetotherium sansaniense* are MN4b–MN8 and MN4b–

MN9, respectively, whereas the genus *Plesiaceratherium* is restricted to MN2b–MN5 (Heissig 1999, 2012, Antoine and Becker 2013). The species *Hispanotherium matritense*, from Western European localities, is so far known in the biozones MN4–MN5, but the genus *sensu lato* (i.e. including *H. corcolense*, *H. beonense* and *H. grimmi*) range extends up to MN8 in Turkey (Heissig 1999; Antoine 2002). Regarding these above-mentioned biostratigraphic considerations, the rhinocerotid assemblage from Gračanica is

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characteristic of the Orleanian European Land Mammal Age (ELMA) and should be constrained to the standard biozones MN4–MN5 (late early to early middle Miocene; Fig. 5). This result remains hypothetical because the stratigraphic range of *Plesiaceratherium balkanicum* sp. nov. is not yet really known and the one of *H*. cf. *matritense* from Gračanica is not directly comparable with confidence to the range of *H. matritense*, whose known distribution is so far restricted to the Iberian Peninsula and Western France (Antoine 2002).

The genera *Brachypotherium*, *Lartetotherium*, *Plesiaceratherium* and *Hispanotherium sensu lato* are common Orleanian rhinocerotids of Europe, mostly considered as Asiatic migrants whose closely related species have earlier FAD in Pakistan and surrounding areas (e.g. Antoine et al. 2010). Among the earliest *Brachypotherium*, *B. perimense* is recorded in the late early Miocene of Pakistan (Heissig 1972a, Welcomme et al. 1997). *Plesiaceratherium* is well documented throughout the early and early middle Miocene of Asia (Yan and Heissig 1986; Lu et al. 2016), notably with the supposed earliest representative, *Plesiaceratherium naricum* (Pilgrim, 1910), from the basal Miocene of Pakistan (Antoine et al. 2010) and the Chinese *P. gracile* from the Shanwang Basin in Linqu County (Lu et al. 2016). Western European Elasmotheriinae (including *Hispanotherium sensu lato*), whose known record encompasses the Iberian Peninsula and France, seem to have an origin in the early Miocene of the Bugti Hills in Pakistan with the early elasmotheriine *Bugtirhinus praecursor* Antoine and Welcomme, 2000. Concerning *Lartetotherium*, its origin is more uncertain because the only species of the genus, *L. sansaniense*, is only known in Europe. However, its sister-group according to recent phylogenies (Antoine et al. 2003; Lu et al. 2016), *Gaindatherium* Colbert, 1934 is already known from the early Miocene of Siwaliks of Pakistan with *G*. cf. *browni* (Antoine et al. 2013, Khan et al. 2013). *Lartetotherium* may thus have an Asian origin too.

The four genera are recorded for the first time in a single locality at Gračanica. Also, the specific assignations permit a better understanding of the Miocene Bosnian fossil record, only known so far from the out-of-date faunal list of Malez and Slišković (1976). This record is also significant for the biogeographical distribution of these taxa at the European scale. Indeed, the taxa *B. brachypus* and *L. sansaniense* are notable widespread species (Heissig 2012), but the genera *Plesiaceratherium* and *Hispanotherium* underline specific distributions that seem to be influenced by geographical area (*P. lumiarense*, *P. mirallesi* and *H. matritense* in Iberian Peninsula and France, *P. platyodon* and *H. beoense* in France, *P. fahlbuschi* in Germany and *Plesiaceratherium balkanicum* sp. nov. and *H*. cf. *matritense* in Bosnia; Cerdeño 1992b, Heissig 1999, Antoine 2002).

From an ecological point of view, *Brachypotherium brachypus* is characterised by a large body mass (around 2700 kg; calculation after the m1 dimensions as a predictor for body weight, as proposed by Legendre 1989), an advanced brachypody, a low head posture and brachyodont cheek teeth, indicating a regular browser adapted to short vegetation feeding Becker et al. (2009). However, according to authors such as Fortelius et al. (2003), the palaeoecology of *Brachypotherium* remains enigmatic. A hippopotamus-like lifestyle is possible, but this proposal lacks direct support. Heissig (2012) suggested a humid forest dweller, but not a swampy forest dweller. From the dental wear, the animal seems to have been a mixed feeder (Fortelius 1990, Fortelius and Solounias 2000). Based on enamel carbon and oxygen isotopic compositions, *Brachypotherium* could have fed in a rather closed woodland environment (Aiglstorfer et al. 2014a).

Lartetotherium sansaniense, *Plesiaceratherium balkanicum* sp. nov. and *Hispanotherium matritense* are three small-sized brachyodont rhinoceroses (body mass less than 1000 kg; calculation after the m1 dimensions as a predictor for body weight, as proposed by Legendre 1989, for *L. sansaniense* and *H. matritense*, and after the M3 ectoloph length, as proposed by Fortelius and Kappelman 1993, for *Plesiaceratherium balkanicum* sp. nov.). Regarding the postcranial bone proportions and the skull morphology of *L. sansaniense* (Guérin 1980, Heissig 1999), we can identify a mediportal locomotion type and a regular browser feeding posture, very close to the extant *D. sumatrensis*, which lives in cloud forests close to water beds or swamps (Becker et al. 2009). After Tütken and Venneman (2009) and Aiglstorfer et al. (2014a), *L. sansaniense* was probably a nonselective feeder, living in a mixed mesic woodland environment, encompassing both closed and open areas. It is in agreement with Guérin (1980) and Heissig (2012) who described it as a rather ubiquist rhinoceros bound to a wide living area. Additionally, Heissig (2012) argued that the strong cingulum reduction would indicate the absence of gum protection during feeding. By analogy, the postcranial bones of *Plesiaceratherium gracile* (Guérin 1980, Yan and Heissig 1986) may indicate a probable gracile and cursorial locomotion type for *Plesiaceratherium balkanicum* sp. nov. The running skills of *Plesiaceratherium* would thus indicate a rather open environment (Becker et al. 2009). According to Antoine (2002), the middle Miocene Elasmotheriina of Europe would have been adapted to open forested environment under rather dry and hot conditions. Moreover, the onset of a climatic degradation (cooling and humidity increasing just after the mid-Miocene climatic Optimum; Zachos et al. 2001) in MN5 of Europe coupled with the ecological competition due to migrating faunas would have resulted in the regional disappearance of the Elasmotheriina (Cerdeño and Nieto 1995, Antoine et al. 2000, Antoine 2002), which may also be the case for the genus *Plesiaceratherium*. After Cerdeño (1992a) and Cerdeño and Nieto (1995), the low head posture and the abundance of dental cement indicate that *Hispanotherium matritense* may have been a grazer and open habitat dweller, associated to a gregarious behaviour and a dry and arid climate.

Its limbs are rather adapted to a cursorial locomotion, without being as slender as those of pure running herbivorous mammals.

More data would be obviously needed to reconstruct the precise ecological adaptations of the rhinocerotid assemblage of Gračanica. However, from the above-mentioned considerations, we can admit the co-occurrence of four rhinocerotids living in a vast woodland area. *Brachypotherium brachypus* could be a territorial mega herbivore occupying a close and humid zone of the woodland in the proximity of water beds or swamps. *Lartetotherium sansaniense*, as a more ubiquist species, partly shared the same habitat while extending its occupation area to more open spaces. *Plesiaceratherium balkanicum* sp. nov. and *H.* cf. *matritense* would be partly allopatric, incoming within the habitat of *B. brachypus* opportunistically to access water supplies.

Compliance with ethical standards

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