



The Carnivora (Mammalia) from the middle Miocene locality of Gračanica (Bugojno Basin, Gornji Vakuf, Bosnia and Herzegovina)

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Abstract

The Carnivora (Mammalia) yielded in the coal mine Gračanica in Bosnia and Herzegovina are composed of the caniform families Amphicyonidae (*Amphicyon giganteus*), Ursidae (*Hemicyon goeriachensis*, *Ursavus brevirohinus*) and Mustelidae (indet.) and the feliform family Percrocutidae (*Percrocuta miocenica*). The site is of middle Miocene age and the biostratigraphical interpretation based on molluscs indicates Langhium, correlating Mammal Zone MN 5. The carnivore faunal assemblage suggests a possible assignment to MN 6 defined by the late occurrence of *A. giganteus* and the early occurrence of *H. goeriachensis* and *P. miocenica*. Despite the scarcity of remains belonging to the order Carnivora, the fossils suggest a diverse fauna including omnivores, mesocarnivores and hypercarnivores of a meat/bone diet as well as Carnivora of small (Mustelidae indet.) to large size (*A. giganteus*). Faunal similarities can be found with Prebreza (Serbia), Mordoğan, Çandır, Paşalar and İnönü (all Turkey), which are of comparable age. The absence of Felidae is worthy of remark, but could be explained by the general scarcity of carnivoran fossils. Gračanica records the most eastern European occurrence of *H. goeriachensis* and the first occurrence of *A. giganteus* outside central Europe except for Namibia (Africa). The Gračanica Carnivora fauna is mostly composed of European elements.

Keywords *Amphicyon* · *Hemicyon* · *Ursavus* · *Percrocuta* · Carnivora · Gračanica

Introduction

New material belonging to the order Carnivora from the middle Miocene locality Gračanica (Bugojno Basin, Gornji

Vakuf, Bosnia and Herzegovina) is presented herein. Gračanica is of great interest due to its geographic position and its middle Miocene age: carnivoran material of middle Miocene age is rare (e.g. Mayda et al. 2015) and Gračanica is located in the Balkans and in time between well-known other middle Miocene sites such as Sansan in France (Peigné 2012) in the West, Steierregg, Voitsberg and Göriach in Austria (Hofmann 1887, 1892; Thenius 1949a, b), Steinheim and Sandelzhausen in Germany (Heizmann 1973; Nagel et al. 2009) in the Northwest, Prebreza in Serbia (Marković et al. 2012), Mordoğan, Çandır, Paşalar, İnönü, Sinap Formation in Turkey (Kaya et al. 2003; Nagel 2003; Viranta and Andrews 1995; Viranta and Werdelin 2003) in the Southeast, Antonios, Chios Island in Greece in the South (Koufos 2008, 2011) and Belometcheskaya in the Northern Caucasus further East (Pickford et al. 2000). Material from Gračanica thus contributes to the knowledge of middle Miocene Carnivora in Southeastern Europe.

In this article, we discuss the assignment of the carnivoran specimens, the age and palaeoecological inferences based on the carnivoran association.

This article is a contribution to the special issue “The drowning swamp of Gračanica (Bosnia-Herzegovina) - a diversity hotspot from the middle Miocene in the Bugojno Basin”

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Locality and stratigraphy

Gračanica is a still active opencast coal mine near the village Gračanica between the cities of Bugojno and Gornji Vakuf in western Bosnia and Herzegovina (Fig. 1). First coal exploitations at Gračanica started in 1939 as underground mining. The locality is situated in the Bugojno Basin, a large intra-mountain basin in the Dinarides, filled with lacustrine deposits (Mandic et al. 2016) (Fig. 1). The sediment exposed in the coal mine represents the lowermost of three lacustrine deposition cycles (Čičić 1976; Mandic et al. in prep., this issue). The lower half of the section in the Gračanica coal mine, of about 20 m thickness, contains the intercalations of lignite deposits, exploited by the mining company. The upper half of the section, also about 20 m thickness, is dominated by clear marly sediment, representing an open lake environment. The mammalian remains come from the lignite rich, lower half of the section, which is indicated by the predominantly dark brownish colour of the fossils. This lignite-bearing part of the section is interpreted as deriving from a swampy environment. The lacustrine deposits overlying the lignite deposits in the Gračanica mine contain a mollusc fauna typical of the early middle Miocene of the Dinaride Lake System (Mandic et al. 2016; Mandic et al. in prep., this issue); this age was confined to the early Langhian, correlating Mammal Zone MN 5 (Harzhauser et al. in press, this issue). The scanty small mammal fauna from the lignite-bearing deposits in the Gračanica section indicates an age ranging between the Mammal Zones MN4 and MN5 (Wessels et al. in press, this issue).

Material and methods

All fossils presented in this article are housed in the Natural History Museum Vienna, in Austria (Figs. 2, 3, and 4). Dental measurements (given in mm) were taken with a caliper to the nearest 0.1 mm and are plotted for the carnassials in Fig. 5. Terminology and nomenclature of tooth morphology follow Van Valen (1994) and Smith and Dodson (2003), whereas definitions of dental measurements follow Peigné and Heizmann (2003). We refer herein to the greatest mesiodistal length of the crown simply as length (= L) and to the greatest labiolingual width as width (= W) of the tooth. Measurements given in quotes (“”) indicate that the measurement is affected by strong wear or fractures. The abbreviation “frag.” indicates that the specimen is fragmented.

Anatomical abbreviations: c, lower canine; P/p, upper/lower premolar, M/m, upper/lower molar

Institutional abbreviations: IPUW, Department for Paleontology, University of Vienna; NHMW, Fossil Vertebrate Collection, Natural History Museum Vienna, Austria

Systematic palaeontology

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Amphicyonidae Haeckel, 1866

Genus *Amphicyon* Blainville, 1841

Amphicyon giganteus Sz, 1825

(Fig. 2, Table 1)

Material: p4-m2 dex. with p4 slightly damaged (NHMW 2015/0009/0001 a–c); these three lower teeth were found together and most probable derive from the same individual.

Remarks: Amphicyonids radiated from southern North America and represent caniform carnivorans ranging in time from the Middle Eocene to the late Miocene (Tomiya and Tseng 2017). The genus *Amphicyon* is diverse and known from numerous species from Europe (e.g. Viranta 1996), Asia (e.g. Peigné et al. 2006a), Africa (e.g. Morales et al. 2016) and North America (e.g. Hunt 1998). The stratigraphic range of *A. giganteus* was assumed for MN 3–MN 5 (Viranta 1996), but shifted recently to MN 4–MN 6 with the youngest record in Europe in MN 6 in Arroyo del Val in Spain (Peigné et al. 2006b). Ginsburg (2000) included earlier forms, identified as *A. lathanicus* and *A. laugnacensis* (MN 3), but Peigné et al. (2008) commented on their similarity to *A. giganteus*. Furthermore, *A. giganteus* was mentioned from the late Miocene locality Kohfidisch (Austria, MN 11) in De Beaumont (1984), but this material was later identified by Viranta (1996) as *A. gutmanni*.

Description: The p4 is slightly damaged, preserving the main cuspid and the distal accessory cuspid. The root is broken. The possible presence of an anterior accessory cuspid cannot be assessed. The posterior accessory cuspid is about half as high as the main cusp and is separated by a deep notch. The cingulid is more developed lingually and reaches to the distal part of the p4. The cingulid is crenulated and forms a small cusplet aligned with the main cuspid and the posterior accessory cuspid at the mesial/distal part.

The m1 has an overall robust appearance with two strong roots. The paraconid-protocoid blade shows a shearing facet at the disto-labial side of the paraconid and the mesio-labial side of the protocoid. The protocoid is the highest cuspid of the trigonid. The metaconid is very close to the protocoid, subequal in height with the paraconid and leans slightly distally. Therefore, it is visible also in labial view. The talonid makes up about one third of the tooth. It carries a hypoconid, which is formed into a prominent cutting edge and a small entoconid. A second wear facet is present labially at the hypoconid between the talonid and the protocoid. The largest width can be measured in the centre of the m1 at the level of the protocoid and metaconid.

In occlusal view, the m2 is semicircular-shaped. The protocoid is the highest cuspid. A small notch is visible



Fig. 1 Geographic position of the locality Gračanica in Bosnia-Herzegovina (left) and within the Bugojno Basin (right), modified after Mandić et al. (2012) and Mandić et al. (2016)

mesially between the protoconid and the paraconid. The metaconid is well developed, but much lower than the paraconid that approaches the protoconid in height. A low crest extends from the metaconid disto-lingually. The cingulid is most pronounced labially at the talonid. The enamel of p4-m2 is wrinkled where no wear facets are present.

Comparisons: Other contemporaneous genera considered for comparisons, such as *Cynelos*, *Ysengrinia* and Haplocyoninae, are at least 20% smaller, with *Ysengrinia* (m1 L:30) being closest to the m1 studied herein (Peigné and Heizmann 2003).

The genus *Amphicyon* is defined by the presence of diastemata between the premolars, the single-rooted p2, the enlarged M2 and the presence of an entoconid on m1 (Viranta 1996).

Several diagnostic features for *A. giganteus* mentioned by Viranta (1996) are verifiable in the present material, such as the presence of a posterior accessory cuspid on p4, the overall stout impression of m1, the small metaconid on m1, the massive talonid with the hypoconid as most prominent cusp and a m2 of subequal height as the talonid on m1. In addition, the lack of a talonid basin confirms the affiliation of the m1 to *A. giganteus* in contrast to *A. major*. Comparative material from Chilleurs-aux-Bois (France; MN 3 in Steininger 1999 but without absolute dating) housed in the Museum of Basel shows similar dental measurements (pers. comm. Loïc Costeur; see Table 1; included in *A. giganteus* in Viranta 1996). The Gračanica specimen is of greater size (Fig. 5) than the specimen from Chilleurs-aux-Bois. Measurements given in Morales et al. (2003) for *A. giganteus* from the middle Miocene of Namibia are also similar to the material described herein. Therefore, we assign the Gračanica specimens to *A. giganteus*.

Family Ursidae Fischer von Waldheim, 1817

Genus *Hemicyon* Lartet, 1851

Hemicyon goeriachensis Toulou, 1884

(Fig. 3(a–z), Table 1)

Material: (NHMW 2013/0009/0001 a–e) isolated p4 dex. (a), m1 dex. (b), m2 sin. (c) and dex. (d), m3 fragment (e); (NHMW 2013/0009/0002 a–e) isolated m1 sin. (a), P4 fragments sin. (b) and dext. (c), fragmented tooth root (d), fragmented maxillary (e) and bone fragments; (NHMW 2015/0008/0001–0004) isolated P4 dex. (0001), M1 sin. frag. (0002), M2 sin. (0003), M2 dex. (0004).

Remarks: The majority of the material could potentially belong to one individual with p4, m1-2 (NHMW 2013/0009/0001) and M1-2 (NHMW 2015/0008/0001–0004), showing a similar degree of wear. However, as the tooth position of P4 dex. is preserved two times, these remains represent at least two individuals.

The taxonomic affiliations of *Hemicyon* and its species were subject to revisions and are still discussed (see Ginsburg and Morales 1998; Nagel 2003; or Thenius 1979 for an overview). The genus *Hemicyon* includes besides others the European species *H. gargan*, *H. stehlini*, *H. majorali*, *H. sansaniensis* and *H. goeriachensis* and material of those taxa was included in different species over time (Ginsburg and Morales 1998). *H. goeriachensis* is known so far from the Mammal Zones MN 5–MN 8 and shows a hypocarnivore tendency, whereas *H. sansaniensis* is characterised by a hypercarnivore tendency (Ginsburg and Morales 1998).

Description: The mandibular material consists of p4 dex., m1 dex., m2 dex. and sin., m3 fragment (NHMW 2013/0009/0001 a–e), and m1 sin. (NHMW 2013/0009/0002 a). The morphology

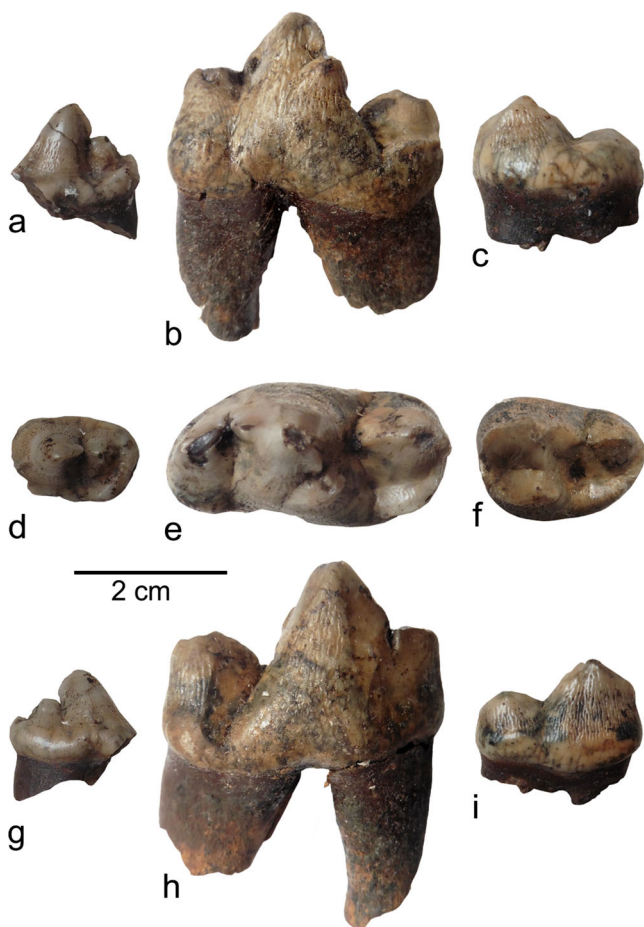


Fig. 2 Teeth of *Amphicyon giganteus* from the middle Miocene of Gračanica, probably of one individual. **a, d, g** p4 dex. (NHMW 2015/0009/0001a). **b, e, h** m1 dex. (NHMW 2015/0009/0001b). **c, f, i** m2 dex. (NHMW 2015/0009/0001c). In lingual view (**a–c**), occlusal view (**d–f**) and labial view (**g–i**)

of the representatives of the same tooth position does not vary and the description is based on both teeth where applicable.

The p4 possessed two roots, but its mesial part is fragmented. The main cuspid is situated in the centre of the tooth, no accessory cuspid are present. A small crest runs across the mesial and distal margin of the main cuspid from the tip to the base. A lingual cingulum is present (Fig. 3(a–c)).

The m1 shows a slight wear facet on its paraconid-protoconid cutting blade. The protoconid is the highest cuspid. Paraconid and metaconid are subequal in height. The talonid bears a pronounced hypoconid, a small entoconid and entoconulid. The talonid shows a shallow basin (Fig. 3(d–f)).

The m2 trigonid consists of a small paraconid and a subequal metaconid and paraconid, which are connected by a crest. The metaconid is slightly lower than the paraconid. The talonid is elongated and a hypoconid is developed (Fig. 3(g–i)).

The m3 is only a small fragment showing a crest around the occlusal surface and another short crest running in the centre of the tooth crown (Fig. 3(m)).

The maxillary material consists of P4 dex., M1 sin. frag., M2 sin. and dex. (NHMW 2015/0008/0001-0004) and P4 sin. frag. and P4 dex. frag. (NHMW 2013/0009/0002 b + c). The morphology of the tooth positions is the same if not indicated differently.

The P4 is represented by a right complete one (2015/0008/0001) and two mesial halves of P4 sin. and dex (NHMW 2013/0009/0002 b + c); in the latter one, the protocone is broken (Fig. 3(q–u)). The P4 fragments show no wear facets. The complete P4 has the same degree of wear as seen in the mandibular material. Therefore, it might be possible that the latter two belong to one individual. The tip of the paracone is broken. Paracone and metastyle are subequal in height and length. A notch is present at the centre of the carnassial blade. There is no parastyle. The protocone is semicircular and there is a mesial indentation that gives it a detached appearance. The protocone is more posteriorly situated. A strong cingulum is present on P4 with the lingual cingulum being more pronounced.

The M1 is fragmented labio-distally and preserves only one root (Fig. 3(v, w)). A pronounced paracone is present (the metacone is broken). The M1 is V-shaped in occlusal view. The protocone is small, mesially shifted and accompanied by a cingulum. There is no paraconule or metaconule, instead a smooth crest is developed in their position.

The M2 is similar to the M1 and differs only in being slightly smaller, more rectangular in occlusal view (not V-shaped), the labial and the lingual borders are curved to each other (bowl-shaped) and the metacone is less developed than the paracone (Fig. 3(w)). The last feature cannot be directly compared to the fragmented M1, but is known from Thenius (1949b).

Comparisons: Phoberocyoninae including *Plithocyon* show a hypercarnivore tendency and morphological differences to *Hemicyon* (Ginsburg and Morales 1998), including a parastyle on P4, more developed entoconid and entoconulid on m1 and sharper cusps on m2. *Zaragocyon* included in Hemicyoninae differs from *Hemicyon* by a more rectangular M2 and smaller labial cusp on the lower molars (Ginsburg and Morales 1998). *Dinocyon* (Hemicyoninae) is characterised by an absent or weak parastyle on P4, a much shorter talonid on the lower molars and a higher hypoconid on m1 if compared to *Hemicyon* (Ginsburg and Morales 1998).

Within the genus *Hemicyon*, several species can be excluded for the present material from Gračanica: *H. gargan* due to its much smaller size, *H. stehlini* due to its slightly smaller size, its more mesially situated protocone on P4 and its m1 and m2 being of the same size (Ginsburg and Morales 1998) and *H. mayorali* due to its mesio-lingual crest on the paracone of P4, a more rectangular M2 and a more developed entoconid on m2 (Astibia et al. 2000).

H. goeriachensis is similar to *H. sansaniensis* especially in size (see Peigné 2012; Peigné et al. 2006b; Thenius 1949b; Zapfe 1950 for measurements of *H. sansaniensis*), but the

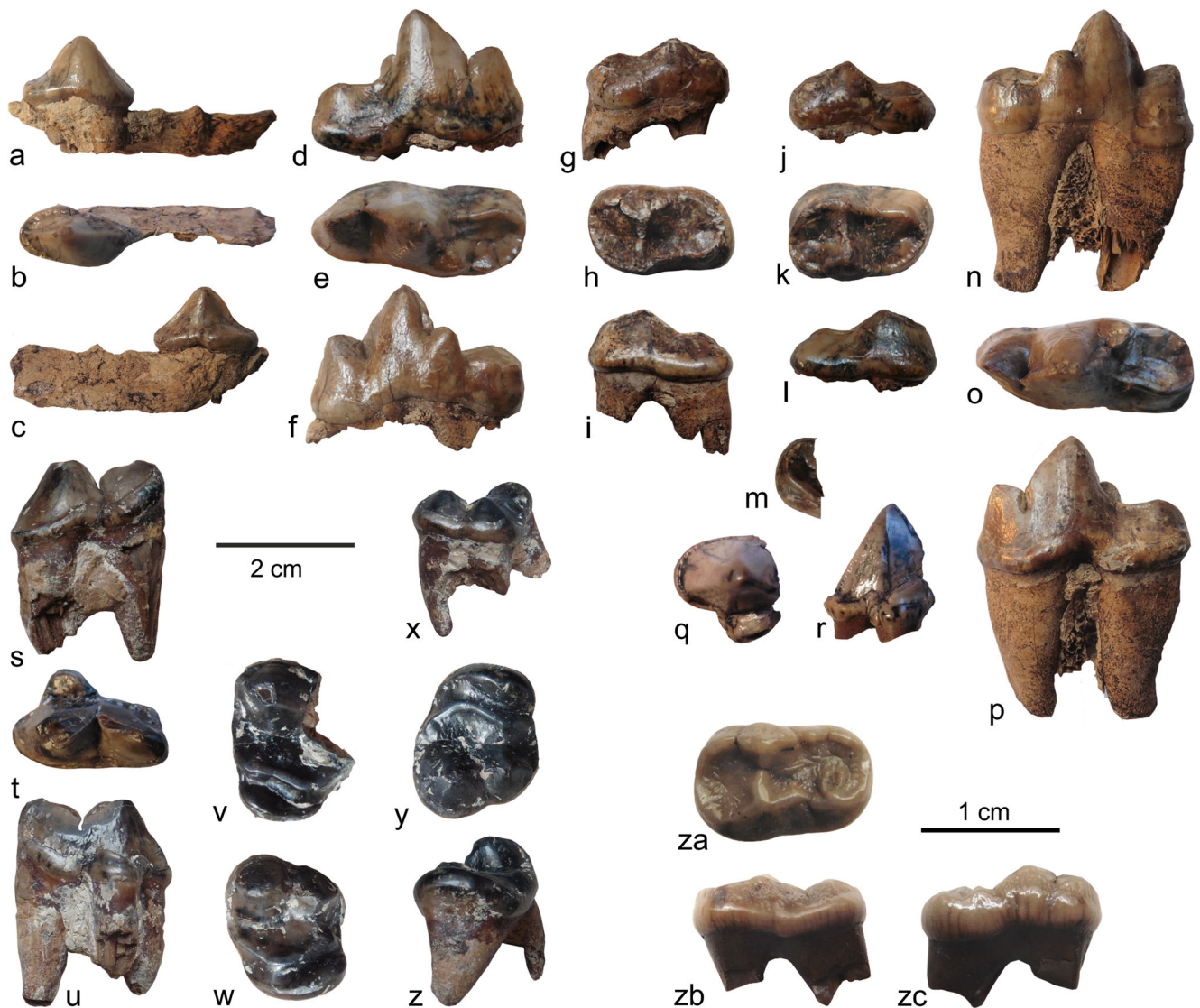


Fig. 3 Teeth of the Ursidae *Hemicyon goeriachensis* and *Ursavus brevirohinus* from the middle Miocene of Gračanica. *Hemicyon goeriachensis*: (a–c) p4 dex. (NHMW 2013/0009/0001a); (d–f) m1 dex. (NHMW 2013/0009/0001b); (g–i) m2 dex. (NHMW 2013/0009/0001d); (j–l) m2 sin. (NHMW 2013/0009/0001c); (m) m3 frag. (NHMW 2013/0009/0001e); (n–p) m1 sin. (NHMW 2013/0009/0002a); (q, r) P4 frag.

Sin. (NHMW 2013/0009/0002b); (s–u) P4 dex. (NHMW 2015/0008/0001); (v) M1 frag. sin. (NHMW 2015/0008/0002); (w) M2 sin. (NHMW 2015/0008/0003); (x–z) M2 dex. (NHMW 2015/0008/0004). *Ursavus brevirohinus*: (za–zc) m2 dex. (NHMW 2015/0010/0001). In occlusal (b, e, h, k, m, o, q, t, v, w, y, za), labial (a, d, g, l, p, s, x, zc) and lingual view (c, f, i, j, n, r, u, z, zb)

former is characterised by the absence of paraconule and metaconule in the upper molars and by a weaker cingulum and thus more elongated appearance as well as by the absence of the parastyle on P4 (Nagel 2003). After Ginsburg and Morales (1998), *H. goeriachensis* further differs from *H. sansaniensis* as follows: paracone and metacone on M1–2 are lower, the lower premolars are lower, mesio-labially not concave, but mesio-labially narrower and concave disto-lingually, m1 with entoconid and entoconulid and a slightly higher hypoconid, m2 much lower and with a lower protoconid than metaconid. The M1 in *H. sansaniensis* shows a U-shaped M1, whereas the M1 is V-shaped in *H. goeriachensis*. Peigné et al. (2006b) added that *H. goeriachensis* possesses a less developed entoconid and

entoconulid on m1 and a lower metaconid than protoconid on m2. The metrics of the specimens described herein match the measurements of the species’ material in Ginsburg and Morales (1998) and in Heizmann (1973). The carnassial data plot close to comparative material of *H. goeriachensis* (Fig. 5).

Genus *Ursavus* Schlosser, 1899
Ursavus brevirohinus Schlosser, 1899
 (Fig. 3(za–zc), Table 1)

Material: m2 dex. (NHMW 2015/0010/0001)
Remarks: The genus *Ursavus* comprises a couple of different species and its affiliations are discussed since a long time (e.g.



Fig. 4 Fragmentary mandibles of a Mustelidae indet. and *Percrocuta miocenica* from the middle Miocene of Gračanica. **a** Mustelidae indet. mandible sin. with c+p1-3/p2-4? (NHMW 2015/0006/0001) in labial view. **b–d** *Percrocuta miocenica* mandible sin. with c+p2-m1 (NHMW 2015/0007/0001) in occlusal (**b**), labial (**c**) and lingual (**d**) view

Thenius 1979). Some species are meanwhile excluded (Abella et al. 2011; Qiu et al. 2014) such as *U. elemenis* and *U. depereti* (Kretzoi 1942; Ginsburg and Morales 1998) with the former one considered as *Ballusia* and the latter one considered as *Agriarctos*, although not all material of *U. depereti* is now referred to *A. depereti* (Kretzoi 1942). Ginsburg and Morales (1998) consider *Ballusia* as the earliest member of Ursinae which gave rise to the lineage of *Ursavus* and *Ursus*. Currently, five species from Europe (*U. isorei*, *U. brevirhinus*, *U. intermedius*, *U. primaevus*, *U. ehrenbergi*), two species from Asia (*U. sylvestris*, *U. tedfordi*) and one species from North America (*U. pawniensis*) are considered as belonging to the genus of *Ursavus* (Qiu et al. 2014). The species *U. brevirhinus* is known from MN 4 to MN 9 (Qiu et al. 2014) and well known from the Austrian localities Steieregg and Voitsberg (MN 5) and Göriach (MN 5; Hofmann 1887, 1892; Thenius 1949a, b).

Description: The m2 is completely preserved with fragmented roots (Fig. 3(za–zc)). The trigonid consists of the protoconid and metaconid. The metaconid is stronger developed than the protoconid. Both are connected by a ridge. The mesial part of the trigonid is semi-circular (“shoe”-shaped) and about half the length of the distal part of the tooth. The talonid is characterised by a labio-lingual narrowing and a labial constriction. The hypoconid is situated distal to this constriction and developed as a low cuspid. A small entoconid is developed as well. The enamel of the occlusal surface is wrinkled.

Comparisons: *Pseudarctos* differs from the *Ursavus* specimen from Gračanica because its m2 is more elongated and misses the “shoe”-shaped trigonid besides its (*Pseudarctos*) smaller size (e.g. Thenius 1949b). The m2 of *Adelpharctos* shows a shorter trigonid (de Bonis 2011). *Indarctos* is larger and preserves two lingual cupids on the talonid (Koufos 2011; Peigné 2016).

The m2 of *Ursavus brevirhinus* was described by Schlosser (1899) as a molar with a low protoconid, a strong metaconid and no paraconid, a state preserved also in the specimen described herein. The morphology of the specimen also fits the description given by Thenius (1949b) for *U. brevirhinus*. The Gračanica specimen presented here (NHMW 2015/0010/0001) differs from those descriptions in a more structured talonid, preserving more cusps than the hypoconid. A similar talonid condition is described for *U. elemensis*, which is of smaller size, though (Dehm 1950). We owe this to the intra-specific morphological variation noted by Thenius (1949b) for *U. brevirhinus*. The systematic identification of the m2 further is supported by the tooth dimensions, which fit the published measurements for that species (Heizmann 1973; Qiu et al. 2014; Thenius 1949b; Zapfe 1950).

Family Mustelidae Swainson, 1835

Mustelidae indet.

(Fig. 4a, Table 1)

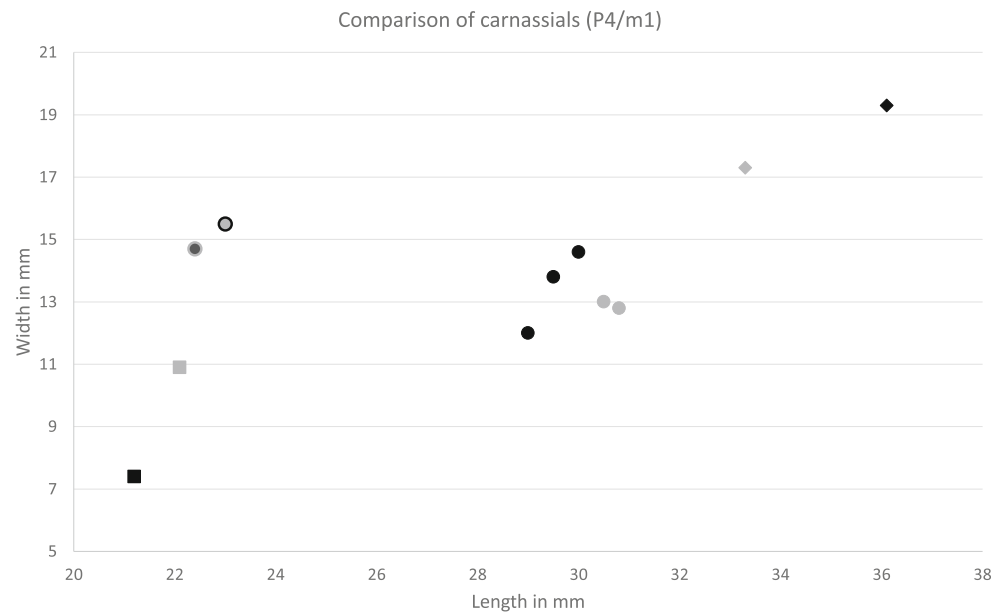
Material: mandible sin. with c, p1-3/p2-4? partly covered in surrounding material (NHMW 2015/0006/0001).

Remarks: A more specific taxonomic assignment is omitted due to the fragmentary nature of the specimen.

Description: The mandible fragment preserves the canine and the first three premolars (Fig. 4a). The canine is about twice the height of the first premolar (p1/2?). There is a strong labial ridge that runs from the base of the tooth until the tip of the canine.

The most mesial premolar (p1/2?) possesses two roots and is a simple tooth consisting of a main cuspid and a cutting edge running mesially to the tip and distally from the tip. The main cuspid is shifted mesially. A labial cingulid is present. The canine and the first premolar are tilted mesially, whereas the following two premolars are tilted distally forming a right

Fig. 5 Comparison of the dental measurements of the carnassials P4/m1. *A. giganteus*: m1 (diamonds), *H. goeriachensis*: m1 (circles), P4 (circles with borders), *P. miocenica*: m1 (squares). Material from Gračanica is in black, whereas comparative material is in grey (for references see Table 1)



angle between cutting edges of the first and the second premolar position from a labial view.

The following premolar (p2/3?) is similar to the preceding tooth, but is larger and preserves a main cuspid situated in the middle of the tooth crown. A cutting edge is present as well. A faint lingual cingulid is developed in addition to the labial cingulid. The latter one is more pronounced.

The most distal preserved premolar (p3/4?) is significantly larger than the preceding tooth position, but of similar morphology. The cingulid is more pronounced than in the preceding premolars. No accessory cuspids are present.

There are no diastemata between the preserved teeth.

Comparisons: The missing carnassial and the combination of absent diastemata and accessory cuspids on the premolars complicate the affiliation of the specimen. In general, the Gračanica specimen resembles most the early “otter-like” genera (Grohé et al. 2010) and we discuss here rejected and possible affiliations.

The following taxa of Mustelidae can be excluded due to the following differences:

Martes (e.g. *muncki/sansaniensis*) shows accessory cuspids on its premolars (Ginsburg 1961; Ginsburg and Bulot 1982; Peigné 2012). *Plesictis* is different in more spaced premolars and accessory cuspids on the premolars (Dehm 1950). *Ischyriactis zibethoides* is larger and its premolars are more spaced (Ginsburg 1961; Peigné 2012). *Proputorius* possesses diastemata and is smaller (Ginsburg 1961; Peigné 2012). *Trocharion albanense* is of comparable size and shows a pronounced cingulid on its premolars, but possesses only one alveolus for the p1, a parastyle appears in outlines on p3 and is present on p4 (Zapfe 1950). Robles et al. (2010) describes the lower premolars as unicuspid and increasing in size from mesial to distal and note that the retained single-rooted p1 is a

plesiomorph character. *Taxodon* (e.g. *sansaniensis*) shows wider premolars respective to their length and their height is not much increasing distally (Ginsburg 1961).

Possible affiliations within Mustelidae: Mustelidae of similar dental morphology and size are represented in the middle Miocene in Europe (*Lartetictis dubia*, *Trochictis*, *Adroverictis*), in North America (*Mionictis*) and in Southeastern Asia (*Siamogale thailandica*; Grohé et al. 2010). This refers especially to the former European “*Mionictis*” species, which are now assigned to *Lartetictis*, *Trochictis* and *Adroverictis* (Ginsburg and Morales 1996) and make them possible candidates:

Taxonomic position and affiliation of some specimens still await revision. This prevents a determination of the present fragmentary mandible, but a short overview shall be given here with the limitation that M1 is not preserved, but the most important element to distinguish the taxa discussed in the following: Thenius’ (1949b) “*Mionictis dubia*”, *Lartetictis dubia* in Ginsburg and Morales (1996), shows similarities to the specimen described herein. Its affiliation has still to be discussed (pers. obsv. DN). *Lartetictis* itself is a monospecific genus and was a widespread mustelid genus in the middle Miocene of Europe, but its taxonomical position within Mustelidae is debated (Heizmann and Morlo 1998; Salesa et al. 2013). The separation in size is figured for M1 in Ginsburg and Morales (1996), but no data for premolars is given. “*Mionictis ginsburgi*” (Alcalá et al. 1994), now assigned to *Adroverictis* (Ginsburg and Morales 1996), is most characteristic for its M1.

“*Mionictis artensis*” (Ginsburg 1968), now *Trochictis artensis* (Ginsburg and Morales 1996), is of the same size like the Gračanica mustelid and shows as well no diastemata, cingulids on the premolars and an asymmetrical p2-3 with a

Table 1 Measurements (in mm) of described carnivore teeth from the middle Miocene of Gračanica and of comparative materials. Estimated measurements of slightly damaged teeth are given in brackets. Measurements of canines are taken mesio-distal (length) and labio-

lingual (width). *IPUW* Institut für Paläontologie Universität Wien, *NMB* Naturhistorisches Museum Basel, *MNHN* Muséum National d'Histoire Naturelle Paris, *SMNS* Staatliches Museum für Naturkunde Stuttgart, *UMJ* Universalmuseum Joanneum Graz

Taxon/locality	Material	Length	Width	Reference
<i>Amphicyon giganteus</i>				
Gračanica	NHMW 2015/0009/0001 a–c			
	p4 dex. frag. (a)	16.2	11.0	
	m1 dex. (b)	36.1	19.3	
	m2 dex. (c)	24.2	17.5	
Chilleurs-aux-Bois	NMB S.O.6531			
	p4	18.4	10.0	pers. comm. Loic Costeur
	m1	33.3	17.3	
	m2	24.4	20.4	
<i>Hemicyon goeriachensis</i>				
Gračanica	NHMW 2013/0009/0001 a–e			
	p4 dex.	15.2	8.1	
	m1 dex.	30.5	13.0	
	m2 dex.	21.2	12.7	
	m2 sin.	21.4	12.8	
	m3 frag.		(9.1)	
	NHMW 2015/0008/0001-0004			
	P4 dex.	22.4	14.7	
	M1 sin. frag.	19.5	(22.8)	
	M2 sin.	18.5	22.3	
	M2 dex.	18.5	22.1	
	NHMW 2013/0009/0002 a–c			
	m1 sin.	30.8	12.8	
	P4 dex. frag. with protocone	(13.7)	(15.7)	
	P4 sin. frag. without protocone	(14.7)	(11.9)	
Steinheim	Type material (Fraas 1885)	13.1	8.0	Heizmann (1973)
	p4	30.0	14.6	
	m1	29.5	13.8	
	m1	19.2	14.0	
	m2	19.4	14.0	
	m2	13.4	10.4	
	m3			
Göriach	Type material			
	P4	26.6	–	Thenius (1949b)
	M1	21.0	–	
	M2	19.3	–	
Göriach				
	P4	23.0	15.5	Thenius (1949b)
	M1	20.2	23.2	
	M2	17.8	22.8	
Göriach	Nr. 22			
	p4	15.0	7.5	Thenius (1949b)
	m1	29.0	12.0	
Göriach	Nr. 3476			
	m1	–	13.5	Thenius (1949b)
	m2	–	13.0	
<i>Ursavus brevirohinus</i>				
Gračanica	NHMW 2015/0010/0001			
	m2 dex.	13.5	8.7	
Göriach	UMJ Nr. 4021			
	m2	11.7–11.8	8.4–8.7	Thenius (1949b)
Steyregg	Type material			
	m2	11.8	7.4	Thenius (1949b)
Oppeln	m2	13.8	9.3	Thenius (1949b)
<i>Ballusia elemensis</i>	min.–max. 13751; -55; -58			
Wintershof-West	m2	8.2–10.1	–	Dehm (1950)
Mustelidae indet.				
Gračanica	NHMW 2015/0006/0001			
	c sin.	5.7	4.0	
	p1/2? sin.	5.0	2.5	
	p2/3? sin.	5.3	3.0	
	p3/4? sin.	7.0	3.8	

Table 1 (continued)

Taxon/locality	Material	Length	Width	Reference
<i>Lartetictis dubia</i>				
Sansan	MNHN Sa 801			Grohé et al. (2010: Table 2) and references therein
	p2	–	3.0	
	p3	6.7	3.8	
	p4	9.6	4.6	
Goldberg/Ries	SMNS 44427			Grohé et al. (2010: Table 2) and references therein
	p2	5.9	3.5	
	p3	6.8	4.0	
	p4	9.1	4.7	
<i>Trochictis artenensis</i>				
Artenay	MNHN Ar 21, left mandible			Grohé et al. (2010: Table 2) and references therein
	p2	4.8	2.5	
	p3	5.8	3.4	
	p4	8.5	4.4	
<i>Rhodanictis depereti</i>				
La Grive St. Alban	MNHN M 5313			Grohé et al. (2010) as above Pilgrim (1932)
	p2	5.0	2.8	
	p3	6.0	3.1	
	p4	7.4	3.7	
<i>Percrocata miocenica</i>				
Gračanica	NHMW 2015/0007/0001			
	c sin.	14.8	11.1	
	p2 sin.	12.3	9.3	
	p3 sin.	15.8	10.1	
	p4 sin.	18.2	10.3	
	m1 sin.	21.2	(7.4)	
Prebreza	Holotype, IPUW 4031			
	c sin.	15.1	11.8	
	p2 sin.	12.6	9.8	
	p3 sin.	16.4	10.7	
	p4 sin.	18.2	10.4	
	m1 sin.	22.1	10.9	

symmetrical p4. In addition, the right angle formed in labial view by the cutting edges of the first two premolars figured in Ginsburg (1968) should be noted. The metrics of a *Trochictis artenensis* specimen from Artenay given in Grohé et al. (2010; herein Table 1) are closest to the discussed specimen. It should be noted that *Trochictis depereti* is also of the same size, but is described as having more spaced premolars, a single alveolus for p1 and only a faintly developed cingulid in the distal part of the teeth (Pilgrim 1932; Thenius 1949b).

Another Miocene mustelid taxon from Europe (e.g. Steinheim in Germany (Helbing 1936), La-Grive-Saint-Alban in France (Ginsburg 1968) or Gargano in Italy (Villier et al. 2011)) worthy to be discussed is *Paralutra*. It differs from the Gračanica mustelid in the notably shifted position of the mesial alveolus of the first premolar (p2) and in more pronounced cingulids (Helbing 1936).

Due to the fragmentary nature of the mandible, we assign NHMW 2015/0006/0001 to Mustelidae indet. and only cautiously propose the possibility of the affiliation or proximity to these “otter-like” mustelids sensu Grohé et al. (2010).

Suborder Feliformia Kretzoi, 1945

Family Percrocutidae Werdelin and Solounias, 1991

Genus *Percrocata* Kretzoi, 1938

Percrocata miocenica Pavlovic and Thenius, 1965
(Fig. 4b–d, Table 1)

Material: mandible sin. with c, p2–m1 with m1 strongly worn and canine fragmented (NHMW 2015/0007/0001).

Remarks: The genus *Percrocata* was referred to Hyaenidae in former times until it was placed in its own family, the Percrocutidae (Chen and Schmidt-Kittler 1983; Werdelin and Solounias 1991). A short overview of the genus *Percrocata* and synonyms can be found in Morales and Pickford (2006) and a more detailed review in Koufos (2008). The species *P. miocenica* is known earliest in Europe from MN 6 of Prebreza (Serbia; e.g. Stefanović 2004) and in the Yatağan Basin (Turkey) formerly dated as MN 7–8 (Alçiçek 2010), but now dated as MN 6 (Bouchal et al. 2017).

Description: The fragmented mandible holds the lower canine and p2–m1 (Fig. 4b–d). Two mental foramina are present, one below the anterior root of p2 and one below p3. The tip of the canine is broken off. A diastema is present between the c and the p2.

The p2 consists of a small anterior accessory cuspid, the main cuspid and a small posterior accessory cuspid. The distal part of the tooth displays a lingual extension. The main cuspid is strongly worn. The lingual cingulid is weak.

The p3 resembles the preceding tooth. The lingual extension of the distal part of the tooth is more pronounced besides the overall larger size. The main cuspid of the p3 is strongly worn. The posterior accessory cuspid is present as short cutting edge. The lingual cingulid is weak.

The p4 consists of an anterior accessory cuspid, the main cuspid and the posterior accessory cuspid formed to a short cutting blade. The anterior accessory cuspid was higher than the posterior accessory cuspid, because it is preserved despite heavy wear at a subequal height. The main cuspid is strongly worn and shows a pronounced buccal wear facet as well as on the posterior accessory cuspid as well. The lingual cingulid is more developed on the distal part of the tooth.

The m1 is heavily worn. A short talonid with a cutting edge and a lingual cingulid are present.

Comparisons: Metric data of different *Percrocuta* species show that the specimen fits to the smaller species such as *P. miocenica* in contrast to a larger species such as *P. tungurensis* (Ghaffar et al. 2011). The mandible of *P. miocenica* from Mordoğan (Turkey) described in Kaya et al. (2003) shows the same morphology and metrics although being slightly larger. Direct comparison with the holotype of *P. miocenica* (Pavlovic and Thenius 1965; IPUW 4031) shows a match with the present specimen with the only difference that NHMW 2015/0007/0001 belonged to an older individual and shows significant tooth wear which is reflected also in Fig. 5 in a similar length, but a lower width of the carnassial.

Discussion

The Carnivora remains from Gračanica are sparse and palaeoecological interpretations are thus limited. However, the known fossils indicate a diverse carnivoran guild composed of omnivores (*U. brevirohinus*; Viranta 1996), mesocarnivores (*H. goeriachensis*; Viranta 1996) and hypercarnivores of a meat/bone diet (*P. miocenica*; Viranta and Andrews 1995; *A. giganteus*; Viranta 1996). The taxa unraveled in Gračanica show a range of estimated body masses from 72 kg (*P. miocenica*; Viranta and Andrews 1995), 80 kg (*U. brevirohinus*; Viranta 1996), 120 kg (*H. goeriachensis*; Viranta 1996) up to 317 kg (for a male *A. giganteus*; 157 kg for a female; Viranta 1996). Small carnivores were present as well, although the scarcity of their remains does not allow further evaluations (Mustelidae indet.).

The absence of Felidae is noteworthy when compared to other (middle) Miocene sites. The felid *Pseudaelurus* is often part of the Miocene carnivoran fauna for example in La Romieu (Roman and Viret 1934) and La Grive St. Alban (Gaillard 1899) in France, Paşalar (Mayda et al. 2015; Viranta and Andrews 1995; Bernor and Tobien 1990) and Çandır (Nagel 2003) in Turkey or Belometchetskaya (Pickford et al. 2000) eastwards in the North Caucasus. However, the lack of felids might

be attributed to the paucity of the Carnivora remains from Gračanica, since there are also records of felids from Greece during MN 4/5 (Koufos 2008). In addition, there is ongoing discussion on the age determination, e.g. if Çandır and Paşalar represent Mammal Zone MN 5 (Begun et al. 2003; Krijgsman 2003) or 6 (Van der Made 2003, 2005).

The deposits of Gračanica are currently assumed to be of Langhian age, correlating Mammal Zone MN 5. The carnivoran assemblage confirms the middle Miocene age: The latest confirmed occurrence of *A. giganteus* is known from MN 6 (Peigné et al. 2006b). The earliest occurrence of *H. goeriachensis* is based on the stratigraphical assignment of Göriach in late MN 5. While *Percrocuta* sp. and Percrocutidae were described for MN 4/5 from Greece before (Koufos 2008), *P. miocenica* from Prebreza is only known from MN 6 (Ginsburg and Morales 1998; Stefanović 2004). Thus, MN 6 would be the age estimation for Gračanica based on Carnivora remains, but would not contradict an age estimation of MN 5.

The following fossil sites, all of MN 6 age (Kaya et al. 2003), are considered to belong to one bioprovince and situated southeastern to Gračanica (Bosnia-Herzegovina): Prebreza in Serbia (Marković et al. 2012); Mordoğan (Kaya et al. 2003), Çandır (Nagel 2003), Paşalar (Viranta and Andrews 1995) and İnönü (Kaya et al. 2003) in Turkey; Belometchetskaya further East in the Northern Caucasus (Pickford et al. 2000). Gračanica (Bosnia-Herzegovina) shares with those sites the occurrence of *Amphicyon*, *Hemicyon*, *Ursavus* and *Percrocuta miocenica*, although there are differences on species-level, e.g. *A. giganteus* instead of *A. major* or *H. goeriachensis* instead of *H. sansaniensis* (see Mayda et al. 2015).

More differences become evident when the fauna of Gračanica is compared with Sandelzhausen (Germany; Nagel et al. 2009), a more northern middle Miocene site (MN 5): felids (*Pseudaelurus*), barbourfelids (*Prosansanosmilus*) and viverrids (*Leptoplesictis*) are known from there with percrocutids being absent.

The determined taxa of Gračanica allow certain geographic inferences: *A. giganteus* occurs in vastly separated regions of Europe (e.g. France) and in Africa (Namibia; Morales et al. 2003). To our knowledge, this is the first evidence of this taxon on a route between central Europe and Africa. The species *H. goeriachensis* was widespread in Europe from Spain, over France, Germany and Austria into the Czech Republic (Ginsburg and Morales 1998). The remains from Gračanica are to our knowledge the hitherto most eastern occurrence of the species. *U. brevirohinus* is a central European species (Qiu et al. 2014) and occurs around the same time quite close in Austrian sites (Hofmann 1887, 1892; Thenius 1949a, b). *P. miocenica* is known from Europe until Turkey (Alçiçek 2010; Stefanović 2004). Gračanica is the northernmost occurrence for *P. miocenica* and the southernmost for *H. goeriachensis* and *U. brevirohinus* so far. Similarities with taxa from Asia (e.g. Turkey) concern only the generic level. The enigmatic

A. giganteus has only been described from Namibia so far (Morales et al. 2003), but remains are always fragmentary. So, the occurrence of a very large amphicyonid is confirmed, but more information about migration routes cannot be gained from that. Concluding, the central European influence is strong in the observed carnivore fauna of Gračanica with few elements from the South.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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