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Dinocrocuta gigantea from the Upper Miocene site of Eldari, Azerbaijan

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Abstract

In this paper we redescribe the specimens of "Eldari hyena" from the Upper Miocene site of Eldari, Azerbaijan. The material, which was previously described as *Hyaena eldarica* includes one maxilla fragment as well as the holotype mandibular fragment with p3-p4 that is unfortunately lost. The upper teeth morphology of Eldari specimen is typical for percrocutids and *Dinocrocuta gigantea* specifically. The teeth size of Eldari hyena also falls within the range of *D. gigantea*. The lost hemimandible exhibits morphology similar to *D. gigantea* and is close to it in size, based on published data. At the same time, it differs from other specimens of *D. gigantea* in having shorter p4 and more pronounced p3 mesial accessory cusps. These are the first *D. gigantea* specimens described from Caucasus.

Keywords: Percrocutinae; Hyaenidae; Neogene; Vallesian; Caucasus

1. Introduction

Percrocutines (*Dinocrocuta* Schmidt-Kittler, 1976 and *Percrocuta* Kretzoi, 1938) are characterized by having unique set of features that are considered derived for Hyaenidae Gray, 1821, like loss of M2 and m2, small P4 protocone enlarged premolars, hypercarnivorous m1 with a reduced talonid and small or absent metaconid, shortened rostrum and domed skull. They also appear much earlier in the fossil record than advanced hyaenids (e.g., *Crocuta* Kaup, 1828, *Pachycrocuta* Kretzoi, 1938) (Howell and Petter, 1985; Werdelin and Solounias, 1991). At first, percrocutines were considered a lineage of Hyaenidae (Kurtén, 1957), but Chen and Schmidt-Kittler (1983) noted that the dp4 of *Percrocuta* has a morphology similar to felids and forms like *Stenoplesictis* Filhol, 1880. Based on this evidence and basicranial morphology that was seemingly different from the "true" hyenas, Werdelin and Solounias (1991) placed percrocutines in a separate family Percrocutidae.

Later detailed study of basicranial morphology showed that *Dinocrocuta* was similar to Hyaenidae in the number of features (Xiong, 2019). The author also noted that the "feloid" pattern of dp4 of percrocutines can be seen not only in *Stenoplesictis* but also in several other Carnivora (*Nimravus* Cope, 1879, *Palaeogale* von Meyer, 1846) and therefore cannot be used as the only evidence for excluding percrocutines from Hyaenidae. Based on this evidence, Xiong (2019) suggested that Percrocutidae could be invalid and percrocutines should be relegated to a subfamily Percrocutinae Schmidt-Kittler, 1976.

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Perhaps the most striking member of the percrocutines is *Dinocrocuta gigantea* (Schlosser, 1903). It is characterized by its large size, exceeding any other members of Hyaenidae. Differentiating dental features of *D. gigantea* include a relatively short m1 talonid, P3 without lingual root, and strongly reduced P4 protocone. Some studies suggested that *D. gigantea* was mainly an active hunter, similar to extant *Crocuta crocuta* (Erxleben, 1777) (Deng and Tseng, 2010; Pérez-Claros, 2022).

D. gigantea is found in localities of Vallesian and Turolian age. The most abundant and complete finds of this species come from those Chinese sites, with latest occurrences of the species dated at MN 11 (Qiu et al., 1988; Deng et al., 2004; Jiangzuo et al., 2023). It is also known from several Vallesian (MN 9–10) localities outside China: Gritsev, Ukraine, Buzhor II (Vangengeim and Pevzner, 1993), Varnitsa (Lungu, 1978) and Pocsesti, Moldavia (Vangengeim and Tesakov, 2008), Blagoevgrad and Nessebar, Bulgaria (Spassov and Koufos, 2002), Pentalophos I, Greece (Koufos, 1995), Bayraktepe II, Turkey (Koufos et al., 2018) (Fig. 1), but the material is much scarcer and is represented by fragmented remains. There are also finds of *D. gigantea* from Altan-Teli, Mongolia (Howell and Petter, 1985; Vislobokova et al., 2001) which are reported to be of Turolian (MN 12) age.

Other species of *Dinocrocuta* include *Dinocrocuta minor* (Ozansoy, 1965) from Astaracian (MN 7/8) of Yassiören, Turkey, *Dinocrocuta grandis* (Kurtén, 1957) from Astaracian, Vallesian and Turolian (MN 7/8–13) Asian localities (Pilgrim, 1932; Howell and Petter, 1985; Pérez-Claros, 2022; Ghaffar et al., 2023), *Dinocrocuta senyureki* (Ozansoy, 1957) from Vallesian (MN 9–10) of Turkey and Turolian (MN 11–12) of Libya (Howell and Petter, 1985; Koufos et al., 2018), *Dinocrocuta salonicae* (Andrews, 1918) from Vallesian or Turolian (MN 9–11) site of Diavata (Koufos, 1995), *Dinocrocuta macrodonta* (Liu et al., 1978) from Lantian basin (MN 10–12), *Dinocrocuta robusta* (Lungu, 1978) from Vallesian (MN 9) site of Kalfa (Lungu, 1978; Vangengeim and Pevzner, 1993; Fig. 1), *Dinocrocuta algeriensis* (Arambourg, 1959) from Algerian sites of Vallesian to Turolian age (MN 9–12) and *Dinocrocuta leakeyi* (Aguirre and Leakey, 1974) from Vallesian (MN 9–10) of Nakali, Kenya (Howell and Petter, 1985; Morales and Pickford, 2006). Soria (1980) reported two species of large-sized percrocutines from Turolian (MN 12) Spanish localities of Ademuz, Los Aljezares and Concud, but specific attribution of this material is debated (Howell, Petter, 1985).

It is believed that *Dinocrocuta* first appeared during the Astaracian. "Explosive" radiation of the genus occurred during the early Vallesian, around the same time as distribution of *Hipparion* across Eurasia (Howell and Petter, 1985). During the Vallesian *D. gigantea* evidently had the widest distribution among *Dinocrocuta*, but sites with *D. gigantea* are only located in two regions in Europe and Asia (Fig. 1). *D. gigantea* is the most studied species among *Dinocrocuta*, but the data on variation of *D. gigantea* teeth size and morphology are still quite limited.

The Caucasus was situated among one of the possible migration routes of large mammals during the late Miocene (Steininger and Rögl, 1984). The presence of *D. gigantea* in Caucasus Miocene sites has been reported, but no specimens have been described (Koufos et al., 2018). In this paper we re-describe *Hyaena eldarica* (Bogatchev, 1927) remains from the upper Miocene site of Eldari (Azerbaijan) as *D. gigantea*.

2. Geological setting and material

The remains of the Eldari *Hipparion* fauna are found in the sedimentary strata of the Eylar-Oyug Mountains. The Eylar-Oyug Mountains are located in the northwestern part of Azerbaijan, on the border with Georgia, on the right bank of the lower reaches of the Iora River (Fig. 1). The main bone-bearing layer of Eldari is located in the middle part of the second suite of Eylar-Oyug sediments. The bone-bearing layer is represented by arenaceous sediments 1.5–2 m thick. It spans along the southern slope of Eylar-Oyug Mountains for 5 km (Gadjiev, 1997).

The main bone-bearing layer of Eldari is dated to Upper Sarmatian (= Vallesian, MN 10) (Vangengeim and Pevzner, 1993; Gadjiev, 1997). Large mammal fauna of Eldari fauna includes *Phoca procaspia*, *Deinotherium giganteum*, *Choerolophodon pentelici*, *Hipparion eldaricum*, *Hipparion* sp., *Eldarotherium burtshaki*, *Aceratherium transcaucasicum*, "*Rhinoceros*" *pachygnatus*, *Achtiaria borissiaki*, *Palaeotragus* sp., *Mirabilocerus eldaricus*, *Tragocerus* aff. *leskewitschi*, *Tragocerus* sp., *Gazella leilae*, *Ictitherium hipparionum*, *Eotragus martinianus*, *Microstonyx major*, *Cervavitus* sp., *Lepus* sp., and *Tetralophodon longirostris* (Gadjiev, 1997). The specimens of Eldari hyena described in this paper come from the same bone-bearing layer.

3. Systematic paleontology

Dental terminology and measurements from Werdelin and Solounias (1991) with modifications. All measurements were made with a 0.01 mm precision electronic caliper. All measurements are given in mm. The specimen is housed in Museum of Natural History, Ministry of Science and Education of Azerbaijan Republic, Baku, Azerbaijan.

Abbreviations: P1 – first upper premolar; P2 – second upper premolar; P3 – third upper premolar; P4 – fourth upper premolar; p1 – first lower premolar; p2 – second lower premolar; p3 – third lower premolar; p4 – fourth lower premolar; L – length; W – width; Lme – metastyle length.

Order Carnivora Bowdich, 1821
Family Hyaenidae Gray, 1821
Subfamily Percrocutinae Schmidt-Kittler, 1976

Genus *Dinocrocuta* Schmidt-Kittler, 1976
Type species: *Hyaena algeriensis* Arambourg, 1959.

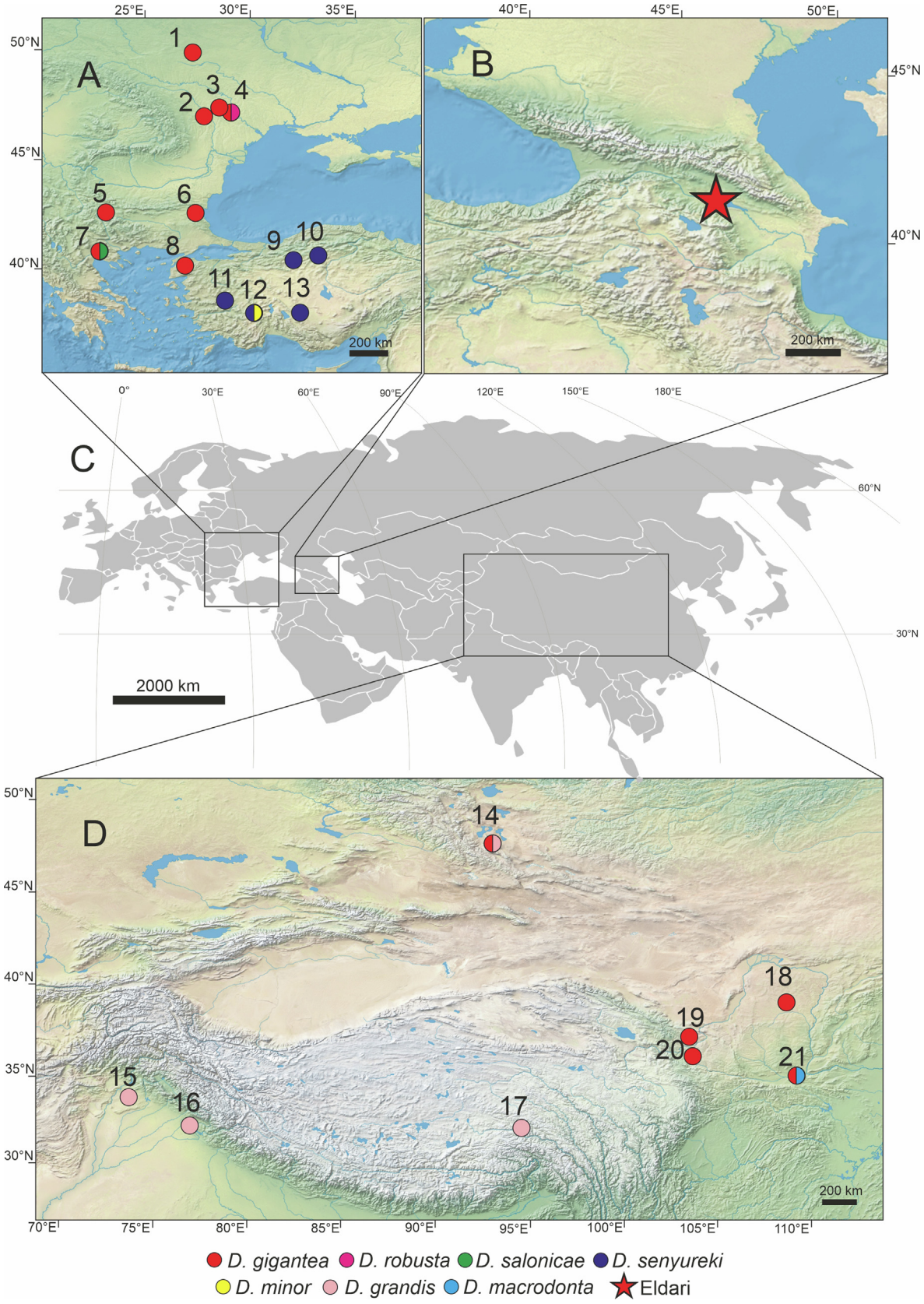

Fig. 1. Eurasian sites with *Dinocrocuta*; (A) South-East Europe; (B) Caucasus; (C) Euraisa; (D) East Asia. 1 – Gritsev; 2 – Buzhor II; 3 – Pocsesti; 4 – Varnitsa, Kalfa; 5 – Blagoevgrad; 6 – Nessebar; 7 – Pentalophos I, Diavata; 8 – Bayraktepe II; 9 – Inönü; 10 –Middle Sinap; 11 – Eşme-Akçaköy; 12 – Yassiören; 13 – Kayadibi; 14 – Altan-Teli, Oshin II; 15 – Markhal, Hasnot, Nila; 16 – Haritalyangar; 17 – Bulong; 18 – Laogaochuan; 19 – Songshan; 20 – Linxia Basin; 21 – Lantian Basin.

Diagnosis: Percrocutines of large to very large size; P3 without lingual root; p4 long relative to p3; p2 hypertrophied with a high robusticity index (modified from Howell and Petter, 1985).

Dinocrocuta gigantea (Schlosser, 1903)
(Fig. 2)

1903 *Hyaena gigantea* – Schlosser, p. 35, pl. 2, figs. 1–3, 6–8.
1927 *Hyaena eldarica* – Bogatchev, p. 201, figs. 1, 2.
1957 *Crocuta* (*Percrocuta*) *gigantea* (Schlosser) – Kurtén, p. 395, fig. 7.
1976 *Percrocuta* (*Dinocrocuta*) *gigantea* (Schlosser) – Schmidt-Kittler, p. 58.
1978 *Crocuta gigantea* (Schlosser) – Zhegallo, p. 340.
1978 *Percrocuta eldarica* (Bogatchev) – Lungu, p. 76.
1978 *Percrocuta gigantea* (Schlosser) – Lungu, p. 73, figs. 18–20.
1982 *Percrocuta (Dinocrocuta) gigantea* (Schlosser) – Zheng, p. 218, p1. 1, fig. 1.
1985 *Crocuta eldarica* (Bogatchev) – Meladze, p. 4.
1985 *Hyaena gigantea* Schlosser – Howell and Petter, figs. 7–13, tables 4, 5.

Material: Left maxilla fragment with canine, P2, P3 and P4 (Eld–42); left hemimandible fragment with p3, p4 and broken p2, no number, current whereabouts unknown.
Diagnosis: Extremely large-sized percrocutine; lower premolars having distinct mesial and distal cuspids; p2 strongly oriented lingually and close to the size of p3; p3 slightly shorter, but greater than or equal to p4 in width; P3 robustly built and widened mesially, due to the presence of large mesiolingual cusp; P4 with extremely reduced protocone, but a strong root remains (modified from Zhang, 2005).
Description:
Maxilla:

All teeth are almost unworn. The enamel on all teeth is wrinkled.

The canine is a large tooth with weak mesial crest and strong distal crest. P1 is missing, its oval alveolus shows that it was a one-rooted tooth. There is a short diastema between the canine and P1 and P1 and P2. P2 is a massive conical tooth. The mesial accessory cusp is absent, but there is a strong cingulum encircling the mesial part of

Fig. 2. Left maxilla fragment of *Dinocrocuta gigantea* from Eldari (Eld–42). (A) Lateral view. (B) Lingual view. (C) Occlusal view.

the tooth. There is also a cingulum on the disto-buccal side of the tooth. The distal accessory cusp is small. P3 is a robust high tooth which is wider in the mesial part because of the strong mesial accessory cusp. The mesial crest of the main cusp and the mesial accessory cusp are shifted lingually. There is a cingulum on the mesial side of the tooth. The distal accessory cusp is well-developed and separated from the main cusp by a groove. There is no third lingual root.

The P4 is a massive, long tooth. It is oriented at an angle relative to P3. The P4 parastyle is a conical cusp, shorter and lower than the paracone but higher than the metacone. The parastyle has no mesial crest, but there is triangle shaped enamel structure at the base of the parastyle on the mesio-buccal side. Parastyle is separated from the paracone by a well-expressed transversal groove. The paracone is a high conical cusp. It is distally inclined, similar to main cusps of P2 and P3. The paracone is separated from metacone by a deep transversal groove. Distal crest of the paracone and the metastyle, positioned at a wide angle relative to each other, form the cutting surface of P4. The horizontal metacone is longer than the paracone. There is a depression on the buccal side of the metacone, which separates it into two parts. The distal part is slightly shifted buccally. There is a weak cingulum on the lingual side of the metacone. The protocone region is greatly reduced with no distinct elevations of the enamel. There is weak crest connecting the protocone with the parastyle. The paracone is shifted mesially slightly, but the mesial border of the protocone does not exceed the mesial surface of the parastyle.

M1 is a short and wide tooth of rectangular shape. The paracone is small and ridge-like, with a mesial crest running to the buccal margin of the tooth and weak distal crest connecting to the distal margin of the protocone. The metacone is greatly reduced and is represented by a small crest located between the paracone and the distal margin of the tooth. The protocone is represented by a strong semicircular crest that is located on the lingual portion of the tooth.

Mandible:

Measurements, description and figures of the lost mandible of *H. eldarica* given by Bogatchev (1927) allow us to use this material for comparison. Here we reproduce the description given by Bogatchev with some modifications: The mandibular fragment is massive and deep, has two mental foramina, one under p2 and another under p3. The p2 is broken off. The p3 is a tooth of almost rectangular shape. It has a strong mesial accessory cuspid that is slightly shifted lingually. The distal accessory cuspid is broken off. Both mesial and distal accessory cuspids of p4 are strongly developed (Fig. 4). The description given by Bogatchev also mentions a p1 alveolus filled with sediments which can't be clearly seen on the original figure.

Dental measurements are presented in Tables 1, 2.

4. Comparison and discussion

4.1. Maxilla

The Eldari hyena was first described under the name *Hyaena eldarica* Bogatchev, 1927 based on the mandibular fragment with complete p3 and p4 (Bogatchev, 1927). The mandible was later lost (Gadjiev, 1997). Bogatchev pointed out that the description of this material under the name *H. eldarica* does not indicate the belief that it is a truly distinct species, the name was given just as a geographical distinction. Later, the maxilla fragment described above was ascribed to the same species. Gadjiev (1961) gave the description of this maxilla and concluded that *H. eldarica* should be recognized as a separate species, although Lungu (1978) suggested that this maxilla might belong to *D. gigantea* based on known measurements.

There are several diagnostic features of *D. gigantea* on upper dentition: P3 has no lingual root, and is robustly built and widened mesially due to the size of mesial accessory cusp. P4 has a greatly reduced protocone and elongated metacone which is longer than the paracone. The mesial border of P4 protocone does not exceed the mesial surface of the parastyle (Howell and Petter, 1985; Bonis and Koufos, 1994; Zhang, 2005). Teeth of the studied specimen from Eldari possess all these features.

The P3 and P4 of hyena form Eldari are larger than the respective teeth of *D. algeriensis*, *D. salonicae*, *D. grandis*, *D. robusta*, *D. leakeyi*, and *D. macrodonta* and fall within the range of *D. gigantea*. The teeth dimensions of large-sized *D. senyureki* from Turkey are close to those of *D. gigantea* and Eldari hyena but are still clearly different from them (Fig. 3). Additionally, *D. senyureki* differs from *D. gigantea* and Eldari hyena in having a less reduced P4 protocone that is significantly mesially shifted, with the mesial border of the protocone exceeding the mesial surface of the parastyle. *D. senyureki* also has a more pronounced P3 mesial accessory cusp than the Eldari specimen (Howell and Petter, 1985). Therefore, teeth morphology and dimensions of maxilla fragment from Eldari allow us to attribute it to *D. gigantea*.

4.2. Mandible

The described p3 and p4 of the lost hemimandible of the Eldari hyena possess features typical for *D. gigantea*: p3 crown of almost rectangular shape, lingually shifted p3

Table 1
Measurements (in mm) of *Dinocrocuta* upper teeth.

Locality	P2		P3		P4			Source
	L	W	L	W	L	W	Lme	
Eldari	28.6	19.0	33.7	24.2	53.6	27.1	23.6	This study
D. gigantea								
Shanxi			30?	23.5	54.0	25.0		Schlosser, 1903; Zhang, 2005
Nessebar					50.8	25.0		Spassov and Koufos, 2002
Varnitsa					55.0	27.0		Lungu, 1978
Varnitsa					58.8	27.5		Lungu, 1978
Fugu County	29.7	20.5	30.5	24.0	54.6	25.5		Zhang and Xue, 1996
Lantian			33.5	23.9	59.6			Zhang, 2005
D. senyureki								
Yassioren	27.0	16.0	33.5	21.9	50.6	27.6	19.3	Howell and Petter, 1985
D. salonicae								
Diavata	22.5	15.0	28.0	19.0	45.0	25.0	15.0	Howell and Petter, 1985
D. grandis								
Hasnot			26.0	18.0	41.0	21.0	15.0	Kurtén, 1957
D. algeriensis								
Bou Hanifia	24.0	17.0	26.5	21.4	40.6	25.5	14.4	Howell and Petter, 1985
Menacer			30.0	a21	41.0	24.0	15.1	
D. robusta								
Kalfa	23.0	14.0	27.0	18.0	42.0			Lungu, 1978
Kalfa	24.0	14.5			44.0			
D. leakeyi								
Nakali			30.4	19.0	44.7	22.0	16.6	Howell and Petter, 1985
D. macrodonta								
Baho	23.2	17.0	29.0	21.5	49.6	21.4	19.0	Howell and Petter, 1985

Table 2
Measurements (in mm) of *Dinocrocuta* lower teeth.

Locality	p3		p4		Source
	L	W	L	W	
Eldari	28.0	18.5	32.0	19.5	Bogatchev, 1927
D. gigantea					
Lantian	32.0	21.0	36.1	20.7	Zhang, 2005
Fugu	30.5	19.0	34.5	19.4	Zhang and Xue, 1996
Tianzhu	30.5	21.3	34.3	18.4	Zheng, 1982
Lantian	28.3	19.5			Kurtén, 1957
Shanxi	28.0	19.0	34.0	19.0	Howell and Petter, 1985
Shanxi	28.3	19.5			Howell and Petter, 1985
Shanxi	28.0	19.3			Howell and Petter, 1985
Songshan	30.5	21.3	34.3	18.4	Howell and Petter, 1985
Altan Teli	29.5	20.2	33.9	20.4	Howell and Petter, 1985
Pentalophos 1	27.5	19.5	34.3	19.5	Koufos, 1995
Bayraktepe	28.8	18.1			Koufos et al., 2018
D. algeriensis					
Bou Hanifa	24.3	17.3	28.5	16.3	Howell and Petter, 1985
Menacer	25.0	18.0			
D. senyureki					
Yassioren	a27		32.6	17.0	Howell and Petter, 1985
Yassioren	26.5	16.5	30.0	16.8	
Sahabi	26.7	~17.3	29.1	a16	
D. grandis					
Nila			29.5	17.3	Kurtén, 1957
D. robusta					
Kalfa	24.0	16.0	27.0	16.0	Lungu, 1978
Kalfa	25.0	16.5	28.0	17.0	

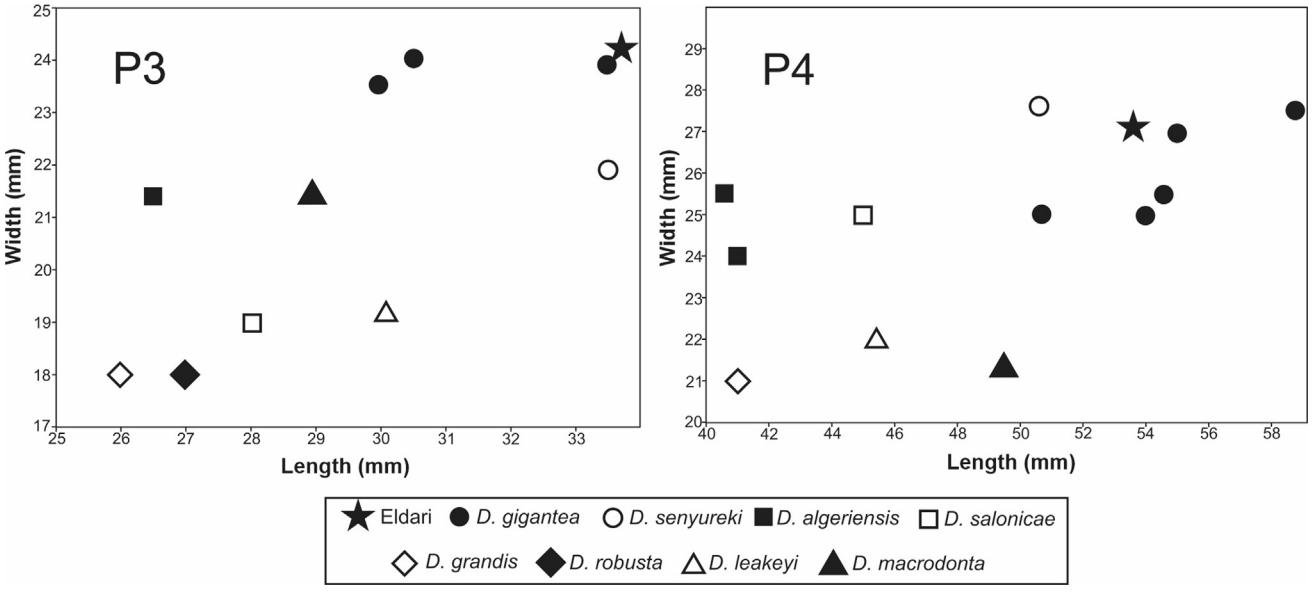

Fig. 3. Bivariate diagram comparing P3 and P4 size of Eldari hyena with *Dinocrocuta* from various localities. Data from Table 1.

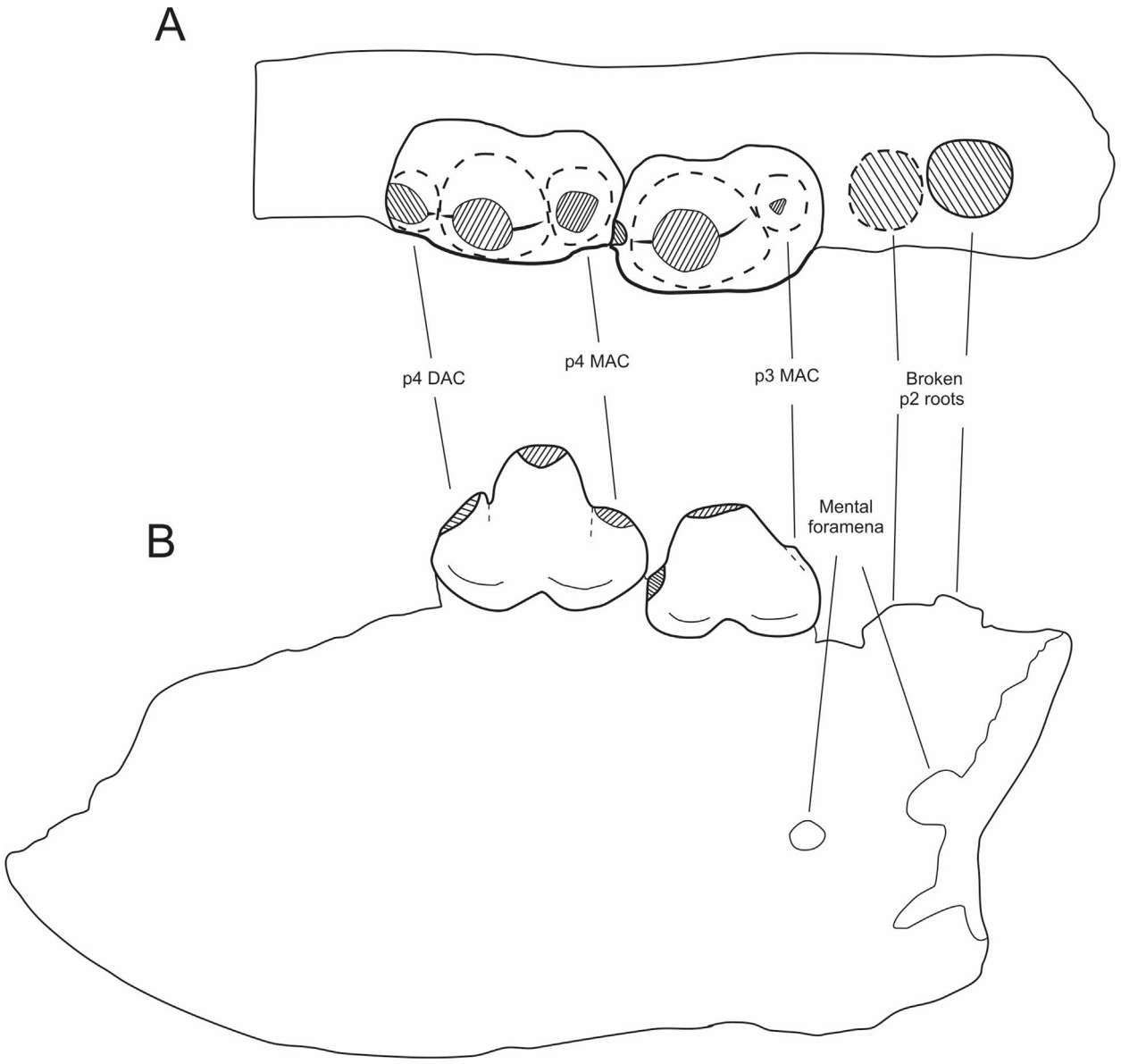

Fig. 4. Schematic diagram showing morphology of the lost mandible fragment of Eldari hyena, not to scale; diagram is based on figures from Bogatchev (1927, table 1, figs. 1, 2). (A) Occlusal view. (B) Buccal view. DAC – distal accessory cusp; MAC – mesial accessory cusp.

mesial accessory cuspid and p4 with strong mesial and distal accessory cuspids (Howell and Petter, 1985; Koufos et al., 2018). It is worth mentioning that p3 mesial accessory cuspid of Eldari specimen is more developed than in the *D. gigantea* type specimen or in specimen from Bayraktepe II (Koufos et al., 2018).

Bogatchev (1927) has compared dimensions of p3 and p4 of Eldari specimen with material of *D. gigantea* (= *H. gigantea*) published by Schlosser (1903), but unfortunately, he confused measurements of upper and lower teeth and used P3 and P4 dimensions for comparison. This led Bogatchev to believe that p3 and p4 of Eldari hyena are too small to be attributed to *D. gigantea*. Comparison with teeth of *Dinocrocuta* from other localities does show that p4 of Eldari hyena is somewhat shorter than that of other *D. gigantea* but is noticeably wider than p4 of other species. Dimension of p3 of Eldari hyena fall within the range of *D. gigantea* (Table 2; Fig. 5).

There are other metric features that distinguish *D. gigantea*: p3 is shorter than p4 but has equal or greater width

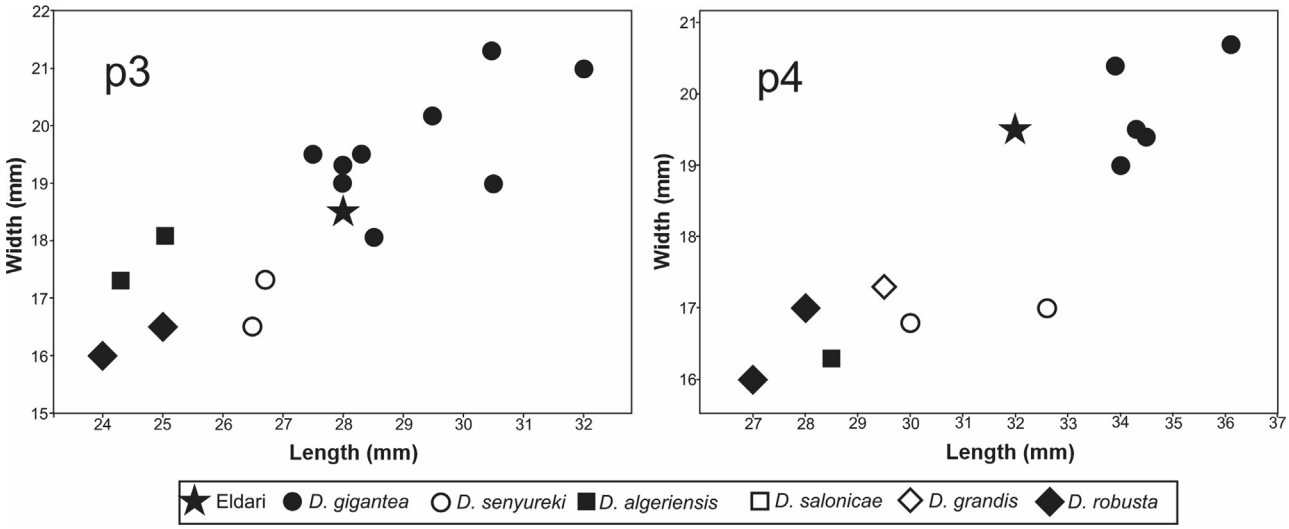

Fig. 5. Bivariate diagram comparing p3 and p4 size of Eldari hyena with *Dinocrocuta* from various localities. Data from Table 2.

(Zhang, 2005). The p3 of the Eldari specimen is shorter than p4 and has almost the same width. Morphology and dimensions of p3 and p4 from the lost Eldari hyena mandible fragment allow us to also attribute it to *D. gigantea*.

5. Conclusion

Analysis of morphology and measurements of maxilla fragment and literature data of mandible fragment of Eldari hyena showed that these specimens belong to *D. gigantea* and can be differentiated from other *Dinocrocuta* species based on the large teeth size and morphological differences.

This is the first described *D. gigantea* material from the Caucasus. This finding contributes to our understanding of geographical variability of this key Miocene species. The relatively shorter p4 and more pronounced p3 mesial accessory cusp of Eldari hyena could be a feature specific to *D. gigantea* from Caucasus, but small sample size does not allow us to state this with certainty.

These results highlight the importance of examining *D. gigantea* specimens from less studied part of its range. Future studies from other regions like the Caucasus, Middle East, and Central Asia can deepen our understanding of distribution and geographical variation of *D. gigantea* and help us better understand its role in late Miocene faunas.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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