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Carnivores from the Late Miocene locality of Hayranlı (Hayranlı, Sivas, Turkey)

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Abstract: The locality of Hayranlı-Sivas is situated in the central Anatolian plateau (Sivas, Turkey) and includes many fossil remains, including carnivores collected from 2 different spots. The aim of this study is to contribute to knowledge of carnivore evolution in Turkey based on the fossil specimens in Hayranlı-Sivas. The studied collection indicates the presence of the following taxa: *Hyaenictitherium wongii*, *Hyaenictitherium intuberculatum*, *Lycyaena dubia*, and *Machairodus giganteus*. *L. dubia* is the first record from Anatolia. The material of each taxon was described and determined by comparison with other materials from various Eurasian localities. During the Early or Middle Turolian 9–7 Ma. (MN11–12), shrubland and open savanna grassland ecosystem habitats might have contributed to rich faunal diversity in the Hayranlı location. Moreover, carnivores of the area, represented by 4 taxa biochronologically, were adapted to this ecology during the evolutionary processes. *M. giganteus* in closed ecosystem locality HAY-91 and *H. wongii*, *H. intuberculatum*, and *L. dubia* in open ecosystem locality HAY-2 were probably the most dominant carnivores of the survey area.

Key words: Carnivore, fossil, *Machairodus giganteus*, *Hyaenictitherium wongii*, *Hyaenictitherium intuberculatum*, *Lycyaena dubia*, evolution, Miocene, Sivas, Turkey

1. Introduction

Compared with the many studies of Neogene Carnivora from neighboring regions, such as Greece and Iran (e.g., Solounias, 1981 and references therein), the Carnivora fauna of Turkey have been studied relatively little (Viranta and Werdelin, 2003). However, there are many Late Miocene fossil mammal-bearing localities in Anatolia, most of which have yielded carnivore remains mentioned or studied by researchers (Nafiz and Malik, 1933; Yalçınlar, 1946, 1950; Şenyürek, 1952, 1953, 1954, 1957, 1958, 1960; Ozansoy, 1957, 1961a, 1961b, 1965; Tekkaya, 1973; Schmidt-Kittler, 1976; Sen, 1990; Bonis, 1994; Bonis et al., 1994; Kazancı et al., 1999; Lunkka et al., 1999; Viranta and Werdelin, 2003).

Fossil sites at Sivas were first discovered in 1993 by the Turkish Vertebrate Fossil Beds Research Project, a collaborative survey effort that included Ankara University (one of the authors, ES Güleç), the General Directorate of the Mineral Research Exploration in Turkey (Turkish acronym: MTA), and the Human Evolution Research Center, University of California at Berkeley (FC Howell and T White). The current survey area included a number of localities within an area encompassing roughly 50 km^2 (Figure 1), centered around 39°44′47″N, 36°48′52″E. Excavations in the first locality began in 2002 and continued yearly until 2010. The total number of fossils recovered by surface collection and excavation is currently 673, of which 25 are carnivores (Table 1).

1.1. Brief geological background

Located at the intersection Asia, Europe, and Africa, Anatolia's geological structure is the product of those continents' tectonic movement history. Turkey's basic rock structure has evolved through the subduction-collision process by combining and accumulating with the Gondwana disposition in the south and the Eurasial disposition in the north, together with the Phanerozoic Paleo and Neotethyan territories, and the last tectonic movement, which continued until the end of the Middle Miocene period, starting in the Late Mesozoic, between the Arabian and Eurasial plates (Şengör and Yılmaz, 1981; Bozkurt and Mittwede, 2001; Kaymakçı et al., 2006). From the orogenic records, the Anatolian peninsula witnessed the development of large depressions by the beginning of the Cretaceous period and the Neotethyan suture zones include outcrop plains and valleys between mountains (Kaymakçı, 2000). The central Anatolian plains were

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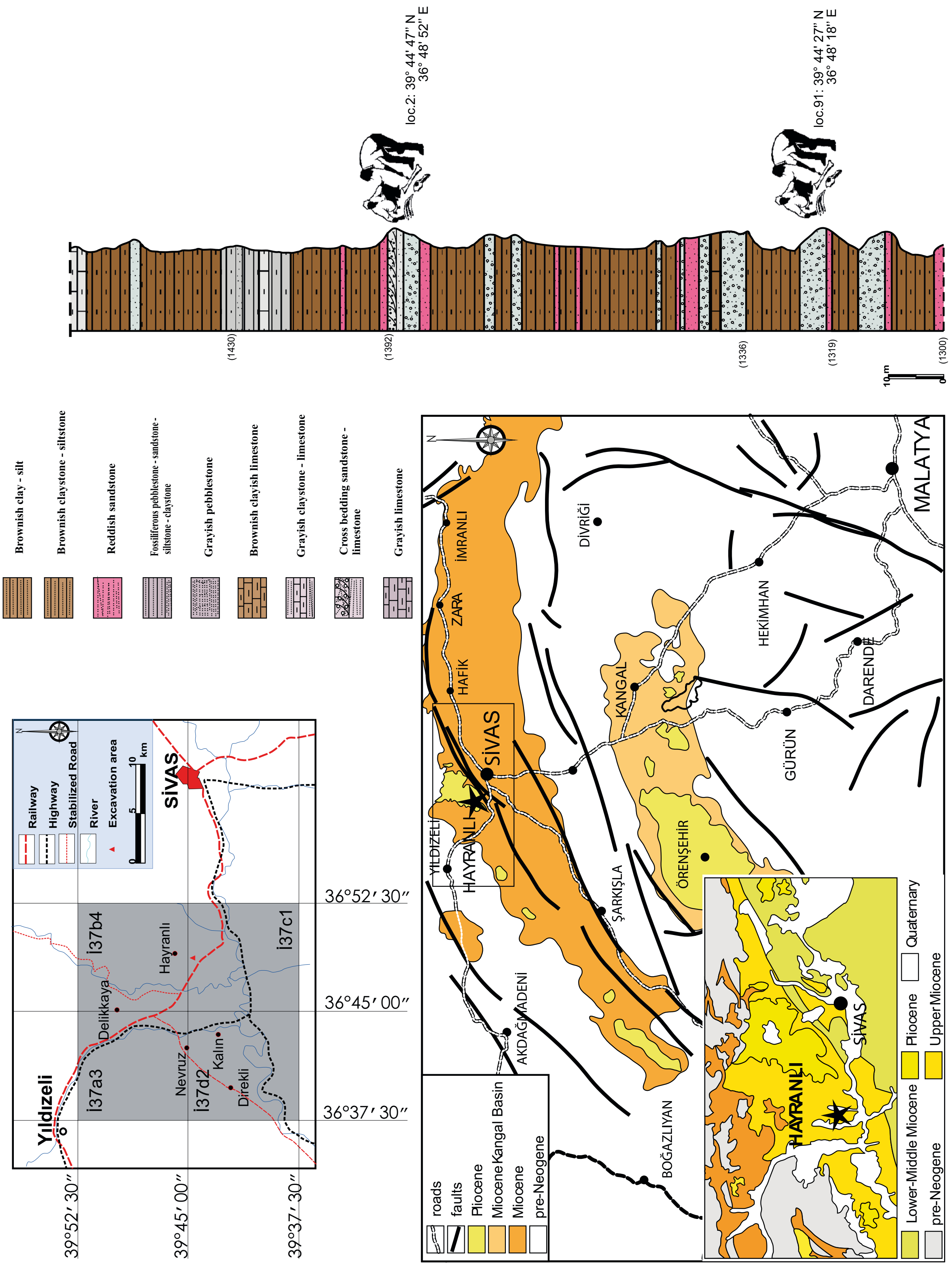

Figure 1. Position of the localities on a geographic and geologic map, and in a stratigraphic column of part of the İncesu formation. Localities 2 and 91 are situated in the stratigraphic column.

formed from marine deposits until a large part of the surface in Anatolia rose in the Eocene period (Görür et al., 1998; Kaymakçı, 2000). The undertaking of the terrestrial deposit regime went on into the Late Eocene. The chordate fossils are protected on the high parts of the terrestrial depressions from the Oligocene to the Miocene. The fossils of this study are from the Derindere region of the İncesu formation, from the Sivas plain. The Sivas plain is located in east-central Anatolia, between the Taurides in the south and Eurasia in the north. This formation includes marine deposits of thicker than 3 km from the Late Paleocene to the Middle Eocene, and Early Miocene depressions with more than 2 km of Oligocene and Pliocene terrestrial depressions (Kaymakçı, 2000).

The İncesu formation is characterized by the presence of limestone and gesso, together with the salty lake wetlands on the mountainsides of the temporarily dry land fluvial deposits, which lay improperly dominant on the Middle Miocene red seams and Early Miocene marine sediments (Kaymakçı, 2000). The fluvial deposits are larger than 200 m and show a clay stone series with conglomerates refining progressively upwards. This serial creates lake-like structures leading progressively upward toward the hills. Fossil horizons are formed 50 m beneath the series (N. Kaymakçı, personal communication). Sivas fossil Bovidae show the typical characteristics of the Greek-Iranian and Afghanistan paleobiological area and can be compared with the classical Turolian lands of Samos, Pikermi, and Maragheh (Bibi and Güleç, 2008). *Microstonyx major* (Made et al., 2013), Gliridae (Kaya and Kaymakçı, 2013), and Lipotyphla fossils (Furio et al., 2014) give an Early or Middle Turolian (MN11–12) age for Hayranlı. Figure 1 gives the map and position of the locality, as well as the Neogene deposits and stratigraphy of the area.

2. Materials and methods

The specimens are stored at the Department of Anthropology of Ankara University, Turkey. The specimen numbers, including the regional, locality, and individual information, are given in Table 1. For example, for

Table 1. Carnivore fossils of the Hayranlı localities.

No.	Specimen	Fossil	Order	Family	Genus	Species
1	58-HAY-1996 Yüzey	Maxilla (right): I1–I3, P2–P4, M1–M2; (left): I1–I3, P2–P4, M1–M2	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. wongii*
2	58-HAY-2/187	Maxilla (left): I1–I2	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. wongii*
3	58-HAY-2/51	Mandibula (right): c, p1–p3; (left): c, p2–p4, m1	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. wongii*
4	58-HAY-2/243	Mandibula (right): c, p2–p2	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. wongii*
5	58-HAY-2/223	Mandibula (right): c, p2–p3	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. wongii*
6	58-HAY-2/102	Mandibula (right): p3, p4	Carnivora	Hyaenidae	*Hyaenictitherium*	*H.* cf. *wongii*
7	58-HAY-2/222	Maxilla (right): I1–I3, P1–P4, M1–2; (left): I2–I3, P1–P4, M1–M2	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. intuberculatum*
8	58-HAY-2/75	Maxilla (right): I1–I3, C, P1	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. intuberculatum*
9	58-HAY-2/168	Maxilla (right): P3, P4	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. intuberculatum*
10	58-HAY-2/101	Maxilla (right): P4, M1	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. intuberculatum*
11	58-HAY-2/57	Maxilla (right): I1–3	Carnivora	Hyaenidae	*Hyaenictitherium*	*H. intuberculatum*
12	58-HAY-2/151	Maxilla (left): P1–P4, M1	Carnivora	Hyaenidae	*Lycyaena*	*L. dubia*
13	58-HAY-2/152	Maxilla (left): P3–P4, M1	Carnivora	Hyaenidae	*Lycyaena*	*L. dubia*
14	58-HAY-2/132	Right lower canine	Carnivora	Hyaenidae	*Ictitherium*	sp.
15	58-HAY-2/138	Right lower canine	Carnivora	Hyaenidae	*Ictitherium*	sp.
16	58-HAY-2/53	Left lower canine	Carnivora	Hyaenidae	*Ictitherium*	sp.
17	58-HAY-91/33	Left upper canine	Carnivora	Undefined	Undefined	Undefined
18	58-HAY-2/130	Right upper canine	Carnivora	Undefined	Undefined	Undefined
19	58-HAY-2/252	Izole (right): m1	Carnivora	Hyaenidae	Undefined	Undefined
20	58-HAY-91/8	Metatarsal II (right)	Carnivora	Felidae	*Machairadus*	*M. giganteus*
21	58-HAY-91/5	Metatarsal III (right)	Carnivora	Felidae	*Machairadus*	*M. giganteus*
22	58-HAY-91/7	Astragalus (right)	Carnivora	Felidae	*Machairadus*	*M. giganteus*
23	58-HAY-2/55	Humerus (distal part)	Carnivora	Undefined	Undefined	Undefined
24	58-HAY-2/54	Phalanx	Carnivora	Undefined	Undefined	Undefined
25	58-HAY-2/244	Distal phalanx	Carnivora	Undefined	Undefined	Undefined

specimen 58-HAY-2/187, '58' is the geographic code for the Sivas region; 'HAY' refers to Hayranlı, the site area encompassing the fossil localities; '2' refers to the fossil locality number; and '187' is the specimen number. For the teeth, capitals denote upper teeth (e.g., P4) and lowercase letters denote lower teeth (p4).

The dental nomenclatures used are those by Schmidt-Kittler (1976) and von den Driesch (1976). All of the measurements were taken by electronic caliper in mm.

This material was compared with materials from other localities, which are kept in institutes indicated by the following acronyms:

IPUW	Institut für Paläontologie der Universität, Vienna
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Musée National d'Histoire Naturelle, Paris
MTA	Maden Tetkik ve Arama (geological survey), Ankara
NHMW	Naturhistorisches Museum, Vienna
AUCT	Aristotle University of Thessaloniki, Thessaloniki

3. Systematic paleontology

Order: Carnivora Bowditch, 1821
Family: Hyaenidae Gray, 1821
Genus: *Hyaenictitherium* Kretzoi, 1938
Species: *Hyaenictitherium wongii* (Zdansky, 1924)

1862–1867 *Ictitherium hipparionum* (Gervais) - p. 68, Pl. 12: 1–2; 1887 *Palhyaena hipparionum* (Gervais) - Kittl, pp. 333–335, Pl. 18: 2–7; 1924 *Ictitherium wongii* sp. nov. - Zdansky, pp. 73–84, Figs. 4–6, Pls. 14: 3–6, 15: 1–4, and 16: 1–2; 1925 *Ictitherium hipparionum* (Gervais) - De Mecquenem, p. 50, Pl. 9: 3; 0 1938 *Ictitherium wongii* Zdansky - Kretzoi, p. 113; 1938 *Palhyaena hipparionum* (Gervais) - Kretzoi, p. 113; 1939 *Ictitherium hipparionum* (Gervais) - Krokos, p. 160; 1952 *Hyaenalopex atticus* gen. et sp. nov. - Kretzoi, p. 21; 0 1980 *Palhyaena wongii* (Zdansky) - Howell and Petter, pp. 584 and 588; 1980 *Ictitherium hipparionum* (Gervais) - Koufos, pp. 56–65, Figs. 18–19, Pls. 7: 2–3, 8: 1; 1981 *Thalassictis wongii* (Zdansky) - Solounias pp. 71–74, Fig. 17; 1985 *Thalassictis mesotes* sp. nov. - Kurten pp. 81–82, Figs. 1–2; 1988 *Thalassictis wongii* (Zdansky) - Werdelin, pp. 223–230, Fig. 9; 1989 *Hyaenotherium magnun* gen. et sp. nov. - Semenov, pp. 94–105, Figs. 28–31; 1989 *Hyaenotherium wongii* (Zdansky) - Semenov, pp. 105–118; Werdelin & Solounias 1991: 33; and Bonis 1994: 21.

Locality: Hayranlı.

Age: MN11–12; Late Miocene, 9–7 Ma.

Material: 58-HAY-1996 Sivas Yüzey. Complete skull with right I1–I3, P2–P4, and M1–M2, and left I1–I3, P2–P4, and M1–M2; 58-HAY-2/187, maxillary fragment with left I1–I2; 58-HAY-2/51, mandibular fragment with left I1, c, and p2–p4, and right m1–c and p1–p3; 58-HAY-2/243, right mandibular fragment with c and p2–m2; 58-HAY-2/223, right mandibular fragment with c and p2–p3; and 58-HAY-2/102, right mandibular fragment with p3 and p4.

Description

Skull: 58 HAY 1996 Sivas Yüzey (Figure 2, 1a and 1b). The skull is clear but it has been displaced from its original position because of the sediment pressure of the nasal bones, from cranial to caudal. Due to the pressure applied from the top, the frontal area, which connects to the dorsal nasal bones, is crushed through to the inside, while the sagittal crest on the caudal skull is completely intact. The zygomatic arches are broken. The posterior part of the skull is protected; mastoids and occipitals are in their original position. The right P1 and C are missing and I3 is displaced from its enamel in the tooth arrangement. On the left, the carnassial composition is broken, and P1 and C are missing. The nasal aperture is in an elliptic and vertical position. The nasal cavity starting from the prosthion remains vertical up to the middle of the canine. The snout is narrow and ends at the anterior or the orbits. The front part of the skull bones ends in the middle of the orbits. The infraorbital foramen lies on the contact points of P3 and P4. The orbits are oval, the front parts end between P3 and P4, and there is visible postorbital narrowing. The zygomatic arches are strong-thick and have a tubercle through the buccal. The cranial part is relatively small and round. The sagittal suture starts at the front of the postorbital bulges and forms the crest by connecting in the middle of the neurocranium and ending in the acrocranion. The occipitals are strong, and the occipital line has a bulge through the posterior and connects with the sagittal crest coming from the dorsal at the hind of the occipital condyle. The condyles are relatively weak and are laterally connected to the occipital bones. The foramen magnum is robust and round. The postglenoid tubercles are large. The bullae are relatively small and elliptical shaped, and the front part is a little behind that of the front surfaces of the postglenoid region. The palate is short and relatively narrow. The width of the palate is parallel until P2, where it then narrows through the buccal and hits its largest point in the distal part of P4. The incisive are lined up and touch each other, but do not overlap. There is a small diastema between the canine and I3, and a smaller diastema between the canine and P1. Specimen 58-HAY-2/187 (Figure 2, 2) is a nasal piece of bone formed by I1 and I2. The cranial dimensions of *H. wongii* are given Table 2.

Upper teeth: In the right tooth sequence, P1 and C are missing, and I1 is displaced from its enamel. In the left tooth sequence, the carnassial is broken, and P1 and C are missing. The rest are in good condition.

I1, 2: Incisives are based on a curvy line, and there is a cingulum torus in the elliptic cusp and buccal.

I3: Looks like a canine and there is a clear tuber cingulum bending to the lingual.

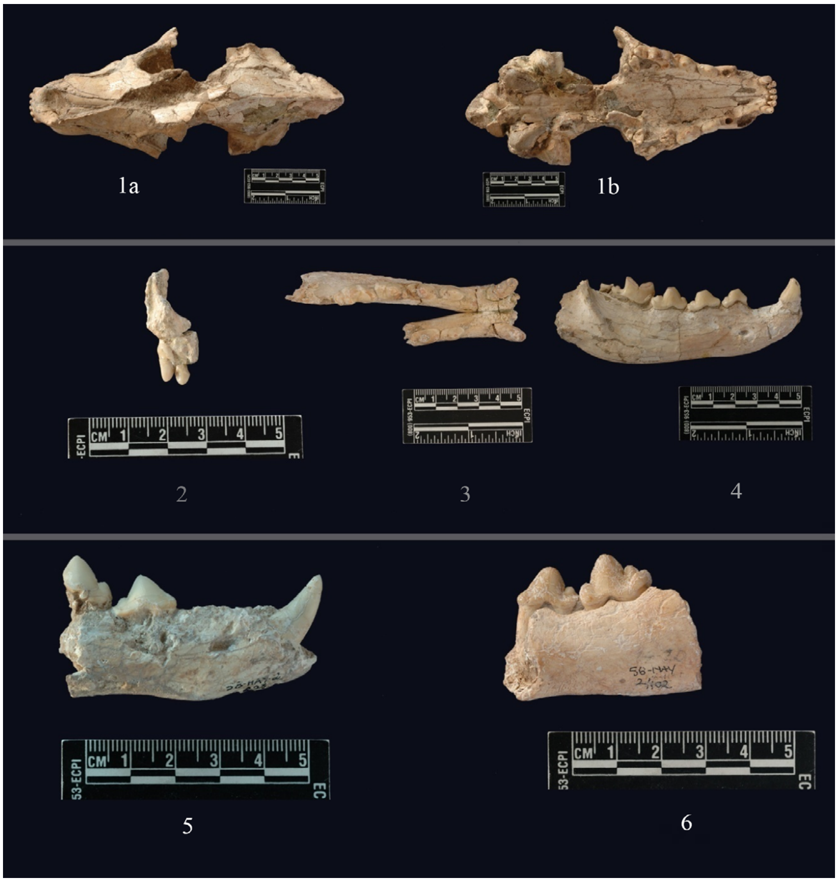

Figure 2. *Hyaenictitherium wongii* from Hayranlı-Sivas (Zdansky, 1924). Skull 58-HAY-1996 Sivas Yüzey, 1a. dorsal, 1b. occlusal; maxilla 58-HAY-2/187, 2. occlusal, mandible; 58-HAY-2/51, 3. lateral, mandible; 58-HAY-2/243, 4. buccal, mandible; 58-HAY-2/223, 5. buccal, mandible; and 58-HAY-2/102, 6. lingual.

P2: Short and large. There is no supporting cusp in the mesial. There is a small cingular tuber in the mesiolingual corner of the anterior of the tooth, connected by a crest, starting from the top of the main tubercle. The cingular is based in the distal of the torus and there is a well-raised cusp in the distal. There is a well-raised cingulum around the tooth.

P3: Relatively short and large. There is a large cavity in the lingual half of the tooth at the distal end, caused by a cingular eminence. On the mesiolingual corner of the tooth, there is a small anterior cusp. In the posterior, there is a large small cusp.

P4: The carnassial is in a long and narrow structure. There is a protocone formed along and apart from the parastyle. The mesial edge of the protocone is a little behind the anterior edge of the parastyle. The parastyle is long and a little smaller than the paracone. The sharp part of the metacone is relatively long and curves toward the buccal. There is a certain strong lingual cingulum.

M1: Long, triangular, and there is a paracone tubercle through the labial. The metacone is small, while the protocone is long and high.

M2: Is a very small tooth with an elliptic cusp.

The upper tooth measurements of the *H. wongii* specimens are given in Table 3.

From the Greco-Iranian province, comparisons of the teeth of the most common hyaenid *H. wongii* with *L. dubia*, *L. chaeretis*, and *T. hyaenoides* are given in Figure 3.

Mandible: 4 mandible remains belonging to the *H. wongii* species from Hayranlı localities. 58-HAY-2/51, (left) I1, c, and p2–p4, and (right) m1, c, and p1–p3 (Figure 2, 3); 58-HAY-2/243, (right) c and m2–M2 (Figure 2, 4); 58-HAY-2/223, (right) c and p2–p3 (Figure 2, 5); and 58-HAY-2/102, (right) p3 and p4 (Figure 2, 6) are in the list. The symphysis is relatively lengthened, narrow, and has a certain lean toward the back. Many of the mandibular rami are missing, broken, or lost. The ramus is round in shape and the anterior part starts beneath m2. The mandibular corpus is quite thin. It evolves from anterior to posterior and m1 leans to the interior. There is only 1 fossa beneath p2. The mandibular dimensions of *H. wongii* are given in Tables 4 and 5.

Table 2. Cranial dimensions of *H. wongii* and *Hyaenictitherium intuberculatum* from Hayranlı-Sivas and various localities.

		H. wongii	*H. wongii*	*H. wongii*	*H. wongii*	*H. wongii*	58-HAY-1996 Sivas Yüzey *H. wongii*	58-HAY-2/222 *H. intuberculatum*
		Koufos, G.D., 2009. Mytilini-1A	Koufos, G.D., 2009. Mytilini-1A	Koufos, G.D., 2009. Mytilini-1A	Koufos, G.D., 2009. Mytilini-1A	Koufos, G.D., 2009. Mytilini-1A	Maxilla (right): I1–I3, P2–P4, M1–M2; (left): I1–I3, P2–P4, M1–M2	Maxilla (right): I1–I3, P1–P4, M1–M2; (left): I2–I3, P1–P4, M1–M2
		MN12	MN12	MN12	MN12	MN12		
		MTLA-200	MTLA-1	NM-M.4161	NHMW-SAM-A.4746	NHMW-SAM-A.4749		
	Maxillary measurements							
1. Prosthion - acrocranion	MAX1	196.4	-	-	204.0	-	250.1	-
2. Prosthion - basion	MAX2	164.5	-	-	181.0	-	210.8	-
3. Prosthion - choanae	MAX3	93.5	-	-	100.0	-	115.8	-
4. Prosthion - middle of the line connected the posterior borders of P4	MAX4	78.0	90.0	-	91.0	-	78.03	-
5. Prosthion - mandibular fossa	MAX 5	124.5	-	-	140.0	-	164.0	-
6. Prosthion - middle of the line connecting the anterior borders of bullae	MAX 6	130.6	-	-	147.0	-	174.0	-
7. Prosthion - anterior border of the orbit	MAX 7	75.5	73.5	-	78.0	-	93.01	70.62
8. Basion - anterior border of choanae	MAX 8	71.0	-	-	81.5	70.0	87.7	-
9. Basion - anterior border of the orbit	MAX 9	100.0	-	-	119.0	98.5	132.2	-
10. Basion - middle of the line connecting the posterior borders of P4	MAX10	86.5	-	-	90.0	76.5-	135.8	-
11. Breadth at the base of the zygomatic arcs	MAX11	54.5	-	59.8	60.0	-	65.4	-
12. Maximal breadth at the zygomatic arcs	MAX12	102.0	-	-	122.5	80.0	-	-
13. Breadth at the posterior borders of the orbits (in projection)	MAX13	46.8	-	49.2	53.7	38.0	(33.7)	-
14. Breadth of the occipital condyles (external)	MAX14	32.2	-	-	37.4	33.5	41.37	-
15. Breadth of foramen magnum	MAX15	17.4	-	-	15.8	-	22.85	-
16. Height of foramen magnum	MAX16	18.8	-	-	14.3	-	21.72	-
17. Height: occipital condyles-occipital protuberance	MAX17	60	-	-	53.7	-	59.47	-
18. Maximal height: posterior end of choanae - frontal	MAX18	67.2	-	-	62.0	55.0	63.39	-
19. Length of bulla	MAX19	31.0	-	-	32.5	-	32.15	-
20. Breadth of bulla	MAX20	17.0	-	-	18.0	-	18.48	-
21. Breadth of maxilla between C (in the middle)	MAX21	22.2	21.2	26.1	23.7	-	-	35.89
22. Idem in P2	MAX22	24.1	25.7	29.3	28.5	20.5	50.59	35.21
23. Idem in P3	MAX23	28.1	31.5	38.7	36.8	28.5	64.04	48.68
24. Idem in the posterior ends of P4	MAX24	56.4	61.0	68.4	65.0	49.0	(82.68)	66.98
25. Idem in M2	MAX25	31.5	32.5	38.9	35.2	26.3	56.56	-
26. Breadth of the incisor	MAX26	24.7	22.3	-	24.5	-	28.8	-
27. Diastema C-I3	MAX27	5.1	6.0	-	5.1	-	-	7.73
28. Idem C-P2	MAX28	10.1	10.0	14.0	9.6	-	-	8.88
29 Idem P2-I3	MAX29	25.1	26.0	-	27.5	-	32.65	24.32

Table 3. Upper tooth measurements of *H. wongii* from Hayranlı-Sivas and various localities.

	H. wongii	*H. wongii*	*H. wongii*	*H. wongii*	58-HAY-1996 Sivas Yüzey	58-HAY-2-187
Upper dentition	Koufos, G.D., 2009, Mytilinii-1A	Koufos, G.D., 2009, Mytilinii-1A	Koufos, G.D., 2000, Vathylakkos-2	Koufos, G.D., 2000, Vathylakkos-2	Maxilla (right): I1–I3, P2–P4, M1–M2	Maxilla (left): I1–I2
	MTLA-200 (right)	MTLA-1 (right)	VTK-38 (right)	VTK-55 (right)		
LI1	-	3.7	4.7	-	3.85	-
BI1	-	2.5	3.3	-	5.13	-
LI2	-	4.5	4.5	-	5.24	3.96
BI2	-	3.7	4.1	-	5.66	4.94
LI3	5.5	7.3	6.1	-	6.53	5.20
BI3	5.2	5.6	-	-	7.37	5.51
LC	9.3	-	12.5	-	-	-
BC	6.8	-	9.1	-	-	-
LP1	5.2	-	6.0	-	-	-
BP1	4.5	-	5.2	-	-	-
LP2	12.0	13.2	-	12.1	15.62	-
BP2	6.4	6.6	-	6.4	8.54	-
LP3	15.0	17.0	-	15.5	19.64	-
BP3	9.1	9.0	-	8.4	10.89	-

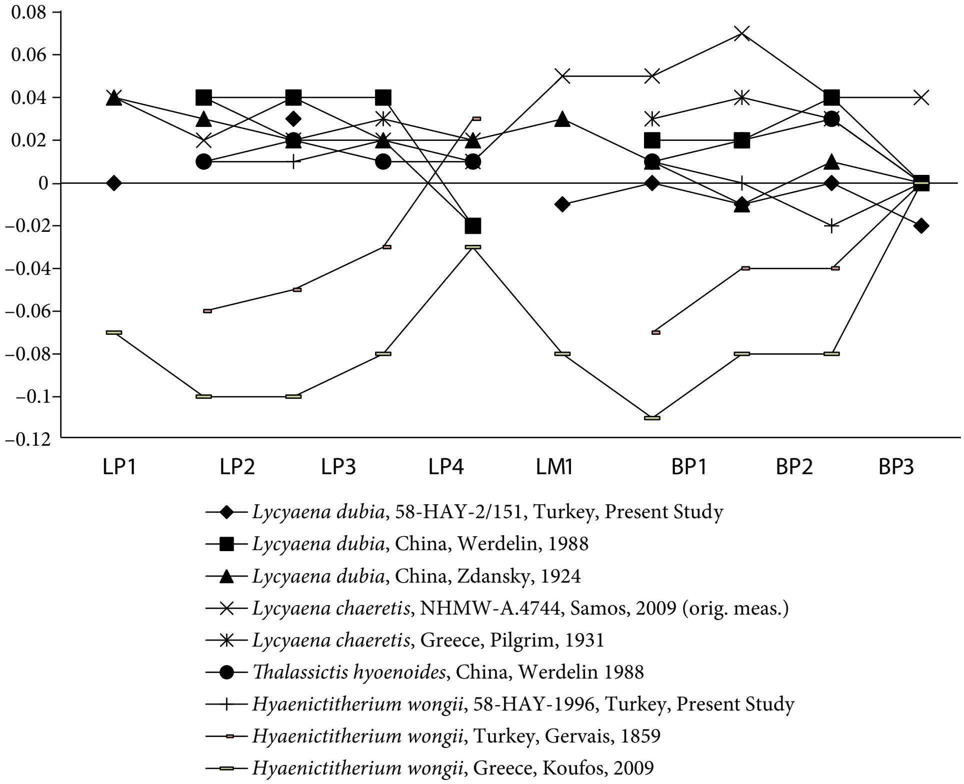

Figure 3. Logarithmic ratio diagram comparing the teeth of *L. dubia*, *L. chaeretis*, *T. hyaenoides*, and *H. wongii* from various localities.

Table 4. Mandibular dimensions of *H. wongii* from Hayranlı-Sivas and various localities.

		58-HAY-2/51 Mandibula (right): c, p1–p3	58-HAY-2/51 Mandibula (left): c, p2–p4, m1	58-HAY-2/243 Mandibula (right): c, p2–m2	58-HAY-2/223 Mandibula (right): c, p2–p3	HAY-2/102 Mandibula (right): P3, P4	Koufos, G.D., 2009, Samos NHMW-SAM-A,4745	Koufos, G.D., 2009, Samos NHMW-SAM-A,4743	Koufos, G.D., 2009, Samos NHMW-SAM-nn-1	Koufos, G.D., 2009, Samos NHMW-SAM-nn-2	Koufos, G.D., 2000, Axios valley LGPUT-RZ1-2
1. Length anterior c - coronoid process	MAN1										
2. Length anterior c - condyle	MAN2										
3. Height inferior border at angle - coronoid	MAN3							49.5			
4. Height inferior border at angle - condyle	MAN4							22.3			
5. Height condyle - coronoid	MAN5										
6. Symphysis length	MAN6	24.39	24.39				32		32.5		37
7. Height in front of p2	MAN7	21.71	21.28	19.98	19.26		20.6	20	25	24.5	23.2
8. Idem in the middle of p3 (lingual)	MAN8			23.79	18.74	20.12	19	18.5	23	24	23
9. Idem in p4 (lingual)	MAN9		23.54	25.34	19.09	21.27	20	20.5	25	25	25.5
10. Idem in m1 (lingual)	MAN10		26.51	27.48			24.3	25	27	26.5	28.8
11. Idem behind m2	MAN11		30.96	27.9			24.5				24
12. Diastema p2-c	MAN12	15.46	12.09	13.82			7.8		11	12.5	13.6
13. Diastema p2-i3	MAN13	23.46	23.74								22.6
14. Diastema i3-c	MAN14						0				
15. Length p2-m1	MAN15		39.9	61.12			61.2	61.8	63	62	
16. Length c-m1	MAN16		85.07	84.57			80.8		86.2	84.1	
17. Length p2-p4	MAN17		42.07	42.89			42.7	44	45.3	42.2	
18. Length p3-m1	MAN18		48.33	49.66			49	49.5	50.3	49.8	
19. Length p2-m2	MAN19		53.88	67.2							
20. Length c-m2	MAN20		90.59	90.58							
21. Length p1-m2	MAN21										

Table 5. Mandibular dimensions of *H. wongii* from Hayranlı-Sivas and various localities.

	Koufos, G.D., 2000, Axios valley MNHN-SLQ-929	Koufos, G.D., 2000, Axios valley MNHN-SLQ-930	Koufos, G.D., 2009, Mytilini-1A MTLA-2	Koufos, G.D., 2009, Mytilini-1A MTLA-237	Koufos, G.D., 2009, Mytilini-1A MTLA-266	Koufos, G.D., 2009, Mytilinii-1A MTLA-468	Koufos, G.D., 2009, Mytilini-1B	Koufos, G.D., 2009, Mytilinii-1B MTLB-100	Koufos, G.D., 2009. Mytilini-1B MTLB-171	Koufos, G.D., 2009, Mytilinii-1C MTLC-18	Koufos, G.D., 2000, Axios valley LGPUT-RZO-10	Koufos, G.D., 2000, Axios valley LGPUT-RZO-100
MAN1	143											136.5
MAN2	154											
MAN3	67											61.3
MAN4	31										26	27
MAN5	36											35.2
MAN6	37	36										23.7
MAN7	29	25	24.5	21		17.6			20.6	21.5		22.7
MAN8	29.5	29	24.7	22	19.6	20.5			22.4	26	23	24
MAN9	30	34	26.8	22.5				20.5	24	26.9	26.5	28.4
MAN10	33		31.5				22	22.1	28.6	30.6	29.8	26
MAN11	32	11					22		25.3	31.7	18.5	13.3
MAN12	13		11.5	6.4		13.6			58.8	17		
MAN13			87.5	80.5					82.2	67		
MAN14			44.3	48					40.7	95.7		
MAN15									25.5	47.5		
MAN16									47			
MAN17									64.7	53.8		
MAN18									88.2			
MAN19												
MAN20												
MAN21												

Mandibular teeth: Four different mandibles are used in the study and all of the specimens are in good condition, except for the incisive.

c: The canine is strong and the root is larger than the petal. The root is round at the connection point in between the root and the petal. This roundness extends to the distal crest, starting from the top of the mesiolingual and canine.

p1: Has a very small, single-rooted, and rounded petal.

p2: There is no secondary mesial tubercle and it is lengthened through p3. The posterior secondary tubercle is strong and based in the distal part of the cingulum. The posterior secondary has a powerful lingual and a weak buccal cingulum.

p3: There is an anterior cuspid that is relatively short and large, and is not totally evolved. The posterior cuspid is small and there is a large distal cingular bulge that looks like a talonid. There is a well-developed buccal cingulum.

p4: Short and large, with a strong anterior cuspid and a very strong posterior cuspid based in the distal cingular position. The lingual level of the distal cingular structure is high and it has a crest form similar to the entoconid. There is a well-evolved buccal cingulum.

m1: Has a relatively small, narrow, and short talonid. The metaconid is relatively half the size of the protoconid. The trigonid length is two-thirds the length of the tooth. The protoconid and paraconid have a blade-like edge and are separated by a deep carnassial notch. The hypoconid is strong and based in the center of the talonid. The entoconid is smaller and combined with the hypoconulid by a crest covering the distal limit of the talonid. A crest starting from the top of the hypoconid increases in size and faces the metaconid and protoconid where they join. A well-evolved cingulum makes the tooth prominent. The lower tooth measurements of the *H. wongii* specimens are given in Table 6.

Comparisons

The taxonomy of small- to medium-sized Late Miocene Hyaenidae is complex. These hyaenids are known as 'ictitheres' and have a long taxonomic past (Kurten, 1982; Semenov, 1989; Werdelin and Solounias, 1991; Koufos, 2000; Bonis, 2005). In Greece, in the Late Miocene, ictitheres have been found in various localities, such as Pikermi, Samos, Axios Valley, Perivolaki (Thessaly), and Kerassia (Evia Island) (Koufos, 2006). Among the Pikermi ictitheres, there is a species that is smaller than *Adrocuta eximia* and bigger than *Ictitherium viverrinum*, which was for a long time called *Ictitherium hipparionum*. The generic name of this species was changed to *Palhyaena*, *Thalassictis*, *Ictitherium*, and *Hyaenotherium*. The name *Palhyaena hipparionum* was given to a specimen by Gervais (1859) in Mt. Luberon, France, and the type sample of this taxon was placed in the Avion museum, but the type specimen has since been lost (Kurten 1982). This hyaenid is nomen dubium and can only be included in the taxon defined by the type specimen of Mt. Luberon until the Mt. Luberon type specimen is found (Werdelin, 1988; Werdelin and Solonuias, 1991).

Similar hyaenids were defined as *Ictitherium wongii*, which has characteristics between those of *Adrocuta eximia* and *Ictitherium viverrinum* from the Late Miocene and from China (Zdansky, 1924). After these, similar European materials were included with these species. As a result, these hyaenids were included in the genus *Hyaenotherium*, with *Hyaenotherium wongii* as the type species of the genus (Semenov, 1989). Thus, another medium-size hyaenid, called *Ictitherium hyaenoides* in China by Zdansky, was transferred to the *Hyaenictitherium* by Kretzoi (1938). These 2 hyaenids should be included in the same genus even though they are different at the species level, and because *Hyaenictitherium* has priority, these 2 species were included in the genus *Hyaenictitherium* (Zhang et al., 2002; Bonis, 2004, 2005). Therefore, Late Miocene hyaenids between *Adcrocuta eximia* and *Ictitherium viverrinum* are known as *Hyaenictitherium wongii* (Zdansky, 1924).

Similar Hyaenidae from Turkey were recorded from Elmadağ - *I. robustum* and *I. hipparionum* (Şenyürek, 1960); Çobanpınar - *I. hipparionum* and *H. eximia* (Ozansoy, 1965); Kemiklitepe - *H. wongii*, *A. examina*, and *L. chaeretis* (Bonis, 1994); Sinap - *H. intuberculatum* and *H. wongii* (Viranta and Werdelin, 2003); and Akkaşdağı - *H. wongii*, *A. eximia*, and *I. viverrinum* (Bonis, 2005). All of these *I. hipparionum* records from Turkey are considered as *H. wongii* because it is a valid taxon.

58-HAY-1996 Sivas Yüzey. Complete skull with right I1–I3, P2–P4, and M1–M2, and left I1–I3, P2–P4, and M1–M2; 58-HAY-2/187, maxillary fragment with left I1–I2 compared with Greek specimens in the Aristotle University of Thessaloniki Mytilini-1A: MTLA-200 and MTLA-1; Maragheh specimens in the Natural History Museum of Paris: MAR 3353, MAR 3354, MAR 3355, MAR 3356, and MAR 3357; Samos specimens in the Natural History Museum of Vienna: NHMW-SAM-A.4743, NHMW-SAM-A.4745, NHMW-SAM-A.4746, and NHMW-SAM-A.4749 Mar-0019 and Mar-0019/1 (A4803). Comparisons of the cranial dimensions and upper tooth measurements of *H. wongii* from Hayranlı-Sivas and various localities showed that the specimens belong to the *H. wongii* taxon (Tables 2 and 3; Figures 4 and 5).

58-HAY-2/51 specimens, mandible fragment with left I1, c, and p2–p4, and right m1–c, p1–p3; 58-HAY-2/243, right mandible fragment with c and p2–m2; 58-HAY-2/223, right mandible fragment with c and p2–p3; and 58-HAY-2/102, right mandible fragment with p3 and p4. Fifty-one specimens compared with Greek specimens in the Aristotle University of Thessaloniki: MTLA-2, MTLA-237, MTLA-266, MTLA-468, MTLB-1, MTLB-100,

Table 6. Lower tooth measurements of *H. wongii* from Hayranlı-Sivas and various localities.

	58-HAY- 2/ 51 Mandible (right): c, p1–p3	58-HAY-2/51 Mandible (left): c, p2–p4, m1	58-HAY-2/243 Mandible (right): c, p2–m2	58-HAY-2/223 Mandible (right): c, p2–p3	HAY-2/102 Mandible (right): P3, P4	Bonis, L., 1994 Kemiklitepe, KTA23	Bonis, L., 1994 Kemiklitepe, KTB5	Bonis, L., 1994 Kemiklitepe, KTB90	Bonis, L., 1994 Kemiklitepe, bKTB90	Bonis, L., 2005, Akaşdağı; AKK-115	Koufos, G.D., 2009, Mytilinii-4 MLN-42	Koufos, G.D., 2009, Mytilinii-1A MTLA-468	Koufos, G.D., 2009, Mytilinii-1B MTLB-100	Koufos, G.D., 2009, Mytilinii-1C MTLC-18	MN12 Viranta & Werdelin Sinap AS,94,1283
Li1												3.5			2.5
Bi1												2.1			-
Li2												4.3		4.1	3.5
Bi2												2.8		3.2	-
Li3												4.9		4.8	5.8
Bi3												4		4.4	-
Lc	11.02	11.35	9.85	8.69						10.9	7	9.6		10.7	8.0
Bc	8.62	7.72	8.96	6.79						7.9	5.5	6.7		8	11.7
Lp1	4.12													3	3.1
Bp1	2.95													3	3.0
Lp2	11.32	11.15	11.7					11.6		11.4	9.5	11		13	12.5
Bp2	6.28	6.27	5.78					6		6.7	4	5.5		6.1	6.2
Lp3	14.5	15.01	15.21	13.87	14.98			14.4		15.6	11.5	14.3			15.3
Bp3	7.07	7.37	7.14	7.97	7.24			7		7.8	4.6	7.3		8	7.2
Lp4		16.36	16.62		17.01					16.5	12		16.3	17.9	18.0
Bp4		8.3	7.84	7.97	8.23					8.7	5.3		8.1	8.8	8.7
Lm1		20.1	19.46			19	18.9	20.3	23.5	20.2	15.5		20.5	21.8	20.4
Bm1		8.53	8.2			14	13.4	14.8	18.7	9.5	6.9		9.3	9.5	9.4
Lm1tal		10.08	10.37			8.7	8.4	8.9	8.7				4.6	5.7	-
Lm2										5.7					-
Bm2										5.1					-

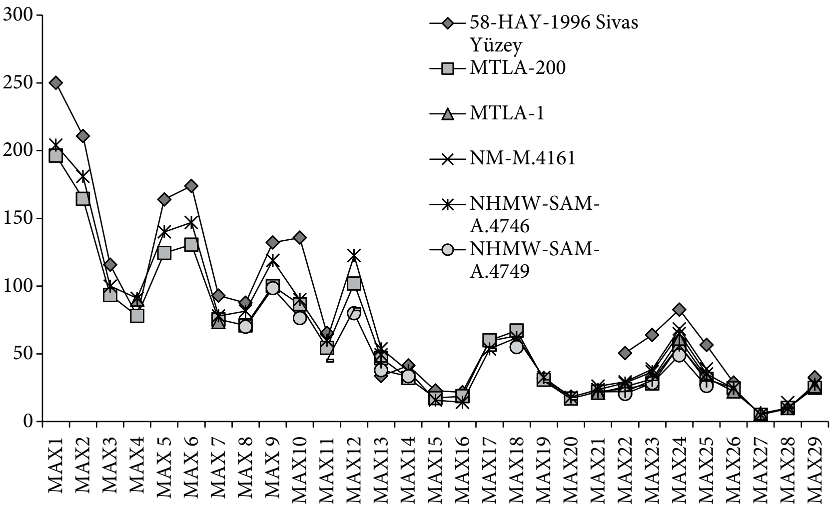

Figure 4. Comparison of the cranial dimensions of *Hyaenictitherium wongii* from Hayranlı-Sivas and various localities.

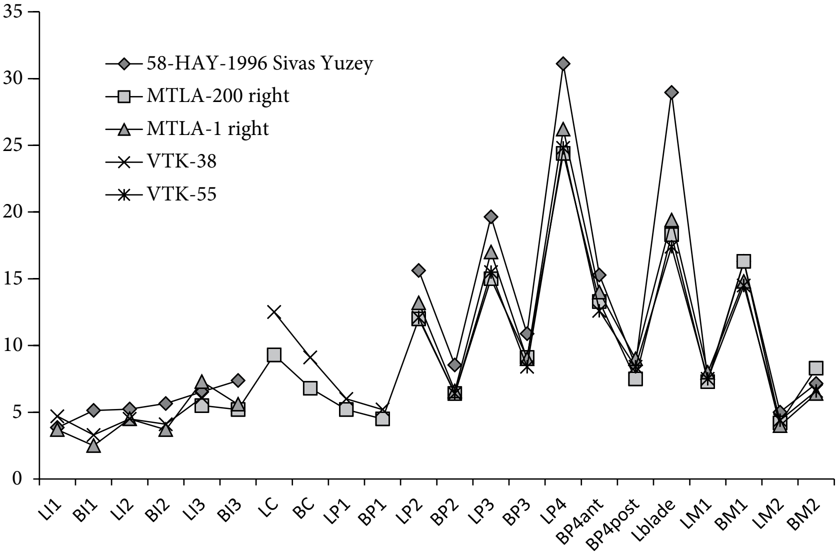

Figure 5. Comparison of the upper tooth measurements of *Hyaenictitherium wongii* from Hayranlı-Sivas and various localities.

MTLB-171, MTLC-18, LGPUTRZ1-2, LGPUTRZO-10, and LGPUTVAT-100; Thessaloniki specimens in the Natural History Museum of Paris: MNHNSLQ-929 and MNHNSLQ-930; and Samos specimens in the Natural History Museum of Vienna: NHMWSAMA.4745, MHNWSAMA.4743, NHMWSAMnn-1, and NHMWSAMnn-2. This showed that these mandible specimens belong to the *H. wongii* taxon. Comparisons of the mandibular dimension and lower tooth measurements of *H. wongii* from Hayranlı-Sivas and various localities are given Table 4 and Figures 3, 6, and 7.

Genus: *Hyaenictitherium* Kretzoi, 1938

Species: *Hyaenictitherium intuberculatum* (Ozansoy, 1965)

Locality: Hayranlı.

Age: MN11–12; Late Miocene, 9–7 Ma.

Material: 58-HAY-2/222, maxillary fragment with right I1–I3, P1–P4, and M1–M2, and left I2–I3, P1–P4, and M1–M2; 58-HAY-2/75, maxillary fragment with right I1–I3, C, and P1; 58-HAY-2/168, maxillary fragment with right P3 and P4; 58-HAY-2/101, maxillary fragment with right P4 and M1; and 58-HAY-2/57, maxillary fragment with left I–1–3.

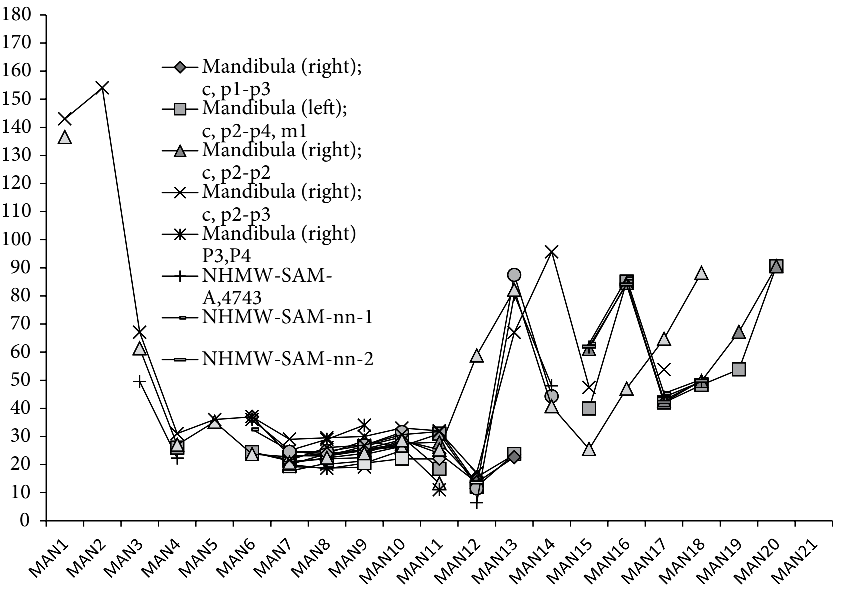

Figure 6. Comparison of the mandibular dimensions of *Hyaenictitherium wongii* from Hayranlı-Sivas and various localities.

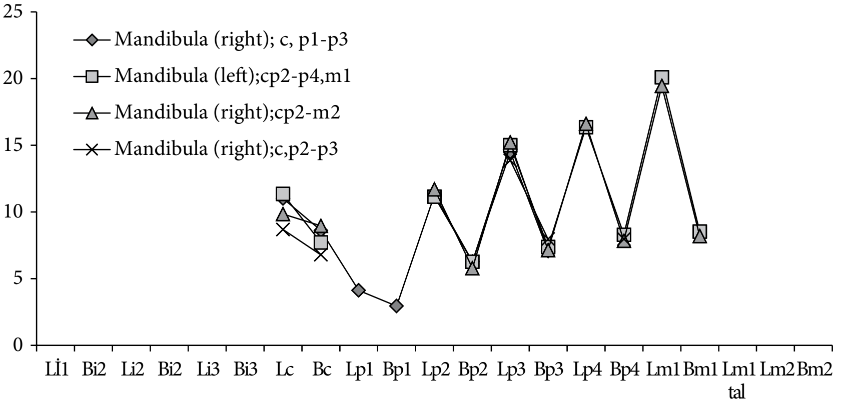

Figure 7. Comparison of the lower tooth measurements of *Hyaenictitherium wongii* from Hayranlı-Sivas and various localities.

Description

Maxilla: 58-HAY-2/75, maxillary fragment (right) I1–I3, C, and P1 (Figure 8, 2c); 58-HAY-2/168, maxillary fragment (right) P3–P4 (Figure 8, 2d); 58-HAY-2/101, maxillary fragment (right) P4–M1 (Figure 8, 2e); 58-HAY-2/57, maxillary fragment (left) I–1–3 (Figure 8, 2f); and 58-HAY-2/222, maxillary fragment (right) I1–I3, P1–P4, and M1–M2, and (left) I2–3, P1–P4, and M1–M2 (Figure 8, 2a and 2b). The maxillary tooth specimens are in good condition, except for the left canine. The palate was originally well fossilized and the skull's anterior orbits are missing, but the frontal part is intact. There is only a small depression because of the pressure applied to the nasal bones. The nasal space-hole is elliptic and vertical. The nasal space starting from the prosthion is in a vertical position up to the area behind the canine. The nasals are narrow and go to the anterior of the orbits. The infraorbital foramen lays on the contact point of P3 and P4. The orbits are round, extroversive front points that end between P3 and P4, and there is a postorbital narrowing (Figure 8, 2a and 2b). The palate is short. From the prosthion to P2's mesial has the same width, gets larger from the middle of P2 to the nuchal, and has its largest point in P4's distal. M1 is settled through the buccal at a 90° angle in the distal of p4. The incisives are settled straight without overlapping; only the coronal parts are in contact. There is a small diastema between the canine and I3, and a smaller diastema between the canine and P1. The I3s have higher coronals than the other incisives. The cranial dimensions of *H. intuberculatum* are given in Figure 8.

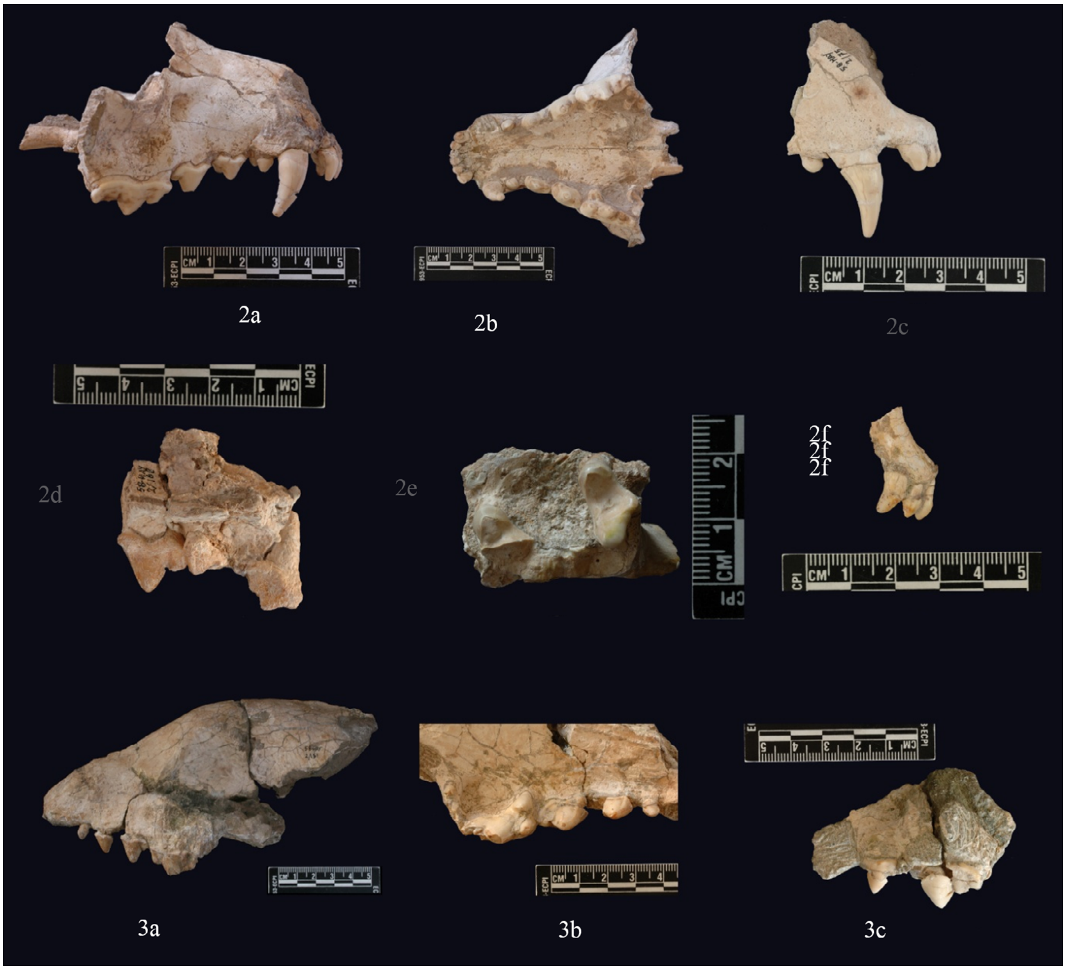

Figure 8. *Hyaenictitherium intuberculatum* Ozansoy, 1965, from Hayranlı-Sivas, maxilla 58-HAY-2/222, 2a. lateral, 2b. occlusal; maxilla 58-HAY-2/75, 2c. lateral; maxilla 58-HAY-2/168, 2d. occlusal; maxilla 58-HAY-2/101, 2e. occlusal; maxilla 58-HAY-2/57: 2f. lateral; *Lycyaena dubia* Zdansky, 1924, from Hayranlı-Sivas, maxilla 58-HAY-2/151, 3a. lateral, 3b. occlusal; and maxilla 58-HAY-2/152, 3c. lateral.

Upper teeth: In the right tooth sequence, P1 and C are missing, and I3 is detached from its enamel. In the left tooth sequence, the carnassial is broken, and P1 and C are missing. Apart from these, the rest are in good condition.

C: The canine is strong, located through the tooth sequence, and is leaning slightly. It has the same position as the incisive. It is pressed up against by the buccal lingual, is strong, and there is a larger root than cusp and a round root coronal pass. This roundness is mesiobuccal. The distal crest, starting from the top of the canine and the crest in the mesial lingual, extends to the root coronal pass.

I1, 2: The incisive are located on a curvy line.

I3: Looks like a canine and there is certain cingulum process bending through the lingual.

P1: Round and small. There is very certain cingulum in the buccal. The coronal part of the lingual is flattened and there is a small crest starting at the mesial of the cingulum ending on the top.

P2: Is a short and large tooth. There is no supporting cusp in the anterior. It is based at the distal of the cingular eminence and there is a cusp in the posterior. There is a well-developed cingulum around the tooth.

P3: Is a relatively short and large tooth. In the distolingual, there is a cavity caused by a certain-strong cingular eminence. On the mesiolingual corner of the tooth, there is a small anterior cusp. There is a crest starting from this cusp going to the top. There is a little cusp in the posterior and a weak crest extends to the top from this cusp.

P4: The carnassial is lengthened and the metacone in the distal is sharpened. The metacone has a 2-sided shape in the buccal. The distal part of the paracone forms the highest point of the carnassial and it is higher than its part in the mesial, and in between there is a buccalingual sulcus. The protocone is lower than the metacone and paracone, and it is located through the lingual with an angle to the paracone on the top. The posterior edge of the protocone begins one-third of the way behind the paracone and the whole coronal part of the carnassial leans through the distal on the cingulum. The distal parts of the paracone and metacone form the cutter. There is a certain cingulum all around the tooth.

M1: Has a large and spandrel paracone having an eminentia to the labial. The protocone is small as the paracone is long and high. There is a curve from the paracone to the protocone and the metacone is located in the middle distal of this curve. M1's lingual edge is in the proximal when compared with its buccal edge. Moreover, it is located in the proximal with P4 at a slight angle. The dental measurements of *H. intuberculatum* are given in Table 7.

Comparisons

This species was described from Sinap (Turkey) by Ozansoy (1965) as *Ictitherium intuberculatum* and later transferred to *Hyaenictitherium* (Bonis, 2004), in Yassıören, with 4 maxilla and 5 mandible items ground on. Ozansoy (1965) did not indicate a holotype for this species and, because of this, Werdelin and Solounias (1991) determined the mandible given by Ozansoy (1965 Pl, 2:3) to be a lectotype. However, Bonis (2004) cited Ozansoy (1965) in his Paris MNHN collection, and by examining specimens TRQ 1192 maxilla (P1–M1), TRQ 1191 maxilla (P3–M2), TRQ 1012 maxilla (P2–M1), TRQ 1013 (C, P3–M2), and hemimandibular TRQ 1014 (C, P2–M1), he was able to evaluate the TRQ 1012, TRQ 1013, and TRQ 1014 specimens as holotype. Ozansoy (1965) defined *H. intuberculatum*; the upper carnassial protocone is clear, is higher than that of Pikermi, Marageh *I. hipparionum*, and the protocone is in the anterior of the paracone. The first tuberculum of *Ictitherium* carnassials found in Sinap shows a bigger character. This type is more evolved than other *Ictitherium*. *H. intuberculatum* is bigger than *I. robustum* and smaller than *I. hipparionum*. Because of these data, *H. intuberculatum* shows a great difference from *I. hipparionum* of China, Greece, Iran, and Turkey. Werdelin and Solounias (1991) stated that this species' dimensions and metric characters are very close to those of Polgardi *I. pannocinum* and might be conspecific to the Hungarian form, but there are some differences in terms of the rates of M2 and M1. Hence, the 2 species are not synonymous. This species' approximate phylogenetic position is next to *I. viverium* Werdelin and Solounias (1991).

Viranta and Werdelin (2003) recorded *H. intuberculatum* from Sinap when they found specimens AS.92.223, AS.93.63, S.91.653, S.91.654, S.91, Sc.1, and S.91.854. The comparison of the maxillary tooth sizes of Ozansoy (1965), mid Sinap and Viranta and Werdelin (2003), and Sinap with the 58-HAY-2-222, 58HAY-2/75, 58-HAY-2/168, 58-HAY-2/10, and 58-HAY-2/57 specimens of Sivas-Hayranlı showed similarities. After the Paris MNHN collection, TRQ 1192 maxilla (P1-M1), TRQ 1191 maxilla (P3-M2), and TRQ 1012 maxilla (P2-M1) were seen by Özkurt; 58-HAY-2/222, maxillary fragment with right I1–I3, P1–P4, and M1–M2, and left I2–I3, P1–P4, and M1-M2; 58-HAY-2/75, maxillary fragment with right I1–I3, C, and P1; 58-HAY-2/168, maxillary fragment with right P3 and P4; 58-HAY-2/101, maxillary fragment with right P4, M1; and 58-HAY-2/57, maxillary fragment with left I-1-3 were included with the *H. intuberculatum* taxon. Comparisons of the upper tooth measurements of *H. intuberculatum* from Hayranlı-Sivas and various localities are given in Table 7 and Figure 9.

Family: Hyaenidae Gray, 1821

Genus: *Ictitherium* Wagner, 1848

Species: *Ictitherium* sp.

Locality: Hayranlı.

Age: MN11–12; Late Miocene, 9–7 Ma.

Material: 58-HAY-2/132, canine (lower right); 58-HAY-2/138, canine (lower right);

58-HAY-2/53, canine (lower left); and 58-HAY-2/252, part of isolated m1.

Description

Canine: Is strong, the posterior is curvy from the top of the corona, pressed from the sides, has a powerful root that is larger than the coronal part, and a round root coronal pass. There is a posterior crest that ends in the bulb of the distal part, which is not very clear. There is a certain mesial crest. The corona has a sharp and pointed top (Figure 10, 5a, 5b, 5c). The canine measurements of *Ictitherium* sp. are given in Table 8.

m1: Is considered as belonging to the *Ictitherium* species (Figure 10, 5f).

Comparisons

58-HAY-2/132, 58-HAY-2/138, and 58-HAY-2/53 left canine samples are evaluated as *Ictitherium* sp. after being matched with *Ictitherium* specimens in morphological and morphometric comparisons. 58-HAY-2/252 isolated (right); it is clear that m1 belongs to Hyaenidae.

Genus: *Lycyaena* Schaub, 1941

Species *Lycyaena dubia* Zdansky, 1924

Lycyaena dubia sp. nov. Zdansky, 1924; 1981 *Thalassictis* (*Lycyaena*) sp. nov. - Solounias & De Beaumont, 1981; *Thalassictis* (*Lycyaena*) *dubia* (Zdansky) - Qiu, 1985; and *Thalassictis* (*Lycyaena*) *dubia* (Zdansky) - Werdelin, 1988.

Locality: Hayranlı.

Age: MN11–12; Late Miocene, 9–7 Ma.

Material: 58-HAY-2/151, maxillary fragment with left P1–P4 and M1; 58-HAY-2/152, maxillary fragment with left P3–P4 and M1.

Description

Maxilla: 58-HAY-2/152, maxilla left P3–P4 and M1 (Figure 8, 3c); 58-HAY-2/151, maxilla left P1–P4 and

Table 7. Upper tooth measurements of *H. intuberculatum* from Hayranlı-Sivas and various localities.

	H. intuberculatum	*H. intuberculatum*	*H. intuberculatum*	*H. intuberculatum*	*H. intuberculatum*	*H. intuberculatum*	*H. intuberculatum*	*H. intuberculatum*	58-HAY-2/222	58-HAY-2/75	58-HAY-2/168	58-HAY-2 /101	58-HAY-2/57
Upper dentition	OZANSOY, 1965, Orta SİNAP	MN9 Viranta & Werdelin Sinap AS,92,223	MN9 Viranta & Werdelin Sinap AS,93,63	MN9 Viranta & Werdelin Sinap AS,92,276	MN9 Viranta & Werdelin Sinap S,91,653	MN9 Viranta & Werdelin Sinap S,91,654	MN12 Viranta & Werdelin Sinap Sc,1	MN12 Viranta & Werdelin Sinap S,91,854	Maxilla (right): I1–I3, P1–P4, M1–M2	Maxilla (right): I1–I3, C, P1	Maxilla (right): P3 and P4	Maxilla (right): P4, M1	Maxilla (left): I-1-3
LI1									3.40	3.47	-	-	3.48
BI1									3.94	4.22	-	-	4.80
LI2				4.5				4.2	4.57	4.27	-	-	5.08
BI2				5.3				5.5	4.88	4.73	-	-	5.20
LI3								6.8	6.33	5.49	-	-	6.39
BI3								4.2	6.50	5.95	-	-	6.41
LC								12.1	9.92	7.12	-	-	-
BC								8.0	6.81	9.81	-	-	-
LP1			6.1					5.1	6.35	5.00	-	-	-
BP1			4.1					4.8	5.15	4.05	-	-	-
LP2	13.0		12.6		11.7				12.23	-	-	-	-
BP2	5.8		6.5		6.0				6.16	-	-	-	-
LP3	16.0	17.1					17.3		15.79	-	16.33	-	-
BP3	7.8	10.1					9.5		8.15	-	9.49	-	-
LP4	24.0	24.2				16.8	26.4		25.44	-	-	-	-
BP4 ant.	13.0	15.3				8.5	14.7		13.53	-	-	-	-
BP4 post.									7.58	-	-	-	-
L blade									25.44	-	-	-	-
LM1	9.6	10.7					15.7		8.28	-	-	7.98	-
BM1	17.4	16.6					9.4		15.33	-	-	13.31	-
LM2		11					8.4		-	-	-	-	-
BM2		6					4.3		-	-	-	-	-

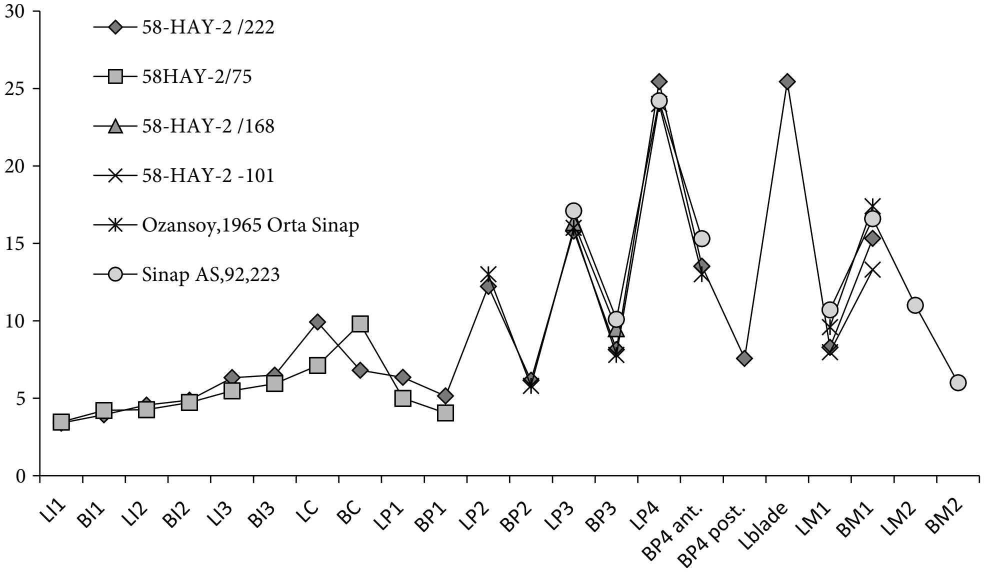

Figure 9. Comparison of the upper tooth measurements of *H. intuberculatum* from Hayranlı-Sivas and various localities.

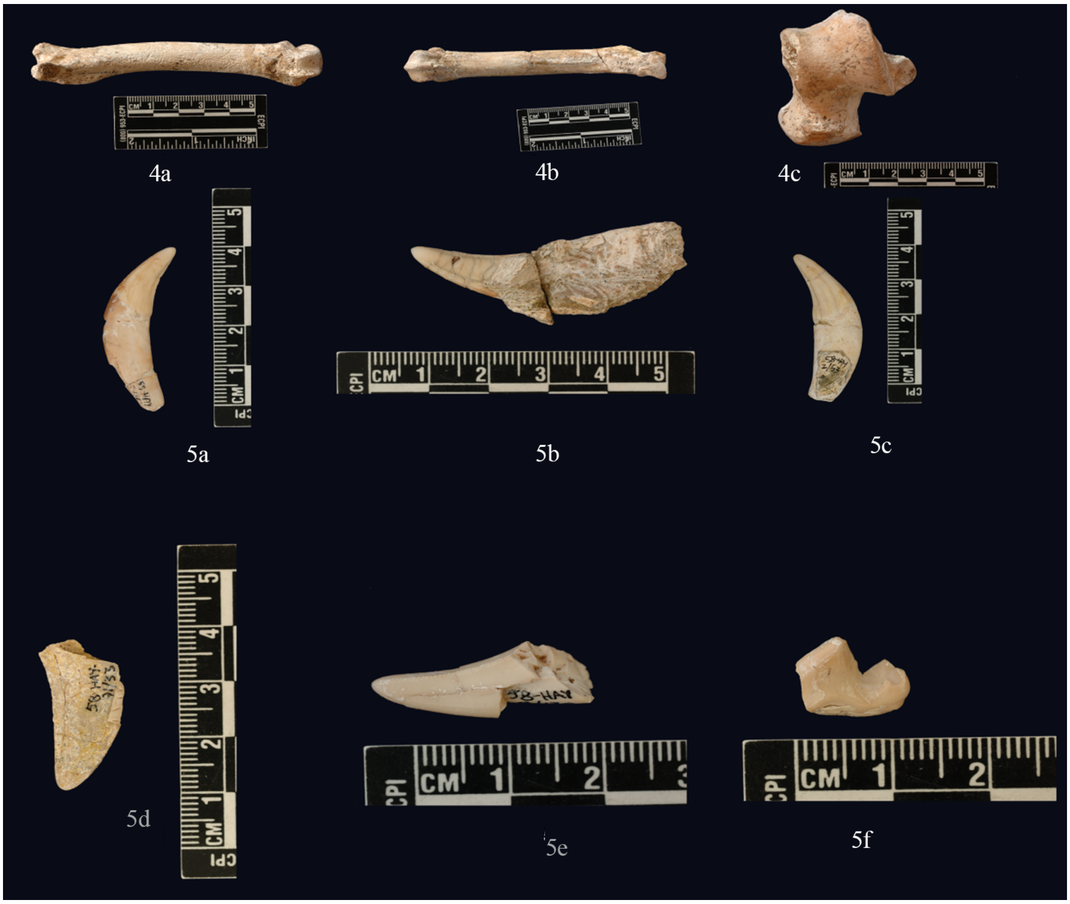

Figure 10. *Machairodus giganteus* (Wagner, 1848). Metatarsal III 58-HAY-91/5, 4a; Metatarsal II 58-HAY-91/8, 4b; Astragalus 58 HAY-91/7, 4c; *Ictitherium* sp., canine 58-HAY-2/132, 5a; canine 58-HAY-2/138, 5b; canine 58-HAY-2/53, 5c; Carnivora, canine 58-HAY-91/33, 5d; canine 58-HAY-2/130, 5e; and part of isolated m1 58-HAY-2/252, 5f.

Table 8. Canine measurements of *Ictitherium* sp. from Hayranlı-Sivas.

Specimens	58-HAY-2/132	58-HAY-2/138	58-HAY-2/53
Material	Canine (lower right)	Canine (lower right)	Canine (lower left)
Lc	6.74	9.98	8.51
Bc	9.74	6.79	10.51
Height of canine	20.56	18.90	22.81

M1 (Figure 8, 3a and 3b). The right part of the specimen, except for the left part carrying canines P1–P4 in the frontal, incisive, and dorsal parts of the skull, is lost. Has a higher skull than *H. intuberculatum* and *H. wongii*. The frontal part of the skull is relatively short (Figure 8, 3a, 3b, and 3c).

Upper teeth: On the left tooth sequence, the metacones and paracones of P1–P4 are broken near the buccal.

P1: Round, small, very certain cingulum in the buccal; the coronal part in the lingual is flattened, and there is a small crest starting from the mesial side of the cingulum, ending on the top.

P2: Is a short and large tooth. There is no supporting cusp in the anterior. The coronal height is quite large. On the mesiolingual corner of the tooth's anterior, there is a cingular eminentia, and there is a weak crest starting from the top of the cusp that becomes more defined near the cingulum. There is a cingulum all around the tooth, but it is stronger in the lingual.

P3: Has larger characteristics compared to the other P3s in the study. There is a large cavity in the distal of the tooth caused by a certain strong cingular eminence. On the mesiolingual corner of the tooth, there is a small cingular eminentia. A weak crest starting from the top of the cusp in the posterior goes through the cingulum. The cingulum is quite clear, especially in the labial.

P4: The carnassial is curved toward the dorsal side, and there is a certain cingulum, especially in the labial of the metacone. The protocone is located on the same plaque as the paracone in the buccalingual position, which means that the anteriors of the protocone and paracone start from the same point. The protocone is smaller, located in the paracone, and the paracone is smaller and located in the posterior part of metacone. There is a certain hole in the diagonal palate that was formed from the combination of the P4's dorsal edge and m1. The location of m1 has an angle larger than 90° through the dorsal when compared to P4. The dental measurements of *L. dubia* are given in Table 9.

Comparisons

A comparison of the measurements of the specimens of 58-HAY-2/151 with *L. dubia* from China and *L. chaeretis* from Samos, which are in between those of *L. dubia* and *L. chaeretis*, shows that they are generally bigger than those of *H. wongii* (Table 9). According to the size of the idems in the posterior ends of P4 and BP4 (anterior), *L. dubia* is a little larger than *H. wongii* and *H. intuberculatum*. *L. dubia* has a wider palate in between P4 but a shorter diastema, and comparatively has a bigger P4 according to 58-HAY-2/151 *L. dubia* than the *H. wongii* 58-HAY-1996 Sivas Yüzey and *H. intuberculatum* 58-HAY-2/222 specimens.

In the structure of the P4 carnassial, the protocone is settled lower compared to the paracone, the metacone has 2 parts and is located at approximately a 90° angle compared to M1 and P4, and the enamel in the lingual of P3 is very clear. 58-HAY-2/151 P4 has a higher paracone

Table 9. Upper tooth measurements of *L. dubia* from Hayranlı-Sivas and Hyaenids from several localities.

	LP1	LP2	LP3	LP4	LM1	BP1	BP2	BP3	BP4 ant,	BM1
L. dubia, 58-HAY-2/151, Turkey, Present Study	6.11	-	20.33	-	-	5.3	8.4	10.67	15.97	15.35
L. dubia, China, Werdelin, 1988	-	16.53	20.83	32.03	7.34	-	8.76	11.61	17.27	16.2
L. dubia, China, Zdansky, 1924	6.7	16.40	19.8	31.1	8.1	5.8	8.6	10.8	16.3	16.3
L. chaeretis, Austria, Samos, 2009	6.71	15.7	21	31	8	6.02	9.3	13	17.5	17.7
L. chaeretis, Greece, Pilgrim, 1931	-	16.7	19.8	31.5	8.1	-	9	12	17	16.3
T. hyoenoides, China, Werdelin, 1988	-	15.44	19.74	29.99	7.95	-	8.57	11.38	17.01	16.3
H. wongii, 58-HAY-1996, Turkey, Present Study	-	15.62	19.64	31.11	7.44	-	8.54	10.89	15.28	16.3
H. wongii, Turkey, Tekkaya, 1972	-	13.3	17.1	27.5	8.3	-	7.1	10	14.4	16.3
H. wongii, Greece, Koufos, 2009	5.2	12	15	24.4	7.3	4.5	6.4	9.1	13.3	16.3

than *H. wongii* and *H. intuberculatum*, M1 is wider and larger, and P3 is bigger and has a strong and recognizable crest from the bottom to the tip at the mesial side.

According to Werdelin (1988), the upper dentitions are fewer and less informative. The most marked feature is a tendency for the specimens of *Lycyaena* to have a narrow P4 blade, and 58-HAY-2/151 has this feature.

Specimens 58-HAY-2/151 and HAY-2/152 were compared with *Miohyaena montadai*, from Przeworno MF/1991/91 (Heizmann and Kubiak, 1992) in the Polish National Academy of Science in Krakow, and, as a result, they were found to be different from *M. montadai*.

Werdelin (1988) showed that *L. dubia* is close to *L. chaeretis* from Samos and Pikermi, so close that they may be conspecific. However, until sufficient material has been recovered of the latter species, it is better to consider *L. dubia* a distinct species of *Lycyaena*, since *L. dubia* is the better known of these species.

Werdelin (1988) mentioned that *L. dubia* is close to *L. chaeretis*; however, a comparison of the 58-HAY-2/151 specimens with Samos A. 4744-*Lycyaena chaeretis* and Zdansky, 1924 M. 3856-*Lycyaena dubia* shows that it more closely resembles *L. dubia*, especially because the skull height from a lateral view is the same. The most recognizable feature of Sivas 58-HAY-2/151 is the height of the skull. 58-HAY-2/151 has a higher skull than *H. intuberculatum* and *H. wongii*, and also higher than Samos A. 4744 *L. chaeretis*, and the frontal part of the skull is relatively short.

As a result of the morphological and morphometric comparisons of the study findings, it was decided that the specimens 58-HAY-2/151, a maxillary fragment with left P1–P4 and M1, and 58-HAY-2/152, a maxillary fragment with left P3–P4 and M1, should be included in the *Lycyaena* aff. (conf.) *dubia* taxon.

Family: Felidae Gray, 1821
Genus: *Machairodus* Kaup, 1833
Species: *Machairodus giganteus* (Wagner, 1848)
Locality: Hayranlı.
Age: MN11–12; Late Miocene, 9–7 Ma.
Material: 58-HAY-91/5, metatarsal III (right); 58-HAY-91/8, metatarsal II (right); 58 HAY-91/7, astragalus (right).

Description

Metatarsal III (right) (Figure 10, 4a): The proximal joint face is spandrel and has a concave shape, leaving a groove in the middle. There is a very clear tubercle at the end of the surface where it connects with metacarpal 2, which has a sagittal orientation. The body has a slight curve, just like metacarpal 2. The trochlea, which is on the distal joint surface, is divided into 2 equal pieces, with a clear crest in the middle. The measurements of metatarsal III are given in Table 10.

Metatarsal II (right) (Figure 10, 4b): The joint part of the proximal edge in the medial is broken, hence making an anatomic determination from this specimens not possible. The axle is slightly curved. The medial and lateral parts of the trochlea that are on distal edge are the same size and the crest between them is quite clear. The measurements of metatarsal II are given in Table 10.

Astragalus (right) (Figure 10, 4c): Covers a larger area than the tibia surface of the lateral medialin. The additional surface of the lateral is quite smooth and is in a half-moon shape. The lateral surface is concave, while the medial surface is convex. The tuber calcanium is quite certain. Measurements of the astragalus are given in Table 10.

Comparisons

Bonis (1994) mentioned that a *Machairodus aphanistus* was found in the lower level localities of Kemiklitepe, which would indicate that it was from the Late Vallesian or Early Turolian. A skull and associate mandible from the upper level of Kemiklitepe is one of the most complete known specimens of *M. giganteus* UEK-124, recorded in the Late Miocene fauna of Kemiklitepe by Geraads et al. (2004). According to previous findings, *M. giganteus* was distributed in Anatolia in Late Miocene carnivore fauna.

The third metatarsal III of 58-HAY-91/5 is almost the same in dimensions to that of *M. giganteus* (AMPG PA 3256/91) from Pikermi (maximum length: 119.7 mm, distal breadth: 22.3 mm) (Roussiakis, 2002).

In the Paris MNHN collection of PIKERMI, for Greek specimens of *M. giganteus* PIK 3278 metatarsal III of the proximal tip is broken, PIK 3279 metatarsal III of the proximal part, the PIK 3244 metatarsal III proximal tip is broken, the PIK 3240 metatarsal II proximal part is broken, the PIK 3280 metatarsal II proximal tip is broken,

Table 10. Measurements of the *M. giganteus* metatarsal III, metatarsal II, and astragalus from Hayranlı-Sivas.

Specimen	58-HAY-91/5	58-HAY-91/8	58-HAY-91/7
Material	Metatarsal III	Metatarsal II	Astragalus
Maximum length	118.00	133.7	52.90
Distal breadth	22.24	22.00	-

and they all have the same features as the 58-HAY-91/8 metatarsal II and 58-HAY-91/5 metatarsal III, and as the unpublished specimens of metatarsal III and metatarsal II of *M. giganteus* of Dr Koufos of the University of Thessaloniki, Greece.

In the Madrid MNCN (Madrid Natural History Museum) collection of Los Valles De Fuentidueña specimens of metatarsal II MNCN 65889, 68890, and 65891 of *Machairodus alberdiae* are almost the same in terms of their anatomy but they are quite small. A comparison of the maximum length shows the *M. giganteus* 58 HAY-91/8 metatarsal II as 133.7 mm and the MNCN *M. alberdiae* 65891 metatarsal II as 108.05 mm.

On the other hand, *Machairodus aphanistus* specimens from Batallones (Madrid) of B-1894 show metatarsal II (max length: 138.31 mm, distal breadth: 22.41 mm), metatarsal III (max length: 128.34 mm, distal breadth: 19.84 mm), B-707 metatarsal II (max length: 135.80 mm, distal breadth: 20.13 mm), metatarsal III (max length: 131.50 mm, distal breadth: 18.82 mm), B-7157 metatarsal II (max length: 142.70 mm, distal breadth: 26.40 mm), metatarsal III (max length: 141.80 mm, distal breadth: 19.57 mm), B-2695 metatarsal II (max length: 130.10 mm, distal breadth: 23.67 mm), and metatarsal III (max length: 128.00 mm, distal breadth: 19.23 mm). The average Batallones (Madrid) specimen has a metatarsal II maximum length of 136.72 mm, metatarsal III maximum length of 132.41 mm, metatarsal II distal breadth of 23.15 mm, and metatarsal III distal breadth of 19.36 mm. According to these measurements, *M. giganteus* is smaller than *M. aphanistus* but larger than *M. alberdiae*.

All of these comparisons show that 58-HAY-91/8 metatarsal II and 58-HAY-91/5 metatarsal III belong to the *M. giganteus* taxon. The 58-HAY-91/8 metatarsal II, 58-HAY-91/5 metatarsal III, and 58 HAY-91/7 astragalus were found together and were associated with each other, which is most probably because they belong to the same specimen and taxon.

The Madrid MNCN collection of Concud (Tervel) *Amphimachairodus giganteus* specimen of astragalus MHCN 14.669 has a maximum length of 51.90 mm, and the Batallones (Madrid) *Machairodus aphanistus* specimens B-6029, B-633, and B-2024 of the astragalus have maximum lengths of 66.38 mm, 61.00 mm, and 57.85 mm, respectively.

58 HAY-91/7 astragalus has the same dimensions as Concud Astragalus MHCN 14.669, but is smaller than Batallones (Madrid) *Machairodus aphanistus* B-6029, B-633, and B-2024.

The specimens of 58-HAY-91/7 astragalus were deemed to include the *M. giganteus* taxon according to the comparisons of the Concud (MN12) (Tervel) specimens of the astragalus MHCN 14.669 and unpublished specimens of the astragalus of *M. giganteus* of Dr Koufos of the University of Thessaloniki, Greece.

Order: Carnivora Bowditch, 1821

Locality: Hayranlı.

Age: MN11–12; Late Miocene, 9–7 Ma.

Material: 58-HAY-91/33, canine (upper left); 58-HAY-2/130, canine (upper right); 58-HAY-2/55, distal part of the humerus; 58-HAY-2/244, distal phalanx; and 58-HAY-2/54, medial phalanx.

Description

Canine: Is very strong, there is a certain and blade mesial ridge (Figure 10, 5d, 5e). Has a larger and shorter corona compared to the other canines.

Humerus: Is a part of the humerus trochlea (Figure 11, 6). In the morphology of the trochlea, it is defined as carnivore indet.

Distal phalanx (claw) (Figure 11, 7): The joint surface in the distal has a subversion. A quite clear sulcus can be seen from the plantar.

Medial phalanx (Figure 11, 8): The proximal edge of the medial phalanx is stable but the distal part is broken. The crista in the trochlea divides the joint surface into 2 pieces.

Comparisons

58-HAY-91/33, left upper canine; 58-HAY-2/130, right upper canine; 58-HAY-2/157, cranium; 58-HAY-2/55, humerus (distal piece); 58-HAY-2/244, distal phalanx; and 58-HAY-2/54, the medial phalanx specimen shows that these are carnivore, but they do not have a diagnostic characteristic to make a detailed taxonomic evaluation.

4. Discussion

According to the results of this study, carnivores *H. wongii*, *H. intuberculatum*, *L. dubia*, and *M. giganteus* lived in Sivas-Hayranlı habitats. However, it is certain that with future studies these biological diversifications will increase. Moreover, the *L. dubia* taxon is a first record for the fossil fauna of Turkey.

In this study, 25 different fossil specimens (Table 1) were evaluated from the Sivas-Hayranlı location, and 4 species, 4 genera, 2 families, and 1 order are listed. From these definitions, there were 4 carnivore species living in Hayranlı in the Late Miocene. Of these carnivores, *M. giganteus* is a large carnivore and *H. wongii*, *L. dubia*, and *H. intuberculatum* can be listed as medium-sized carnivores.

4.1. Paleoecology and paleoenvironments of the Sivas carnivore fauna

The carnivore fossils described in this study derived from the Derindere Member of the İncesu formation, located in the Sivas Basin. The Sivas Basin is located in east-central Anatolia and straddles the Eurasian Plate in the north and the Taurides (of Gondwanan affinity) in the south. Akgün

Figure 11. Carnivora Bowditch, 1821. Distal part of the humerus 58-HAY-2/55, 6; distal phalanx 58-HAY-2/244, 7; and medial phalanx 58-HAY-2/54, 8.

et al. (2000) defined the paleoecology of the Sivas region and the plant association shows forest associations of the riversides or/and lakesides, while the mixed forest shows plains and grassy biotopes and also shows a seasonally moist and warm climate that has an exception in summer heat. The İncesu formation of Late Miocene Düzyayla is located 50 km northeast of Hayranlı; therefore, both belonged to the same ecosystem during the Late Miocene and the fossils of the mammals symbolize forest and grassy lands. In Hayranlı-Sivas, having 6 bovid species shows the suitability of the ecosystem for carnivores (Bibi and Güleç, 2008). We might say that this ecosystem had a fauna that allowed 4 species of carnivores, *H. wongii*, *H. intuberculatum*, *L. dubia*, and *M. giganteus*, to survive, which were determined in this study. The carnivore fauna at the MN11 localities was 68% Hyaenidae and 12% felids, and they were large-sized, terrestrial, and cursorial, mainly carnivorous-hypercarnivorous and bone/meat predators. According to the carnivore fossil fauna, the Hayranlı fossil localities, as a part of the Greco-Iranian biogeographic province at the Late Miocene, were open and dry environments.

H. wongii, which is very well known at the Late Miocene sites of China and lived in a large area spanning all the way to Greece; *H. intuberculatum*, represented by a few areas in Anatolia and Greece; *L. dubia*, spanning a large area from Asia to Spain; and *M. giganteus*, which is the common cat of the Late Miocene, were all definitely among the hunters of the Hayranlı locality. The Hayranlı predators would have been well suited for the Late Miocene ecosystem, which was dry, grass-dominant, and mosaic savanna vegetation open habitats compared to the early and Middle Miocene ecosystem, which was described by Akgün et al. (2007) and Akkiraz et al. (2011). Anatolia was wet, warm, and humid (the suggested mean annual precipitation was between 1000 and 1400 mm, and the mean annual temperature was between 16.5 and 20.8 °C) from the Early Miocene to the Middle Miocene. The mean faunal hypsodonty index for all of the large mammal and plant-dominated taxa from Greece to Afghanistan shows that open and grassland ecosystems appeared in the eastern Mediterranean by the Middle Miocene, and the habitat reconstruction derived from the paleosols data establishes that more open deciduous woodland and arid habitats were present at that time in central Anatolia (Fortelius et al., 2002; Strömberg et al., 2007; Eronen et al., 2009, 2010).

During the Late Miocene of the eastern Mediterranean, herb and grassland ecosystems became dominant and the number of mammal species adapted to an open habitat increased. This climatic cooling event during the Late Miocene coincides with Zachos et al.'s (2001) marine isotopes. Strömberg et al. (2007) conducted fossil vegetation analyses in Turkey and Greece. According to that work, from the Middle Miocene to the Late Miocene and around Turkey, the existence of grass-dominant and mosaic savanna vegetation open habitats can be seen.

Hayranlı predators were suited for the ecological area described by Zachos et al. (2001), Koufos (2005, 2011), and Strömberg et al. (2007), which was sometimes shrubbery and shrublands, and partly open grasslands. The fossil specimens of *Hipparion*, bovids, suids, and giraffe and rhino in the excavation area all support this thought. More specifically, *M. giganteus*, which had short legs that would not have been suitable for a long chase, probably hunted big and slow-moving animals. The hyena group applied their hunting strategy with small groups on a hierarchical order. Of this group, *L. dubia* is important because of its adaptation to long-range running due to its long metapoids and because it is the first example from Turkey. Moreover, *H. intuberculatum*, which also had short, slender legs and could survive among the great predators of Eurasia, is quite remarkable.

The other fauna members discovered at the Hayranlı locality, such as Suidae (Made et al., 2013), Gliridae (Kaya and Kaymakçı, 2013), Bovidae (Bibi and Güleç, 2008), and Lipotyphla (Furio et al., 2014) describe the existence of shrubland and savanna-like grassland geography when evaluated as a whole. The average hypsodonty value, according to the big mammal findings of herbivore-omnivores that were discovered at the Hayranlı locality, supports this finding (Kaya and Kaymakçı, 2013). Additionally, there were no primate fossils at the Hayranlı locality, while *Ankarapithecus meteai* and *Ouranopithecus turkae*, seen in Anatolia during this time period, point to a more open area.

4.2. Biochronology and paleobiogeography of the Sivas fossil beds

The geographic area that presently incorporates the southern Balkans, Turkey, and part of the south peri-Pontic region formed during the Late Miocene western domain of the so-called Greco-Iranian biogeographic province (Bonis de et al., 1992). The fossils of Hayranlı in this study were from the Derindere region of the İncesu formation, from the Sivas plain, belonging to the Greco-Iranian biogeographic province.

According to Koufos (2011), it is quite clear that the majority of the localities of the Greco-Iranian province included in biozones MN9–12 are fluvial. As a locality of the Greco-Iranian province, the Hayranlı localities show a fluvial feature. The findings of Kaymakçı (2000) support the fluvial feature of the Hayranlı localities. Kaymakçı (2000) indicated that the İncesu formation to which Hayranlı belongs is characterized by the presence of limestone and gesso, together with the salty lake wetlands on the mountainsides of the temporarily dry land fluvial deposits. The majority of the localities included in the biozone MN9–12 mammal fauna are thanatocoenoses, consisting of elements carried by water from a wider area and living in different habitats (Koufos, 2011). The fossilization type of the Hayranlı localities indicates that the fauna of the Hayranlı localities is a thanatocoenosis.

The carnivore fossils examined in this study derive from the HAY-2 and HAY-91 localities. According to the excavations at the HAY-2 locality, the fauna comprise 45% Equidae, 30% Bovidae, 17% Carnivora, 5% Suidae, 3% Elephantidae, and 5% Rhinoceortidae, Giraffidae, and some unknown taxa. At the Hay-91 locality, the fauna comprise 51% Bovidae, 16% Equidae, 12% Carnivora, and 6% Elephantidae, and the rest are Suidae and some unknown taxa. The Hayranlı carnivore faunas at the MN11 localities comprise 68% Hyaenidae and 12% felids, and they are large-sized, terrestrial, and cursorial, mainly carnivorous-hypercarnivorous and bone/meat predators. The Sinap carnivores are relatively abundant [23% (87% hyaenids, 17% felids)]. Koufos (2005) reported that the best documented Vallesian locality (MN9) fauna is that of the Sinap localities in Turkey. The MN10 faunas of the southeastern Mediterranean are poorly documented, mainly from Greece and Turkey, and 1 locality in Bulgaria. Carnivores are also abundant (22%) and their composition includes a high percentage of Hyaenidae (64%) and felids (29%). If compared with the Vallesian locality (MN9) Sinap localities in Turkey and the Vallesian faunas of western and central Europe (MN10), the findings indicate that Hayranlı is Turolian (MN11–12). The varieties and the great deal of mammal fossils of the Sivas-Hayranlı localities found in the eastern Mediterranean are quite significant, providing a good base for further comparisons and discussion. The geological age of the faunas and the paleogeography of Haliminhanı are already well known as MN11–12 from previous studies, and, essentially, this one.

The arrival of *Hipparion* in Eurasia from America, known as *Hipparion*-datum, was a major event used extensively in biostratigraphy and biochronology as a marker of the beginning of the Late Miocene (MN9). A strong sea level drop around 11.0 Ma reopened the Beringian land-bridge (Haq et al., 1988; Kufos et al., 2005) and some North American mammals entered Eurasia. In the eastern Mediterranean, recent magnetostratigraphic data from Turkey suggest an age of 10.7 Ma (Kappelman et al., 2003). Thus, presently, the beginning of the Late Miocene (arrival of *Hipparion*) must be considered at 10.7 in the eastern Mediterranean. Hipparions constitute a great deal of the fossils coming from Hayranlı, especially at the 58-HAY-19 locality and surrounding area (Güleç et al., 2007). Hayranlı localities at the same stratigraphic levels give various paleontological and sedimentological differences. The faunal and stratigraphic results show that locality 2 shows a more open area than locality 91. The observed difference after the excavations at the Hayranlı localities shows that the Sivas Basin has a very rich fauna. Even though the Sivas fossils mostly give us MN11 or early MN12 biozones, the existence of Tethytragus is a good example of fossils giving MN5 and MN8 biozones (Bibi and Güleç, 2008). Another example is the 0.6-Ma-year difference between localities 2 and 91 (Made et al., 2013).

The open/dry conditions continued during the Turolian in the eastern Mediterranean region. The analysis of the mammal faunas suggests an open environment of extended grasslands with small trees, bushes, and shrubs, with seasonal rainfall followed by dry periods. The environment was characterized by a gradual increase in aridity from west to east (Koufos, 2011). The cooling down of the climate towards the end of Turolian caused the appearance of open life systems such as dessert, graze lands, and tundra, and also resulted in the reduction of closed ecosystems such as forests. As a result, the diversity of mammal fauna in Anatolia was at its highest and there was a great deal of mammal migration into Anatolia when the geographic barriers occasionally disappeared between the continents.

The faunal variety, as a result of the Messinian crisis, began to reduce by the end of the Turolian and this continued until the end of the Ruscinian and Villanian. Anatolia is regarded as an important domain for mammal exchanges between Asia, Europe, and Africa during the Neogene. In this geographic region, migration pathways between the 3 continents crossed (Kufos et al., 2005).

Participating in the Greco-Iranian province, *Gazella* cf. *G. capricornis*, *Prostrepsiceros houtumschindleri syridisi*, cf. *Protoryx* sp., *Tethytragus* cf. *T. koehlerae*, and *Tragoportax* cf. *T. amalthea* (58-HAY/14, 19, 23, and 70) have been assigned to late MN11 or early MN12 (Bibi and Güleç, 2008). Additionally, a lower MN11 age is suggested for Hayranlı (58-HAY/2 and 19) based on the evolutionary stage of the suid (*Microstonyx major*) collection (Made et al., 2013). Made et al. suggested that *Microstonyx* showed changes in incisor morphology, which are interpreted as a further adaptation to rooting. This probably occurred during a short period between 8.7 and 8.121 Ma and was possibly a reaction to environmental changes (Made et al., 2013). Moreover, Gliridae (Mammalia, Rodentia) including *Microdyromys koenigswaldi* and *Myomimus maritsensis* were yielded from the 58-HAY/84 locality (Kaya and Kaymakçı, 2013). Thus, there is a significant faunal exchange from forest dwellers to ground-dwelling species, which is characterized by the increase in *Myomimus* finds from a number of localities during the Late Miocene, probably attributable to the vegetational shift from predominating forested wetland environments to open woodland and steppe-like environments. Furthermore, Furio et al. (2014) found an almost identical faunal content of the localities from Hayranlı (58-Hay/80-82-83-84-85), including 1 erinaceid (*Schizogalerix sinapensis*), 5 soricids (including *Paenelimnoecus* sp., *Amblycoptus oligodon*, *Petenyia dubia*, Soricinae indet., and Crocidurinae/Crocidosoricinae indet.), and 2 talpids (*Desmanella* aff. *cingulata* and *Desmanodon larsi* sp. nov.). The insectivore assemblage is typical for the Late Miocene. It points to an Early or Middle Turolian (MN11–12) age (Furio et al., 2014). Additionally, during this time-span, a significant number of hominoids appeared, representing *Ankarapithecus meteai* and *Ouranopithecus turkae* in Anatolia.

4.3. Conclusions

In this study, the fossil specimens of Turkey and the surrounding localities were evaluated to see the biochronological relationship between various localities and Sivas/Hayranlı. Kınık (Tekkaya et al., 1972) MN12, Sinap (Viranta, 2003) MN9, Çobanpınar (Şenyürek, 1960) MN12, Akkaşdağı (Bonis, 2005) MN12, Mordoğan (Kaya et al., 2003) MN6, Kemiklitepe (Bonis, 1994) MN11, Paşalar (Viranta and Andrews, 1995) MN6, and Çandır (Nagel, 2003) MN5–6 of Greece are from Pikermi (Forsyth Major, 1894; Pilgrim, 1931; Solounias, 1981; Bernor et al., 1996; NOW, 2007–2008; Koufos, 2009). The MN12, Axios valley (Koufos, 2000) MN12, Mytilini (Koufos, 2009) MN11–12, and Maragheh (Mecquenem, 1924–1925; Campbell et al., 1980; and Bernor, 1986) MN11–12 localities show that Sivas/Hayranlı localities are dated as MN11–12.

According to their biochronological relationships, the Sivas carnivores expanded mainly between European MN11 and 12, or 8.7–6.6 million years ago. The geographic area that presently incorporates the southern Balkans, Turkey, and part of the southern peri-Pontic region formed the western domain of the so-called Greco-Iranian biogeographic province during the Late Miocene (Bonis de et al., 1992). Kostopoulos (2009) emphasized that the early Turolian large mammal association of southeastern Europe, although it followed general trends, seemed to absorb most of the environmental vibrations that provided more vigorous reactions in the eastern sector (i.e. Anatolia). While Anatolia experienced a phase of increasing species richness during this period, mainly controlled by successive immigration/origination waves of perissodactyls and artiodactyls, the western sector shows remarkable faunal stability. At the same time, faunal exchanges between the southern Balkans and Anatolia appear to be low, implying a kind of geographic isolation. Strömberg et al. (2007) summarized earlier views supporting a climatic and vegetational gradient across the Greco-Iranian province, with increasing aridity and decreasing tree coverage toward the east. Although a climatic gradient might well have existed, it seems insufficient to fully explain the observed faunal differences and the apparent faunal-swap restrain between the southern Balkans and Anatolia. Other lines of evidence point to a real physiogeographic barrier between these 2 geographic sectors. During the Late Miocene, a great number of mammal taxa from Asia and Africa arrived in Europe using Anatolia as an access road. The mammalian localities in Turkey are quite abundant and provide good knowledge of the faunas (Koufos, 2003). The importance of migration through this geographic region is that the various mammalian dispersal events can be used for a biostratigraphic division.

The Sivas fossil carnivore faunas in the MN11–12 zone, being typical for the Turolian, are quite similar to those of the Greek Pikermi, Axios Valley, and Mytilini and Turkish Kınık and Kemiklitepe locations, which are about 8.2–6.4 million years old. Moreover, they are also similar to those of the Sinap locality, which is 11 million years old, in the MN9 zone. Furthermore, these data support that the Sivas fossil localities are Turolian, in the MN11–12 zone, and are 7–9 million years old by means of their biochronological relationship.

In the Sivas fossil localities, the ecological characters of the carnivore fossil fauna symbolize that the seasonal moist and warm climate of the ecosystem had a grass-dominant mosaic savanna vegetation character, as described by Strömberg et al. (2007).

After the evaluations about noncarnivore fauna at the Sivas localities, it was understood that the ecosystem had a partially shrubland and partially savanna-like geographical structure.

It was also understood that the carnivores obtained from the Sivas localities were suited for an ecological environment that was sometimes shrub- and bushland, and partially open grassland. Even the stratigraphic differences among Haliminhanı localities make it difficult to determine the countless fossil environments, and the differences between localities 2 and 91 are important. When we look at the topographic localities as a whole, where the HAY-2 and HAY-91 localities are situated, you can see that they are geomorphologically stable. In Figure 1, the stratigraphic view shows that the HAY-2 locality is situated at 1382 m and the Hay-91 locality is situated at 1319 m. This positioning shows that the HAY-2 locality is older than the HAY-91 locality. Adapted to a more closed ecological environment, *M. giganteus* was probably the most dominant carnivore of the HAY-91 locality. *H. wongii*, *H. intuberculatum*, and *L. dubia* of the HAY-2 locality take their place in the literature as carnivores that preferred a more open ecosystem. The differences between these 2 localities show a diversion in the vegetation, from a humid forest environment to an open forest steppe-like environment, due to a reduction in rainfall.

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