

Tip-Tugai Cave, the First Cave Hyena *Crocota spelaea* (Goldfuss, 1823) Den Found in the Urals

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Abstract—The Tip-Tugai Cave (52°59′28.6″ N, 57°00′22.3″ E) is described as a new site with cave hyena *Crocota spelaea* fossils. The bone-bearing layer was dated to marine isotope stage (MIS) 3 based on the species composition of the fauna of large and small mammals. Finds of abundant remains of cave hyenas of different ages and bones of large herbivores with hyena gnaw marks indicated that the Tip-Tugai Cave was used as a hyena den in the Late Pleistocene. This is the first cave hyena den described in the Urals.

Keywords: *Crocota spelaea*, Late Pleistocene, hyena den, Southern Urals

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Ancient dens of carnivorous mammals provide a unique subject of paleontological studies. Studies of such localities yield data not only on the history of vertebrate fauna, but also on the ecology and ethology of extinct carnivores. Dens utilized by a single carnivore species are of particular interest, but are found rarely [1, 2].

The cave hyena *Crocota spelaea* (Goldfuss, 1823) is one of the species that utilized caves as dens. The cave hyena was a key member of the carnivore guild in Late Pleistocene faunas of Eurasia [3]. More than 100 localities with *C. spelaea* remains are currently known in Europe [4]. However, only some of them have been described unequivocally as hyena dens [2, 5, 6]. These localities are even fewer in Russia and include Barakievskaya Cave in the North Caucasus and Denisova Cave in Altai [2]. In the Urals, *C. spelaea* fossils have been found in 14 localities, but the finds usually consist of individual teeth or bones, and none of the localities has been described as a hyena den [7, 8].

Cave hyena dens have several features in common. Hyena remains are abundant, accounting for 10–30% of the total amount of remains of large mammals, and include fossils of individuals of different ages. Traces of hyena activities are detectable in dens: bones of large herbivores have gnawing marks, there are bones and teeth with digestion traces, and hyena coprolites might be found [2, 9]. Cannibalism signs, that is, hyena bones with hyena gnawing signs, are characteristic of dens [10]. A predominance of juvenile individ-

uals in the age composition indicates that the cave might be used as a natal den (maternal chamber) [5]. The so-called nibbling sticks are fragments of long bones of large mammals showing signs of gnawing by hyena cubs at one or both ends [11].

The Tip-Tugai Cave was discovered in 2021 by members of the Protei speleologists' club of Magnitogorsk. The locality is among the largest in the Urals in terms of the abundance of cave hyena fossils, along with the Smelovskaya II and Ust'-Katavskaya caves [8, 12]. The objective of this work was to analyze the fossils of hyenas and the accompanying fauna of large mammals in order to determine the taphonomic type of the locality in the Tip-Tugai Cave.

The Tip-Tugai Cave is located in the Bashkiriya National Park in Burzhanskii District of the Republic of Bashkortostan (52°59′28.6″ N, 57°00′22.3″ E), on the right bank of the Belaya River, at an altitude of 365 m. The cave is of a passageway type; the mouth faces southward; the floor is rising gradually; a main passageway is 83 m long and has a mean width of 2.2 m, a height of 1.5 m, and an amplitude of 7 m.

An excavation site was 40 m away from the mouth and was 1.5 × 1.5 m in dimensions. Loose deposits consist of brown clay loam and are approximately 1 m deep. The deposits are rather uniform lithologically and lack distinct stratigraphic horizons; only a slight darkening of the deposits is seen in lower horizons (at a depth of 0.8–1.0 m). Subrounded limestone pieces ranging in size from 1 to 10 cm are found both on the surface and within the deposit depth; their number substantially decreases with depth. The deposits were excavated by conventional 10-cm horizons parallel to the surface. All of the soil was washed on sieves with a mesh size of 0.1 cm. Bone remains were detected in all

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Table 1. Age composition of cave hyenas from the Tip-Tugai Cave

Age class	Juvenile		Subadult	Adult	Old
	2–8 months	8–12 months	1–3 years	3–16 years	>16 years
Number of teeth	8	10	7	8	2
Minimum number of individuals	3	4	5	3	1

horizons. The greatest amount of fossil bones was excavated from a depth of 40–60 cm.

Two types of bone remains were possible to recognize by the extent of fossilization and coloration. One type included slightly fossilized bones, cream colored or light yellow. Most bones of the type were found on the cave floor and in upper horizons (to a depth of 0.4 m). These were Holocene-type bones.

The other type is represented by fossilized bones that were black, dark yellow, and dark gray in color. Most bone remains of the type were found in the middle part of the deposits (at a depth of (40–60 cm). Bones of the type were occasionally found on the cave floor as well. These bones were of a Late Pleistocene age. Bones of both types could be detected in the same horizon. Only bones that belong to the second type by the extent of fossilization and coloration were considered in this work.

A collection of bone remains from the Tip-Tugai Cave was deposited in a museum of the Institute of Plant and Animal Ecology (coll. no. 2400).

The large herbivorous mammalian fauna included the mammoth *Mammuthus primigenius* Blumenbach, 1799; horse *Equus* sp.; woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799); Irish elk *Megaloceros giganteus* (Blumenbach, 1799), steppe bison *Bison priscus* Bojanus, 1827; saiga antelope *Saiga tatarica* (L., 1776); and camel *Camelus* sp.

Predatory mammals included the family Hyaenidae, which was represented by remains of the cave hyena *C. spelaea*. In addition, there were remains of species belonging to the families Canidae: the wolf *Canis lupus* L., 1758 and fox *Vulpes vulpes* (L., 1758); Ursidae: the brown bear *Ursus arctos* L., 1758 and large cave bear *U. kanivets* Vereshchagin, 1973; Mustelidae: the marten *Martes* sp.; wolverine *Gulo gulo* L., 1758; steppe polecat *Mustela eversmanii* Less., 1827; least weasel *M. nivalis* L., 1766; stoat *M. erminea* L., 1758; and *Mustela* sp.; and Felidae: the cave lion *Panthera spelaea* Goldfuss, 1810.

The species composition of small mammals included species of three orders (Eulipotyphla, Lagomopha, and Rodentia): the common mole *Talpa europaea* L., 1758; hare *Lepus* sp.; Eurasian beaver *Castor fiber* L., 1758; shrew *Sorex* sp.; pika *Ochotona* sp.; ground squirrel *Spermophilus* sp.; bobak marmot *Marmota bobak* (Muller, 1776); great jerboa *Allactagula major* (Kerr, 1792); lesser jerboa *Allactagulus* sp.; European hamster *Cricetus cricetus* (L., 1758); gray

dwarf hamster *Cricetulus migratorius* (Pallas, 1773); Eversmann's hamster *Allocricetulus eversmanni* (Brandt, 1859); northern mole vole *Ellobius talpinus* (Pallas, 1770); voles *Clethrionomys* ex gr. *rutilus–glareolus*; steppe lemming *Lagurus lagurus* (Pallas, 1773); yellow steppe lemming *Eolagurus luteus* (Eversmann, 1840); European water vole *Arvicola terrestris* (L., 1758); narrow-headed vole *Lasiopodomys gregalis* (Pallas, 1779); tundra vole *Alexandromys oeconomus* (Pallas, 1776); and gray vole *Microtus* ex gr. *arvalis–agrestis*.

The large and small mammal faunas correspond to Late Pleistocene faunas of the Southern Urals [13] and can be dated to the middle of the Late Pleistocene (marine isotope stage (MIS) 3). Their age is supported by data from a morphological analysis of teeth of *Lasiopodomys gregalis*, a dominant species of the small mammal fauna.

In total, 43 cave hyena bones were found in the Tip-Tugai Cave, including 3 mandibular fragments, 35 individual teeth, 1 skull fragment, and 7 limb bones. The other large carnivorous mammals were represented by single finds, and cave hyena remains accounted for 33% of the total number of large mammal fossils.

The ages of individual hyenas were inferred from tooth characteristics and the extent of epiphyseal fusion [14, 15]. Deciduous teeth without signs of wear (2–8 months of age), deciduous teeth with signs of wear, and permanent teeth whose roots are not fully developed (8–12 months of age) were assigned to juvenile hyenas. Permanent teeth with slight, if any, signs of wear were assigned to subadults (1–3 years of age). Teeth with moderate crown wear were assigned to adults (3–16 years of age). Teeth with a crown worn down heavily almost to its base were assigned to old hyenas (>16 years of age).

Teeth of hyenas representing all of the age classes were found in the Tip-Tugai Cave (Table 1). Juvenile hyenas accounted for 44%; subadults, 31%; adults, 19%; and old hyenas, 6% of the total number (Table 1). All limb bones showed complete epiphyseal fusion and belonged to at least a single adult hyena.

Hyena gnawing marks were detected on the majority (>90%) of bones of large herbivores (Figs. 1a–1f) and all *C. spelaea* (Figs. 1g and 1h) mandibles found in the cave. Bones with signs of digestion (Fig. 1d) and fragments of long bones of large mammals with signs

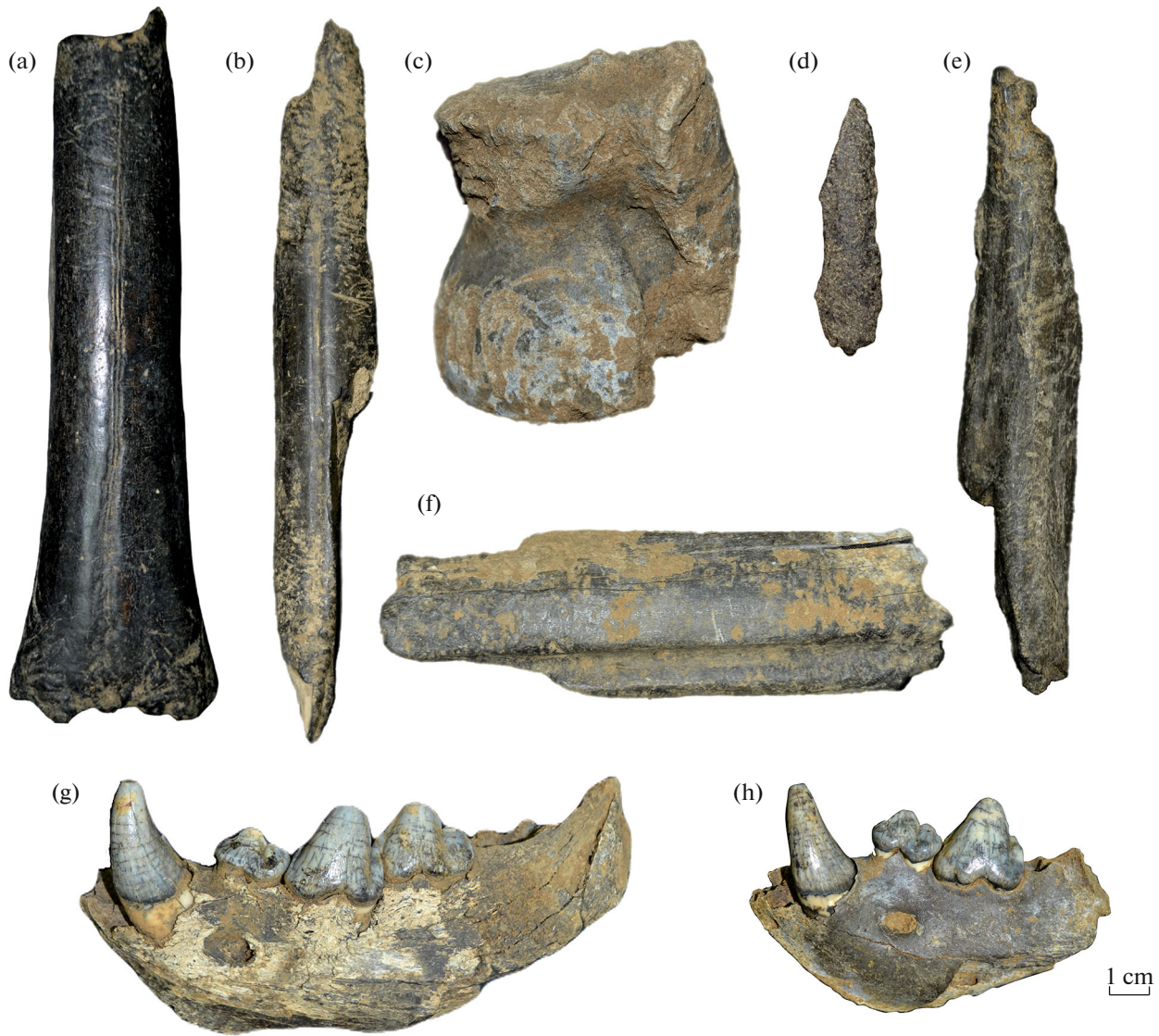


Fig. 1. Large mammal bones with marks left by *C. spelaea* teeth from the Tip-Tugai Cave: (a) a metapodium of *Camelus* sp., (b, f) metapodia of *M. giganteus*, (c) a talus of *C. antiquitatis*, (d, e) bones of unknown taxonomic affiliation, and (g, h) mandibles of *C. spelaea*.

of gnawing by hyena cubs (Figs. 1b, 1e, 1f) were also found.

Thus, the cave hyena substantially affected the formation of the taphocenosis of the Tip-Tugai Cave. Characteristic hyena gnaw marks were observed on the majority of bones of large herbivores, including bison, horses, woolly rhinoceroses, and mammoths. These species are a typical prey of the cave hyena [11, 16]. Cannibalism signs and bones with digestion signs were additionally found in the cave. The finds suggest a presence of a hyena den in the Tip-Tugai Cave. Many remains found in the cave belonged to juvenile hyenas aged 2–12 months (44%). Juveniles and subadults were the most abundant (75%). Large mammal bones gnawed by hyena cubs were found as well. Taken together, the finds indicate that the Tip-Tugai Cave was used as a natal den, where hyenas raised their cubs.

The Tip-Tugai Cave in the first cave hyena den described reliably from the Urals.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects. Only fossil specimens were used in the study.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

1. Jimenez, E., Germonpré, M., and Boudin, M., New insights into cave hyena ethology and the implications for territorial competition with hominins in Late Pleistocene north-west Europe: the case of Caverne Marie-Jeanne (Belgium), *Quat. Sci.*, 2022, vol. 37, no. 4, pp. 593–611.
2. Baryshnikov, G.F., Cave hyena (*Crocota spelaea*): taphonomy and adaptation, in *Aktual'nye voprosy evrazijskogo paleolitovedeniya* (Actual Problems of Eurasian Paleolithology), Novosibirsk: Inst. Arkheol. Etnogr. Sib. Otd. Ross. Akad. Nauk, 2005, pp. 15–16.
3. Baryshnikov, G.F. and Vereshchagin, N.K., Brief overview of Quaternary hyenas (family *Hyaenidae*) of Russia and adjacent territories, *Tr. Zool. Inst. Ross. Akad. Nauk*, 1996, vol. 270, pp. 7–65.
4. Lewis, M.E. and Werdelin, L., A revision of the genus *Crocota* (Mammalia, Hyaenidae), *Palaeontographica*, 2022, vol. 322, nos. 1–4, pp. 1–115.
5. Diedrich, C.G., Late Pleistocene *Crocota crocuta spelaea* (Goldfuss, 1823) clans as Prezewalski horse hunters and woolly rhinoceros scavengers at the open air commuting den and contemporary Neanderthal camp site Westeregeln (central Germany), *J. Archaeol. Sci.*, 2012, vol. 39, no. 6, pp. 1749–1767.
6. Harrison, R.A., The Uphill Quarry caves, Weston-Super-Mare, a reappraisal, *Proc. Univ. Bristol Spelaeol. Soc.*, 1977, vol. 14, no. 3, pp. 233–254.
7. Kropacheva, Yu.E., Cave hyena in the Urals, *Materialy konferentsii molodykh uchenykh* (Proc. Conf. Young Sci.), Yekaterinburg: Akademkniga, 2003, pp. 96–98.
8. Kuz'mina, S.A., Faunal data on the Late Paleolithic site Smelovskaya II in the Southern Urals, in *Pleistotsenovye i golotsenovye fauny Urala* (Pleistocene and Holocene Urals faunas), Chelyabinsk, 2000, pp. 137–153.
9. Rivals, F., Baryshnikov, G.F., Prilepskaya, N.E., and Belyaev, R.I., Diet and ecological niches of the Late Pleistocene hyenas *Crocota spelaea* and *C. ultima ussurica* based on a study of tooth microwear, *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 2022, vol. 601, pp. 111–125.
10. Diedrich, C.G., An Ice Age spotted hyena *Crocota crocuta spelaea* (Goldfuss 1823) population, their excrements and prey from the Late Pleistocene hyena den of the Sloup Cave in the Moravian Karst, Czech Republic, *Hist. Biol.*, 2012, vol. 24, no. 2, pp. 161–185.
11. Diedrich, C.G. and Žák, K., Prey deposits and den sites of the Upper Pleistocene hyena *Crocota crocuta spelaea* (Goldfuss, 1823) in horizontal and vertical caves of the Bohemian Karst (Czech Republic), *Bull. Geosci.*, 2006, vol. 81, no. 4, pp. 237–276.
12. Kosintsev, P.A. and Bachura, O.P., Late Pleistocene and Holocene mammal fauna of the Southern Urals, *Quat. Int.*, 2013, vol. 284, pp. 161–170.
13. Danukalova, G., et al., Quaternary deposits and biostratigraphy in caves and grottoes located in the Southern Urals (Russia), *Quat. Int.*, 2020, vol. 546, pp. 84–124.
14. Kruuk, H., *The Spotted Hyena: a Study of Predation and Social Behaviour*, Chicago: Univ. of Chicago Press, 1972.
15. Jimenez, I.J., et al., Ontogenetic dental patterns in Pleistocene hyenas (*Crocota crocuta* Erxleben, 1777) and their palaeobiological implications, *Int. J. Osteoarchaeol.*, 2019, vol. 29, no. 5, pp. 808–821.
16. Diedrich, C.G., Europe's first Upper Pleistocene *Crocota crocuta spelaea* (Goldfuss 1823) skeleton from the Koněprusy Caves: a hyena cave prey depot site in the Bohemian Karst (Czech Republic), *Hist. Biol.*, 2012, vol. 24, no. 1, pp. 63–89.

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