

## HELMINTH EGGS FROM *PACHYCROCUTA BREVIROSTRIS* (CARNIVORA, HYAENIDAE) COPROLITES FROM TAURIDA CAVE (EARLY PLEISTOCENE, CRIMEA)

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### KEY WORDS ABSTRACT

Helminth  
*Pachycrocuta brevirostris*  
Trematoda  
*Toxocara*  
*Capillaria*  
*Taenia*  
Toxocariasis  
Coprolite  
Early Pleistocene  
Crimea  
Taurida Cave

Twenty-seven *Pachycrocuta brevirostris* coprolites from Taurida Cave (Early Pleistocene) were studied. Eggs of parasitic worms were found in 6 of them (22.2%). Eggs of Trematoda species were identified among them, as were eggs of *Taenia*, *Toxocara*, and *Capillaria*. *Toxocara* eggs were the most common; they were found in 15% of the coprolites. This is the earliest evidence of *P. brevirostris* infection by these groups of helminths.

The phenomenon of parasitism on Earth is closely related to the evolution of the entire organic world. Some researchers even link the origin of life to parasitism, meaning that the parasitism of 1 living organism by another can be dated to 4.4–3.8 billion years ago (Araujo et al., 2003). Most fossil parasite taxa are morphologically similar to modern parasites (Dittmar, 2009). Therefore, the study of parasites of fossil mammals can help to understand aspects of their ecology and patterns of the evolution of parasite–host relationships (Jouy-Avantin et al., 1999; Cascardo et al., 2021). One of the most common places where the remains of helminths are found is fossil animal feces, i.e., coprolites. Many paleoparasitological studies are devoted to the investigation of coprolites (Dentzien-Dias et al., 2013; Perri et al., 2017).

Hyena coprolites are found at many Pleistocene localities in Eurasia, some of which contain several hundred specimens (Horwitz and Goldberg, 1989; Ferreira et al., 1993; Scott et al., 2003; Perri et al., 2017; Keiler, 2019; Espigares et al., 2023). This high degree of preservation is related to the presence of a large number of bones in the diet of bone-cracking Hyaenidae. Such a diet leads to a high concentration of calcium compounds in their feces, thereby making them more likely to be preserved in the fossil record (Larkin et al., 2000). Hyena coprolites usually have a spherical or oval shape because of the natural segmentation of a long fecal “sausage” into individual pellets (Diedrich, 2012).

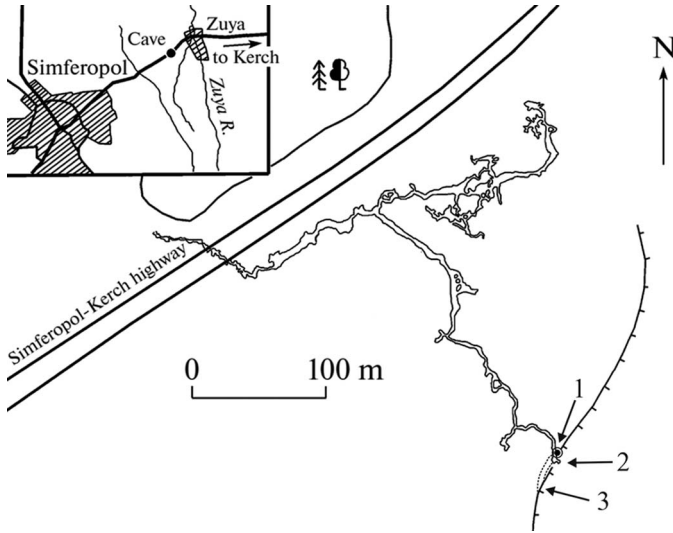
Studies on hyena coprolites are usually focused on their diet and environmental conditions (pollen composition), and research on parasites from coprolites is less common (Horwitz and Goldberg, 1989; Diedrich, 2012; Keiler, 2019; Espigares et al., 2023). For example, larvae of unidentified nematodes have been found in hyena coprolites from Pleistocene localities of Fontana Acetososa, Costa San Giacomo, Grotto Guatarri, and Grotto del Fosellone in Italy (Ferreira et al., 1993).

There are also few data on parasites in coprolites of the short-faced hyena *Pachycrocuta brevirostris* (Gervais, 1850) in particular. *Pachycrocuta brevirostris* coprolites containing a nematode egg of the genus *Toxocara* have been found only at the Haro locality in Pakistan and are dated to 1.2 Ma (Perri et al., 2017). Hyena coprolites have been found at one of the largest *P. brevirostris* sites in Europe (Untermassfeld) with only indirect evidence of infestation (Keiler, 2019).

### MATERIALS AND METHODS

#### Geological and faunal setting

In this paper, we describe helminth eggs from hyena coprolites from Taurida Cave. It is located on the Crimean Peninsula, 15 km east of Simferopol. This site was discovered in 2018 during the construction of the Taurida federal highway (Fig. 1).



**Figure 1.** The geographical location and the plan of Taurida Cave. (1) Coprolite assemblage; (2) excavated entrance; (3) possible Early Pleistocene entrance.

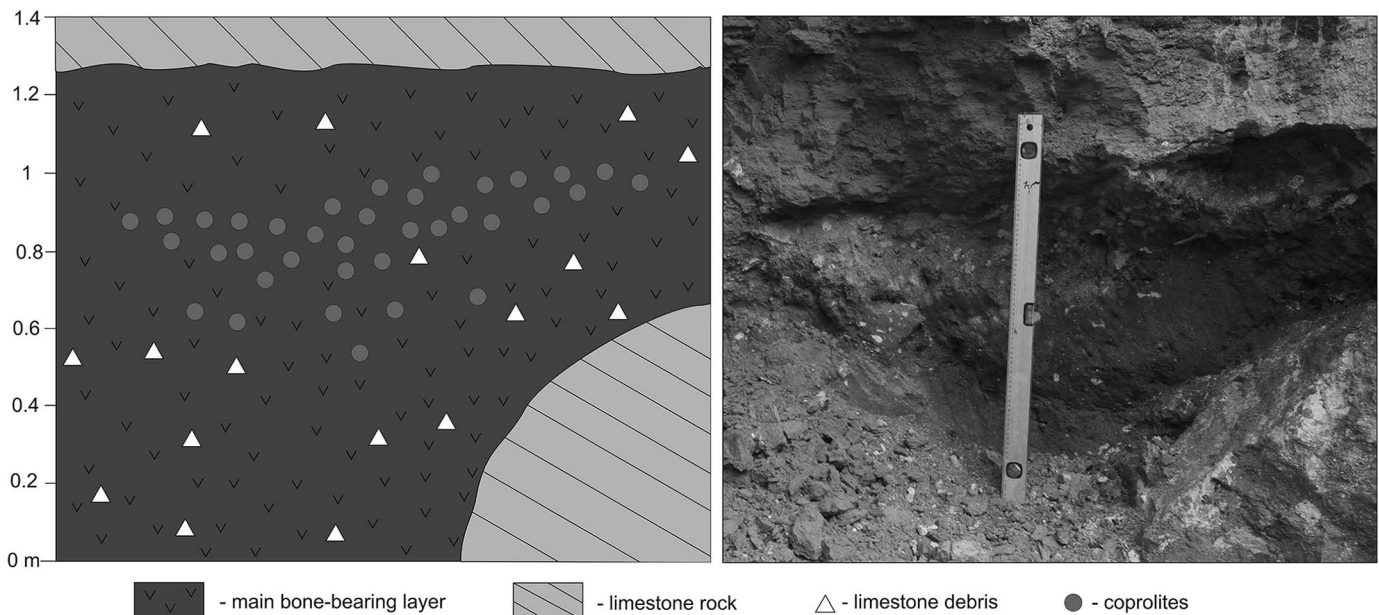
A large number of bones have been found in the red-brown subaerial loams of the cave (Oksinenko and Lavrov, 2021). The fossil fauna of Taurida Cave includes members of the following families: Canidae: *Canis* sp., *Vulpes alopecoides*, and *Vulpes* cf. *vulpes* (Gimranov et al., 2021); Ursidae: *Ursus etruscus* (Gimranov et al., 2020); Felidae: *Homotherium crenatidens*, *Megantereon adroveri*, and *Lynx issiodorensis* (Lavrov et al., 2020, 2021b, 2022a); Hyaenidae: *Chasmaporthetes lunensis* and *P. brevirostris* (Lavrov et al., 2021a, 2022b); and Mustelidae: *Mustela palerminea* (Gimranov et al., 2023). Many large herbivorous mammalian taxa have also been found in the cave. The list of species from Taurida Cave deposits corresponds to the Psekupian faunal complex (Early Pleistocene, Late Villafranchian, MQR10, 1.8–1.6 Ma;

Lopatin, 2019, 2021; Lopatin et al., 2019; Lopatin and Tesakov, 2024; Gimranov et al., 2020; Vislobokova et al., 2020).

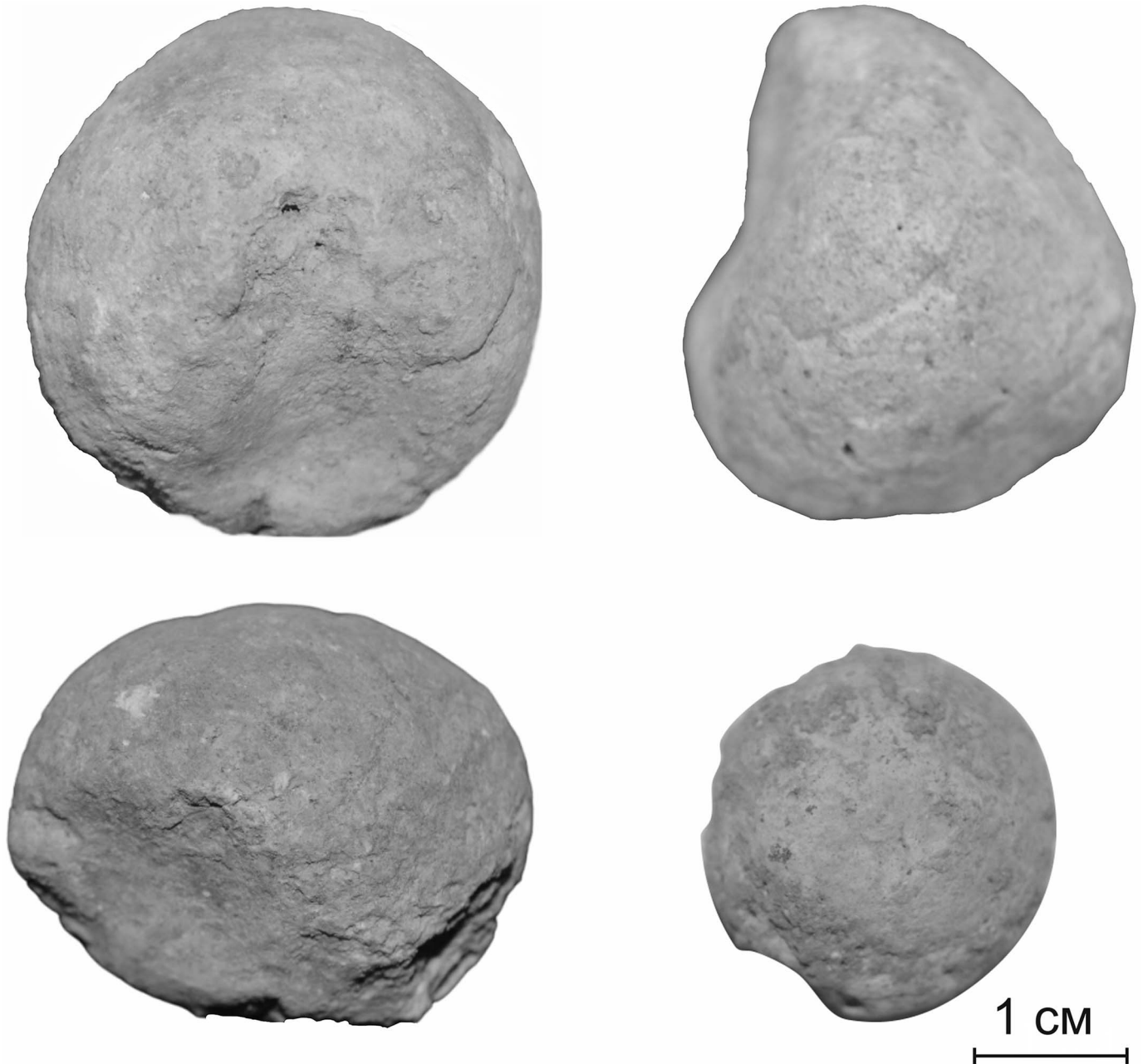
The sample of *P. brevirostris* is the largest among other Carnivora. Characteristic features of *P. brevirostris* include massive teeth and a skull with a powerful sagittal crest, which allowed these animals to crack the bones of large herbivores (Turner and Anton, 1996). Short-faced hyenas had exceeded all modern and fossil Hyaenidae sensu stricto in size, weighed ~110 kg, and had a height of more than 1 m (Palmqvist et al., 2011).

Almost a hundred teeth and several jaws and limb bones of *P. brevirostris* in total from at least 2 dozen individuals were found in the southern corridor of Taurida Cave. The bone-bearing layer also contained many bones of large ungulates with characteristic hyena gnawing. In addition, approximately 1,300 coprolites were found. Most of them proved to be concentrated in 1 place in the southern corridor, where a layer of coprolites reached the height of 10–20 cm in an area of ~5 m<sup>2</sup> (Figs. 1, 2).

Coprolites from Taurida Cave have a shape and size typical of modern and fossil large bone-eating predators: segments of round or oval shape, with rare inclusions of bone fragments (Diedrich, 2012; Wang et al., 2018). Only 1 large bone-eating predator, *P. brevirostris*, has been recorded in the faunal complex of Taurida Cave. Coprolites of members of Canidae have a more elongated shape, on average smaller size, and a much higher content of small-mammal bones (Oshmarin and Pikunov, 1990; Bravo-Cuevas et al., 2017). The tooth morphology of *Ch. lunensis* indicates that they had primarily consumed meat, not bones (Kurten and Werdelin, 1988); therefore, coprolites of this species most likely had morphology different from that of the feces of bone-eating hyenas. Members of the family Felidae are primarily meat eaters too, and their coprolites have rarely been preserved (Sanz et al., 2016). From these observations, we concluded that the coprolites under study were left by *P. brevirostris*. The first study on parasites from *P. brevirostris* coprolites from Taurida has shown the presence of *Toxocara* sp. eggs in hyena coprolites (Sivkova et al., 2022b).



**Figure 2.** The coprolite assemblage in the southern corridor of Taurida Cave.



**Figure 3.** Coprolites of *Pachyrocuta brevirostris* (Early Pleistocene, Crimea). Photo by D. R. Khantemirov.

The discovery of the large number of hyena coprolites made it possible to conduct a comprehensive parasitological study aimed at establishing the species composition of the parasites using morphological features. The abundance of coprolites collected in Taurida Cave provides a unique opportunity to expand our understanding of *Pachyrocuta* endoparasites. The aim of this study was the detection of parasite eggs in coprolites of *P. brevirostris* and the characterization of these eggs.

#### Coprolite examination

All the examined specimens come from a large coprolite assemblage (discovered during excavations in 2020) in the southern

corridor of the cave. This assemblage constitutes a part of the main bone-bearing layer. The coprolites together with the soil were transported to the Laboratory of Paleocology at the Institute of Plant and Animal Ecology, the Russian Academy of Sciences, where they were cleaned and catalogued.

Each coprolite was placed in a sterile plastic bag and labeled. Subsequent analysis was carried out in the Laboratory of Parasitology, the Faculty of Veterinary Medicine and Zootechnology, Perm State Agro-Technological University (Russia). For the study, 27 coprolites were selected and weighed on BW-500 scales, model ML-A01, max. 100 g,  $d = 0.01$  (Lin'an CF Co., Ltd., Hangzhou, China). The diameter was measured using a Topex digital caliper (Grupa Topex, Warsaw, Poland).

Each coprolite was disinfected by flaming before examination. All further work was carried out with adherence to sterility rules to prevent contamination of the material with modern parasites. Disinfection of utensils and instruments was also performed by flaming.

Coprolites were ground in a mortar, rehydrated with a 0.5% trisodium phosphate solution for 1 wk at 4 C, and examined by the sedimentation method. Between 39 and 281 slides from each coprolite specimen were inspected (an average of 134.1 slides per specimen). The total number of examined slides was 3,620.

The specimens were viewed under a Meiji microscope (Meiji Techno, Saitama, Japan) with eyepiece magnification of  $\times 10$  and a  $\times 10$  or  $\times 40$  objective, and were photographed using a Vision CAM V500 camera (West Medica, Wiener Neudorf, Austria) for light-field microscopy (1.5 megapixels). Paleoparasitological analysis of the specimens was carried out according to the internationally accepted procedure (Bouchet et al., 2003). Morphometry of eggs was performed in PhotoM 1.21 software (A. Chernigovsky, Russia). Parasites were identified according to the VIGIS atlas (Cherepanov et al., 2001) as well as descriptions from researchers (Shulak and Arkhipov, 2010; Traversa et al., 2011; Panova and Khrustalev, 2017; Abou-El-Naga, 2018; Hendrix and Robinson, 2022; Ualiyeva, 2023). Additionally, we determined the main indices accepted in parasitology: the frequency of parasite occurrence (prevalence) and the number of parasite eggs per coprolite specimen and gram of fossilized feces.

## RESULTS

Weighing of the coprolite specimens showed that their weight ranged from 4.06 to 27.43 g and averaged  $10.20 \pm 4.34$  g (mean  $\pm$  SD). The diameter of the pellets ranged from 21.8 to 41.0 mm ( $28.1 \pm 3.6$  mm). All coprolites had a similar rounded shape (Fig. 3).

The parasitological analysis detected helminth eggs in some specimens. The results of the microscopic examination of coprolites are summarized in Table I.

Among 27 analyzed coprolites, 6 (22.2%) contained helminth eggs of various taxa. In 4 specimens (14.8%), eggs of *Toxocara* sp. were detected. Overall, the number of eggs of this species per gram of coprolites was rather low: 0.02.

The detected eggs of *Toxocara* sp. had sizes comparable with modern ones (Fig. 4; Table II) and characteristic spherical shape, a thick shell with granulated surfaces, and a dark gray color, which are identical to morphological characteristics of members of this genus detected in extant predators.

In 2 coprolite specimens (7.4%), eggs morphologically similar to the eggs of trematodes were found. They had an ovoid shape and a “cap” at one of the poles. In the absence of a cap, there was an “orifice” at the pole of the egg. The frequency of occurrence was 0.01 eggs per gram (epg) of coprolites.

In specimen No. 24, the trematode eggs were smaller in size, with a length of 67.1  $\mu$ m and a width of 42.3  $\mu$ m. Their shape was slightly asymmetrical. In specimen No. 25, the egg had larger dimensions, with a length of 126.3  $\mu$ m and a width of 79.0  $\mu$ m. These eggs were almost symmetrical, but their shell had signs of deformation (Fig. 5). The slight deformation of eggs may be explained by processes of diagenetic transformations of fossil

**Table I.** Results of parasitological analysis of *Pachyrocuta brevirostris* coprolites (Early Pleistocene, Crimea).

Specimen ID	Weight (g)	Diameter (mm)	Number of slides	Result (number of eggs)
1	6.26	31.0	89	Negative
2	7.92	35.0	137	Negative
3	5.50	28.0	138	<i>Toxocara</i> sp.: 1
4	6.42	24.0	97	Negative
5	17.80	41.0	145	Negative
6	4.06	23.0	91	Negative
7	7.39	29.0	111	Negative
8	13.97	29.5	166	Negative
9	5.43	22.0	105	Negative
10	13.47	30.0	170	Negative
11	11.94	26.2	157	Negative
12	11.64	33.5	39	Negative
13	8.53	25.1	100	Negative
14	12.09	24.0	123	Negative
15	12.73	29.0	96	<i>Toxocara</i> sp.: 1
16	27.43	33.3	243	Negative
17	5.52	27.4	87	Negative
18	7.14	25.5	99	Negative
19	6.79	23.4	100	Negative
20	15.08	32.9	127	<i>Toxocara</i> sp.: 1
21	16.13	24.2	182	<i>Taenia</i> sp.: 1
22	14.60	31.6	182	Negative
23	14.05	26.5	281	Negative
24	6.84	27.9	177	<i>Toxocara</i> sp.: 3 <i>Capillaria</i> sp.: 2 Trematoda: 2
25	5.95	21.8	128	Trematoda: 1
26	6.06	25.8	132	Negative
27	4.53	24.8	118	Negative
Mean $\pm$ SD	10.20 $\pm$ 4.34	28.1 $\pm$ 3.6	134.07 $\pm$ 36.94	Total: Trematoda: 3 <i>Taenia</i> sp.: 1 <i>Capillaria</i> sp.: 2 <i>Toxocara</i> sp.: 6

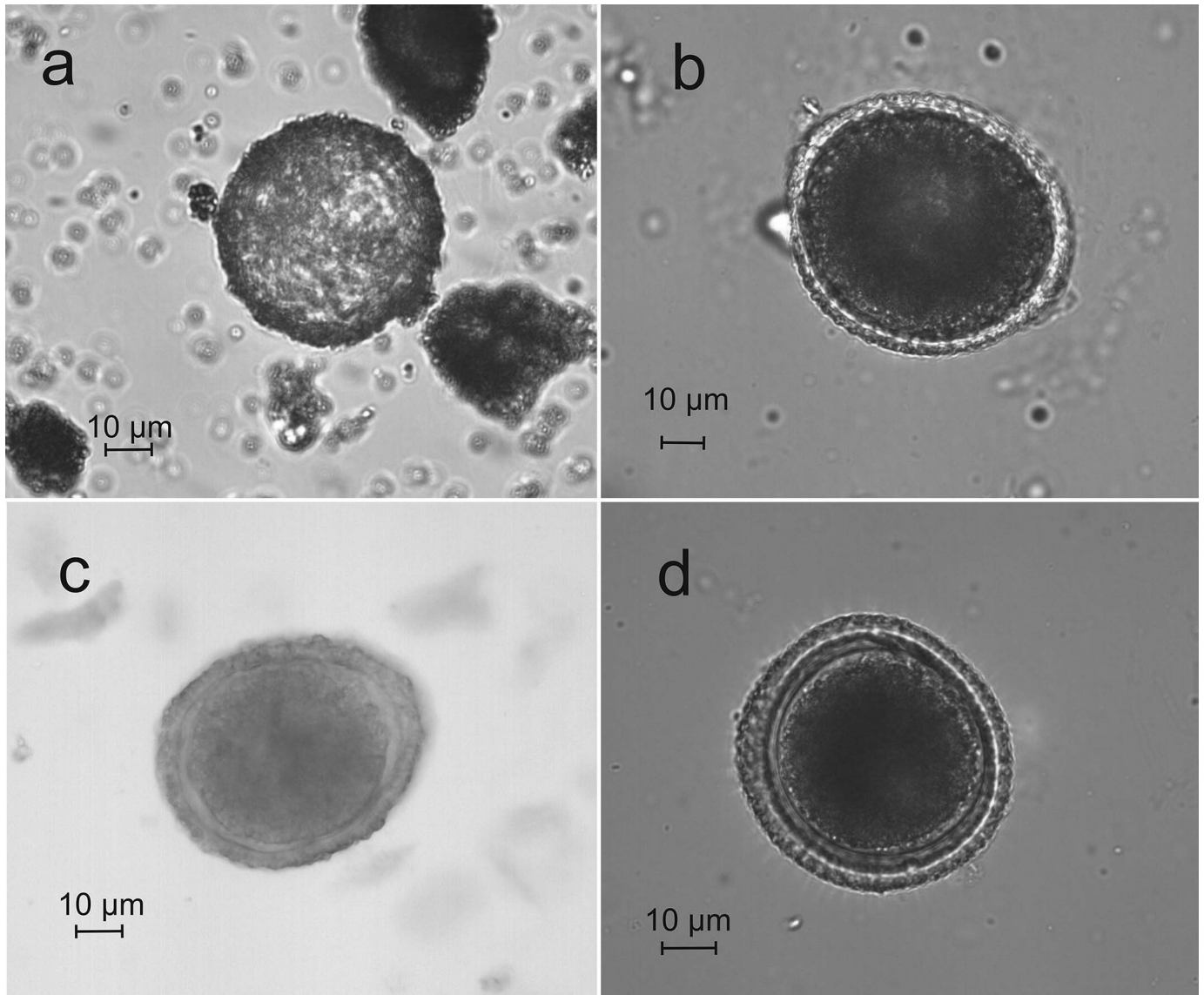
biological objects, which has been noted in earlier papers on sediments from archeological sources (Kumm et al., 2010; Sivkova et al., 2022a).

In 1 case, the egg had morphology characteristic of *Taenia* sp. (0.004 epg of feces): It contained a visible striated oncosphere. Besides, in 1 coprolite, eggs of capillariid nematodes (Capillariidae) were registered (0.007 epg of coprolites; Fig. 6). The eggs of capillariids from the analyzed coprolites are similar to modern capillariids in terms of size, the presence of some asymmetry, and the presence of well-visible “corks” at the poles.

## DISCUSSION

The eggs most frequently found here in *P. brevirostris* coprolites from Taurida Cave belong to the genus *Toxocara*. One *Toxocara* egg has been detected in a *P. brevirostris* coprolite from Pakistan, as mentioned previously (Perri et al., 2017). Toxocariasis could have been a common infestation in short-faced hyenas, but further research is needed to prove this notion. Toxocariasis has also been diagnosed in modern spotted hyenas *Crocuta crocuta* (Mozgovoy, 1953).

Trematodes (Trematoda or Digenea) are often found in extant carnivores (Romashova, 2016, 2019; Otranto and Deplazes,



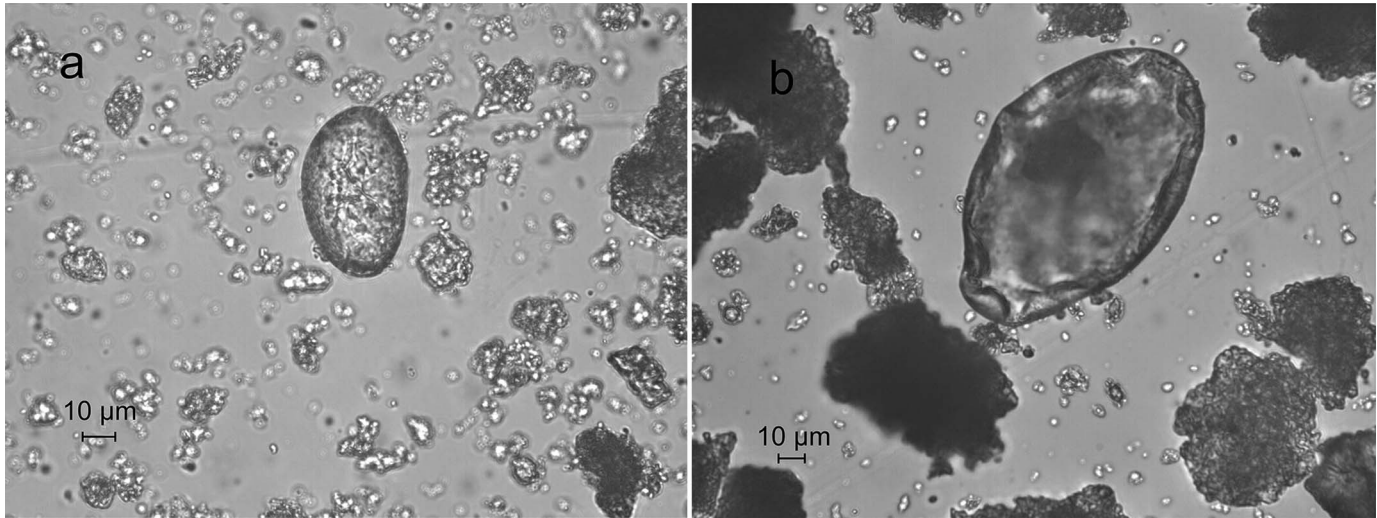
**Figure 4.** Comparison of *Toxocara* eggs by morphology. (a) *Toxocara* sp. egg from coprolites of *Pachyrocuta brevirostris* (Early Pleistocene, Crimea); (b) an egg of modern *Toxocara* sp. from *Vulpes vulpes*; (c) an egg of modern *Toxocara* sp. from *Lynx lynx*; (d) an egg of modern *Toxocara* sp. from *Canis familiaris*. Photos by T. N. Sivkova.

2019). This class includes more than 2,700 nominal genera and ~18,000 species (Petrov and Podvyaznaya, 2019). It is one of the most numerous and widespread groups of helminths. All of them are characterized by a complex developmental cycle with obligatory residence in a terrestrial or aquatic mollusc as an intermediate

host. Such molluscs likely lived in the vicinity of Taurida Cave in the Early Pleistocene. For most trematode species found in carnivorous mammals, the cycle involves additional or reservoir hosts (Bennet et al., 2020), which may be amphibians, reptiles, birds, or mammals of other taxa. Likely, the trematode eggs

**Table II.** Comparison of sizes (micrometers) between modern helminth eggs and helminth eggs from coprolites of *Pachyrocuta brevirostris* (Early Pleistocene, Crimea).

Helminth taxa	<i>Pachyrocuta brevirostris</i> coprolites (Taurida Cave, Crimea)	Orlov (1953)	Cherepanov et al. (2001)	Shulak and Arkhipov (2010)
<i>Toxocara</i> sp.	71.3	65–67	75–85	66–85 × 64–77
<i>Taenia</i> sp.	46.8 × 38.67	38–39 × 34–35	28 × 36	—
<i>Capillaria</i> sp.	63.32 × 30.70	62–77 × 33–37	—	56–69 × 35–40



**Figure 5.** Trematode eggs from *Pachycrocuta brevirostris* coprolites (Early Pleistocene, Crimea). (a) A trematode egg from specimen No. 24; (b) a trematode egg from specimen No. 25. Photos by T. N. Sivkova.

registered in small numbers in *P. brevirostris* coprolites come from their prey.

In their life cycle, taeniids have an obligatory intermediate host in the form of various herbivorous animals, and the definitive host is a carnivorous mammal. Judging by the abundance of ungulate bones with hyena gnaw marks in sediments in Taurida Cave, such a cycle could have been present in this biotope. Modern spotted hyenas are also often infested by aphids, with at least 2 new species identified recently (Terefe et al., 2014). The finding of only 1 taeniid-type egg in the coprolites analyzed here is explained by the structure of mature chainworm segments, in which the uterus is represented by a trunk with lateral branches, from which eggs are released only via the destruction of the segment itself, which often occurs in the external environment during movement of a detached proglottid. In modern carnivores, eggs of taeniids—even in the case of infestation—are not always detectable either (Abuladze, 1964).

Different *Capillaria* spp. have either a direct or complex developmental cycle involving molluscs or worms, depending on the species. It should also be noted that their various species invade not only the digestive system, but also the parenchymatous organs, the bladder, and the respiratory organs of mammals. In all cases, eggs of the parasite are excreted in large quantities with feces (Hodžić et al., 2016). The detection of a *Capillaria* egg in only 1 coprolite specimen in our work may mean that this infestation was relatively rare in *P. brevirostris*.

Among extant members of Hyaenidae, 3 species can crack large bones and regularly use them in their diet just as *P. brevirostris* could: the spotted hyena *C. crocuta*, the brown hyena *Parahyaena brunnea*, and the striped hyena *Hyaena hyaena*.

Some morphological features of *P. brevirostris* point to a possible similarity of their feeding habits with those of *H. hyaena* and *Par. hyaena*. Proportions of the short-faced hyena's cheek teeth indirectly indicate that *P. brevirostris* preferred scavenging to

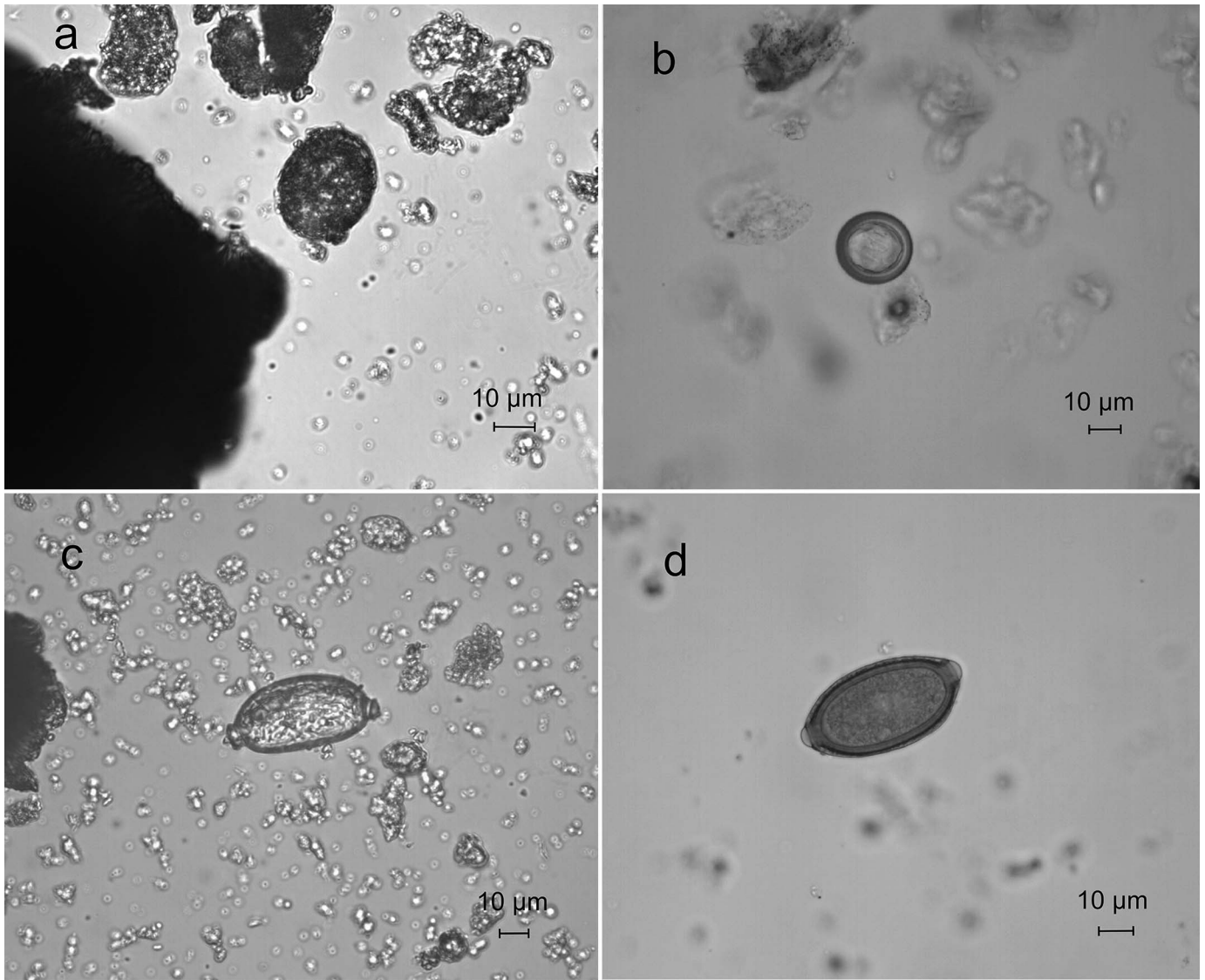
active hunting, similar to modern striped and brown hyenas (Coca-Ortega and Pérez-Claros, 2019). Furthermore, the distal limbs of *P. brevirostris* are shortened, which allows them to carry animal carcasses over long distances more efficiently, thereby also pointing to the predominance of scavenging (Palmqvist et al., 2011).

Additionally, out of all the extant hyenas, *C. crocuta* is closest to *P. brevirostris* in body size, and the prey species of *P. brevirostris* (*Equus stenosis*, *Gazellospira torticornis*, and *Bison* sp.) had a size class and ecological niches similar to those of typical prey of *C. crocuta* (*Equus quagga*, *Connochaetes gnou*, and *Syncerus caffer*; Kruuk, 1972). The presence of *Toxocara* eggs in coprolites of *P. brevirostris* from Taurida Cave also implies a similarity in feeding behavior between short-faced and spotted hyenas.

The finding of a large assemblage of coprolites (Fig. 2) may indicate that *P. brevirostris* lived in groups. All modern hyenas use feces to mark their territories, and this process often results in clusters of droppings (Gorman and Mills, 1984). This phenomenon is especially evident in the behavior of *C. crocuta*. Dozens of individuals from the same clan may use the same latrine, often located near their den, thus causing excrement accumulations of up to 100 m<sup>2</sup> (Kruuk, 1972; Mills and Gorman, 1987). The accumulation of the *P. brevirostris* coprolites in question may have resulted from the burial of such a latrine.

The coprolites of *P. brevirostris* contained eggs of *Toxocara* sp. (6 eggs), Trematoda (3 eggs), and *Capillaria* (2 eggs). An egg of *Taenia* sp. was found only once. Further research on coprolites from Taurida Cave can confirm the observed prevalence rate of helminth infestations in *P. brevirostris*.

This is the earliest evidence of infestation of *P. brevirostris* by these helminth taxa. The parasite fauna detected in short-faced hyenas' coprolites from Taurida Cave is similar to that of modern predators and may indicate a similarity in food species and lifestyle between fossil *P. brevirostris* and modern hyenas, in particular *C. crocuta*.



**Figure 6.** Comparison of helminth egg morphology. (a) A *Taenia* sp. egg from a coprolite of *Pachyrocuta brevirostris* (Early Pleistocene, Crimea); (b) an egg of modern *Taenia* sp.; (c) an egg of *Capillaria* sp. from a coprolite of *P. brevirostris* (Early Pleistocene, Crimea); (d) an egg of *Capillaria aereophila* from modern *Vulpes vulpes*. Photo by T. N. Sivkova.

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