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ARTICLE

ELASMOTHERIUM CHAPROVICUM (PERISSODACTYLA: RHINOCEROTIDAE) FROM THE EARLY PLEISTOCENE TAURIDA CAVE, CRIMEA

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ABSTRACT—This paper describes a representative collection of deciduous and permanent teeth, as well as postcranial skeletal elements of *Elasmotherium*, from the abundant Early Pleistocene locality at Taurida Cave (Crimean Peninsula). The age of the large and small vertebrate assemblage from this locality is estimated to be between 1.8 and 1.6 Ma (late Villafranchian), which inhabited in a savanna-like environment. The morphological features of the teeth support the attribution of the *Elasmotherium* remains from Taurida to the species *E. chaprovicum* Shvyreva, 2004, which is known from the Khaprovian Faunal Assemblage of the south of Eastern Europe (middle Villafranchian). The finds from Taurida Cave indicate that in Crimea this species was also characteristic of the Psekupsian Faunal Assemblage (late Villafranchian). The development of enamel structures at different stages of crown wear in various tooth generations was analyzed. The milk upper teeth of *Elasmotherium* are described for the first time.

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INTRODUCTION

The history of the genus *Elasmotherium* is currently considered to be relatively well-studied (Antoine, 2002; Kosintsev et al., 2019; Shvyreva, 2015, 2016; Zhegallo et al., 2005). However, questions remain regarding the taxonomic composition of the genus, the stratigraphic distribution of certain species, and their phylogenetic relationships. The origin of the genus *Elasmotherium* is quite ancient. According to current understanding, the Elasmotheriinae lineage diverged from other rhinoceroses in the early Oligocene (Antoine, 2002; Antoine et al., 2010; Liu et al., 2021; Shvyreva, 2016) or possibly as early as the Eocene (Kosintsev et al., 2019). During their independent evolution, the Elasmotheriinae developed a number of morphological features that distinguish them from other members of the Rhinocerotidae. The genus *Elasmotherium* likely appeared in the Late Pliocene and persisted until the Late Pleistocene (e.g., Kosintsev et al., 2019; but see Sun et al., 2022). Its range extended from the northwestern Black Sea region to eastern Asia (Kožamkulova, 1981; Shvyreva, 2016).

Certain species of elasmotheres have been used to characterize the Pleistocene faunal units of Eastern Europe (Alexejeva, 1977, 1989; Bajgusheva et al., 2001; Gromov, 1948; Titov, 2008; etc.). Shvyreva emphasized the important biostratigraphic significance of *Elasmotherium*. She proposed the following sequence of species in relation to Eastern European faunal assemblages: *Elasmotherium chaprovicum* Shvyreva, 2004 (Khaprovian Faunal Assemblage, middle Villafranchian), *E. peii* Chow, 1958 (Psekupsian Faunal Assemblage, late Villafranchian), *E. caucasicum* Borissiak, 1914 (Tamanian Faunal Assemblage, late Villafranchian–Early Galerian), and *E. sibiricum* Fischer, 1809 (Tiraspolian, Khasarian and Mammoth faunal assemblages, Late Galerian–Aurelian) (Shvyreva, 2015). Recently, a new species, *Elasmotherium primigenium* Sun, Deng & Jiangzuo, 2022, was described from the Upper Miocene of China (Yangjing locality, Shaanxi Province). The authors considered it to be the most primitive representative of the genus (Sun et al., 2022).

Some researchers question the validity of the species *Elasmotherium peii* and *E. chaprovicum*, recognizing only *E. caucasicum* and *E. sibiricum* as valid species (e.g., Antoine, 2002, etc.). The independence of these species is doubted due to the limited material on which they were described.

The unique material discovered in recent years from the abundant new Early Pleistocene locality at Taurida Cave makes it possible to confirm the validity of the species *Elasmotherium chaprovicum*. The main bone-bearing layer, associated with reddish-brown subaerial loams, contains numerous remains of Early Pleistocene animals. The mammalian assemblage correlates with the beginning of the Calabrian, zone MNQ18/MQ1, and is dated to 1.8–1.6 Ma (Lopatin et al., 2019; Lopatin & Tesakov, 2024). Bone accumulation at the site occurred primarily

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due to hyena activity in several grottos and galleries of the cave. Most bones bear gnawing marks from large predators, porcupines, and small rodents. The richest vertebrate assemblage discovered in the cave can be attributed to the Psekupsian Faunal Assemblage of Eastern Europe. To date, the Early Pleistocene fauna of Taurida Cave comprises over 100 taxa of terrestrial vertebrates, including small and large mammals, birds, reptiles, and amphibians (Lopatin et al., 2019; Lopatin & Tesakov, 2024; Lopatina et al., 2024). Large mammals identified from the locality include *Canis etruscus* Forsyth Major, 1877, *Vulpes alopecoides* (Del Campana, 1913), *Ursus etruscus* Cuvier, 1823, *Pachycrocuta brevirostris* (Gervais, 1850), *Chasmaporthetes lunensis* (Del Campana, 1914), *Homotherium crenatidens* (Fabrini, 1890), *Megantereon adroveri* Pons-Moyà, 1987, *Lynx issiodorensis* (Croizet & Jobert, 1828), *Acinonyx pardinensis* (Croizet & Jobert, 1828), *Archidiskodon meridionalis* (Nesti, 1825), *Equus* cf. *stenonis* Cocchi, 1867, *Equus* sp., *Sus* sp., *Paracamelus gigas* Schlosser, 1903, *Arvernoceros verestchagini* David, 1992, *Megaloceros* cf. *stavropolensis* Titov & Shvyreva, 2016, *Eucladoceros orientalis* (Radulesco & Samson, 1967), *Dama pontica* Vislobokova, 2024a, *Gazellospira torticornis* (Aymard, 1854), *Pontoceros ambiguus* Vereschagin et al., 1971, *Gazella* cf. *subgutturosa* (Güldenstädt, 1780), *Tavridia gromovi* Vislobokova, 2023b, *Leptobos etruscus flerovi* Vislobokova et al., 2025, *Bison* (*Eobison*) *constantini* Vislobokova et al., 2026, *Soergelia minor* Moya-Sola, 1987, *Megalovis latifrons* Schaub, 1923, *Ovis gracilis* Vislobokova, 2023c, *Capra crimiensis* Vislobokova & Yarmolchyk, 2025, and others (Gimranov et al., 2023, 2024; Lavrov et al., 2021, 2022a, 2022b, 2024; Lopatin, 2025; Lopatin et al., 2019; Vislobokova, 2022, 2023a, 2023b, 2024a, 2024b; Vislobokova et al., 2019, 2025, 2026; Vislobokova & Titov, 2020; Vislobokova & Yarmolchyk, 2025). Two rhinocerotid taxa have been reported, *Stephanorhinus* sp. and *Elasmotherium* sp. (Lopatin et al., 2019). Data on the vole association indicate that the Early Pleistocene phase of sediment accumulation in Taurida Cave occurred between 2.1 and 1.6 Ma. However, the main bone-bearing layer (containing all large-sized remains) was formed during the second half of the existence of the Psekupsian Faunal Assemblage, approximately 1.8–1.6 Ma (Lopatin & Tesakov, 2024). The composition of the assemblage indicates the existence of a savanna-like landscape in the vicinity of the cave (Lopatin et al., 2019). This is supported by paleobotanical studies based on palynomorph and phytolith analysis, which reveal the predominance of habitats with grass-forb meadow associations and the presence of patches of pine-oak forests (Lopatina et al., 2024).

MATERIALS AND METHODS

The measurements of the teeth and limb bones were taken according to Guérin (1980) and, in part, Shvyreva (2016). The nomenclature of enamel structures in the teeth is based on the works of Gromova (1959) and Shvyreva (2016), with additions from the papers of Borissiak (1914) and Teryaev (1929). The description of the dental structures was carried out with consideration of their variability along the crown height, including the use of 3D tomography. Tomography was performed using Neoscan N80 (PIN) and ELTECH-Med (SSC) X-ray scanners. In total, 33 teeth of different generations (Table 1; Fig. 1) and 137 limb bone specimens (Tables 2–6; Figs. 2–5) were studied. Measurements are given in millimeters (mm), and indices in percentages. The material is stored in the collections of the PIN (Moscow) and the scientific speleological-paleontological complex "Taurida Cave" of the Vernadsky Crimean Federal University (Zuya Village, Belogorsk District).

TABLE 1. Measurements (in mm) of cheek teeth of *Elasmotherium chaprovicum* (n = number of specimens) from Taurida Cave, Lower Pleistocene, Crimea (coll. PIN, CFU) (min–med–max).

Teeth	Crown length	Crown width	Crown height
dP1, n = 1	31.5	25.6	(30)
dP2, n = 5	33.4–36.12–37.3	34.9–36.64–39	19.5–44
dP3, n = 6	39.4–44.04–49.2	31.3–37.58–47.2	38–64
dP4, n = 5	48.5–52.2–64.7	41.1–43.21–46.9	58–84
P2, n = 1	40.7	35.2	67
P4, n = 3	48.8–51.41–55.7	58.3–61.35–64.4	80–100
M1, n = 7	49.75–62.42–69.8	41.9–55.44–69	97–116
M2, n = 1	72.0	56.4	181
dp4, n = 2	47.5; –	21.5; 21.9	40–41
m1, n = 2	45.5; 63.5	35.9; 26.4	54–65

Institutional Abbreviations—**PIN**, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **CFU**, Vernadsky Crimean Federal University, Simferopol, Crimea; **ROMK**, Rostov Regional Museum of Local History, Rostov-on-Don, Russia; **SSC**, Southern Scientific Centre RAS, Rostov-on-Don, Russia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, Beijing, China.

Measurement Abbreviations—**APD artic**., transverse diameter of the articular block; **APD bec**., transverse diameter of the calcaneus (along the coracoid process); **APD corp. sommet**., transverse diameter of the calcaneal tuber; **APD diaph**., transverse diameter of the diaphysis; **APD dist**., transverse diameter of the distal epiphysis; **APD int**., maximum transverse diameter of the astragalus; **APD prox**., transverse diameter of the proximal epiphysis; **APD sommet**., transverse diameter of the calcaneal tuber; **H**, greatest height; **L**, greatest length**; L corp. sommet**., length of the calcaneal tuber body; **TD corp. sommet**., width of the calcaneal tuber body; **TD diaph**., width of the diaphysis; **TD dist**., width of the distal epiphysis; **TD prox**., width of the proximal epiphysis; **TD sommet**., width of the calcaneal tuber; **TD sust**., width of the calcaneus (at the sustentaculum tali); **W**, greatest width; **W artic**., width of the articular block; **W artic. dist**., width of the distal trochlea.

SYSTEMATIC PALEONTOLOGY

Family RHINOCEROTIDAE Gray, 1821
Subfamily ELASMOTHERIINAE Bonaparte, 1845
Tribe ELASMOTHERIINI Bonaparte, 1845
Genus *ELASMOTHERIUM* Fischer, 1808
ELASMOTHERIUM CHAPROVICUM Shvyreva, 2004

Elasmotherium chaprovicum: Shvyreva, 2004:163, text-fig. 1 (original description).

Elasmotherium sibiricum: Gaponov, 1948:39, text-figs. 1–3 (initial definition).

Elasmotherium caucasicum: Bajgusheva, 1971:21, pl. V, figs. 5 and 6 (previous definition).

Elasmotherium caucasicum: Svistun, 1973:53, text-fig. 2 (previous definition).

Elasmotherium cf. *caucasicum*: Bajgusheva et al., 2001:134 (previous definition).

Elasmotherium peii: Shvyreva, 2016:43, text-figs. 12 and 13 (previous definition).

Elasmotherium sp.: Lopatin et al., 2019:40 (previous definition).

Holotype—Left M2 (ROMK L-1439).

Type Locality—Liventsovka sand pit, Rostov Region, Russia, Early Pleistocene, middle Villafranchian.

Description

The remains of elasmotheres from Taurida Cave are represented by isolated upper and lower teeth, fragments of tooth

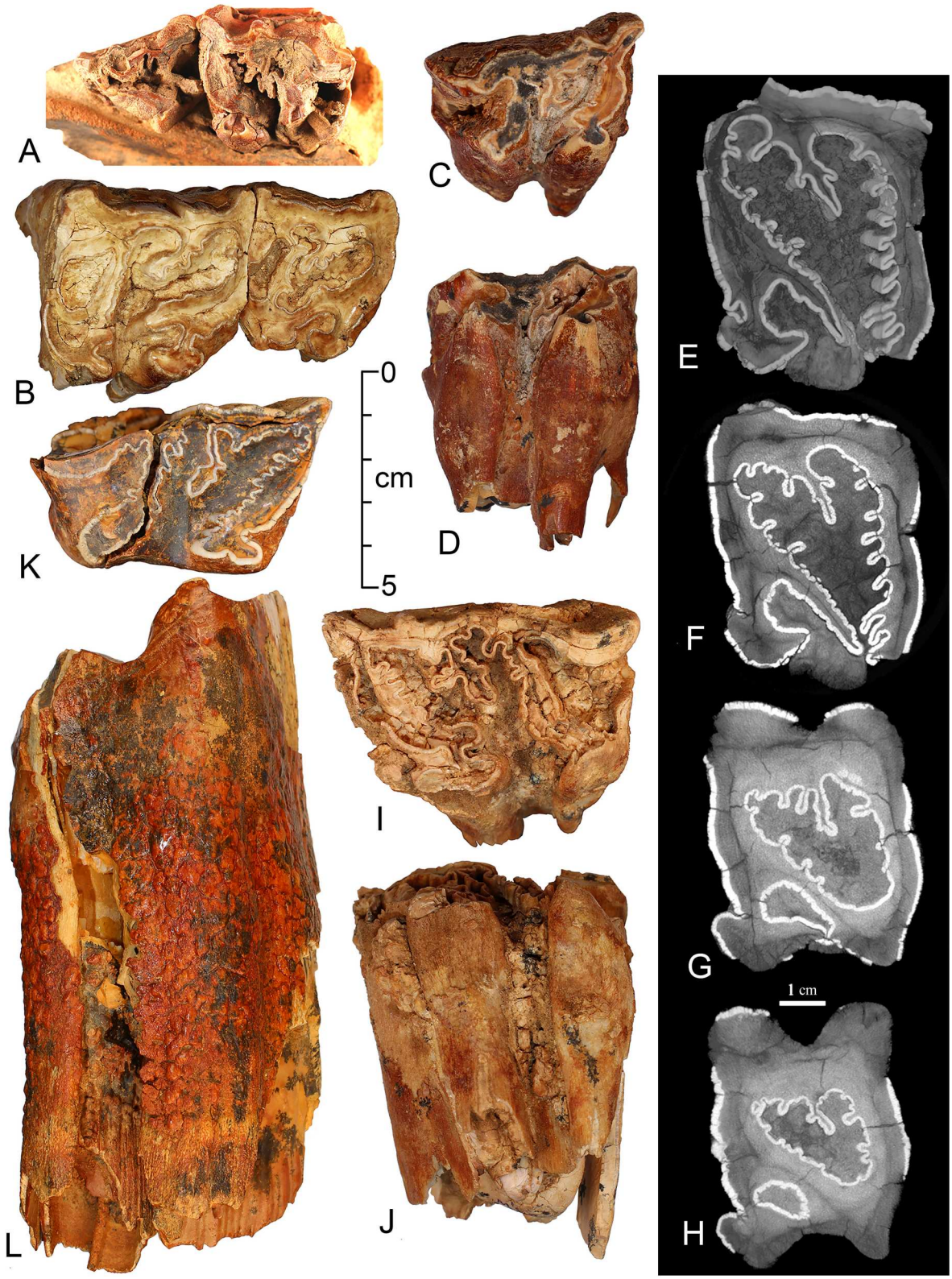


FIGURE 1. Upper teeth of *Elasmotherium chaprovicum* from Taurida Cave, Lower Pleistocene, Crimea. **A**, CFU Tavr-El/1, left dP1–dP2, occlusal view; **B**, CFU Tavr-El/2, right dP2–dP3, occlusal view; CFU Tavr-El/8, right dP4 in occlusal, **C**, and buccal, **D**, views; PIN 5644/3051, transverse sections of right P4 at the following levels: occlusal surface, **E**, 4 cm below the occlusal surface **F**, 7 cm below the occlusal surface **G**, 9 cm below the occlusal surface, **H**; CFU Tavr-El/12, left M1 in occlusal, **I** and buccal, **J** views; CFU Tavr-El/13, right M2 in occlusal, **K**, and buccal, **L**, views.

TABLE 2. Main measurements (in mm) and indices (%) of the humerus, radius, and ulna of *Elasmotherium chaprovicum* (n = number of specimens) from Taurida Cave, Lower Pleistocene, Crimea. Values are presented as min–med–max where applicable. See Abbreviations section.

Parameters	Humerus n = 2	Radius n = 4	Ulna n = 8
L	472.0 (n = 1)	–	550.0 (n = 1)
TD prox.	–	96.1–120.1–143.8	102.1–119.4–130.5
APD prox.	–	67.6–85.3–101.4	–
TD dist.	171.4–220.4	>94.6–116.5 (n = 2)	48.8 (n = 1)
APD dist.	141.2–147.4	86.1–116.1 (n = 2)	65.5 (n = 1)
TD dia.	92.5–97.1	44.9–62.9–83.5	–
APD dia.	117.1–137.9	30.5–42.0–52.1	–
Indices			
TD prox. : L max.	–	–	21.8 (n = 1)
TD dist. : L max.	46.7 (n = 1)	–	–
TD dia. : L max.	19.6 (n = 1)	–	8.9 (n = 1)
APD prox. : TD prox.	–	67.7–69.7–71.6	–
APD dist. : TD dist.	76.7 (n = 1)	99.7 (n = 1)	–
APD dia. : TD dia.	126.6 (n = 1)	62.4–67.4–71.6	134.2 (n = 1)

TABLE 3. Main measurements (in mm) and indices (%) of metacarpal bones of *Elasmotherium chaprovicum* (n = number of specimens) from Taurida Cave, Lower Pleistocene, Crimea. Ranges are shown as min–med–max. See Abbreviations section.

Parameters	Metacarpal II n = 9	Metacarpal III n = 22	Metacarpal IV n = 15
L max.	236.3–245.7–253.8	230.7–251.7–272.0	206.7–229.1–241.4
TD prox.	60.7–67.5–74.5	80.8–87.7–101.3	54.4–66.1–74.0
APD prox.	53.1–60.0–70.9	60.0–65.8–91.6	53.1–60.9–70.5
TD dist.	61.1–69.2–77.3	90.0–96.1–105.8	71.3–77.4–85.1
APD dist.	55.1–62.2–68.4	62.2–66.0–97.2	52.8–61.5–66.4
TD dia.	53.0–62.7–69.0	63.2–70.8–84.0	48.8–57.3–62.9
APD dia.	25.7–29.3–32.0	27.8–33.6–41.6	26.8–31.7–36.7
Indices			
TD prox. : L max.	27.5–29.1–30.9	13.8–28.1–32.2	30.4–31.1–32.2
APD prox. : TD prox.	82.8–88.9–101.6	69.3–73.9–80.6	83.0–92.9–97.9
APD dist. : TD dist.	92.8; 114.7 (n = 2)	69.1–71.2–73.8	74.1–79.5–89.1
TD dist. : L max.	27.1–30.2–33.2	15.3–38.2–39.0	33.1–34.4–35.6
TD dia. : L max.	25.6–28.0–29.6	11.8–28.1–30.0	24.2–25.0–25.8
TD dia. : TD prox.	86.8–91.2–98.9	76.6–80.8–88.9	79.5–86.6–93.3
APD dia. : TD dia.	45.1–46.8–48.8	41.4–47.2–52.6	48.6–55.7–59.6

TABLE 4. Main measurements (in mm) and indices (%) of calcanei of *Elasmotherium chaprovicum* (n = number of specimens) from Taurida Cave, Lower Pleistocene, Crimea. Values are given as min–med–max. See Abbreviations section.

Parameters	Calcaneum n = 14
L max.	161.4–172.5–182.6
DT sust. (= W max.)	91.4–109.0–126.7
DAP bec. (= DAP max.)	86.5–103.9–122.3
DT sommet.	69.9–74.6–81.0
DAP sommet.	92.7–100.1–113.1
L corp. sommet.	94.6–107.3–124.2
TD corp. sommet.	49.4–57.7–66.7
APD corp. sommet.	72.6–80.9–89.3
Indices	
DT sust. : L max.	56.1; 69.4 (n = 2)
L. corp. sommet. : L max.	55.2–63.8–68.0
DT sommet. : DAP sommet.	61.7–69.6–76.8
DT sommet. : DT sust.	77.9 (n = 1)

TABLE 5. Main measurements (in mm) and indices (%) of astragali of *Elasmotherium chaprovicum* (n = number of specimens) from Taurida Cave, Lower Pleistocene, Crimea. Data are presented as min–med–max. See Abbreviations section.

Parameters	Astragalus n = 18
H max.	103.7–115.4–122.2
W max.	118.9–130.4–140.4
APD int.	66.9–80.2–96.2
W artic.	109.8–119.9–127.7
W artic. dist.	99.3–110.2–122.0
Indices	
W max. : H max.	102.0–112.9–125.5
APD int. : W max.	57.4–62.2–77.5
W artic dist. : W artic.	84.9–95.0–125.2
W artic. dist. : W max.	81.1–85.9–90.8

TABLE 6. Main measurements (in mm) and indices (%) of metatarsals of *Elasmotherium chaprovicum* (n = number of specimens) from Taurida Cave, Lower Pleistocene, Crimea. Ranges are indicated as min–med–max. See Abbreviations section.

Parameters	Metatarsal II n = 6	Metatarsal III n = 14	Metatarsal IV n = 13
L	209.5; 222.8 (n = 2)	231.4–244.7–257.0	212.2 (n = 1)
TD prox.	35.8–42.0–51.1	54.2–70.0–82.8	59.9–65.2–72.3
APD prox.	47.6–49.2–51.5	42.4–57.1–68.7	56.8–66.1–72.7
TD dist.	50.2 (n = 1)	75.3–81.2–86.9	50.7 (n = 1)
APD dist.	50.5 (n = 1)	56.9–59.1–61.7	47.9 (n = 1)
TD dia.	27.3–33.2–37.9	51.6–60.2–65.4	40.2–46.4–52.7
APD dia.	32.5–37.1–44.0	30.7–35.6–41.2	31.3–35.9–38.9
Indices			
TD prox. : L max.	17.1; 22.9 (n = 2)	24.0–28.2–30.6	30.2 (n = 1)
APD prox. : TD prox.	100.8–118.0–126.8	64.5–83.0–111.3	95.2–102.4–114.5
APD dist. : TD dist.	100.6 (n = 1)	67.9–72.9–75.6	94.5 (n = 1)
TD dist. : L max.	24.0 (n = 1)	34.1–34.7–36.3	23.9 (n = 1)
TD dia. : L max.	16.8; 17.0 (n = 2)	22.3–23.9–25.4	18.9 (n = 1)
TD dia. : TD prox.	53.4; 79.8 (n = 2)	76.9–84.9–101.1	62.8–70.7–80.0
APD dia. : TD dia.	92.1–104.6–161.1	57.5–60.5–65.7	66.2–78.0–82.1

rows (dP1–dP2 and dP2–dP3), and both complete and fragmentary bones of the postcranial skeleton (Figs. 1, 2).

The collection predominantly contains teeth of juvenile individuals, including deciduous teeth, as well as a few permanent premolars, fairly numerous M1, and single examples of M2 and M3 (Table 1). The pattern of enamel structures in all teeth varies depending on the degree of wear. The folding of the enamel on the inner walls of all fossettes is extremely weak. The upper deciduous cheek teeth are represented by dP1–dP4. The permanent upper teeth include P2–M3; P1 was not found. The age of individuals ranges from newborns with unworn and unerupted dP2 to specimens over 30 years old (by analogy with the white rhinoceros, *Ceratotherium simum* (Burchell, 1817), see Hilmann-Smith, 1986).

Upper Teeth—The fully-formed deciduous cheek teeth dP1–dP4 have well-developed roots. Their crowns are covered with a layer of cementum to varying degrees, both externally and within the valleys. The single, slightly worn dP1 has a subtriangular shape in cross section (Fig. 1A). On the buccal side of the crown, the parastyle, paracone, and metastyle ribs are well developed, while the metacone rib is poorly discernible. On the lingual side, a weakly expressed anterior valley and protocone rib are noticeable. The median valley is narrow and similar in length to the protoloph. It closes at the level of the dorsal third of the crown height. Small folds of the crista and crochet unite to form an additional fossette (~2 mm in diameter) within the



FIGURE 2. Limb bones of *Elasmotherium chaprovicum* from Taurida Cave, Lower Pleistocene, Crimea. PIN 5644/3065, right humerus in anterior **A**, and inferior, **B**, views; PIN 5644/3066, proximal fragment of the right radius in anterior, **C**, and posterior, **D**, views; PIN 5644/3067, distal fragment of the left radius in anterior, **E**, and posterior, **F**, views; PIN 5644/3073, left ulna in medial, **G**, and anterior, **H**, views; PIN 5644/3209, right calcaneus in medial, **I**, and anterior, **J**, views; PIN 5644/3218, right astragalus in anterior, **K**, and inferior, **L**, views; PIN 5644/3139, right second metacarpal (Mc II) in dorsal, **M**, anterior, **N**, and palmar, **O**, views; PIN 5644/3149, right third metacarpal (Mc III) in dorsal, **P**, anterior, **Q**, and palmar, **R**, views; PIN 5644/3177, left fourth metacarpal (Mc IV) in dorsal, **S**, anterior, **T**, and palmar, **U**, views; PIN 5644/3252, right second metatarsal (Mt II) in dorsal, **V**, anterior, **W**, and plantar, **X**, views; PIN 5644/3267, left third metatarsal (Mt III) in dorsal, **Y**, anterior, **Z**, and plantar, **A′**, views; PIN 5644/3274, right fourth metatarsal (Mt IV) in dorsal, **B′**, anterior, **C′**, and plantar, **D′**, views.

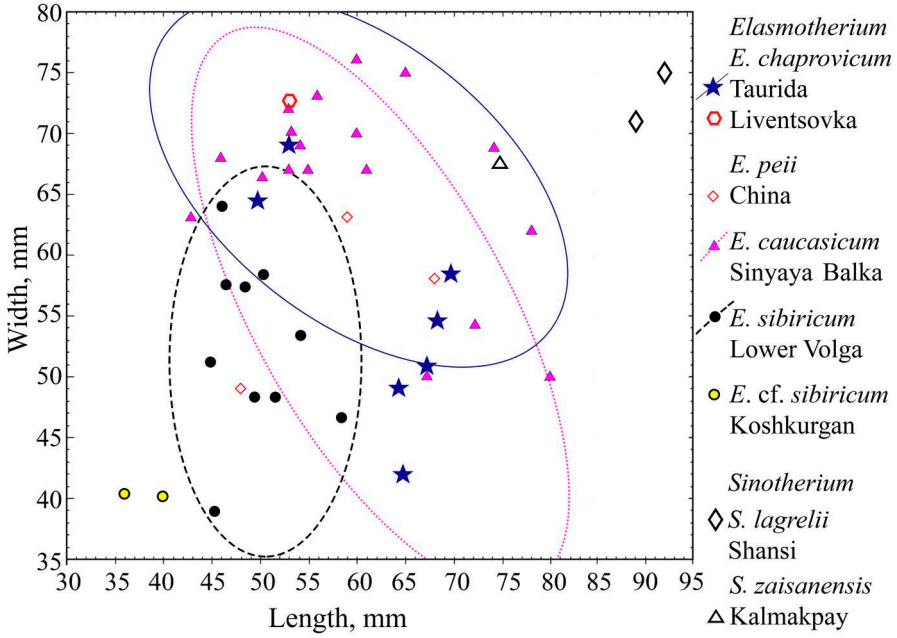


FIGURE 3. Ratio of length to width in M1 teeth of the *Elasmotherium* and *Sinotherium* species.

valley, even in slightly worn teeth. A subtriangular open posterior valley is present on the posterior side of the crown. As wear progresses, it decreases in size and closes approximately at the dorsal third of the crown.

The dP2 specimens range from unworn to heavily worn (Fig. 1A, B). The crown cross-section is sub-square. In slightly worn teeth, the length of the tooth is slightly greater than its width. Buccally, the parastyle and metastyle ribs are well developed. The noticeable paracone rib fades toward the base of the crown. The protoloph is wider than the metaloph. The shape of the protocone changes from subrounded in slightly worn teeth to suboval in heavily worn teeth. The median valley closes only in heavily worn teeth due to the fusion of the antecrochet and the anterior wall of the metaloph. The crista in the lingual part is divided into two or three folds. The crista and crochet are close to each other, but the formation of an additional valley is not observed even in heavily worn teeth. The posterior valley is open only in slightly worn teeth and closes approximately at the level of the ventral third of the crown height. A closed posterior valley is also present in heavily worn teeth. The hypocone is weakly separated from the metaloph.

Teeth dP3 are represented by specimens of varying degrees of wear. Their morphology is largely similar to that of dP2 (Fig. 1B). The differences lie in the slightly larger dimensions of dP3. The median valley has a relatively wide exit and does not close, even in heavily worn teeth. The crista is less branched, but its

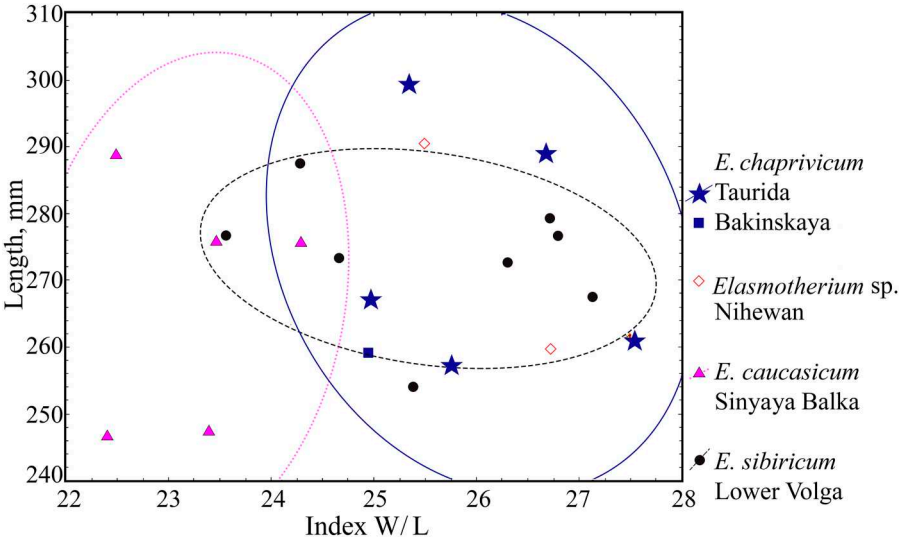


FIGURE 4. Ratio of length to the slenderness index (diaphyseal width/length × 100) of the third metacarpal (Mc III) in the *Elasmotherium* species.

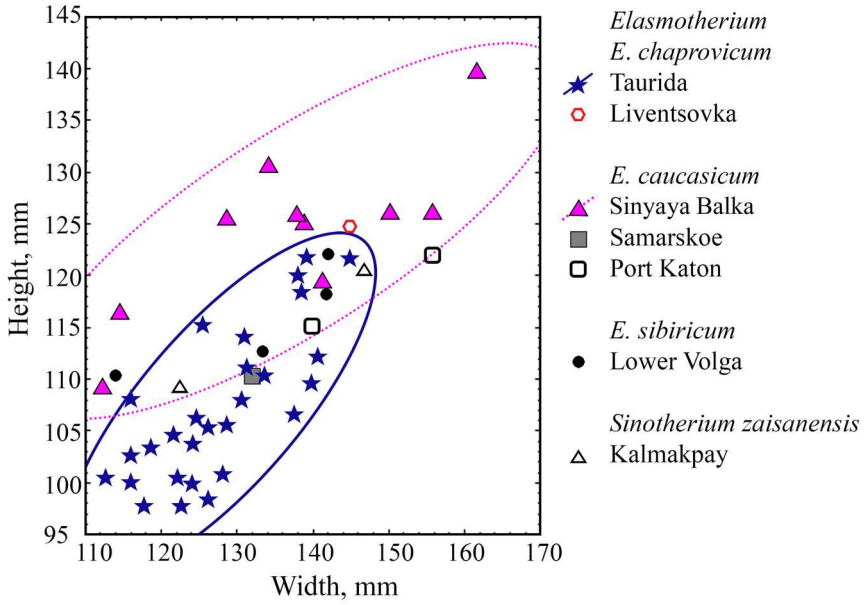


FIGURE 5. Ratio of height to width in the astragals of *Elasmotherium* and *Sinotherium* species.

walls in moderately and heavily worn teeth are composed of relatively plicated enamel. The crochet is well expressed in slightly worn teeth, but completely absent in heavily worn ones. The shape of the protocone also varies from subcircular to suboval; but its length is somewhat greater than that of dP2. The posterior valley also closes at the level of the ventral third of the crown height.

Teeth dP4 are presented with both incompletely formed, unerupted crowns and slightly worn ones. In slightly worn teeth, the crown noticeably widens from the grinding surface to the base (Fig. 1C, D). On the buccal side of the crown, the parastyle and metastyle ribs are clearly visible. In slightly worn teeth, the paracone rib is also noticeable, but it nearly disappears at the level of the ventral third of the crown height. The anterior sinus is weakly expressed. The opening of the median valley is relatively wide. The crista is simple or bears additional enamel structures. In occlusal view the protocone is suboval; its length increases toward the base of the tooth. The posterior valley closes at approximately two-fifths of the crown height.

Permanent upper cheek teeth differ from deciduous ones by their larger crown dimensions, higher hypsodonty, and more distinct enamel plication on the walls of the median valley, and, in moderately to heavily worn teeth, also on the anterior wall of the posterior valley. The crown is covered with external cement.

A single incompletely formed P2 was identified in the jaw above a heavily worn dP2. The crown of this tooth is characterized by clearly expressed parastyle, metastyle, and paracone ribs on the buccal side. The anterior valley and anterior sinus are relatively well developed. The exit of the median valley in the apical part of the crown is wide, narrowing toward its base. The posterior valley is open only in slightly worn teeth. A weak crista, represented by a minor enamel fold, appears only at the apical part of the unworn crown.

P4 are represented by both unerupted and slightly worn teeth, as well as extremely worn ones with closed roots and decreased crown due to basal wear. The cross-section of the crown is subtrapezoidal due to weak pressure from the preceding tooth. On the buccal side, the parastyle, paracone, and metastyle ribs are expressed. In moderately and heavily worn teeth, a closed additional valley is formed due to the fusion of the crista and crochet (Fig. 1E–H). The protoloph is relatively narrow. In moderately worn teeth, the roots are fully formed but not closed; closed roots are observed in heavily worn specimens.

Among seven M1 specimens in the collection, both unformed crowns and heavily worn teeth with closed roots are present. The crown cross-section varies from subtrapezoidal in slightly worn teeth to subrectangular in heavily worn ones (Fig. 1I, J). In less worn teeth, the crown length exceeds the width, while in heavily worn ones, the width exceeds the length. On the buccal wall of the ectoloph, the parastyle and metastyle ribs are clearly expressed. The metastyle is relatively long on the grinding surface side in slightly worn teeth, and short in moderately and heavily worn ones. The paracone rib is only observed in the apical part of the crown in slightly worn specimens. The exit of the median valley is wide; it closes due to fusion of the antecrochet with the metaloph near the base of the crown. The posterior valley is open only in very slightly worn teeth. With wear, it closes (forming a postfossette) and disappears from the occlusal surface in heavily worn specimens. In a heavily worn tooth with a crown height of 116 mm, the roots are already fully closed. The crista is long and narrow in slightly worn teeth, becoming spoon-shaped or branched as wear progresses. The cristella is separated from other folds of the median valley only in moderately and heavily worn teeth. A small antecrochet is present in slightly and moderately worn teeth, becoming long and narrow in heavily worn specimens. The protocone is suboval and elongates with progressive crown wear. Root formation begins in teeth with only a little degree of wear.

A single M2 is preserved, slightly worn, with a crown height of 181 mm, and has no formed roots (Fig. 1K, L). The parastyle and metastyle ribs are well expressed on the ectoloph wall. On the occlusal surface, the metastyle is relatively short in the apical part of the crown and becomes very short with significant tooth wear. The paracone rib is barely noticeable. The median valley has a wide exit, which likely never closes. The crista is rather narrow. The cristella is small. The protocone is elongated. The posterior valley closes only in the dorsal half of the crown; at the base, it forms a large subcircular enamel island with sparse folds.

There is only one fragment of a rather heavily worn M3, allowing for assessment of the structure of the median valley. Its walls

are composed of highly plicated enamel. The crista is small, with a number of enamel folds on the anterior wall. The cristella is not expressed. Notably, despite the remaining crown height of at least 152 mm, the bottom of the median valley is closed. Due to preservation, root development cannot be confidently assessed, however based on other teeth, root formation likely began in this specimen. Apparently, this tooth belonged to an old individual, likely over 30 years old.

Lower Teeth—Only a few lower teeth are present in the collection. The crown surfaces are covered with cementum, which is strongly developed in the valleys. Enamel folding is insignificant and is more pronounced on the walls of the posterior internal valley in moderately and heavily worn teeth.

There are two slightly worn dp4, in which the lophids on the occlusal surface are not yet fused. Their roots are formed but not closed. Between the roots, pressure areas from forming permanent p4 teeth are visible. The anterior and posterior internal valleys are wide, closing only near the crown base due to the fusion of the metaconid and entoconid. The metaconid is quite large; in slightly worn teeth, it is well separated from the posterior wall of the protoconid and bears two large enamel folds directed posteriorly (aborally).

There are also only two m1, one of which has not yet erupted, and the other is strongly worn. The metaconid is also quite large, subcircular in slightly worn tooth and suboval in more worn specimen. The hypolophids are nearly sagittally aligned. The posterior internal valley is wider and closes later than the anterior one during crown wear process. In heavily worn teeth, the crown length is greatly reduced, and the roots are closed.

Postcranial Skeleton—The postcranial skeleton is mostly represented by limb bones and their fragments (Fig. 2). Nearly all bones of the forelimb are present, along with the metatarsal and tarsal elements of the hindlimb. Bones of adult animals are the most abundant in the collection. Remains of juvenile elasmotheres are few in number and usually heavily fragmented. Therefore, the work provides a description restricted to the postcranial skeleton of adult individuals.

The humerus (Fig. 2A, B) has a relatively short diaphysis (Table 2). The articular head is wide and slightly convex, oriented posteriorly and slightly medially. The distal epiphysis is very wide, with a large lateral ligamentous tubercle constituting about one-third of its width and displaying clear muscle attachment surfaces. The epicondylar crest (crista epicondylaris) is wide and high, positioned significantly medially to the lateral epicondyle (epicondylus lateralis). The distal trochlea of the humerus is relatively small; in PIN 5644/3065 its width is about one-third of the total length of the humerus and is not much thicker than the diaphysis (the ratio of the total length to diaphysis width is 23.1). The medial ridge is significantly larger than the lateral one. The median groove of the trochlea is wide and shallow. The median sulcus of the trochlea is flat and broad, separating the trochlea from the medial ligamentous tubercle. From above, the distal trochlea is bounded by the radial fossa (fossa radialis) anteriorly and the olecranon fossa (fossa olecrani) posteriorly. The fossa radialis is smooth, shallow, and moderately wide. Fossa olecrani is also weakly defined, broad, and deep. The medial epicondyle is less prominent than the lateral one. The diaphysis is wide and short, proximally subtriangular in cross-section, with an anteroposterior width comparable to that of the distal epiphysis. The humeral crest (crista humeri) is narrow and high in the middle part.

The radius is long and slender (Fig. 2C–F). The proximal epiphysis is moderately wide and flattened both medially and laterally. The trochlear notch (incisura trochlearis) has a slightly concave profile, with a low transverse ridge. The transverse palmar crest is high and sharp. The medial ligamentous tubercle is rounded and prominent, strongly protruding palmarly. The diaphysis is weakly convex anteriorly in cross-section. The distal epiphysis is slightly larger than the proximal one (Table 2). The scaphoid articular facet is more concave than the lunate articular facet. The overlying transverse ridge (crista transversa radii) is wide and low.

The ulna is long and straight, without a pronounced curvature (Fig. 2G, H). The proximal epiphysis is wide (Table 2). The lateral margin is broad and high, while the medial margin is thin and extends far medially. The semilunar notch (incisura semilunaris) is moderately deep and opens widely in the mediodistal direction. The anconeal process (processus anconeus) is wide and slightly deflected downward. The distal epiphysis is comparatively narrow. The diaphysis is moderately wide, with a sharp, high ridge separating its anterior and lateral surfaces.

The second metacarpal (Fig. 2M–O) has a similar width along its entire length. The proximal facet for the trapezoid bone is slightly concave anteriorly and flat posteriorly. The facets for the third metacarpal and capitate (os magnum) bones are wide. A large ligamentous tubercle is present distally. The diaphysis is strongly flattened in the dorsal-palmar direction and curves slightly medially in its distal part. The distal articular block is inclined laterally. In the transverse plane above it, there is a large ligamentous tubercle.

The third metacarpal is wide and massive (Fig. 2P–R). Due to the development of lateral ligamentous tubercles, the widths of the proximal and distal epiphyses are similar. The facets for the fourth metacarpal bone are relatively small. The diaphysis is wide and dorsopalmarly flattened.

The fourth metacarpal is the shortest among the metacarpals, but slightly more robust than the second metacarpal bone (Fig. 2S–U). The diaphysis is noticeably curved mediolaterally and is less flattened compared with the other metacarpals. The profile of the distal block is subquadrate, distinguishing it from the other metacarpals.

The calcaneus has a wide calcaneal tuber and an articular block (Fig. 2I, J). In some specimens, the calcaneal tuber is less inflated. In most specimens, the coracoid and sustentacular facets approach closely but do not fuse. The sustentaculum tali is wide and massive. The proximal process of the calcaneal tuber projects forward more strongly than the coracoid process, slightly overhanging it. The calcaneal tuberosity occupies about 80% of the body of the calcaneal tuber.

The astragalus has a low articular block, which is weakly convex both medially and laterally (Fig. 2K, L). The articular block is tilted at an angle of about 30° relative to the distal block of the bone. The lateral margin of the distal block projects noticeably forward. The medial tubercle is high, about one-third of the total bone height, and projects distinctly backward. The facet for the scaphoid bone is ribbon-shaped, and in some specimens, its lower margin merges with the sustentacular facet.

The second metatarsal is relatively thin and slender with a slight mediolateral curve (Fig. 2V–X). The proximal epiphysis is narrow in the longitudinal plane and wide transversely, while the distal epiphysis is wide transversely and narrow longitudinally. The facet for the third metatarsal is equal to or smaller than that for the third cuneiform bone.

The third metatarsal is slender (Fig. 2Y–A'). The distal expansion is comparatively weak. The distal epiphysis is wide, but comparatively short in the dorsoplantar direction.

The fourth metatarsal is significantly more robust than the second metatarsal (Fig. 2B'–D'). The dorsoplantar diameter of the proximal epiphysis slightly exceeds the mediolateral one. The diaphysis is rounded in cross-section and is less twisted along its axis than that of the second metacarpal.

Comparisons

The enamel folding in teeth from Taurida Cave on the inner walls of all the valleys is less pronounced than that of *Elasmotherium caucasicum*, that existed during the late Early

Pleistocene (late Villafranchian–early Galerian). A sufficiently representative collection of *E. caucasicum* teeth from the type locality of the Tamanian Faunal Assemblage, Sinyaya Balka/Bogatyri (Taman Peninsula), made it possible to study in detail the pattern of age variability of the enamel structures of hypsodont teeth in this species (Bajgusheva et al., 2011). In the elasmothere from Taurida Cave, the degree of hypsodonty is lower than in *E. caucasicum*. The crown height of slightly worn M1 (with forming roots) is less than that of *E. caucasicum* (average 150.2 mm). The only M2 from Taurida Cave, at an incipient stage of wear, also has a smaller crown height (181 mm) compared to those of *E. caucasicum* from the type locality Sinyaya Balka, where crown height reaches 210–240 mm (in teeth beyond the initial wear stage). In the Taurida form, the closure of the posterior valleys on M1–M2 occurred later in ontogeny. The closed posterior valley (postfossette) is present in these teeth almost to the base of the crown, unlike in the Caucasian elasmothere, where in M1, the posterior valley disappears completely by the ventral third of the crown and is not observed on heavily worn M2. In the elasmothere from Crimea, root formation on the upper premolars and first molar occurred already in slightly worn teeth, unlike in *E. caucasicum*, in which the presence of roots, both closed and open, was noted only in the very heavily worn P4–M3 (Table 7).

Compared to the Middle and Late Pleistocene species *E. sibiricum*, the teeth from Taurida Cave are distinguished by relatively larger crown dimensions (Fig. 3), a lower degree of hypsodonty, less pronounced plication, and less orderliness of the enamel folds.

The relatively low-hypsodonty for elasmotheres, the relatively early formation of roots, the delayed closure of the posterior valley, and its presence even in heavily worn M1 and M2 support the attribution of the Crimean specimens to *E. chaprovicum*, described from the Liventsovka sand pit in the Northeastern Azov region (middle Villafranchian) (Bajgusheva, 1971; Shvyreva, 2004, 2016; Titov, 2008).

The teeth from Taurida Cave share several features with *E. peii* specimens from central China (early Early Pleistocene), including similar sizes, a relatively low degree of crown hypsodonty, the preservation of a closed posterior valley (postfossette) almost to the base of the M1–M2 crowns, and the onset of root formation in moderately worn teeth (Chow, 1958; Tong et al., 2014). However, the Crimean elasmothere differs from this Asian form by exhibiting a twofold greater degree of enamel folding in the permanent upper teeth (especially in the ventral half of the crown). *Elasmotherium peii* has the least pronounced enamel plication among all representatives of the genus. For example, for similar wear stages of M2, the posterior wall of the protoloph displays 12 folds of 1.6–4.9 mm width at Taurida and only 6–7 folds in *E. peii* (2.8–7 mm width: IVPP V-962; 2.1–6 mm: IVPP V-967). M3 from Taurida has a higher M3 crown, likely due to a greater sagittal curvature of the ultimate molar.

Postcranial bones of different *Elasmotherium* species are morphologically very similar. Most apparent differences are likely expressions of age variability and/or sexual dimorphism, and their evaluation requires a separate study. A comparison of the humerus, radius, ulna, astragalus, and metapodial bones of *E. chaprovicum* from Taurida with those of *E. caucasicum* from Sinyaya Balka and *E. sibiricum* from various localities in Siberia and the Volga region shows a relative closeness between *E. chaprovicum* and *E. sibiricum* (Figs. 4, 5). According to major proportions and bone indices, these two species exhibit very similar values, whereas the bones of *E. caucasicum* are larger and more massive. At the same time, based on many morphological features of the postcranial skeleton, *E. chaprovicum*, more closely resembles *E. caucasicum* than *E. sibiricum*.

Among the most notable features distinguishing *E. chaprovicum* from Taurida Cave from *E. sibiricum* are the following:

1. On the humerus, the distal epiphysis has a width comparable to that of *E. sibiricum*, but the distal trochlear block is wider and less oblique, with a more prominently developed fossa for the lateral digital extensor.
2. In the radius, the diaphysis is more flattened, and the styloid process on the distal epiphysis is shorter than in *E. sibiricum*.
3. The ulna is straighter (whereas in *E. sibiricum* it is much more curved in lateral view). The proximal epiphysis is wider in specimens of comparable individual age. The semilunar notch is less deep in *E. chaprovicum*, the anconeal process protrudes farther forward, and the olecranon is broader distally.
4. The calcaneus has a more developed calcaneal tuber, a lower neck, and is somewhat more gracile than in *E. sibiricum*, while maintaining similar width proportions.

In the morphology of the astragalus and metapodial bones, differences from *E. sibiricum* lie in the sizes and relative proportions of the facets. However, the available sample does not allow these differences to be confidently interpreted as species-diagnostic. In terms of overall dimensions, these bones in *E. chaprovicum* fall within the same size range as those of *E. sibiricum*, but they are generally smaller and more gracile than those in *E. caucasicum*.

The only find of "*Elasmotherium*" *primigenium* from the Late Miocene of Yangjing locality (Dingbian County, Shaanxi Province, northwestern China) has heavily worn M2, which is located in the jaw (Sun et al., 2022). This fact complicates comparison. It can be noted that the M2 dimensions of the

TABLE 7. Main species parameters of several species of *Elasmotherium* and "*E*". *primigenium* upper permanent teeth. *, data on material from Taurida Cave, Crimea; **, detailed data is not available.

Parameters	*E. peii*	*E. chaprovicum**	*E. caucasicum*	*E. sibiricum*	"*E*". *primigenium*
Enamel plication on the inner walls	weakly pronounced	relatively weakly pronounced	relatively irregular significant plication	ordered significant plication	relatively weakly pronounced
Closed postfossette in M1/M2	present in the middle part of the crown**	present almost to the base of the crown	disappears completely by the apical third of the crown	present only in the apical third of the crown	present in the middle part of the crown**
Roots	occurred in all moderately worn teeth**	occurred in slightly worn P2–M3	occurred only in heavily worn P2–M3	unknown in M2–M3	–
Height of M1 crowns with initial wear stage, mm	–	97–116	181–182	184–207	–
Height of M2 crowns with initial wear stage, mm	>152	~181	210–240	198–267	–

elasmothere from Taurida Cave are generally similar to those of representatives of various species of *Elasmotherium* and *Sinotherium*, including the find from Yangjing. It can be assumed that the closed postfossette in the find from China is present at the level of the mid-height of the crown or even in its basal third. This feature is characteristic for both the Early Pleistocene *E. peii* and *E. chaprovicum*, and representatives of the genus *Sinotherium*. The significant degree of tooth wear in the Chinese find makes proves difficult comparing the enamel plication pattern.

The teeth of elasmothere from the Taurida Cave differ from latest Neogene *Sinotherium lagrelii* Ringström, 1923 and *S. zaisanensis* Bayshashov, 1986 in having a greater crown height and noticeably greater plication of enamel on the grinding surface.

DISCUSSION

A study of representative samples of elasmothere teeth from several localities (Taurida, Sinyaya Balka, Bolshoy Karaman, Rasshevatskaya) has revealed significant variability in enamel structures depending on the degree of crown wear. The current species diagnoses within the genus were established without considering changes in the expression of occlusal surface structures during ontogenesis. In addition, it is likely that the number of premolars in all species was the same; however, researchers have not previously accounted for developmental features of the dental system in these rhinoceroses, in which the premolars P2/p2 and P3/p3 fell out with age after complete wear, resulting in a reduced tooth row length. Therefore, a revision of species diagnoses is necessary, based on updated data.

The chronological sequence of species proposed by Shvyreva (2015), *E. chaprovicum–E. peii–E. caucasicum–E. sibiricum*, in our opinion, requires revision and supplementation in light of new finds. In support of this sequence, Shvyreva (2015, 2016) classified elasmothere remains from a few localities in the Northern Black Sea region (Tokmak, Zhevakhova Gora, Kuyalnik) and Ciscaucasia (Rasshevatskaya) as the species *E. peii*. However, the teeth of these specimens are characterized by degrees of hypsodonty, enamel folding, and the development of additional structures that are comparable to those of *E. chaprovicum*. The morphological features that, according to Shvyreva (2015), distinguish this elasmothere from *E. chaprovicum* fall within the limits of intraspecific variability demonstrated by the material from Taurida. We therefore suggest that the so-called "*E. peii*" from the Northern Black Sea region also belongs to *E. chaprovicum*.

Apparently, *E. peii* is most likely the most primitive representative of the genus, based on dental characteristics. This species is currently known only from a few dental specimens from Asia. In addition to its type locality, Sanmen in Shanxi Province (Pinglu County, China), finds of *E. peii* have been reported from the Kayrakkum locality (Fergana, Uzbekistan; collection of the Geological Institute of the Russian Academy of Sciences, Moscow; GIN, no. 2721). The age of the former locality is estimated to be from the earliest Pleistocene (Huang & Ji, 1984; Sun & Deng, 2019), while the latter is correlated with the Gauss–Matuyama Reversal (2.59 Ma) (Bajgusheva & Titov, 2021; Sotnikova et al., 1997). The teeth of this species are characterized by relatively low crowns, delayed root development, and weak folding of the enamel on the grinding surface.

Recently, a new species, "*Elasmotherium*" *primigenium* Sun, Deng & Jiangzuo, 2022, was described from the Upper Miocene of China (Yangjing locality; Sun et al., 2022). However, the lack of clear morphological differences in the skull compared to representatives of the genus *Sinotherium* and the similarity of its dental parameters, particularly primitive features, to those of Late Miocene and Pliocene representatives of that genus, suggest that the find from Yangjing cannot be attributed to *Elasmotherium*. The indicated features of enamel structures on the grinding surface are given without taking into account their variability at different levels of the crown.

Thus, we include four species in the genus *Elasmotherium*. The earliest species is known from Central Asia, while later forms had a wider distribution area, ranging from East Asia to Eastern Europe. The revised chronological succession of Eurasian *Elasmotherium* species is as follows: *E. peii–E. chaprovicum–E. caucasicum–E. sibiricum.*

Elasmotherium peii is currently known only from China (Chow, 1958) and Uzbekistan. The type material consists of a complete tooth row, exhibiting the characteristic hypsodonty and enamel development typical of the genus, but with unusually weak enamel folding and less developed additional structures. Geochronological distribution: Late Pliocene (?)–early Early Pleistocene.

Elasmotherium chaprovicum has been described based on materials from localities of the Khaprovian Faunal Assemblage (2.6–2.1 Ma) of the south of Eastern Europe–the Northeastern Azov region (Khapry, Liventsovka, Mokryi Chaltyr), the Northwestern Black Sea region (Tokmak, Kryzhanovka/Kuyalnik, Novye Tanatary), and Ciscaucasia (Sablya) (Shvyreva, 2016; Titov, 2008). The attribution of specimens from the Xiashagou locality (Nihewan, China) to this species is questionable, as they are represented only by isolated bones of the postcranial skeleton. Geochronological and biostratigraphic distribution: Early Pleistocene, middle Villafranchian.

Elasmotherium caucasicum has been described from several localities of the Tamanian Faunal Assemblage of the south of Eastern Europe–the Sea of Azov and the Lower Don regions (Sinyaya Balka, Tsymbal, Semibalki, Port Katon, Samarskoe, Berdyansk, Mariupol, Sarkel) and, probably, Ciscaucasia. Reported finds of *E. caucasicum* in China require verification (Deng & Zheng, 2005). Geochronological and biostratigraphic distribution: the end of the Early Pleistocene, late Villafranchian–early Galerian.

Elasmotherium sibiricum is known from numerous localities within the Khasarian Faunal Assemblage, ranging from Eastern Europe to the Baikal region. This is the type species of the genus and the best studied (Kožamkulova, 1981; Shvyreva, 2015, 2016; Zhegallo et al., 2005). Geochronological and biostratigraphic distribution: the second half of the Middle Pleistocene to the beginning of the Late Pleistocene, Aurelian.

The evolutionary changes in the characteristics of the dental system from more ancient to chronologically younger species were manifested in increased hypsodonty and prolonged permanent tooth growth, as well as in the enhancement and ordering of enamel folding along the inner walls of all valleys. At the same time, the dental formula of the permanent generation remained unchanged across all species.

The features of the limb bones examined in the study reveal a trend in size variation. During the Early Pleistocene, in the transition from *E. chaprovicum* to *E. caucasicum*, there was a slight increase in body size. In the Middle and Late Pleistocene *E. sibiricum* became smaller, approaching the size of *E. chaprovicum*. However, current understanding of *E. caucasicum* is primarily based on the abundant material from the Sinyaya Balka locality. It remains unclear whether the "gigantism" of *E. caucasicum* is a true species-level trait or a characteristic specific to the Taman population.

As for the morphological features of the postcranial skeleton (excluding the bones, whose features are described above), for the majority of bones found in the Taurida cave (e.g., carpal bones, individual tarsal bones, phalanges), we did not find any

differences in the observation material that could be confidently diagnostic at the species level. Minor variations in the structure and orientation of facets, the development of ligamentous tubercles and similar features are most likely expressions of intraspecific variability and have not yet been systematically considered. The absence of pronounced morphological differences in these bones between early and late representatives of the genus suggests that these animals occupied relatively stable habitats throughout the Pleistocene, despite global climatic and environmental transformations (Titov et al., 2021). However, a more detailed comparative analysis of elasmotheres postcranial skeleton remains a subject for future research.

CONCLUSIONS

The study of fossil material from the Lower Pleistocene deposits of the Crimean Taurida Cave (late Villafranchian, 1.8–1.6 Ma) revealed the presence of the species *Elasmotherium chaprovicum* in the fauna of the Psekupsian Faunal Assemblage at this locality. This species was originally described from localities of the previous Khaprovian Faunal Assemblage in Eastern Europe (middle Villafranchian).

The study provided unique data on the morphological characteristics of teeth across different individual ages, as well as on the bones of the postcranial skeleton of *E. chaprovicum*. For the first time, the deciduous teeth of elasmotheres were described in detail. The dental analysis accounted for enamel variability at different crown levels and included parameters such as the degree of hypsodonty, enamel plication, the timing and degree of root formation, and the stages of posterior and median valley closure, among other features. A high degree of similarity was observed between the morphology of the postcranial skeleton of *E. chaprovicum* and that of *E. caucasicum* and *E. sibiricum*. In terms of the size class, the Taurida specimens of *E. chaprovicum* are comparable to *E. sibiricum* and smaller than *E. caucasicum*.

The finds refine current understanding of the evolutionary history of *Elasmotherium* in the southern part of Eastern Europe. The form previously referred to as "*E. peii*" in this region is here attributed to *E. chaprovicum*, and the revised chronological sequence of species in the northern Black Sea region is established as: *E. chaprovicum–E. caucasicum–E. sibiricum*.

The material from Taurida Cave extends the known chronological range of *E. chaprovicum* and shows that, in Crimea, the Northern Black Sea region, and Ciscaucasia, this species was characteristic of both the Khaprovian and Psekupsian faunal assemblages of Eastern Europe, and existed within the range of 2.6–1.6 Ma.

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AUTHOR CONTRIBUTIONS

CRediT: VVT: Conceptualization, Formal analysis, Investigation, Methodology, Software, Writing – original draft; IAY: Data curation, Investigation, Writing – original draft; VSB: Investigation, Methodology; IAV: Conceptualization, Supervision; AVL: Project administration, Validation, Writing – review & editing. VVT and IAY participated in collection, systematization and description of collection. VSB realized identification and comparison of dentalmaterial. IAV and AVL wrote and edited the manuscript.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials (see Supplementary Information). The CT data are available in MorphoSource:

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

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SUPPLEMENTARY FILES

Supplemental_information_file_1.docx: Supplementary Figures S1–3.

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