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A New Antelope *Tavridia gromovi* gen. et sp. nov. (Artiodactyla, Bovidae) from the Lower Pleistocene of the Taurida Cave in the Crimea

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Abstract—A new form of small antelope is described from the Lower Pleistocene of the Taurida Cave in the Crimea. A new genus and species *Tavridia gromovi* is identified from a fragment of the skull roof with a horn core and the lower jaw. This small antelope differed from all known forms in the morphological features of the horn cores and the dental system. Based on the combination of characters, it is assigned to the tribe Antilopini (Eurasia and Africa, Middle Miocene to Recent). The discovery of *T. gromovi* in the Crimea testifies to the significant diversity of this group of antelopes in the middle of the Early Pleistocene.

Keywords: *Tavridia gromovi* gen. et sp. nov., Antilopini, Early Pleistocene, the Crimea, Taurida Cave
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INTRODUCTION

The Taurida Cave near the village of Zuya, 15 km east of Simferopol, is a large locality of Pleistocene vertebrates in Central Crimea, discovered in 2018 during the construction of the Tavrida federal highway (Lopatin et al., 2019). Material, found in the main fossiliferous layer (MNQ18, 1.8–1.5 Ma) during excavations in 2022, included the remains of a small peculiar antelope of the tribe Antilopini Gray, 1821 of the subfamily Antilopinae Gray, 1821.

The tribe Antilopini comprises antelopes of the genus *Gazella* and related forms. The tribe includes up to 15–16 fossil genera and up to 13 extant genera, of which four: *Gazella* (s.s.), *Antilope*, *Nanger*, and *Eudorcas* belong to true gazelles (McKenna and Bell, 1997; Groves and Grubb, 2011; Hassanin et al., 2012; Bärmann et al., 2013). All these antelopes, mostly small and medium in size, had straight or lyre-shaped horns. Their horn cores lack cavities (sinuses), most are not twisted or are twisted heteronymously (i.e. normally, counterclockwise), less often twisted homonymously (backward, clockwise). Interfrontal and frontoparietal sutures are complicated. The premolar row is shortened to varying degrees, and the second lower premolar (P_2) can be reduced (sometimes poorly developed). The premolar P_4 usually has an open anterior valley (the paraconid and metaconid are not merged together), while the molar M_3 often has a well-developed posterior (third) lobe (Gentry, 1990, 1992; Gentry et al., 1999). In the fossil record, Antilopini are recorded starting from the Middle Miocene. In the Early Pleistocene, they were quite widespread in Europe, Asia and Africa.

So far, five Antilopini species belonging to three genera have been known from the Early Pleistocene of Europe: *Gazella borbonica* Depéret, 1884, MN15–MNQ17, Europe; *G. bouvrainae* Kostopoulos et Athanassiou, 1997, MNQ16b–18, Europe; *G. aegea* Athanassiou, 2002, MNQ17, Greece; *Gazellospira torticornis* (Aymard, 1854), MN16–MNQ18, Europe; *Antilope koufosi* Kostopoulos (1998), MNQ18, Greece (Kostopoulos and Athanassiou, 1997; Kostopoulos, 1998, 2022; Spassov and Crégut-Bonnoure, 1999; Spassov, 2005; Crégut-Bonnoure, 2007; Rodrigo, 2011; etc.). Only one of these species, *G. torticornis*, has been found in the early Pleistocene artiodactyl assemblage from Taurida based on the materials of the first excavations, in 2019–2020. (Vislobokova et al., 2020).

The diagnosis of fossil genera and species of Antilopini is largely based on the features in the morphology of the frontals and horn cores (position on the skull and shape, the nature of the surface, etc.), as well as the features of the dentition (the relative length of the premolar row, the morphology of P_4 and M_3). Based on the combination of morphological characters, the antelope from Taurida differs from all known forms of Antilopini and is assigned to a new genus and a new species.

The discovery of a new antelope in the Taurida Cave improves our understanding of the diversity of fossil Antilopini of Europe and complements the emerging picture of the natural environment of the Crimea in the middle of the Early Pleistocene, the time of the dispersal of early *Homo* in the Black Sea region.

SYSTEMATIC PALEONTOLOGY

Family Bovidae Gray, 1821

Subfamily Antilopinae Gray, 1821

Tribe Antilopini Gray, 1821

Genus *Tavridia* Vislobokova, gen. nov.

Etymology. From the Taurida Cave locality.

Type species. *Tavridia gromovi* sp. nov.

Diagnosis. Size small. The frontal bones between the horn cores are moderately elevated, lying above the level of the orbits, slightly thickened anteriorly, and without sinuses. The supraorbital foramens are in a short distance from the bases of the horn cores, in deep pits. The postcornual fossae are small and laterally located. The pedicle is very short, overlapped anteriorly by a horn core. The horn cores are weakly homonymously twisted, slender, diverging from the base and slightly bent posteriorly, rounded in cross section; their bases are slightly compressed anteroposteriorly, without cavities. The surface on the medial side has a well-defined longitudinal groove starting above the base of the horn core; its sharp posterior edge transforms into a low crest distally. The mandible is of gazelle type, with a convex lower margin. The premolar tooth row is short. P_2 is strongly reduced, with a single root. P_3 and P_4 are short, with a well-developed, lingually protruding parastylid, a metaconid sloping backwards, and a closed posterior lingual valley. The crowns of the lower molars are high, without an ectostylid, with a flattened lingual wall and a slight "goat" fold. M_2 and M_3 are enlarged; the third lobe of M_3 is long and wide, with a facet (mark) and a posterior stylid.

Species composition. Type species from the Lower Pleistocene, Late Villafranchian (MNQ18).

Comparison. The slender horn cores and the gazelle-type mandible, the absence of sinuses in the frontals and horn cores, the flattened lingual wall of the lower molars, the presence of a weak "goat" fold, as well as the structural features of P_4 and M_3 indicate that the antelope from Taurida belongs to the tribe Antilopini.

Homonymous twisting of the horn cores and a considerable reduction in P_2 distinguishes the Taurida antelope from most representatives of Antilopini (including *Antilope* Pallas, 1766 and *Gazellospira* Pilgrim et Schaub, 1939). These features make *Tavridia* similar to *Hispanodorcas* Thomas, Morales et Heintz, 1982 (Late Miocene–Early Pliocene of Europe) and *Antidorcas* Sundevall, 1847 (Late Pliocene–Recent, Africa). In the absence of sinuses and the lateral position of the postcornual fossae, *Tavridia* is similar to *Hispanodorcas*, but differs in the elevation of the interhorn region of the frontal bones above the level of the orbits, the nature of the surface, the more rounded cross-sectional shape of the horn core, the shape of the horizontal branch of the mandible, greater hypsodonty, short premolars, single-rooted P_2 and larger M_3 with a strongly developed third lobe (Thomas et al., 1982; Bouvrain and de Bonis, 1988; Alcalá and Morales, 2006; Kostopoulos, 2014). It differs from *Antidorcas* in the absence of sinuses, the position of the postcornual fossa, the divergence of the horn cores from the base, a less sharp difference in the height of the mandibular body below P_4 and M_3, and the preservation of P_2. In *Antidorcas*, the sinuses are developed at the bases of the horn cores and in the frontals, extending to the supraorbital foramina (Vrba, 1973; Farke, 2010), P_2 is absent, and P_3 is strongly reduced (Gentry, 1966; Vrba, 1973; Gentry and Gentry, 1978). In addition, it differs from *Hispanodorcas* and *Antidorcas* in the anteroposterior compression of the horn cores, larger size, and structure of M_3.

The genus *Tavridia* is similar to *Antilope* in having a weak twisting and a rounded cross section, as well as in the nature of the surface of the horn core, but differs in the type of twisting. In representatives of the genus *Antilope*, it is heteronymous (Pilgrim, 1937, 1939; Gentry et al., 1999; Kostopoulos, 1998, 2022; Khan and Akhtar, 2014). The horn core of *Tavridia* is similar to the holotype of *A. subtorta* Pilgrim, 1937 (AMNH, no. 19989) from the Upper Pliocene of Siswan, Pakistan, in size, shape, and the presence of a well-defined, wide longitudinal groove starting above the base (Pilgrim, 1937, fig. 42; Khan and Akhtar, 2014, Fig. 3). But, unlike *Tavridia*, in *A. subtorta* this furrow extends along the outer surface of the horn core. Differs from *A. koufosi* from Gerakarou (MNQ18), Greece, both in the type of twisting and in the shape of the horn cores; in *A. koufosi*, the twisting is heteronymous and spiral-like (Kostopoulos, 1998, 2022).

It differs from *Gazella* Blainville, 1816 in the lateral position of the horn fossa, shorter pedicles, the twisting of the horn cores and features of their surface, as well as a strong reduction of P_2. In all *Gazella*, the postcornual fossa is displaced posteriorly, the pedicles are longer, the horn cores are not twisted and are usually strongly striated, P_2 has two roots. The size of the antelope from Taurida surpasses the gazelles from the Early Pleistocene of Europe, *G. borbonica*, *G. bouvrainae* and *G. aegea*. It differs from *Gazellospira* Pilgrim et Schaub, 1939 in smaller size, twisting of the horn cores, shorter row of premolars, greater hypsodonty, and the absence of ectostylid on the molars. In *Gazellospira*, the horn cores are heteronymously twisted and spiral-like.

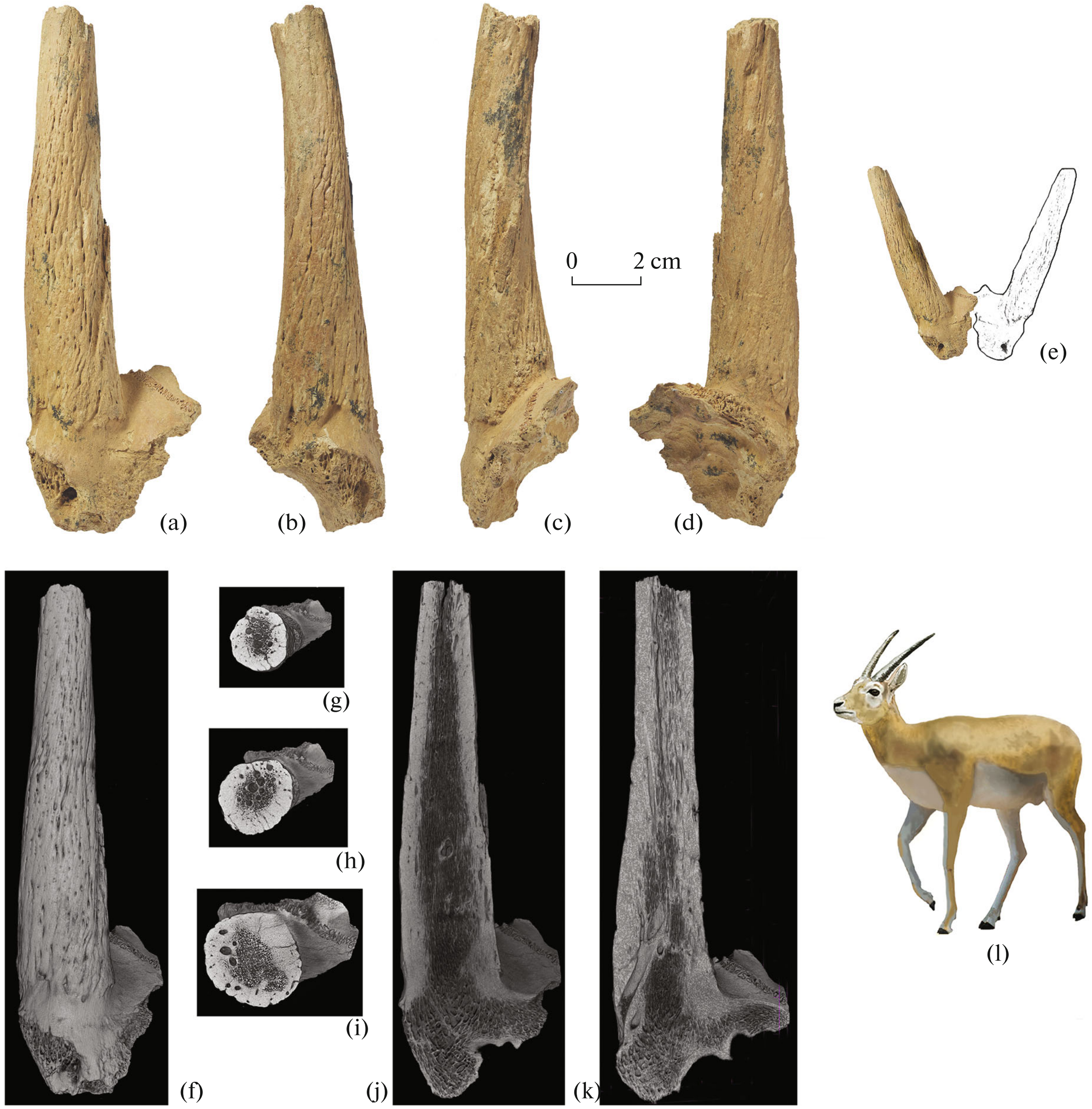

Fig. 1. *Tavridia gromovi* gen. et sp. nov.: (a–k) holotype PIN, no. 5644/306, skull roof fragment with incomplete right horn core: (a) anterior view, (b) lateral view, (c) medial view, (d) posterior view, (e) position of the horn cores; (f–k) CT-scan: 3D models, outside (f), cross sections, at the end (g), in the middle (h), at the base (i); longitudinal sections: along the midline (j) and closer to the surface (k); (l) reconstruction of the appearance of the animal; Crimea, Taurida Cave; Lower Pleistocene.

Tavridia gromovi Vislobokova, sp. nov.

Etymology. Named in honor of V.I. Gromov, the outstanding Russian researcher of the Quaternary.

Holotype. PIN, no. 5644/306, skull roof fragment with incomplete right horn core (Fig. 1); Russia, Crimea, Taurida cave; Lower Pleistocene (Upper Villafranchian, MNQ 18).

Description (Figs. 1, 2). The skull roof of the holotype is broken anteriorly in front of the supraorbital foramen, and posteriorly, behind the frontoparietal suture. The angle between the frontal and parietal surfaces is about 140°. The frontoparietal (coronal) and interfrontal (sagittal) sutures are complicated. The frontoparietal suture is curved, protruding anteriorly at an angle of approximately 140°. The preserved parietal part of the skull roof is flattened. The interhorn region of frontal bones lies above the orbit; it is convex, with a narrow, slight concavity along the medial edge of the base of the horn core. The width of the skull at the point of constriction behind the orbits appears to have been less than 90 mm. The frontals between the supraorbital foramens (for. supraorbitale) may have been slightly concave. The frontal bone is thickened anteriorly (up to 20 mm thick slightly above for. supraorbitale). The base of the horn core is located above the orbit and is only slightly displaced posteriorly. The supraorbital foramen is rather large (up to 4.5 mm in diameter), lying in a deep fossa near the base of the horn core (the minimum distance from the posterior edge of the for. supraorbitale to the base of the horn core is 16.2 mm). The distance between the supraorbital foramens was probably about 50 mm. The pedicle is very short; in anterior view, it is almost not visible (covered by the horn core), and posteriorly, its length does not exceed 5 mm. The contact of the horn core with the frontal anteriorly and with the pedicle is well expressed. The minimum distance from the inner edge of the base of the horn core to the interfrontal suture was about 17.5 mm, and, apparently, the distance between the horn cores slightly exceeded the transverse diameter of the base of the horn core. The angle of inclination formed by the horn core with the preserved parietal part of the skull roof is approximately 76°. The base of the horn core is slightly beveled relative to the longitudinal axis of the skull, the angle of bevel of its maximum axis with respect to the sagittal plane is about 78°. The horn core is relatively thin, gradually narrowing towards the broken margin, directed posteriorly and slightly laterally, slightly homonymously twisted and slightly bent backwards. At the ends, in front of the break, the core has a barely noticeable lateral bend. In anterior view, the horn core looks straight, but from the side it looks slightly curved: the anterior edge of the horn core is straight in the proximal half and slightly convex distally, and its posterior edge is slightly concave. The angle of divergence of the horn cores was acute (probably no more than 40°–50°). The surface of the horn core is almost without grooves and pronounced keels, covered with a series of "reticulate-anastomosing grooves" as in *Antilope subtorta* and *A. cervicapra* (from Pilgrim, 1937, p. 812). A pronounced medial longitudinal groove (up to 5 mm wide) with a sharp posterior edge, turning into an unpronounced crest, begins on the anteromedial part of the surface, at a distance of about 1.5 cm from the base of the horn core, and ends slightly below the broken margin. The crest extends to the broken margin and ends in the middle of its posterior edge. Judging by the position of the ends of the crest, the twisting of the horn core from the base to the break is about 105°. The postcornual fossa is small, located on the lateral surface, slightly closer to the anterior edge of the base of the horn core than to its posterior edge. A very short, narrow groove runs obliquely upwards from the postcornual fossa. Discontinuous oblique grooves are present behind this groove on the outer surface of the horn core, as well as on its posterior surface. The cross section of the horn core is rounded. The base of the horn core is strongly oblique with respect to the longitudinal axis of the horn core and slightly compressed anteroposteriorly; the transverse diameter (DT) of the cross section of the base of the horn core slightly exceeds its anteroposterior diameter (DAP); Compression index—95%.

The CT-scan showed the absence of sinuses in the frontal bone and horn core (Fig. 1f–1k). Bone tissue of the horn core has the canals for vessels, including large ones.

The left ramus of the mandible, PIN, no. 5644/307, is broken off in front of the mental foramen, as well as in the area of the angular region, and partially destroyed behind the tooth row (Fig. 2). A bone height rather sharply increases from P_2 to M_3. The lower edge of the body is convex. The mental foramen is relatively small. The distance from it to the tooth row is less than the length of M_1–M_2. The diastema was apparently short. A very small foramen is found below the anterior edge of P_3. The articular surface of the articular process is concave, but at the medial edge it is slightly convex. The coronoid process is long; it is slightly broken off at the end and probably protruded posteriorly beyond the articular process. The posterior margin of the ascending ramus below the articular process is straight in outline. The shape of the angle is not known, but apparently it was not very protruding.

The teeth are hypsodont. The premolar row is very short. P_2 is strongly reduced: it was single-rooted and probably rudimentary; its alveolus is extremely small (0.95 mm in diameter). The crowns of P_3 and P_4 are relatively short, with a well-developed, strongly protruding lingual parastylid, a relatively unpronounced paraconid, a posteriorly directed metaconid that slightly protrudes lingually and meets the entoconid; the posterior valley is closed. On the buccal side of P_4, the hypoconid is separated from the protoconid by a deep, rather narrow, V-shaped valley. The crowns of the molars are relatively high, without an ectostylid. The lingual walls are relatively flat, with a well-developed parastylid and entostylid, very slightly swollen pillars of the metaconid and entoconid, and without a pronounced metastylid. All molars have a slight "goat" fold. The M_2 and especially M_3 crowns are enlarged. The third lobe of the M_3 crown is long and wide, with an internal mark and a posterior stylid. The buccal wall of the third lobe of M_3 is convex; it is rounded on the occlusal surface. The lingual wall of the third lobe of M_3 has a short lingual pillar, slightly rounded, slightly angular on the occlusal surface. The length of the third lobe is equal to the length of the second, while its width is only a quarter less.

Mesowear relief is relatively high, the labial cusps are mostly sharp, the anterior cusps on M_2 and M_3 are slightly broken off, the depressions between the cusps are shallow on M_1 and deeper on M_3 (Fig. 2d).

Measurements in mm, indexes in %. Holotype PIN, no. 5644/306, frontal: length from posterior edge of supraorbital foramen to frontoparietal suture, 41; maximum pedicle length posteriorly, 5.5;

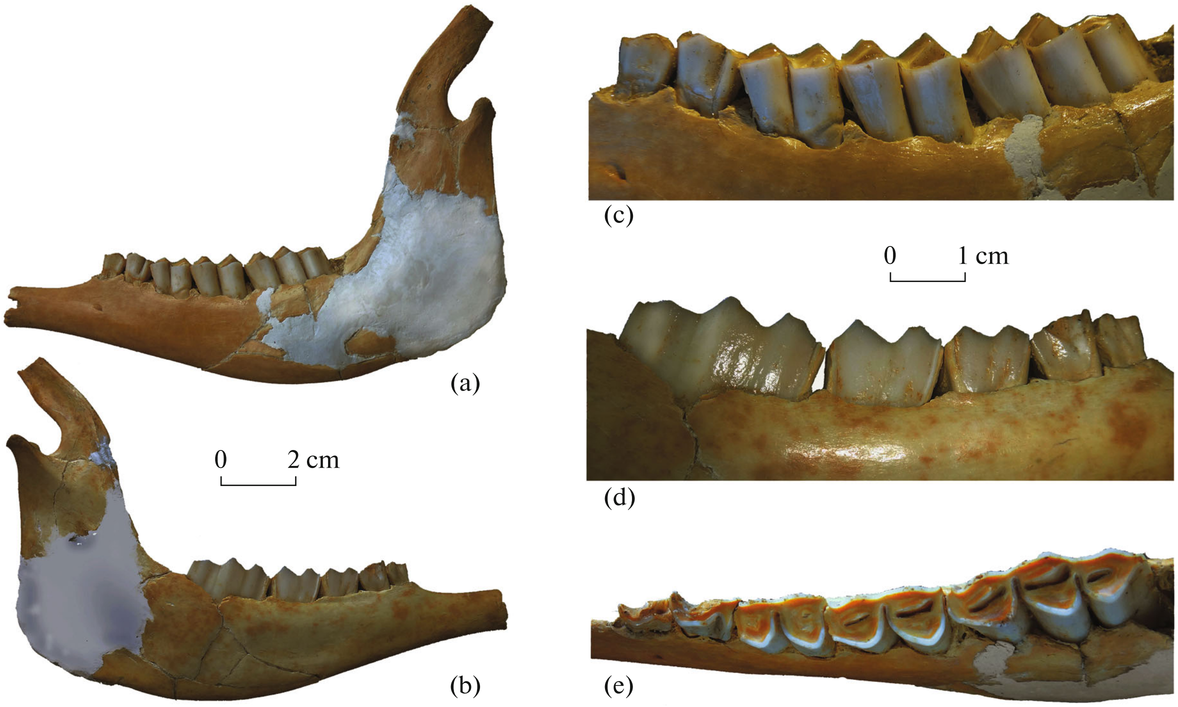

Fig. 2. *Tavridia gromovi* gen. et sp. nov., paratype PIN, no. 5644/307: (a, b) left mandibular ramus with P_3–M_3, lateral view (a), medial view (b); (c–e) P_3–M_3: (c) buccal view, (d) lingual view, and (e) occlusal view; Crimea, Taurida Cave; Lower Pleistocene.

horn core: length (in a straight line) to broken margin 125.5; transverse diameter (DT) and anteroposterior diameter (DAP), DT × DAP, 28.25 × 26.8 at the base, 22.78 × 20.98 in the middle, and 16.53 × 16.18 at the broken margin; DT of the base anteriorly, 32.03; compression index of the base (DAP/DT), 95.

Paratype PIN, no. 5644/307, left ramus of the mandible: length from the posterior edge of the mental foramen to the anterior edge of the alveolus of P2, 21.25; length of tooth row from the alveolus of P_2 to the alveolus of M_3, 71.8; ascending ramus width in the middle, 30.58; minimum diastema height, 12.82; the height of the horizontal ramus below P_2, 19.15, below M_1, 23.86, below M_3, 30.39; the greatest height of the ascending ramus, 103.75; the height of the ascending ramus to the base (notch) of the articular process, 67.14, to the articular process, 75.12.

Teeth: premolar row length (from the alveolus of P_2) 18.4, molar row length, 51.74, along the alveoli, 17.99 and 49.83 respectively (lingual side), 15.57 and 52.81 (buccal side); length and width (L × W) of teeth: P_3, 7.36 × 4.36; P_4, 8.84 × 4.78; M_1, 11.93 × 8.83; M_2, 15.9 × 8.23; M_3, 23.65 × 8.38; length and width of the third lobe of M_3, 8.69 × 6.62. The height of M3 is less than 1.5 times its total length. Index P_2–P_4/M_1–M_3, 36.

Remarks. At present, the genus *Gazella* and related forms are assigned to the tribe Antilopini of the family Antilopinae (McKenna and Bell, 1997; Gentry et al., 1999; Bibi et al., 2009; Gentry, 2010), and are not separated into a separate subfamily Gazellinae, as it is was treated previously, in particular, by E.L. Dmitrieva (1977).

Material. Only the holotype and paratype from the Lower Pleistocene of the Taurida Cave, Crimea.

TAVRIDIA AND SOME ASPECTS OF THE EVOLUTION OF ANTILOPINI

The discovery in the Crimea of a new small antelope that has very weakly homonymously twisted horn cores along an almost straight axis brings us to consider some issues of the evolution of gazelle-like forms of Antilopini with weakly twisted horns which are closest in size and morphologically to the newly found form (*Hispanodorcas*, *Antidorcas,* and *Antilope*).

The main evolutionary trends of these Antilopini, as well as other ungulates, are associated with the expansion of their habitats in the context of climate and landscape change. In different lineages, there was a gradual expansion into the semi-open, and then open biotopes, which was accompanied, among other things, by changes in skull morphology, the shape of the horn cores, and the dental system.

The main changes in the evolutionary development of horn cores in gazelle-like Antilopini have been the increase in their size, increased twisting and spiraling, posterior inclination, axis bending, base compression, and the appearance of keels. The bases of the horn cores are usually located above the orbits, but in some taxa they are displaced posteriorly. The frontal sinuses are only developed in some taxa. They are most strongly developed and extend into the base of the horn core in *Antidorcas*, while in some species of *Antilope* and *Gazella*, small sinuses lie rostral to the supraorbital canal (e.g., Farke, 2010). In the course of evolution, various representatives of the Antilopini group developed and gradually strengthened adaptations to grazing and mixed feeding: increased hypsodonty, a reduction in the relative length of the premolar row, an increase in the size of molars and, accordingly, in the height and width of the body of the mandible below the molars.

The phylogeny of Antilopini shows especially clear examples of mosaic evolution, parallelisms, different rates of evolutionary development of similar characters, the appearance of similar characters at different geological times, as well as occurrence of different combinations of similar morphological characters in different forms.

The Taurida antelope exhibits a unique combination of primitive and advanced characters characteristic of the gazelle-like Antilopini, as well as specialized traits. This combination distinguishes *Tavridia* from all known genera. Plesiomorphies found in the holotype of *T. gromovi* sp. nov. include: (1) the absence of sinuses in the frontal bones and horn cores, (2) the position of the bases of the horn cores above the orbit, (3) the divergence of the horn cores from the bases, (4) the unpronounced bending of the horn cores, (5) the unpronounced posterior inclination of the horn cores and 6) the rounded cross-section. The apomorphies include: (1) the position of the interhorn region of the frontal bones above the level of the orbit, (2) the position of the supraorbital foramen in a deep fossa, (3) the lateral position of the postcornual fossa, and (4) a short pedicle. The main specialized characters in *Tavridia* are: (1) weak homonymous twisting of the horn core, (2) a very low position of the anterior edge of the base of the horn core (overlapping the pedicle anteriorly), and 3) the presence of a medial longitudinal groove with a sharp posterior edge, passing into a crest at the distal end.

Plesiomorphies in the morphology of the mandible of *Tavridia* include: (1) a relatively low body of the horizontal ramus, (2) great width of the ascending ramus, (3) large angle between the horizontal and ascending rami, (4) small distance between P_2 and the mental foramen. The apomorphies include: (1) convex lower margin of the body of the horizontal ramus; and (2) an increase in body height from P_2 to M_3. In its significant reduction of the premolar row, significant decrease of P_2, length decrease of P_3 and P_4, strong increase of the molars M_2 and M_3, the degree of development of the posterior lobe of M_3, and the absence of ectostylid on molars, *Tavridia* surpasses all known extinct representatives of Antilopini and approaches some modern species.

The genus *Hispanodorcas* was distributed in southern Europe from the Late Miocene to the Early Pliocene and is represented by three species: *H. torrubiae* Thomas, Morales et Heintz, 1982 (type species) from the Concud type locality and the Los Mansuetos locality, Middle Turolian (MN12), Spain; *H. orientalis* Bouvrain et Bonis, 1988 from Ditiko-3, Late Turolian (MN13), Greece; *H. heintzi* Alcalá et Morales, 2006 from La Galera, Early Ruscinian (MN14), Spain (Thomas et al., 1982; Bouvrain and de Bonis, 1988; Alcalá and Morales, 2006). In addition, *H.* cf. *orientalis* is present in the Nikiti-1 locality, Late Vallesian (MN10), Greece (Kostopoulos, 2014, 2022). The type species *H. torrubiae* is known only from horn cores, but other species are represented by more complete fossil material (including mandibles with dentition). In the process of evolution, the twisting, bending, and mediolateral compression of the horn cores increased in *Hispanodorcas*, while the postcornual fossa and the lateral sulcus became smaller (Bouvrain and de Bonis, 1988; Kostopoulos, 2022). *Tavridia* shows similarities with *Hispanodorcas* in its plesiomorphies as well as some apomorphies: e.g., the short pedice, lateral postcornual fossa. But *Tavridia* differs from *Hispanodorcas* in the high position of the interhorn region of the skull in relation to the orbits, the more rounded cross-section of the horn core, and the absence of the anterior keel. The compression index of the base of the horn core in *T. gromovi* (95%), which is higher than in *H. torrubiae* (77.8–90.8%). Specific features of the *T. gromovi* holotype that indicate that *Tavridia* and *Hispanodorcas* belong to different phyletic lineages include its rounded rather than oval cross-section, anteroposterior rather than mediolateral compression of its base, the absence of a flattening on the lateral surface characteristic of *Hispanodorcas*, the presence of a deep medial longitudinal groove, and the shape of the horizontal ramus of the mandible. The affinities of *Hispanodorcas* have been interpreted differently. The genus *Hispanodorcas* is either assigned to Antilopini (McKenna and Bell, 1998; Alcalá and Morales, 2006) or to another Antilopinae group, Oiocerina Pilgrim, 1934 (Kostopoulos, 2014, 2022). The authors of the genus *Hispanodorcas* noted its similarity to *Gazella* (Thomas et al., 1982).

The genus *Antidorcas* has existed in Africa since the Pliocene and is represented in the modern fauna by the species *A. marsupialis* (Zimmermann, 1780), which inhabits the southwestern arid zone and dry savannah of South Africa and is the national emblem of South Africa (Cain III et al., 2004; Castelló, 2016). Antelopes of this genus appeared on the continent 2.8–2.4 Ma and dispersed widely about 2 Ma (Gentry, 1966; Vrba, 1973, 1974, 1995; Sewell et al., 2019). Fossils of these antelopes are also present at early *Homo* sites (e.g., Olduvai, Tanzania; Sterkfontein, South Africa). These antelopes have sinuses developed in the frontals and in the bases of the horn cores. In this character, *Antidorcas* is more advanced than *Tavridia*.

Common apomorphies of these genera are: (1) the position of the interhorn part of the frontal bone above the level of the orbits, (2) the position of the supraorbital foramen in a deep fossa near the base of the horn core, and (3) the convex lower margin of the body of the horizontal ramus, although the increase in body height from P_2 to M_3 is not as sharp in *Tavridia* as *Antidorcas*. In addition, these genera share similar changes in the dental system (strong reduction of P_2, well-developed third lobe of M_3), but differ in the shape of the horn cores. The horn cores of *Antidorcas* are more robust at the base, usually slightly compressed mediolaterally and sometimes have lateral flattening. On the other hand, in *A. recki* (Schwarz, 1932) from Olduvai (Bed II, 1.8 Ma), possibly ancestral to other species of the genus, the base of the horn core of the holotype M 21460 is very weakly compressed (Gentry, 1966; Vrba, 1973). E. Vrba believed that *Antidorcas* branched off from *Gazella* in the Pliocene, earlier than 3 Ma (Vrba, 1973). The origin of *Antidorcas* from *Gazella*, in her opinion, in particular, is indicated by the primitively rounded cross-sectional shape of the horn cores in the early *Antidorcas*, as well as in the early *Gazella*. The oldest Antilopini in Africa have been found in the Middle Miocene (ca. 14 Ma; Vrba, 1985).

The rounded cross-section is also characteristic of antelopes of the genus *Antilope*. These antelopes have been common in South Asia since the Late Pliocene. They may have lived in Africa as well (Gentry, 1976, 1985; Bibi, 2013). In Asia, fossil species of this genus are known from the Upper Siwaliks of Pakistan: *A. subtorta* Pilgrim, 1937 and *A. intermedia* Khan et Akhtar, 2014 from the Tatrot Formation (3.4–2.6 Ma) and *A. cervicapra* (Linnaeus, 1758) from the Pinjor Formation (2.6–0.6 Ma) (Pilgrim, 1937, 1939; Khan and Akhtar, 2014). The species *A. cervicapra* today inhabits the Hindustan Peninsula south of the Himalayas; it prefers grassy areas, shrubs, open forests on plains (IUCN SSC Antelope Specialist Group, 2017). Species of the genus *Antilope* differ from *Tavridia* in the heteronymous type of twisting, but the compression index of the base of the horn core of *T. gromovi* is close to the average between the indexes of *A. subtorta* (99%) and *A. cervicapra* (93.5%) (Pilgrim, 1937, 1939). The twisting of the horn cores in *Antilope* is stronger and increases from *A. subtorta* to *A. cervicapra*; the latter has spiral twisting. In modern *A. cervicapra*, as in *Tavridia*, P_2 is reduced and the third lobe of M_3 is well developed, but P4 is less strongly shortened. In contrast to *Tavridia*, the supraorbital foramina lie primitively at the same level with the forehead, but the horn cores are displaced posteriorly, they do not extend above the orbit, but slightly behind its posterior margin (e.g., Grove and Grubb, 2011).

The relationships of the only European representative of the genus *Antilope*, the species *A. koufosi* (Kostopoulos, 1998) (=*Parastrepsiceros koufosi*) from the Early Pleistocene of Gerakarou (MNQ18), Greece, are not yet clear (Kostopoulos, 2022). In addition to the holotype (horn core, GER-273), the species is represented by three horn cores, two fragments of the upper jaw, a fragment of the mandible with P_3–M_3, and a metacarpal bone stored at the Aristotle University of Thessaloniki. In terms of the size of the horn cores, *A. koufosi* is close to *T. gromovi*, but differs in their spiral shape, heteronymous type of twisting, and mediolateral compression of the base (DAP 30.0–34.7 mm, DT 24.0–28.5 mm, DAP/DT 80–84%) (according to: Kostopoulos, 1998). These species are also similar in the shape of the lower margin of the mandible body, P_3–M_3 length (62.3 mm in *T. gromovi* and 62.5 mm in *A. koufosi*, GER-148), and M_3 morphology (Kostopoulos, 1998, text-figs. 3, 4e). However, in *A. koufosi*, the premolars are longer, the metaconid is not inclined backwards on P_4, the molar row is shorter (L M_1–M_3, 44 mm), and there is an ectostylid on the molars. According to these features of the lower teeth, *A. koufosi* is more primitive than *T. gromovi*.

The type of horn cores of early gazelles (slender, slightly bent back, without keels and with a rounded section) could theoretically be ancestral (or close to the ancestral state) both for forms with homonymous twisting (*Hispanodorcas*, *Antidorcas*, *Tavridia*) and for forms with heteronymous twisting (*Antilope*). The appearance of these types of horn cores twisting may have been due to early divergence (or radiation) from a gazelle-like ancestor in the Miocene, or may have occurred repeatedly, perhaps through intermediate forms of gazelle-like antelopes in the Late Miocene – Pliocene. Since the early history of Antilopini has not yet been sufficiently studied, these hypotheses require further confirmation.

The evolutionary history of Antilopini is analyzed not only on the basis of paleontological data, but for modern species also using data from molecular genetics (e.g. Hassanin and Douzery, 1999; Matthee and Robinson, 1999; Hassanin et al., 2012; Bärmann et al., 2013; Lerp et al., 2013; Yang et al., 2013; Bibi, 2013, 2014; Chen, 2019).

Extant species of the genera *Antilope*, *Antidorcas*, and *Gazella* and several other genera are included in a single group of gazelle-like antelopes, recently identified as a subtribe of Antilopina based on complete mitochondrial genomes (Hassanin et al., 2012). A series of analyses using the entire mitochondrial genome as well as combined mitochondrial and nuclear gene data have shown a close relationship between *Gazella* (s.s.) and *Antilope* (*A. cervicapra*) and their divergence with *Antidorcas* (*A. marsupialis*) (Hassanin et al., 2012; Bärmann et al., 2013). According to the molecular clock (based on the complete mitochondrial genome), the adaptive radiation of Antilopina with the appearance of *Gazella* (s.s.), *Antidorcas*, and *Saiga* occurred in the Late Miocene (ca. 8.5–8.0 Ma), while the divergence of *Gazella* and *Antilope* occurred in the Early Pliocene (ca. 4.5–4.2 Ma) (Hassanin et al., 2012) or earlier, at the end of the Miocene (7.4–5.2 Ma) (Bibi, 2013). Phylogenetic analysis based on cytochrome b shows that true gazelles appeared 10.5–6.3 million years ago (Lerp et al., 2013).

Based on phylogenomic data, it is more likely that *Tavridia* originated in the Pliocene or even in the Late Miocene.

The biodiversity of gazelle-like antelopes increased during major global and regional environmental transitions: at the end of the Miocene during the Messinian crisis in the Mediterranean (6 Ma: Boehme et al., 2017), at the Pliocene–Pleistocene boundary (2.6 Ma), and in the middle of the Early Pleistocene (2–1.8 Ma). The increase in biodiversity was associated with the evolution of lineages and dispersal events set against the background of landscape and climate change, increasing climate aridity, and the expansion of grasslands. Changes in Antilopini biodiversity at these boundaries can be traced in Europe, Africa, and Asia (Vrba, 1995; Kostopoulos, 1998; Gentry et al., 1999; deMenocal, 2004; Crégut-Bonnoure, 2007; Khan and Akhtar, 2014). The similarities between the Taurida antelope and some species of *Hispanodorcas*, *Antidorcas*, and *Antilope* are largely due to the general trends in the evolution of Antilopini and to similar adaptations evolving in members of these genera with the transition to more open habitats, an increase in the proportion of grasses in the diet, and the development of grazing. The pattern of evolution of these antelopes was quite complex, with the appearance of many forms with different combinations of ancestral gazelle plesiomorphies and new adaptations. Among true gazelles, lineages can be distinguished with adaptations to arid conditions (savannas, semi-deserts, and deserts) and those adapted to a more humid climate which could disperse along mountain systems (e.g., Lerp et al., 2013).

The morphology of the mandible and the dental system of *Tavridia gromovi* gen. et sp. nov. and modern *Antidorcas marsupialis* and *Antilope cervicapra* are largely similar, although *T. gromovi* shows a different combination of primitive and advanced characters (for example, a relatively low mandibular body and the absence of ectostylid on molars). This suggests that, in terms of the level of adaptation to living in open biotopes, it was quite close to these two species. A significant reduction in the premolar row, as well as rather high crowns and details of molar morphology, in *T. gromovi* are apparently associated with adaptations to feeding on herbaceous plants and grasses. In terms of these adaptations, *T. gromovi* was superior to species of the genus *Hispanodorcas* and *Antilope subtorta*. The antelope from Taurida was most likely a mixed feeder, just as the extant *Antidorcas marsupialis* and *Antilope cervicapra* and the fossil species of *Antidorcas* (e.g. Ecker, 2018; Lozano and Blanco, 2018; Uno et al., 2018; Sewell et al., 2019). In terms of molar wear (mesowear), *T. gromovi* is closest to *A. recki* (see Sewell et al., 2019). As in *A. recki*, the wear pattern in *T. gromovi* retains the relatively high relief of occlusion and sharp cusps characteristic of browsers. Such an antelope could have inhabited savannahs, ecotones on the border of sparse forests and steppes, and shrub plains. In addition to herbaceous plants and grasses, the diet may have included leaves of woody plants and shrubs, as well as fruits.

All these data indicate a significant originality of *Tavridia*. However, additional material and new studies will be needed to clarify the phylogenetic affinities of this antelope.

CONCLUSIONS

The study of fossil remains from the Taurida Cave in the Crimea made it possible to establish the presence of the new genus and species of the tribe Antilopini *Tavridia gromovi* with slightly homonymously twisted horns in the Early Pleistocene fauna of this locality. The phylogenetic affinity of this small antelope is not yet clear, but comparison with other representatives of Antilopini suggests that it belonged to a lineage going back to the Late Miocene. This antelope was been adapted to life in semi-open landscapes. The presence of a new antelope in the Early Pleistocene of Crimea improves our understanding of the diversity of the antelopes of the Antilopini tribe in Europe and its evolution.

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CONFLICT OF INTEREST

The author declares that she has no conflict of interest.

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