

## Early Pleistocene Spiral-Horned Antelopes (Artiodactyla, Bovidae) from the Taurida Cave (Crimea, Russia)

I. A. Vislobokova<sup>a, \*</sup>, V. V. Titov<sup>b</sup>, A. V. Lavrov<sup>a</sup>, D. O. Gimranov<sup>c, d</sup>,  
D. B. Startsev<sup>e</sup>, and K. K. Tarasenko<sup>a</sup>

<sup>a</sup>Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, 117647 Russia

<sup>b</sup>Southern Scientific Center, Russian Academy of Sciences, Rostov-on-Don, 344006 Russia

<sup>c</sup>Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia

<sup>d</sup>Ural Federal University, Yekaterinburg, 620002 Russia

<sup>e</sup>Vernadsky Federal University of Crimea, Simferopol, 295007 Russia

\*e-mail: ivisl@paleo.ru

Received February 5, 2019; revised February 7, 2019; accepted February 12, 2019

**Abstract**—The article describes fossil remains of two spiral-horned antelope species *Gazellospira torticornis* (Aymard, 1854) and *Pontoceros ambiguus* Vereschagin, Alexejeva, David et Baigusheva, 1971 which were found in 2018 in the Lower Pleistocene sediments of the Taurida Cave in Central Crimea. These finds are the first evidence of the occurrence of these taxa on the Crimean Peninsula. This association is correlated with the Late Villafranchian faunas of Europe and the mammal zone MNQ18 (within the time interval 1.8–1.5 Ma). Fossils of *G. torticornis* from the Taurida Cave confirm the tendency towards a reduction in size among the late representatives of this antelope species. *P. ambiguus* from the Taurida Cave is one of the earliest representatives of the species in the south of Europe. Finds of spiral-horned antelopes in the Taurida Cave help elucidate the details of their morphological evolution, refine their geographic and stratigraphic range.

**Keywords:** Early Pleistocene, Crimea, spiral-horned antelopes, *Gazellospira*, *Pontoceros*, stratigraphical distribution, paleogeography

**DOI:** 10.1134/S0031030120010116

The Taurida Cave is a Pleistocene vertebrate fossil locality discovered in 2018 in Central Crimea near Zuya village, 15 km east of Simferopol, during the construction of the federal highway Simferopol–Kerch. Vertebrate fossils of the Psekupsian complex found in the cave are of especial interest because they date to the period of early hominin (genus *Homo*) dispersal in Eurasia.

The Taurida Cave is located on the Inner Range of the Crimean Mountains between Beshterek River and Fundukli River and is incised into limestones of Paleogene age. The bone-bearing layer in the southern gallery is a subaerial-type red-brown loam. The “Hyaena Den” area of the cave has yielded fossils of the hare *Hypolagus brachygnathus* (Kormos, 1930), porcupine *Hystrix (Acanthion) vinogradovi* Argyropulo, 1941, a small wolf *Canis* sp., the giant hyaena *Pachycrocuta brevirostris* (Gervais, 1850), the sabretoothed cat *Homotherium crenatidens* (Fabrini, 1890), elephant *Archidiskodon meridionalis* (Nesti, 1825), two species of stenonian horses, rhinoceroses *Elasmotherium* sp. and *Stephanorhinus* sp., camel *Paracamelus gigas* Schlosser, 1903, deer *Arvernoceros vereschagini* David, 1992, bovines *Leptobos* sp. and *Bison (Eobison)*

sp., as well as two species of spiral-horned antelopes. Preliminary biochronological analysis indicates that the Taurida Cave fauna belongs to the Psekupsian mammal complex of Eastern Europe, Late Villafranchian, mammal zone MNQ18 with an age range 1.8–1.5 Ma (Lopatin et al., 2019). From isotope analysis (<sup>40</sup>Ar/<sup>39</sup>Ar) of fossils from localities in France, zone MNQ18 is approximately equivalent in age to the interval from the Réunion paleomagnetic subchron, 2.19–2.14 Ma, (Senèze fauna) to 1.47 Ma (Peyrolles fauna, MNQ19) (Nomade et al., 2014).

The study of different groups of Bovidae plays an important role in the current research of the evolution of Pleistocene faunas, because paleontological as well as archaeological evidence suggest that migrations of members of this group were associated with hominin dispersal. In this article we give the first description of spiral-horned antelopes from the Taurida Cave. The diagnostics of this group is based on the features of the horn cores and their torsion types (homonymous or heteronymous), as well as postcranial features. The well-preserved fossil material from the “Hyaena Den” indicates the presence of two species of spiral-horned antelopes of genera *Gazellospira* Pilgrim et Schaub,

1939 and *Pontoceros* Vereschagin, Alexejeva, David et Baigusheva, 1971. Occurrence of *Pontoceros* in the Taurida Cave is of especial interest, for it is likely the first occurrence of this genus in the Early Pleistocene of Europe. *Pontoceros* is known from Dmanisi in Georgia (Vekua, 2012), a locality close in age to the Taurida Cave that has yielded fossils of early *Homo* (Lordkipanidze et al., 2013). Also, the Taurida Cave is one of the few localities with the youngest fossils of late representatives of the typical Villafranchian species *Gazellospira torticornis* (Aymard, 1854) and the only Late Villafranchian locality with this species in the south of Eastern Europe.

We use the following abbreviations for measurements of horn cores and metapodia: length (L), transverse diameter (DT), anteroposterior diameter (DAP), proximal (prox), distal (dist), diaphysis (diaph). The following abbreviations are used for institutions: (PIN) Borissiak Paleontological Institute, Russian Academy of Sciences, (IPAE) Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences.

*Gazellospira torticornis* (Aymard, 1854)

**Material.** Fragment of right horn core, PIN 5644/57; fragment of a base of horn core with part of a frontal, IPAE 727/47; right metacarpal, IPAE 727/44; right metatarsal, IPAE 727/45.

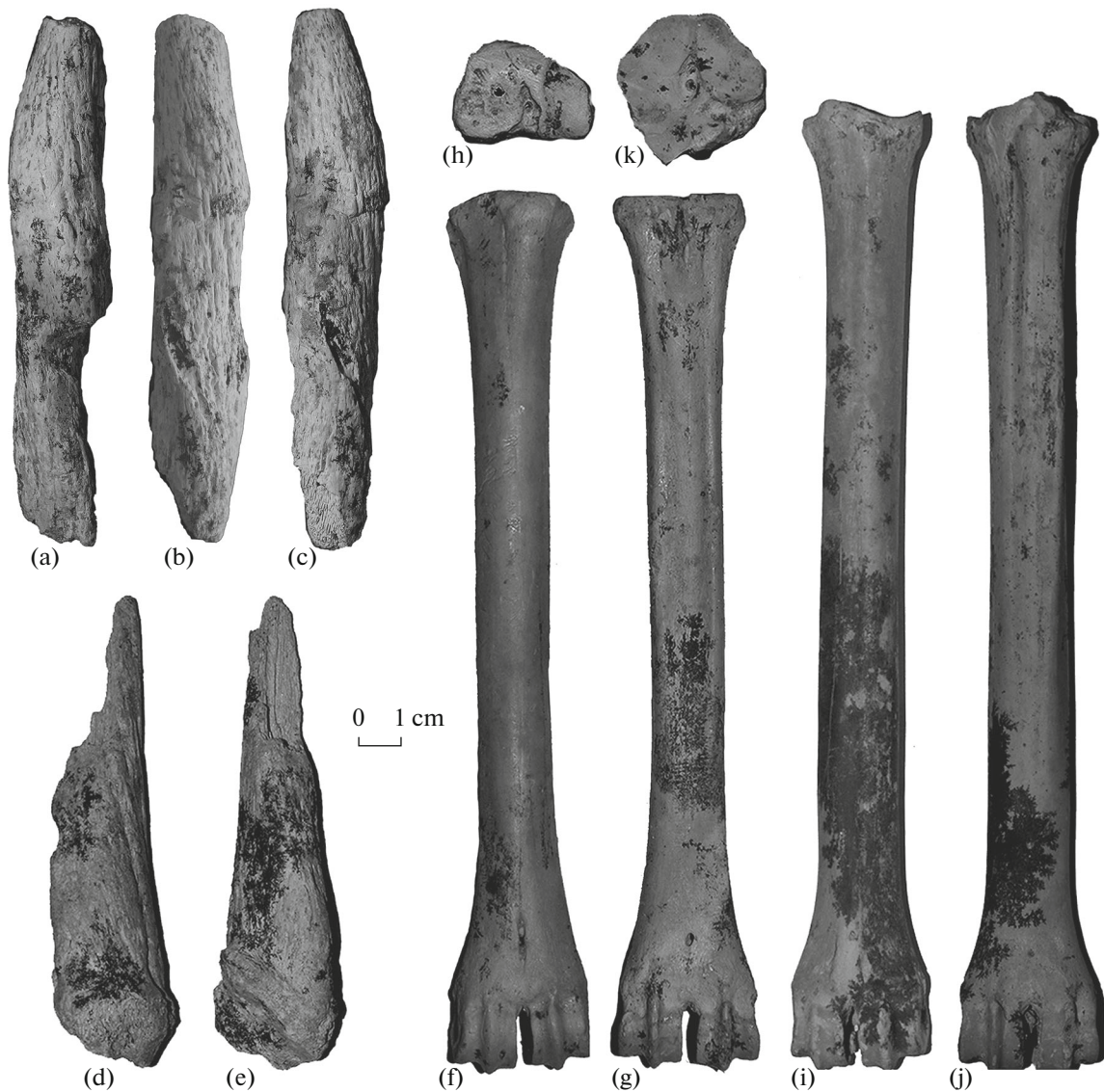
**Description and comparison** (Fig. 1). Horn cores are heteronymously twisted in specimen PIN 5644/57, with two spiral keels, the anterior and the better developed posterolateral. The cross-section at the base of the horn core in specimen 727/47 is almost round, somewhat pointed at the posterolateral keel; in specimen PIN 5644/57 the section is elliptical (somewhat oval). Measurements in mm: IPAE 727/47: L 108; DT × DAP 27.9 × 28.7.

Metacarpal and metatarsal are slender, gracile, expanding gradually towards the proximal and the distal epiphyses. Measurements of metacarpal in specimen IPAE 727/44 in mm: L 219; DTprox × DAPprox 32.5 × 23.7; DTdist × DAPdist 34.7 × 22.9; DTdiaph × DAPdiaph 18.7 × 17.1; robustness index (DTdiaph/L) 0.09; width distal epiphysis index (DTdist/L) 0.14. Measurements of metatarsal IPAE 727/45 in mm: L 247; DTprox × DAPprox 31 × 31.7; DTdist × DAPdist 35 × 26.2; DTdiaph × DAPdiaph 19.5 × 22.9; DTdiaph/L 0.08; DTdist/L 0.14.

The horn cores as well as the metacarpal and the metatarsal of the antelope from the Taurida Cave correspond in morphology and size to *G. torticornis* from the Late Villafranchian of Europe (Fig. 2). The diameter measurements at the base of the horn cores (DT and DAP) are close to the smallest forms of *G. torticornis*. Judging from the length and the proportions of the metacarpal and the metatarsal, *G. torticornis* from the Taurida Cave was relatively small and gracile. The measurements on these bones are close to the largest

ones observed in *G. torticornis hispanica* Garrido, 2008, a small form from the Fonelas P-1 locality in Spain (ca. 2 Ma, MNQ18). The values of DTdiaph/L and DTdist/L are also close for *G. torticornis* from the Taurida Cave and Fonelas P-1. The holotype from Fonelas P-1 has the following measurements: L 235; DTprox × DAPprox 30.49 × 33.31; DTdist × DAPdist 32.47 × 22.71; DTdiaph 16.96; DTdiaph/L 0.07; DTdist/L 0.14; the range of metacarpal lengths in the antelope from Fonelas P-1 (L min–max) 219–246 (Garrido, 2008). Differs from *G. gromovae* Dmitrieva, 1975 from Kuruksay (MNQ17), Tajikistan (Dmitrieva, 1977), in having more slender horn cores and generally smaller size.

**Remarks.** The species *G. torticornis* is quite well represented in the fossil record of Western Europe and has been well studied (Pilgrim and Schaub, 1939; Heintz, 1966, 1970; Duvernois and Guérin, 1989; Kostopoulos, 1997a; Spassov and Crégut-Bonnoure, 1999; Athanassiou, 2005; Lyras and van der Geer, 2007; Garrido, 2008; Bellucci and Sardella, 2015; and others). The holotype of the type species *G. torticornis*, the right horn on a skull fragment from the early Late Villafranchian locality Le Coupet (Musée Crozatier, Le-Puy-en-Velay, France: Dorlhac, 1854, text-fig. 8). This species is characterized by the heteronymous type of horn torsion. Frontals are pneumatized, horn cores lack pneumatized sinuses, are set above the orbits, twisted in a loose coil, with two spiral keels, the cross-section of the horn cores somewhat oval to round, pointed at the better developed posterior keel. Research shows that horn cores in antelopes of this species can vary both in length and in the development of keels, as well as in the number of coils around the long axis of the horn. West European fossils suggest a gradual reduction in size of *G. torticornis* over the Villafranchian of Spain and France (Heintz, 1966; Rodrigo, 2011). The reduction in general size is well traced in antelopes of the beginning of the Late Villafranchian, in particular, from the Fonelas P-1 locality (ca. 2 Ma, MNQ18) in Spain (Garrido, 2008). The population of *G. torticornis* from Fonelas P-1 is one of the latest in the Mediterranean. It has been split into a separate subspecies *G. torticornis hispanica* Garrido, 2008. The holotype for this species is a left metatarsal, FP1-2001-0165, housed in the Museo Geominero del Instituto Geológico y Minero de España, Madrid (Garrido, 2008, text-fig. 16F), while paratypes include fragments of skulls with horn cores, maxilla and mandible, radius and metacarpal. The diagnostic characters of the species include the morphology of the horn cores and teeth and the small size of postcranial bones. Horn cores can be up to 300 mm long in this species, are inclined at an angle of 35°–60° to the cranial roof and are set about 53–63 mm apart. The angle of horn divergence is 64°–76°. The base of the horn core has a well-developed posterolateral keel and sometimes a prominent anterior keel; the location of these keels and the degree of their development are



**Fig. 1.** *Gazellospira torticornis* (Aymard, 1854): (a–c) PIN 5644/57, incomplete right horn core: (a) anterior view, (b) medial view, (c) posterior view; (d, e) IPAE 727/47, fragment of a horn core: (d) anterior view, (e) posterior view; (f–h) IPAE 727/44, right metacarpal: (f) anterior view, (g) posterior view, (h) proximal view; (i–k) IPAE 727/45, metatarsal: (i) anterior view, (j) posterior view, (k) proximal view; Crimea, Taurida Cave, Lower Pleistocene.

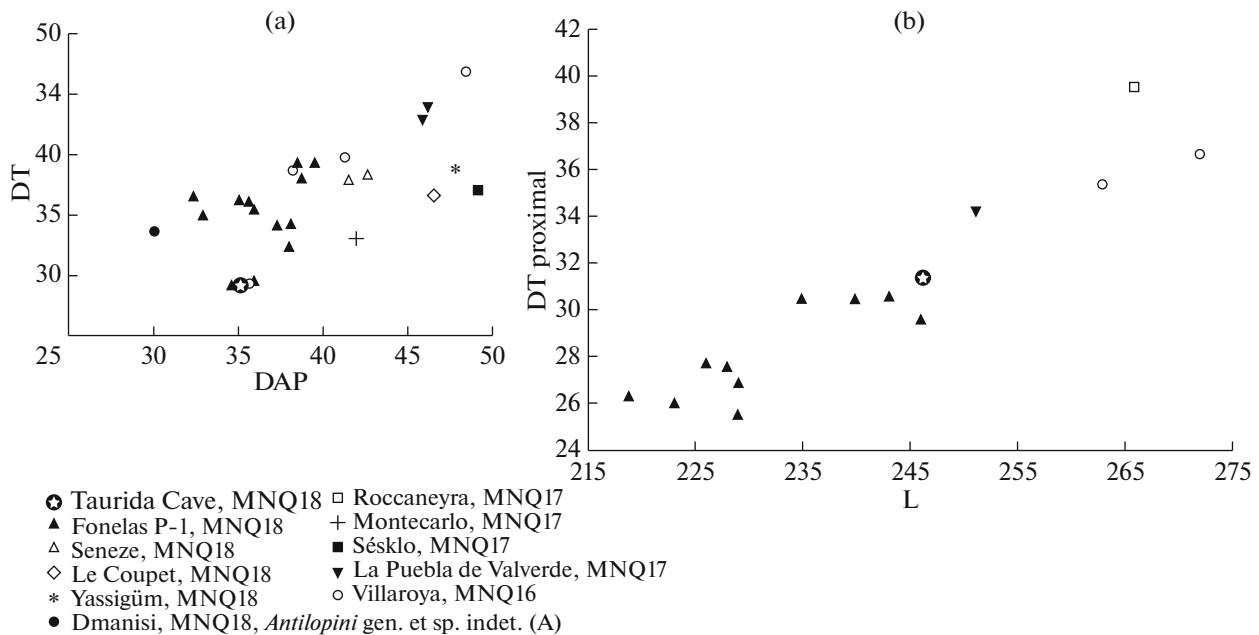
variable; the number of full coils about the long axis of the horn can reach two (Garrido, 2008).

A different species, *G. gromovae* Dmitrieva, 1975, has been described from the Kuruksay locality in Tajikistan correlated with Middle Villafranchian faunas. This species differs from *G. torticornis* in having horn cores that are less divergent at the base, as well as in several characters of the skull base and upper teeth (Dmitrieva, 1975, 1977).

The Taurida Cave fossils are evidence of the occurrence of a rather small form of *G. torticornis* in Crimea, which agrees with the general trend towards a reduction in size of *G. torticornis* at the beginning of the Late

Villafranchian (MNQ18), observed on Western European material.

The most ancient *Gazellospira* are possibly found in the Pliocene locality of Çalta (MN15) in Turkey (Bouvrain, 1998). Definite finds of members of this antelope genus are known from Late Pliocene deposits correlated with zone MN16b, in particular, Villaroya in Spain (Rodrigo, 2011), Kvabebi in Georgia (Bukhsianidze and Koiava, 2018) and Gülyazi in Turkey (Sickenberg, 1974). In the Early Pleistocene, the genus *Gazellospira* was distributed in the European and Asian parts of the Mediterranean zoogeographic subregion of the Palearctic, as well as in some adjacent areas. Generally, the biochronological range of the



**Fig. 2.** Relationship between measurements of (a) horn cores and (b) metacarpals in *Gazellospira torticornis* (Aymard, 1854) (with data from: Athanassiou, 2005; Bukhsianidze, 2005; Garrido, 2008; Rodrigo, 2011; Demirel and Mayda, 2014; Bellucci and Sardella, 2015; etc.).

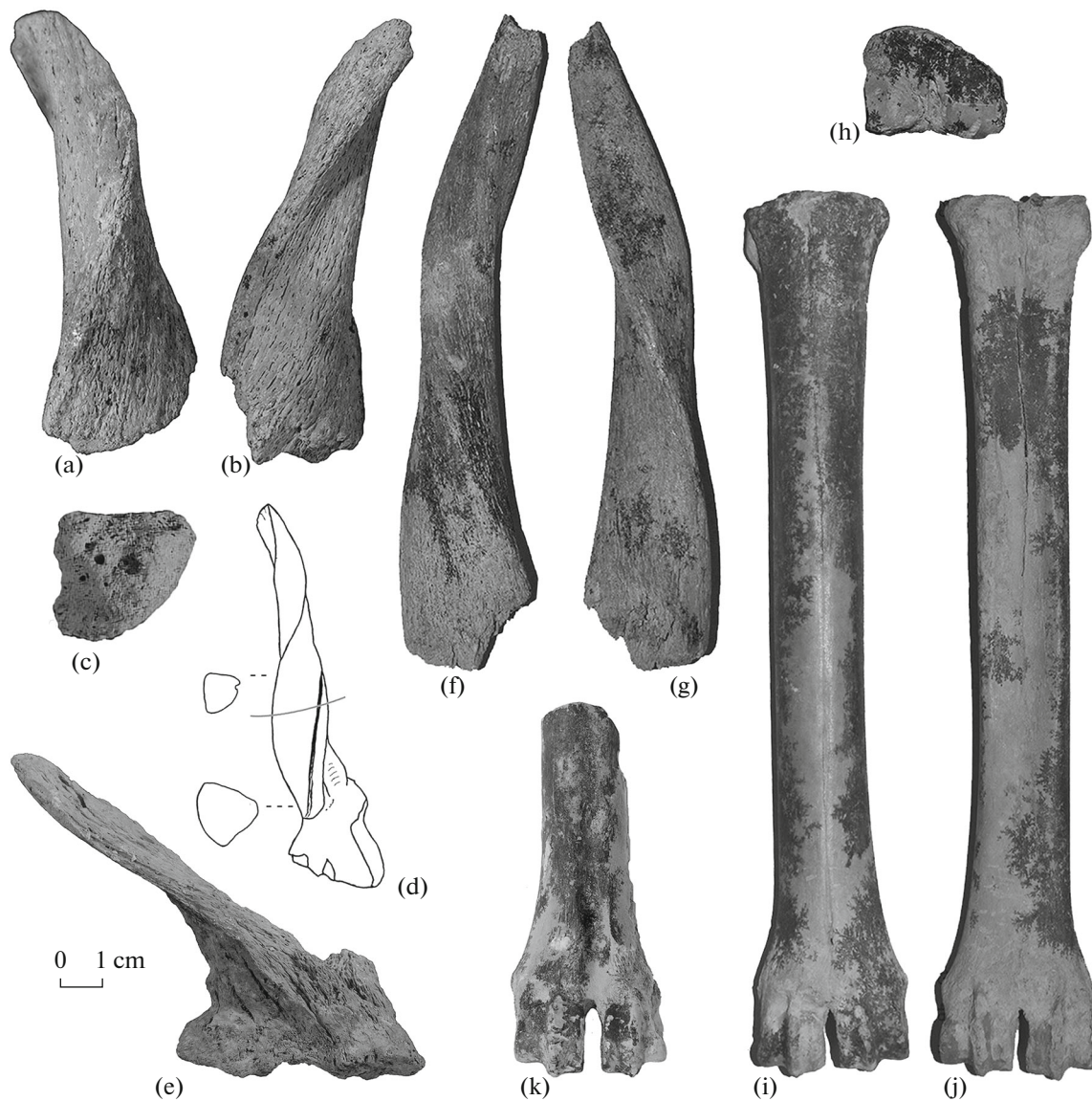
species *G. torticornis* corresponds to zones MN16b–MNQ18. The species was most widely distributed in the Middle and at the beginning of the Late Villafranchian. In the Middle Villafranchian (MNQ17) it occurred over a range from Spain to Turkey. At the boundary of Middle and Late Villafranchian, the range starts contracting, and it disappears completely in post-Olduvai time at the end of the Danubian/Eburonian (the beginning of the zone MNQ19). In Italy, the latest representatives of the species are known from the faunas of Costa San Giacomo (MNQ17) (Bellucci, Sardella, 2015). For the first half of the Late Villafranchian (MNQ18), fossils of this species are known from localities in France (Le Coupet, Chillac, Senezé), Spain (Fonelas P-1), Greece (Gerakarou, Krimni 1, Alykes, possibly, Pirgos, etc.), Germany (Erpfinger Höhle), Romania (Valea Granceanului), Bulgaria (Slivnitsa), Montenegro (Trlica, TRL11-10) and Turkey (Yassigüm, 1.5 Ma) and others (Kostopoulos and Koufos, 1994; Athanassiou, 1996, 2005; Kostopoulos, 1997a, 2014; Spassov and Crégut-Bonnoure, 1999; Koufos, 2001; Kostopoulos et al., 2002; Spassov, 2003, 2016; Rădulescu et al., 2003; Arribas et al., 2004; Radulesko, 2005; Crégut-Bonnoure, 2007; Garrido, 2008; Rodrigo, 2011; Demirel and Mayda, 2014; Vislobokova and Agadzhanian, 2015; Koufos and Kostopoulos, 2016; and others). *G. torticornis* fossils found in the Taurida Cave are the first find in Eastern Europe within a Late Villafranchian fauna. Previously, *Gazellospira* antelopes in this region were only known from two localities of the Khaprovian mammal complex, Liventsovka on the Azov Sea coast

and Bolgrad in the Odessa Oblast, both from the Middle Villafranchian (MNQ17), but represented by very scarce material. These *Gazellospira* fossils were attributed to *G. torticornis* (Alekseeva, 1977) or to *G. gromovae* (Titov, 2008). According to data of Maria Bukhsianidze (2005), the antelopes of Dmanisi (1.75 Ma, MNQ18; Georgia), may include *Gazellospira*. The metacarpals of *Antilopini* gen. et sp. indet. (B) from Dmanisi are close in size and proportions to *G. torticornis* from Middle Villafranchian localities (zone MNQ17) Roccaneyra (Spain) and Senezé (France) (Bukhsianidze, 2005). In the absence of finds of horn cores of *Gazellospira* in Dmanisi, their occurrence in that locality remains unconfirmed.

*Pontoceros ambiguus* Vereschagin, Alexejeva, David et Baigusheva, 1971

**Material.** Fragment of cranial roof with part of a right horn core, PIN 5644/54; incomplete right horn core, PIN 5644/55; incomplete left horn core, IPAE 727/46; right metacarpal, IPAE 727/43; distal end of a metatarsal, PIN 5644/58.

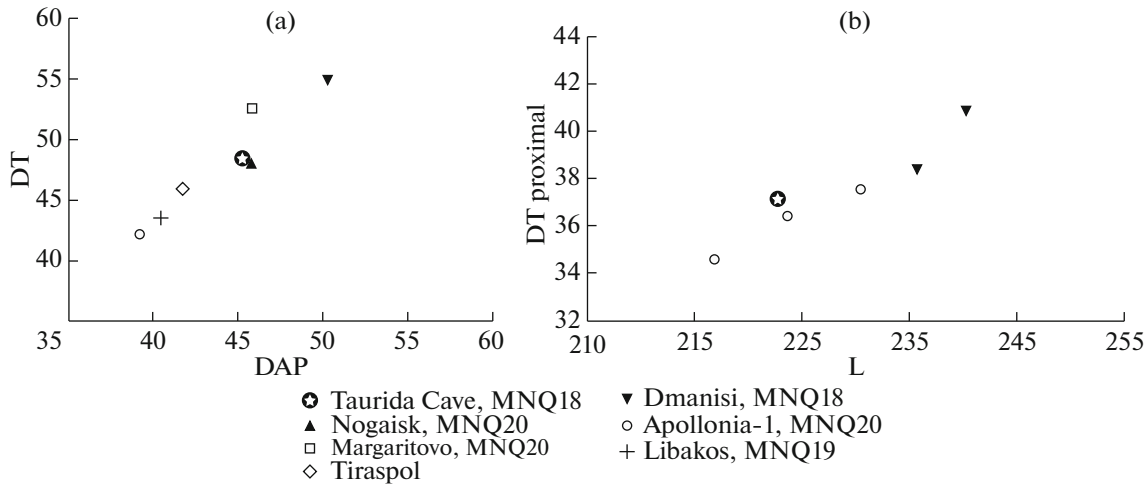
**Description and comparison** (Fig. 3). Horn cores are set above the orbits. They are homonymously twisted, triangular in section. Sinuses at the base of the horn cores are absent. The morphology and size of PIN 5644/55 corresponds well with the upper half of the holotype of the species *P. ambiguus* from Nogaïsk, Ukraine. There are three well-developed keels which are named, in following the nomenclature of the authors of the species, after the location



**Fig. 3.** *Pontoceros ambiguus* Vereschagin, Alexejeva, David et Baigusheva, 1971: (a–c) PIN 5644/55, right horn core: (a) anterior view, (b) posterior view, (c) cross-section of its base; (d) linear drawing of holotype GIN 938-1, from Nogaïsk (after Vereschagin et al., 1971, pl. 34, fig. 1), showing the shape of the sections and a line approximately corresponding to the position of the base of the fragment of the horn core from Taurida; (e) PIN 5644/54, fragment of the cranial roof with part of the left horn core; (e, g) IPAE 727/46, incomplete left horn core: (f) lateral view, (g) medial view; (h–j) IPAE 727/43, right metacarpal: (h) proximal view, (i) anterior view, (j) posterior view; (k) PIN 5644/58, distal end of a metatarsal, anterior view; Crimea, Taurida Cave, Lower Pleistocene.

of their proximal points in the holotype, namely: frontal (anteromedial), posterolateral and posteromedial. The latter is compressed and has the shape of a torus, whereas the anteromedial and posterolateral keels are well-developed and more pointed. The horn is twisted in approximately one coil from the base to the point of the horn, whereas it has 1.25 coils in the holotype. The anterolateral surface of the horn core in PIN 5644/55 along the edge of the anteromedial keel has a long deep furrow; the same furrow in the holotype reaches the base of the horn. The cross-sectional shape at the base of the horn core in PIN 5644/55 is rounded triangular,

similar to the cross-section at midlength of the horn core in the holotype; above it, the cross-section is rounded-triangular as well. PIN 5644/54 has a horn core located above the orbit and is inclined posteriorly at an angle of about  $40^\circ$  to the cranial roof; the horn cores likely diverged very little at the base. Measurements of the horn cores in mm: PIN 5644/54 DAP  $\times$  DT (calculated) 48, PIN 5644/55 DAP  $\times$  DT at the lower breakage point 30  $\times$  42.5; at the base these values may have been similar to those in the holotype: 46  $\times$  48 or somewhat greater; IPAE 727/46 L 177, DT  $\times$  DAP 28.6  $\times$  35.3.



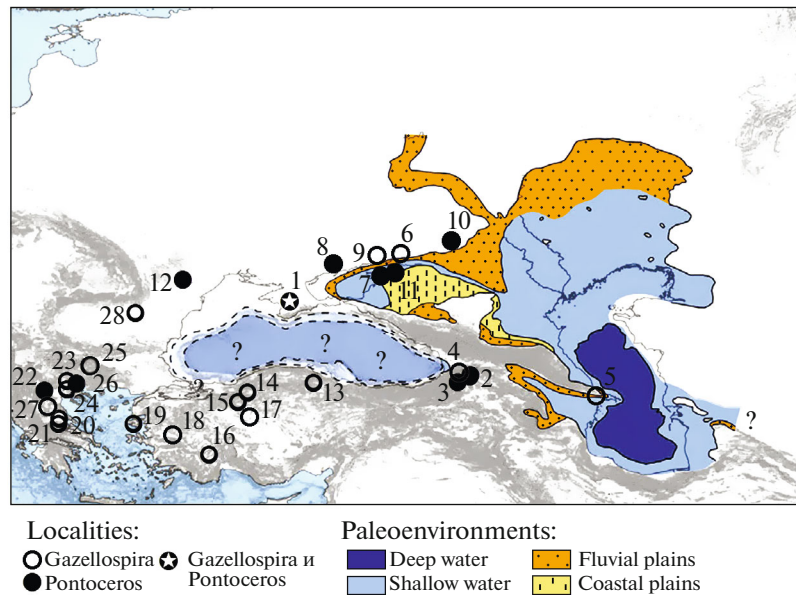
**Fig. 4.** Relationship between measurements of (a) horn cores and (b) metacarpals in antelopes of the genus *Pontoceros* (with data from Vereshchagin et al., 1971; Kostopoulos, 1997b; Bukhsianidze, 2005; Vekua, 2012).

The morphology, size, shape of the cross-section and the inclination angle of the horn cores from the Taurida Cave correspond to the holotype of *P. ambiguus* (Fig. 3c). It differs from *P. ambiguus mediterraneus* Kostopoulos, 1997 from Apollonia-1 (Greece; MNQ20, ca 1 Ma) in having a more distinctly triangular cross-sectional shape and somewhat greater size. In *P. ambiguus mediterraneus* DAP × DT at the base of the horns is 40.5–41.3 × 43.2–44.6 mm, and their cross-section from the base to the middle of horn height is elliptical to subcircular, because the keels are more smoothed (less sharpened) than those in the type form (Kostopoulos, 1997b). The horn cores in this subspecies are inclined at an angle of 30°–40° to the cranial roof, torsioned in one turn and diverge more strongly from the base to the top than in the type form. Furthermore, the anterior part of the frontal in *P. ambiguus mediterraneus* contains numerous small sinuses that are absent in *P. ambiguus* from the Taurida Cave and Nogaisk; an increased pneumatization is a derived character. The antelope from the Taurida Cave differs from the holotype of *P. surprine* Vekua, 2012 from Dmanisi (Georgia; MNQ18, ca. 1.8 Ma) in being somewhat smaller in size, having more posteriorly inclined horns, which are triangular in cross-section and have three keels. In the holotype of *P. surprine*, the horn cores are more massive (DT × DAP 55.5 × 50 mm), twisted in one turn, only one (anterolateral) keel is strongly developed; the horn is inclined posteriorly at an angle of 50° to the cranial roof; the cross-section of the horn base is almost round (Vekua, 2012).

Metacarpal, IPAE 727/44, elongated, slender, but somewhat more massive than in *G. torticornis*. Its morphology, size, and robustness correspond to *P. ambiguus* (Fig. 4). On the proximal articular surface, the os trapezoideocapitatum facet is almost squarish, the crest separating it from the os hamatum facet is low. On the palmar side of the diaphysis, sulcus

longitudinalis palmaris is wide and long, the opening of canalis metacarpi distalis is small. The proximal and distal parts of the diaphysis of the metacarpals and metatarsals expand quite sharply towards the epiphyses; the outline of the distal epiphysis (viewed anteriorly) looks rectangular. The dorsal longitudinal groove on the metatarsal near canalis metatarsi distalis has high, sharp crests. These characters are also observed on the metapodials from Dmanisi identified as *Antilopini* gen. et sp. indet. (B) (Bukhsianidze, 2005, pl. VII-5), but possibly belonging to *Pontoceros*. The length of these bones in *Antilopini* gen. et sp. indet. (B) from Dmanisi is somewhat greater than in *Pontoceros* from the Taurida Cave, but both have similar robustness indices. Measurements of the metacarpal IPAE 727/43 in mm: L 223, DTprox × DAPprox 37.4 × 26.6, DTdist × DAPdist 39.3 × 25.9; DTdiaph × DAPdiaph 23.4 × 20; DTdiaph/L index 0.10; DTdist/L index 0.18. These correspond approximately to measurements and indices of metacarpals in *P. ambiguus mediterraneus*. The last two indices in *P. ambiguus mediterraneus* have values of 0.08–0.09 and 0.15–0.17; in *Antilopini* gen. et sp. indet. (B) the values are 0.10 and 0.16 (Fig. 4b).

**Remarks.** The genus *Pontoceros* was established based on the horn structure from fossil material from Nogaisk and Margaritovo on the Azov Sea Coast, as well as from Tiraspol (Kolkotova Balka) in Moldova (Vereshchagin et al., 1971). The holotype for the type species *P. ambiguus* is a right horn with a skull fragment, GIN 938-1 from the Lower Pleistocene of Nogaisk, supposedly from the lower beds in the section (Vereshchagin et al., 1971, pl. XXXIV, fig. 1–2). According to L.I. Alekseeva (1977), these beds occur below the layers with the Nogaisk small mammal fauna (MNQ20) and contain fauna from the late stage of the Khaprovian (=Psekupsian) complex with the typical *Archidiskodon meridionalis* (= *Mammuthus*



**Fig. 5.** Main fossil localities for spiral-horned antelopes of the Eastern Mediterranean province. Localities: (1) Taurida Cave, (2) Dmanisi, (3) Akhalkalaki, (4) Kvabebi, (5) Palan-Tyukan, (6) Liventsovka, (7) Margaritovo, (8) Nogaïsk, (9) Shirokino, (10) Sarkel, (11) Semibalki, (12) Kolkotova Balka (Tiraspol), (13) Kamişli, (14) Sarikol Tepe, (15) Çalta, (16) Yassigüme, (17) Gülyazi, (18) Bgök, (19) Vaterá, (20) Sésklo, (21) Alykes, (22) Libakos, (23) Gerakarou, (24) Krimini-1, (25) Vólax, (26) Apollonia-1, (27) Dafneró, (28) Bolgrad.

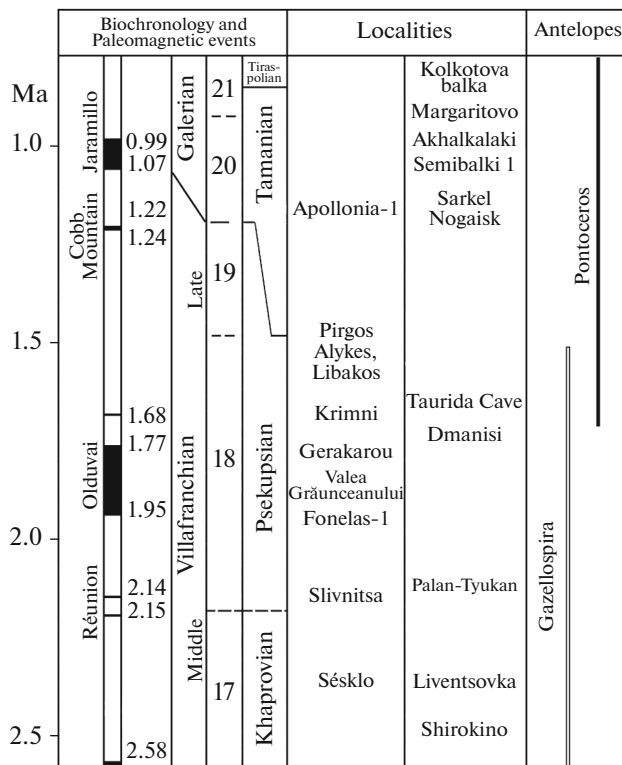
*meridionalis*). In the first description of the genus, the horn core from Margaritovo was assigned to the Tamanian complex (Vereshchagin et al., 1971; Alekseeva, 1977), zone MNQ20, whereas the fossils from Tiraspol (Kolkotova Balka, MNQ21) were assigned to the Tiraspolian complex. The horn core from Margaritovo, judging from its preservation, may originate from beds with a fauna transitional between the Tamanian and the Tiraspolian mammal complexes (Margaritovo 2 locality, MNQ20/MNQ21; Tesakov et al., 2007). *P. cf. ambiguus* occur within the fauna of Semibalki 1 (MNQ20) of the Tamanian faunistic complex of the Northeastern Azov sea coast (Baigushcheva, 2000).

The genus *Pontoceros* existed from approximately the Olduvai paleomagnetic episode to the beginning of the Middle Pleistocene. It is much more poorly represented in the fossil record than *Gazellospira* (Fig. 5). The range of the species *P. ambiguus* stretched from the Northeastern Azov Sea coast to Greece and, possibly, Israel. *Antilopini* gen. et sp. indet. (cf. *Pontoceros ambiguus/Spiroceros* sp.) is found in the fauna of ‘Ubeidiya (1.6–1.2 Ma; Israel) (Martínez-Navarro et al., 2012). Fossils of antelopes of the genus *Pontoceros* are found in faunas of Dmanisi (MNQ18) (Vekua, 2012) and Akhalkalaki (0.98–0.78 Ma, MNQ20) in Georgia (Bukhsianidze et al., 2014), as well as in Libakos (MNQ18), Apollonia-1 (MNQ20) and Platanochori-1 (MNQ20) in Greece (Kostopoulos, 1997a, 2006; Konidaris et al., 2015). *Pontoceros* from Apollonia-1 is morphologically somewhat different from the

type form from Nogaïsk (see above), and D. Kostopoulos (1997) assigned it to a new subspecies *Pontoceros ambiguus mediterraneus*, to which he also referred the form from Libakos (=Antilopinae gen. indet. sp. A.; Steensma, 1988, text-fig. 81).

*Pontoceros* had homonymously torsioned horns, which clearly sets them apart from *Gazellospira*. They are further distinguished from the latter by some details of the structure of metacarpals and metatarsals, in particular, in the shape of the proximal articular surface of the metacarpal and its os trapezoideocapitatum facet, which in *Gazellospira* are more rounded medially. Judging by measurements, representatives of *P. ambiguus* from the Taurida Cave and Apollonia-1 were smaller than *Pontoceros surprine* from Dmanisi.

The authors of the genus *Pontoceros* assigned it to the subfamily Tragelaphinae Pilgrim, 1939 (Vereshchagin et al., 1971), and this systematic position of the genus was accepted in a series of later studies (Baigushcheva, 1971; Alekseeva, 1977; Dmitrieva, 1975, 1977; Titov, 2008). N.K. Vereshchagin et al. (1971) believed that *P. ambiguus* was a large antelope, the size of a gnu, and weighing up to 120–130 kg, resembling a bongo *Tragelaphus eurycerus* Ogilby, 1837. However, the homonymous torsion of *Pontoceros* is unlike modern tragelaphines, which have heteronymously twisted horns. According to recent phylogenetic and genetic studies, this group, closely related to Bovini, is included as tribe within the subfamily Bovinae. Both groups (Bovini and Tragelaphini) are likely derived from the Miocene Boselaphini (Bibi et al., 2009).



**Fig. 6.** Chronological sequence of the main localities of spiral-horned antelopes of the Eastern Mediterranean province.

Some morphological details of the horn core and teeth of *Pontoceros* indicate their kinship with members of the tribe Caprini (Kostopoulos, 1997b, 2006; Vekua, 2012), which are currently assigned to the subfamily Antilopinae (Bibi et al., 2009). Among the modern species of the family Bovidae only about 13% have homonymously twisted horns; these are found among Caprini, Alcelaphini, as well as some Bovini, and almost never occur among the modern Antilopini, except for some individuals of gazelles (Kostopoulos, 2014). Vekua (2012) assigned *Pontoceros* to the tribe Oiocerini Sokolov, 1953 of the subfamily Caprinae based on the morphology of an incomplete skull fragment and on the homonymously torsioned horn cores in *P. surprine*. Further fossil finds are needed to refine the systematic position of *Pontoceros*, along with a detailed comparison with fossil and modern species using ontogenetic and phylogenetic evidence.

\* \* \*

The fossils of spiral-horned antelopes from the Taurida Cave have made it possible to refine the stratigraphic and geographic range, as well as the details of evolution of the species *Gazellospira torticornis* and *Pontoceros ambiguus*. The evidence from the Taurida Cave and the analyzed biostratigraphic range of these spiral-horned antelopes indicate that the association

*Gazellospira torticornis*–*Pontoceros ambiguus* can be considered typical for the first half of the Late Villafranchian, zone MNQ18, time interval ca. 1.8–1.5 Ma. The boundaries of this time interval were determined based on the evidence of the last occurrence of *G. torticornis* and first occurrence of *Pontoceros*. It corresponds to the first half of the Late Villafranchian of Western Europe (MNQ18), Danubian/Eburonian, MIS 65–57.

The discovery of *G. torticornis* in the Taurida Cave showed that its range at the time also covered the southern part of Eastern Europe, in addition to the European coasts of the Mediterranean and Asia Minor. Crimea likely served as one of the few Late Villafranchian refugia of this species. Taurida Cave fossils further confirm the trend towards smaller size in late representatives of *G. torticornis*. The presence of *G. torticornis* in territories adjacent to the European Mediterranean, namely, in Crimea and Turkey, within localities dated to the time interval between 2 and 1.5 Ma (Figs. 5, 6) indicate that a continuous range of this species existed within the Mediterranean zoogeographic subregion of the Palearctic at the beginning of the Late Villafranchian. Antelopes *Pontoceros ambiguus* from the Taurida Cave locality are some of the earliest representatives of the genus. *Pontoceros* appeared in the context of a growing global cooling trend and significant paleobiogeographic change (Kahlke et al., 2011). The range of the genus *Pontoceros* is tied to the Eastern Mediterranean province and included Greece, the southern part of Eastern Europe and Caucasus, and possibly also the Levant. In Greece, the faunas of Libakos and Alykes are close in age and the fossils of *Pontoceros* in Libakos and of *Gazellospira* in Alykes may be evidence of contemporaneous existence of these antelopes in the region in the Late Villafranchian. The faunas of Libakos and Alykes correspond to the Farneta faunal stage in Italy, their age likely being close to 1.5 Ma (e.g., Koufos and Kostopoulos, 2016).

The immediate ancestors of the spiral-horned antelopes of the genera *Gazellospira* and *Pontoceros* are as yet unknown, although many researchers believed that they should be sought in Asia. Further study and new finds should make it possible to elucidate the faunistic links of the Late Villafranchian faunas of Crimea and Caucasus, establish possible phylogenetic affinities between antelopes of this region with forms from Asia and Africa, and further refine the reconstructed links between faunistic events and the migration of early hominins in the Eastern Mediterranean.

#### ACKNOWLEDGMENTS

The authors thank all those who participated in the excavation of the Taurida locality.

#### FUNDING

The study was partially funded under the Fundamental Research Program of the Presidium of the Russian Acad-



emy of Sciences “Evolution of the organic world. The role and influence of planetary processes,” and also under the Russian Foundation for Basic Research project no. 19-05-00982 and as part of the government assignment to the Southern Research Center of Russian Academy of Sciences for 2019, project no. 01201363186.

## REFERENCES

- Alekseeva, L.I., *Teriofauna Rannego Antropogena Vostochnoi Evropy* (Mammal Fauna of Early Anthropogene of Eastern Europe), Moscow: Nauka, 1977.
- Athanassiou, A., Contribution to the study of the fossil mammals of Thessaly (Greece), *Ph.D. thesis*, Athens: Athens Univ., 1996, 353 p.
- Athanassiou, A., *Gazellospira torticornis* (Aymard, 1854) from the late Pliocene locality of Sésklo (Thessaly, Greece), *Quaternaire*, 2005, vol. 2, p. 137–144.
- Azanza B. and Morales J., Los artiodáctilos de Huélago, Huescar-1 y Cúllar de Baza-1 (cuenca de Guadix-Baza, Granada), *Trabajos sobre Neógeno-Cuaternario*, 1989, vol. 11, pp. 289–314.
- Baigusheva, V.S., Fossil mammal fauna of the Liventsovka quarry (Northeastern Azov Sea coast), *Tr. Zool. Inst. Akad. Nauk SSSR*, 1971, vol. 69, no. 49, pp. 5–28.
- Baigusheva, V.S., New data on the Taman faunistic complex from the excavation near the Semibalki village (Azov Sea coast), *Istoriko-arkheologicheskie issledovaniia v Azove i na Nizhnem Donu v 1998 g.* (Historical and Archaeological Research in Azov and the Lower Don River in 1998), Azov: Azov. Istoriko-Arkeol. Paleontol. Kraeved. Mus., 2000, no. 16, pp. 27–57.
- Bellucci, L. and Sardella, R., The last Antilopini bovids from the Early Pleistocene of Italy, *Quatern. Intern.*, 2015, vol. 357, pp. 245–252.
- Bibi, F., Bukhsianidze, M., Gentry, A.W., Geraads, D., Kostopoulos, D.S., and Vrba, E.S., The fossil record and evolution of Bovidae: State of the field, *Palaeontol. Electron.*, 2009, vol. 12, no. 3, 10A.
- Bouvrain, G., Le gisement de vertébrés pliocènes de Çalta, Ankara, Turquie. Bovidés, *Geodiversitas*, 1998, vol. 20, pp. 467–485.
- Bukhsianidze, M., The fossil Bovidae of Dmanisi. *Doct. Thesis*, Ferrara: Univ. Ferrara, 2005. 192 p.
- Bukhsianidze, M., Chagelishvili, R., Hertler, C., Kvavadze, E., and Martkoplshvili, I., New findings about the Akhalkalaki site (Southern Georgia, Caucasus; 0.98–0.78 Ma), *Abstr. Book VI Int. Conf. on Mammoths and their Relatives*, Thessaloniki: Aristotle Univ., 2014, p. 38.
- Bukhsianidze, M. and Koiava, K., Synopsis of the terrestrial vertebrate faunas from the Middle Kura Basin (Eastern Georgia and Western Azerbaijan, South Caucasus), *Acta Palaeontol. Pol.*, 2018, vol. 63, no. 3, pp. 441–461.
- Crégut-Bonnoure, E., Apport des Caprinae et Antilopinae (Mammalia, Bovidae) à la biostratigraphie du Pliocène terminal et du Pléistocène d'Europe, *Quaternaire*, 2007, vol. 18, no. 1, pp. 73–97.
- Demirel, F.A. and Mayda, S., A new Early Pleistocene mammalian fauna from Burdur Basin, SW Turkey, *Russian J. Theriol.*, 2014, vol. 13, no. 2, pp. 55–63.
- Dmitrieva, E.L., *Fossil spiral-horned antelopes of Western Mongolia and some regions of Central Asia, Fauna i Biostratigrafiia Mezozoiia i Kainozoiia Mongolii* (Fauna and biostratigraphy of the Mesozoic and Cenozoic of Mongolia), Moscow: Nauka, 1975, pp. 76–83.
- Dmitrieva, E.L., *Antilopy Neogena Mongolii i Sopredel'nykh Territorii* (Neogene Antelopes of Mongolia and Adjacent Regions), Moscow: Nauka, 1977.
- Dorlhac, J., Notice géologique sur le cratère du Coupet, et sur son gisement de gemmes et d'ossements fossils, *Ann. Soc. Agricult. Sci. Art. Commerc. Puy*, 1854, vol. 19, pp. 597–617.
- Duvernois, M.P. and Guérin, C., Les Bovidae (Mammalia) du Villafranchien supérieur d'Europe occidentale, *Géobios*, 1989, vol. 22, pp. 339–379.
- Ferrera, S.B., Gutiérrez, J.C., Medina, M.D., Alarcón, C.V., Mingorance, J.M., Valsero, J.J., Garrido, G., Baeza, E., Hernández, R.C., and Herrera, A.A., Nuevos registros paleontológicos de grandes mamíferos en la Cuenca de Guadix-Baza (Granada): aportaciones del Proyecto Fonelas al conocimiento sobre las faunas continentales del Plioceno-Pleistoceno europeo, *Bol. Geol. Minerol.*, 2004, vol. 115, no. 3, pp. 567–581.
- Garrido, G., The most recent and complete set of *Gazellospira torticornis* (Bovidae, Artiodactyla, Mammalia) fossils known for the late Upper Pliocene of Western Europe (Fonelas P-1, Gaudix Basin, Granada), in *Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas*, Arribas, A., Ed., Cuadern. Museo Geominero, no. 10, Madrid: Inst. Geol. Minero España, 2008, pp. 413–460.
- Heintz, E., La présence de *Gazellospira torticornis* dans le gisement Villafranchien de Saint-Vallier (Dome). Essai de repartition géographique et stratigraphique, *Bull. Soc. Géol. France*, 1966, vol. 7, no. 8, pp. 25–30.
- Heintz, E., Les Cervidés Villafranchiens de France et d'Espagne, *Mém. Mus. Nat. Hist. Nat. Ser. C.*, 1970, vol. 22, pp. 1–202.
- Kahlke, R.D., García, N., Kostopoulos, D.S., Lacombe, F., Lister, A.M., Mazza, P.P., Spassov, N., and Titov, V.V., Western Palaeartic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe, *Quatern. Sci. Rev.*, 2011, vol. 30, pp. 1368–1395.
- Konidararis, G. E., Tourloukis, V., Kostopoulos, D. S., Thompson, N., Giusti, D., Michailidis, D., Koufos, G.D., and Harvati, K., Two new vertebrate localities from the Early Pleistocene of Mygdonia Basin (Macedonia, Greece): Preliminary results, *C. R. Palevol.*, 2015, vol. 14, pp. 353–362.
- Kostopoulos, D.S., The Plio-Pleistocene artiodactyls from Macedonia, Greece: 2. The fossiliferous locality of Volaks (Volakas Basin, Drama, NE Greece), *Paleontol. Evol.*, 1997a, vol. 30–31, pp. 83–92.
- Kostopoulos, D.S., The Plio-Pleistocene artiodactyls (Vertebrata, Mammalia) of Macedonia 1. The fossiliferous site “Apollonia-1,” Mygdonia basin of Greece, *Geodiversitas*, 1997b, vol. 19, no. 4, pp. 845–875.
- Kostopoulos, D.S., Greek bovids through time, *Ann. Géol. Pays Hellén.*, 2006, vol. 41, no. 1, pp. 141–152.

- Kostopoulos, D.S., Taxonomic re-assessment and phylogenetic relationships of Miocene homonymously spiral-horned antelopes, *Acta Palaeontol. Pol.*, 2014, vol. 59, no. 1, pp. 9–29.
- Kostopoulos, D.S. and Koufos, G.D., The Plio-Pleistocene artiodactyls of Macedonia (Northern Greece) and their biostratigraphic significance, preliminary report, *C. R. Acad. Sci. Sér. 2*, 1994, vol. 318, pp. 1267–1272.
- Kostopoulos, D.S. and Sen, S., Late Pliocene (Villafranchian) mammals from Sarikol-Tepe, Ankara, Turkey, *Mitt. Bayer. Staatsslg. Paläontol. Hist. Geol.*, 1999, vol. 39, pp. 165–202.
- Kostopoulos, D.S., Vassiliadou K. and Koufos G.D., The beginning of the Pleistocene in the Balkan area according to the Mammal record: palaeozoogeographical approach, *Ann. Géol. Pays Hellén.*, 2002, vol. 39, pp. 253–278.
- Koufos, G., The Villafranchian mammalian faunas and biochronology of Greece, *Boll. Soc. Paleontol. Ital.*, 2001, vol. 40, no. 2, pp. 217–223.
- Koufos, G.D. and Kostopoulos, D.S., The Pliocene large mammal record in Greece: Implication for early human dispersal into Europe, *Palaeoanthropology of the Balkans and Anatolia: Human evolution and its context*, Harvati K. and Roksandis M., Eds., Dordrecht: Springer, 2016, pp. 269–280.
- Krijgsman, W., Tesakov, A., Yanina, T., Lazarev, S., Danukalova, G., Van Baak, C.G.C., Agustí, J., Alçiçek, M.C., Aliyeva, E., Bista, D., Bruch, A., Büyükmeriç, Y., Bukhshianidze, M., Flecker, R., Frolov, P., et al., Quaternary time scales for the Pontocaspian domain: Interbasinal connectivity and faunal evolution, *Earth-Sci. Rev.*, 2019, vol. 188, pp. 1–40.
- Lopatin, A.V., Vislobokova, I.A., Lavrov, A.V., Startsev, D.B., Gimranov, D.O., Zelenkov, N.V., Maschenko, E.N., Sotnikova, M.V., Tarasenko, K.K., and Titov, V.V., Taurida cave, a new locality of the Early Pleistocene vertebrates in Crimea, *Dokl. Biol. Sci.*, 2019, vol. 485, no. 3, pp. 381–385.
- Lordkipanidze, D., de León, M. S. P., Margvelashvili, A., Rak, Y., Rightmire, G. P., Vekua, A., and Zollikofer, C. P., A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo, *Science*, 2013, vol. 342, pp. 326–330.
- Lyras, G.A. and van der Geer, A.A.E., The Late Pliocene vertebrate fauna of Vatera (Lesvos Island, Greece), *Cranium*, 2007, vol. 24, no. 2, pp. 11–24.
- Martínez-Navarro, B., Belmaker, M., and Bar-Yosef, O., The bovid assemblage (Bovidae, Mammalia) from the Early Pleistocene site of Ubeidiya, Israel: Biochronological and paleoecological implications for the fossil and lithic bearing strata, *Quatern. Intern.*, 2012, vol. 267, pp. 78–97.
- Nomade, S., Pastre, J. F., Guillou, H., Faure, M., Guérin, C., Delson, E., Debard, E., Voinchet, P., and Messenger, E., <sup>40</sup>Ar/<sup>39</sup>Ar constraints on some French landmark Late Pliocene to Early Pleistocene large mammalian paleofaunas: Paleoenvironmental and paleoecological implications, *Quatern. Geochron.*, 2014, vol. 21, pp. 2–15.
- Pilgrim, G.E. and Schaub, S., Die schraubenhörnige Antilope des europäischen Oberpliocäns und ihre systematische Stellung, *Abh. Schweiz. Paläontol. Ges.*, 1939, vol. 62, pp. 1–30.
- Radulesco, C., Artiodactyles du Pliocène et du Pléistocène inférieur de Roumanie, *Quaternaire*, 2005, vol. 2, pp. 191–200.
- Rădulescu, C., Samson, P., Petculescu, A., and Ştiucă, E., Pliocene large mammals of Romania, *Coloq. Paleontol.*, 2003, vol. 53, no. 1, pp. 549–558.
- Rădulescu, C., Samson, P., and Ştiucă, E., Cadre biostratigraphique du paléolithique inférieur en Roumanie, *Quaternaire*, 1998, vol. 9, no. 4, pp. 283–290.
- Rodrigo, M.A., *Los bóvidos Villafranchienses de la Puebla de Valverde y Villarroya: sistemática, filogenia y paleobiología*, Tesis Doct., Zaragoza: Univ. Zaragoza, 2011. 433 p.
- Sickenberg, O., Etude du “Villafranchien” en Anatolie (Turquie), *Bull. Bur. Rech. Géol. Min.*, 1974, vol. 78, no. 1, pp. 241–245.
- Spassov, N., The Plio-Pleistocene vertebrate fauna in South-Eastern Europe and the megafaunal migratory waves from the east to Europe, *Rev. Paléobiol.*, 2003, vol. 22, pp. 197–229.
- Spassov, N., Southeastern Europe as a route for the earliest dispersal of *Homo* towards Europe: Ecological conditions and the timing of the first human occupation of Europe, in *Paleoanthropology of the Balkans and Anatolia: Human evolution and its context*, Harvati, K. and Roksandic, M., Eds., Dordrecht: Springer, 2016, pp. 281–290.
- Spassov, N. and Crégut-Bonnoure, E., Premières données sur les Bovidae Villafranchiens de Bulgarie, *C. R. Acad. Sci.*, 1999, vol. 328, pp. 493–498.
- Steenma, K.-J., Plio-Pleistozäne Großsäugetiere (Mammalia) aus dem Becken von Kastoral Grevena, südlich von Neapolis–NW-Griechenland, *Doct. Thesis*, Clausthal: Tech. Univ., 1988. 315 p.
- Tesakov, A.S., Dodonov, A.E., Titov, V.V., and Trubikhin, V.M., Plio-Pleistocene geological record and small mammal faunas, eastern shore of the Azov Sea, Southern European Russia, *Quatern. Intern.*, 2007, vol. 160, pp. 57–69.
- Titov, V.V., *Krupnye Mlekopitaiushchie Pozdnego Pliotsena Severo-Vostochnogo Priazov'ia*. (Late Pliocene Large Mammals of the Northeastern Azov Sea Coast). Rostov-on-Don: Yuzhn. Nauchn. Tsentr Ross. Akad. Nauk, 2008.
- Vekua, A., New spiral-horned antelope in Dmanisi fauna, *Bull. Georg. Natl. Acad. Sci.*, 2012, vol. 6, no. 3, pp. 139–144.
- Vereshchagin, N.K., Alekseeva, L.I., David, A., and Baigushcheva, V.S., *Genus Pontoceros, Pleistosen Tiraspolia* (The Pleistocene of Tiraspol), Chişinău: Ştiinţa, 1971, pp. 167–170.
- Vislobokova, I.A. and Agadzhanian, A.K., New data on the large mammals of the Pleistocene fauna of Trlica (Montenegro, Central Balkans), *Paleontol. J.*, 2015, vol. 49, no. 6, pp. 86–103.

Translated by D. Ponomarenko