Late Miocene Bovids from Şerefköy-2 (SW Turkey) and Their Position within the Sub-Paratethyan Biogeographic Province

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Source: Acta Palaeontologica Polonica, 60(1) : 49-66

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2012.0129

Late Miocene bovids from Şerefköy-2 (SW Turkey) and their position within the sub-Paratethyan biogeographic province

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Kostopoulos, D.S. and Karakütük, S. 2015. Late Miocene bovids from Şerefköy-2 (SW Turkey) and their position within the sub-Paratethyan biogeographic province. *Acta Palaeontologica Polonica* 60 (1): 49–66.

We describe new fossil bovid craniodental remains from the Upper Miocene fossil site of Şerefköy-2, Yatağan Basin, SW Turkey. The new material belongs to six species: *Gazella* cf. *G. capricornis*, *Palaeoryx pallasi*, *Sporadotragus parvidens*, *Skoufotragus* cf. *Sk. schlosseri*, *Urmiatherium rugosifrons*, and ?*Sinotragus* sp., which together indicate a latest middle–early Late Turolian (Late Miocene) age. Medium-to-large bovid taxa prevail over small ones, and protoryxoid bovids clearly dominate the assemblage. An analysis of the taxonomic structure, size and diet spectra of several Turolian bovid assemblages from Greece and Turkey reveals Şerefköy-2 to be a member of a mammalian palaeocommunity particular to southwestern Anatolia, which in turn forms part of the sub-Paratethyan biogeographic province.

Key words: Mammalia, Bovidae, Antilopinae, biogeography, Miocene, Turolian, Turkey, Anatolia.

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Received 7 November 2012, accepted 10 June 2013, available online 17 June 2013.

Introduction

Anatolia, located in modern-day Turkey, plays a crucial role in the reconstruction of late Neogene Eurasian palaeozoogeography and palaeoenvironments (e.g., Costeur and Legendre 2008; Eronen et al. 2009; Kostopoulos 2009b), because it represents the natural link between the western and eastern extremes of the so-called Late Miocene sub-Paratethyan biogeographic province (Bernor et al. 1979). There area is rich in Late Miocene fossil sites, but in most cases their contents have only been reported in the form of preliminary faunal lists (e.g., Sickenberg et al. 1975; Alan 1997; Saraç 2003). Pioneer works by Ozansoy (1965), Tekkaya (1973a, b), Senyürek (1952, 1953), Boscha-Erdbrink (1978), and Köhler (1987) only gave a fragmentary view of the rich and abundant Late Miocene bovid assemblage of Anatolia, which were partially, but never entirely, filled by later studies on newly discovered or re-examined material (e.g., Bouvrain 1994; Gentry 2003; Kostopoulos 2005; Geraads and Güleç 1999; Bibi and Güleç 2008).

Thee field seasons at the new locality of Şerefköy-2, discovered in the summer of 2007 in Yatağan Basin, SW Turkey (Fig. 1; coordinates: N 37°21'47.80'', E 28°14'11.10''; see Kaya et al. 2012 for further information on the geological context), yielded more than 1200 identifiable fossil specimens belonging to more than 25 species of mammals. Together, these represent one of the richest Turolian faunas from Anatolia, and offer a chance to (i) test faunal correlations within the sub-Parathethyan biogeographic province and (ii) further develop the local biochronological framework. Here, we provide a detailed description of the bovids forming part of the Şerefköy-2 bovid assemblage, preliminary reported by Kaya et al. (2012). The remaining taxa recovered from this site will be described elsewhere.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; MYŞE PV, collection of the Natural History Museum of Ege University, Izmir, Turkey; KNUA, Kapodistrian National University of Athens, Greece; LGPUT, Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki, Thessaloniki, Greece; MNHN, Museum national d'Histoire naturelle, Paris, France; NHMA, Aegean Museum of the Natural History-Zimalis Foundation, Samos Island, Greece; NHMW; Naturhistorisches Museum Wien, Austria.

Other abbreviations.—APD, anteroposterior diameter; CFA, correspondence analysis; L, length; n, number of specimens; TD, transverse diameter; W, width. Upper and lower case letters denote upper and lower teeth, respectively.

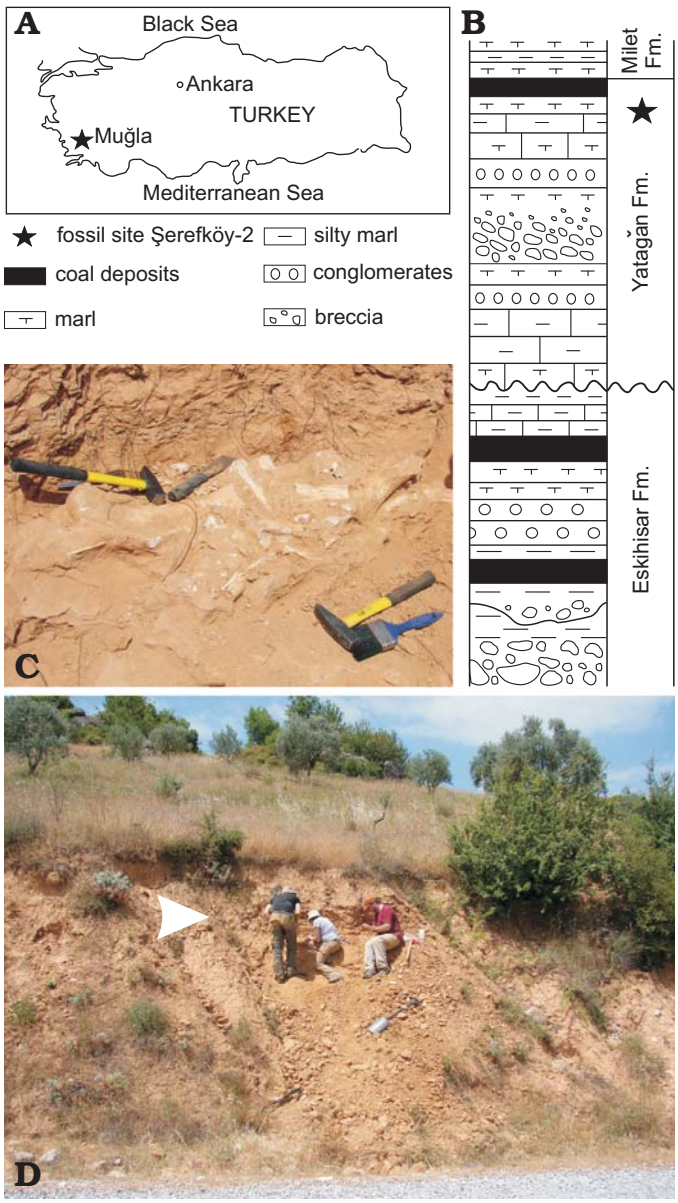

Fig. 1. The fossil mammal site of Şerefköy-2 (Turkey). **A**. Geographical location. **B**. Local lithostratigraphy (modified from Kaya et al. 2012). **C**. Typical fossil accumulation at Şerefköy-2. **D**. View of the fossiliferous site.

Material and methods

Horn core and cranial proportions of different bovids were explored using discriminant and Principal Components analyses. Following Bibi and Güleç (2008), Kostopoulos (2009b), Koufos et al. (2006, 2009a), and Kostopoulos and Bernor (2011), we performed a correspondence analysis (CFA) to investigate the structure of various Turolian (8.7–5.4 Ma; Late Miocene) bovid assemblages from Greece, Turkey and Iran. Following Bibi and Güleç (2008), we first analysed bovid assemblages according to their relative abundances at the genus level. Next, we repeated the analysis by grouping all genera into five units reflective of the basic taxonomic structure of each assemblage. This allowed us to (i) overcome differing taxonomic opinions; (ii) incorporate genera with low abundances; and (iii) emphasise general patterns in taxonomic structure.

Finally, we compared the results the CFA analyses with the size distribution and diet spectra of the involved bovid faunas. The latter reflect crucial ecological parameters (body size and feeding prefeences) that are relevant at the level of both the organism and the community as a whole (e.g., Western 1979; McNaughton and Georgiadis 1986; Eisenberg 1990). Multivariate statistics were performed using PAST version 2.16 (Hammer et al. 2001). Skull and horn core nomenclature follows Gentry (1971, 1992). Dental nomenclature follows Bärmann and Rössner (2011). All measurements are in millimetres (mm). Further details on all the analyses and the data themselves are provided as Supplementary Online Material (SOM 1, SOM 2, available at http://app.pan.pl/SOM/app60-Kostopoulos_Karakutuk_SOM.pdf).

Systematic palaeontology

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1848

Family Bovidae Gray, 1821

Subfamily Antilopinae Gray, 1821 (including all non-Bovinae taxa sensu Kingdon 1982; e.g., Groves and Grubb 2011)

Genus *Gazella* Blainville, 1816

Type species: *Gazella dorcas* Linnaeus, 1758, Recent.

Gazella cf. *G. capricornis* (Wagner, 1848)

Fig. 2.

Material.—MYŞE PV-2501, frontlet; MYŞE PV-1577, PV-1834, right horn cores; MYŞE PV-560, PV-1578, left horn cores; MYŞE PV-1831, PV-1832, partial right horn cores; MYŞE PV-1359, PV-1632, PV-1828, partial left horn cores; MYŞE PV-1360, partial horn core; MYŞE PV-1830, 1633, 1393, distal portions of horn cores; MYŞE PV-2572, palate; MYŞE PV-2575 right upper tooth row P2–M3; MYŞE PV-2000, PV-2558, PV-2562, PV-2564, right mandibular body with p2–m3; MYŞE PV-2557, PV-2563, left mandibular body with p2–m3; MYŞE PV-2565, left mandibular body with p3–m3; MYŞE PV-1526, right m3. All from Şerefköy-2, Turkey, Late Turolian (Late Miocene).

Description.—*Gazella* cf. *G. capricornis* is the only gazelle present at Şerefköy-2, and represented by at least 5 individuals. The supraorbital foramen is located close to the pedicle, within an elliptical and rather narrow depression (Fig. 2C$_1$). The postcornual fossa is oval, small, and moderately deep. The pedicle is moderately high anteriorly (Fig. 2C). The horn cores are short (maximum length: 100 mm along the anterior surface), inserted moderately far apart from each other, and weakly divergent distally (Fig. 2C$_1$). In lateral view, the horn core is slightly curved and moderately inclined posteriorly (Fig. 2A, B, C$_2$), while in cross section it changes from be-

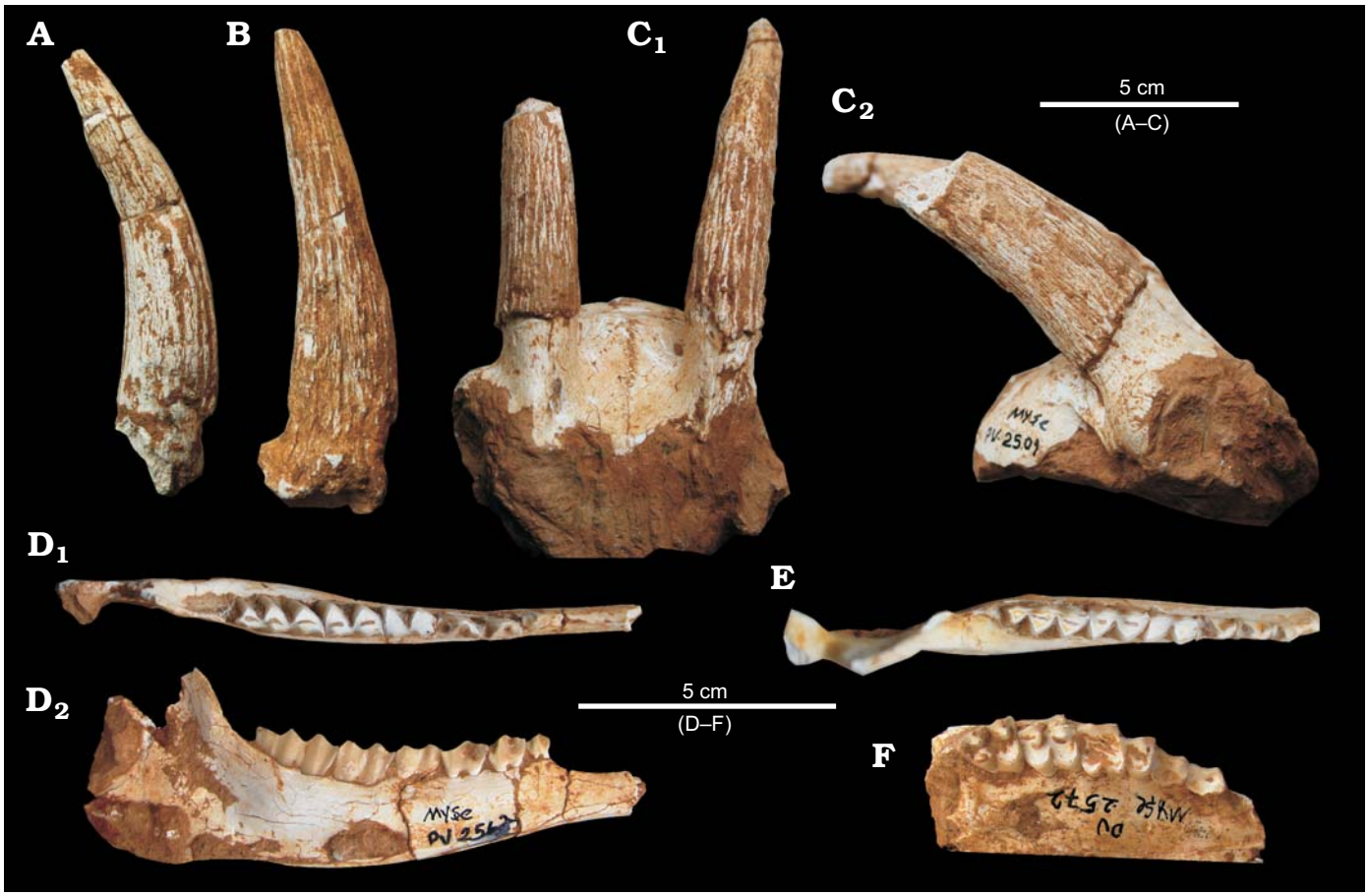

Fig. 2. The bovid artiodactyl *Gazella* cf. *G. capricornis* (Wagner, 1848) from Şerefköy-2 (Turkey), Late Turolian (Late Miocene). **A**. Left horn core (MYŞE PV-1578) in lateral view. **B**. Left horn core (MYŞE PV-560) in lateral view. **C**. Frontlet (MYŞE PV-2501) in frontal (C_1) and lateral (C_2) views. **D**. Left mandibular body (MYŞE PV-2557) in occlusal (D_1) and lingual (D_2) views. **E**. Right mandibular body (MYŞE PV-2564) in occlusal view. **F**. Right P2-M3 of the palate (MYŞE PV-2572) in occlusal view.

ing symmetrically elliptical near the base (owing to weak mediolateral compression) to a more rounded shape towards the tip (TD × 100/APD = 70.4–73.2 at the base, n = 4, and 84.6–104.6 at 7 cm above the base, n = 3; Table 1). Strong, deep, and continuous furrows run along both the anterior and posterior surfaces of the horn core.

The premolars are moderately long compared to the molars (Fig. 2D–F), with the upper and lower premolar/molar ratios equalling about 71% (n = 1) and 54–60% (n = 6), respectively (SOM 3: Tables 1, 2). There is no entostyle on the upper molars. M3 has a strong metastyle and a weak mesostyle (Fig. 2F). The anterior conid of p3 and p4 is weak, but separated from the anterior stylid (MYŞE PV-2000). The mesolingual conid is elongated and oriented posteriorly on p3, but more triangular (during early wear) and located relatively further posteriorly on p4 (Fig. 2D, E). The anterior valley of p3 and p4 is widely open (Fig. 2D, E). The posterior valley of p4 is open in the single unworn specimen (MYŞE PV-2000) and still visible even at advanced stages of wear (Fig. 2D, E). A small ectostylid is present on m1. The mesostylids on m2 and m3 are strong.

Table 1. Horn core measurements (in mm) of *Gazella* cf. *capricornis* from Şerefköy-2 (Turkey). TD, transverse diameter at the base and at 7 cm above the base; APD, anteroposterior diameter at the base and at 7 cm above the base.

Specimen	TDbase	APDbase	TD7	APD7
MYŞE PV-2501	16.4	23.1	12.8	14.8
MYŞE PV-560	17.8	24.3	14.7	14.1
MYŞE PV-1577	15.3	21.7	10.0	11.8
MYŞE PV-1578	16.4	22.2		

Remarks.—The gazelle from Şerefköy-2 is considerably larger than *Gazella ancyrensis* Tekkaya, 1973 from Middle Sinap, as well as *G*. cf. *ancyrensis* from Maragheh (Iran), Samos (Greece), and Kemiklitepe-D (Turkey), but smaller than *Gazella mytilinii* Pilgrim, 1926 from Samos (Bouvrain 1994; Kostopoulos 2009a; Kostopoulos and Bernor 2011). *Gazella pilgrimi* Bohlin, 1935 from Samos and the Axios Valley (Greece) and Akkaşdağı (Turkey) differs from the Şerefköy-2 specimens in having a shorter pedicle, as well as a longer, more mediolaterally compressed, and more strongly inclined horn core (Bouvrain 1996; Kostopoulos 2005, 2009a).

The overall shape of the horn core of the Şerefköy-2 gazelle recalls both *Gazella deperdita* (Gervais, 1847) from Western Europe and the SE European *Gazella capricornis* (Wagner, 1848). However, the horn core of *G. deperdita*

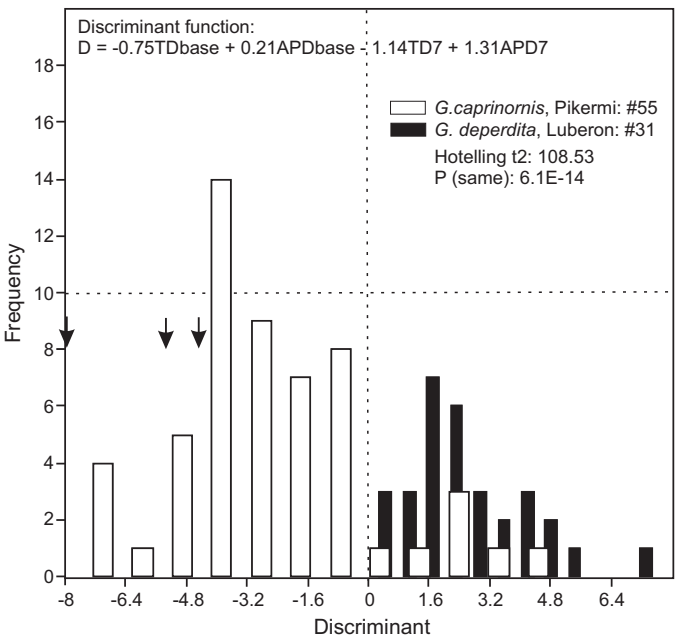

Fig. 3. Discriminant analysis of the horn core proportions of *Gazella deperdita* from Luberon (= Cucuron), Late Miocene, SW Europe and *Gazella capricornis* from Pikermi, Late Miocene, Greece, based on four variables: TD at the base (TDbase), APD at the base (APDbase), TD at 7 cm above the base (TD7) and APD at 7 cm above the base (APD7). Arrows indicate values for the Şerefköy-2 gazelle according to the discriminant function. Abbreviations: APD, anteroposterior diameter; TD, transverse diameter.

is larger (Fig. 3), much more curved in lateral view, more inclined posteriorly, and more mediolaterally compressed along its distal portion. *Gazella capricornis* was originally described from Pikermi (Greece), but similar forms are widely distributed between the Balkans and Iran (Kostopoulos 2005, 2009a; Kostopoulos and Bernor 2011). Both *Gazella* cf. *G. capricornis* from Samos (particularly specimens from Mytilinii-1A) and the Şerefköy-2 gazelle are characterised by an anterior conid distinct from the anterior stylid on p3 and p4, and the closing of the posterior valley of p4 at late wear stages. Together with *G.* cf. *G. capricornis* from Akkaşdağı and Maragheh, they further differ from typical specimens of *G. capricornis* from Pikermi in having slightly shorter premolars compared to the molars (Table 2).

Genus *Palaeoryx* Gaudry, 1861

Type species: *Antilope pallasi* (Wagner, 1857), Pikermi, Greece; Late Miocene.

Palaeoryx pallasi (Wagner, 1857)

Fig. 4.

Material.—MYŞE PV-2573, right upper tooth row with P2–M3; MYŞE PV-1293, right upper tooth row with P3–M3; MYŞE PV-1294/B, partial left upper tooth row with M2–M3; MYŞE PV-1295, partial left upper tooth row with P4–M1; MYŞE PV-1599, left mandibular body with p2–m3; MYŞE PV2574, right mandibular body with p2–m3; MYŞE PV-2552, partial of right mandibular body with m2–m3. All from Şerefköy-2, Turkey, Late Turolian (Late Miocene).

Description.—Specimens from Şerefköy-2 referable to this taxon are limited to some upper and lower tooth rows, representing at least two individuals. The premolars are long compared to the molars (Fig. 4, SOM 3: Tables 1, 2), with upper and lower premolar/molar ratios of 70.8% (n = 1) and 64.3–66.7% (n = 2), respectively. P4 is narrower than both P3 and P2, and P2 is shorter than P3. The anterior style is weakly developed on P2, but sharp, posteriorly curved and joined to the anterolabial cone on P3 (Fig. 4C). The "metaconule" is barely recognisable on P2 and P3, which have a distinctly convex lingual wall, and absent on P4, in which the anterolingual and posterolingual crista of the lingual cone are symmetrically developed (Fig. 4C). The anterior style of P4 is more pronounced than the anterolabial cone, with the latter having a more central position on the labial wall of the tooth than on P3 (Fig. 4C). All upper molars bear a fossetta (central islet) and low, double entostyles, originating from both the protocone and the metaconule (Fig. 4C). The anterior lobe of M1 and M2 is narrower than the posterior one. The development of the mesostyle on the upper molars ranges from weak in MYŞE PV-2573 to strong in PV-1293 and PV-1294.

The p2 has a simple and strong anterior stylid and no anterior conid. The mesolingual conid is also simple, short and placed both anteriorly and almost perpendicularly to the longitudinal axis of the tooth (Fig. 4A, B). The posterior stylid on p3 is much less developed than the posterolingual conid, with both structures becoming fused during late stages of wear (Fig. 4A, B). The anterior conid and the anterior stylid are indistinct, thus forming a robust anterior cuspid. The mesolingual conid is elongated and slants distally, joining the talonid at advanced stages of wear (Fig. 4A). The p4 resembles p3, but is larger, and retains and open posterior valley until the onset of late stages of wear (Fig. 4A, B). The posterolabial conid is indistinct on p2 and p3, and weakly developed on p4. The lower molars have a strong mesostylid,

Table 2. Comparison of *Gazella* cf. *G. capricornis* from Şerefköy-2 with *G.* cf. *G. capricornis* from different localities and with *G. capricornis* from Pikermi. Data are from Kostopoulos (2005, 2009a) and Kostopoulos and Bernor (2011). APD, anteroposterior diameter; L M/m, length of upper/lower molar row; L P/p, length of upper/lower premolar row; TD, transverse diameter at the base and at 7 cm above the base.

	Gazella cf. *G. capricornis*				*Gazella capricornis*
	Şerefköy-2 (Turkey)	Akkaşdağı (Turkey)	Samos (Greece)	Maragheh (Iran)	Pikermi (Greece)
APD × 100/TDbase	135.4–141.8	103.3–137.6	102.6–139.7	112.2–147.4	102.5–139.2
APD × 100/TD7	95.9–118.0	100.0–128.9	100.0–125.0	103.8–128.7	85.0–136.4
LP/LM × 100	71.1–71.2	67.7–74.6	67.0–73.0	76.5	75.4–78.4
Lp/Lm × 100	54.0–60.2	55.2–56.4	58.0	58.8–61.8	59.7–70.8

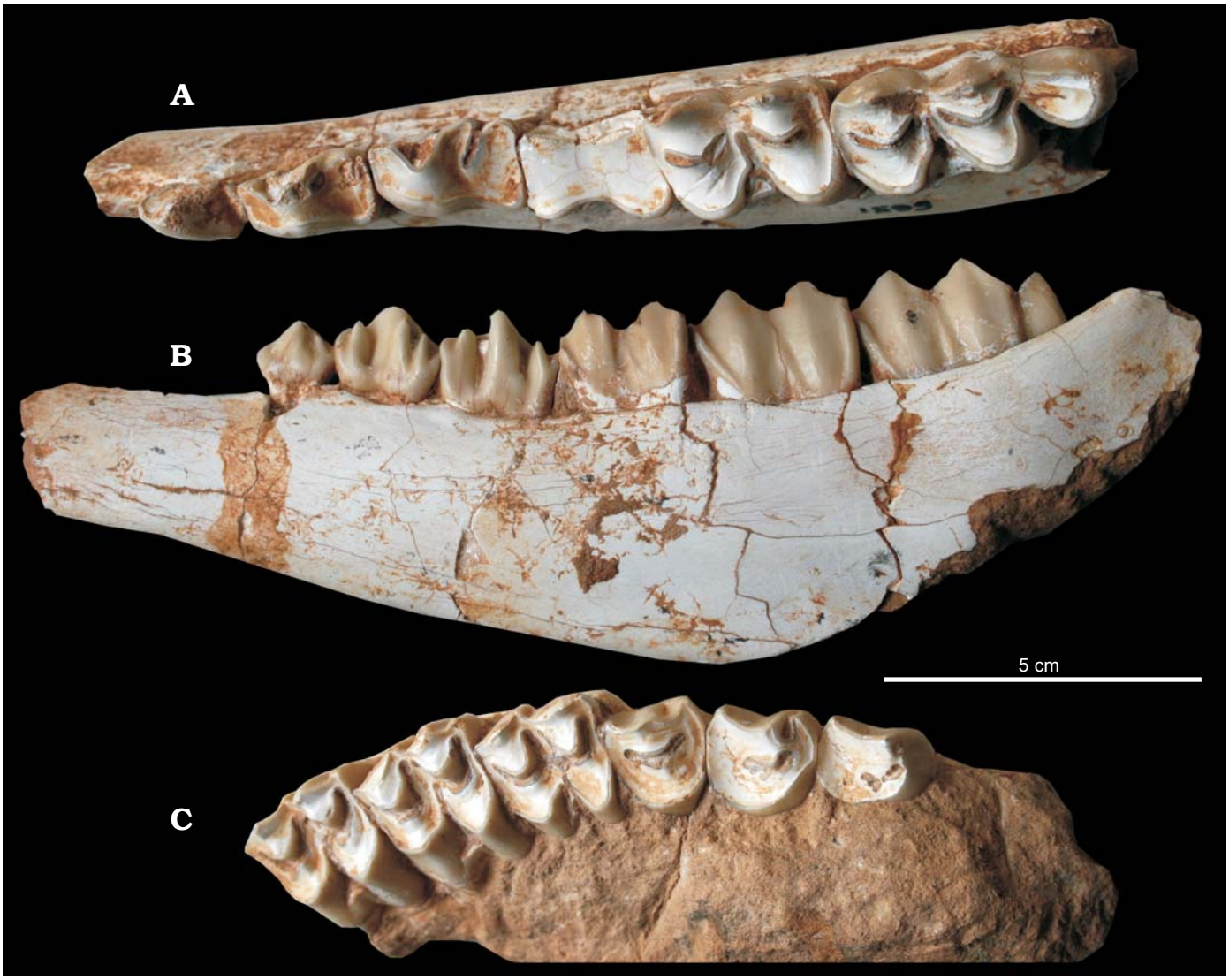

Fig. 4. The bovid artiodactyl *Palaeoryx pallasi* (Wagner, 1848) from Şerefköy-2 (Turkey), Late Turolian (Late Miocene). **A**. Left mandible (MYŞE PV-1599) in occlusal view. **B**. Right mandible (MYŞE PV-2574) in lingual view. **C**. Right upper tooth row (MYŞE PV-2573) in occlusal view.

moderate ectostylids (basal pillars), and no anterior cingulid (goat fold). The third lobe of m3 is rather large and bears a flat entoconulid, as well as a bulbous hypoconulid (Fig. 4A).

Remarks.—*Palaeoryx* Gaudry, 1861 is mainly known from Turolian sites of the sub-Paratethyan zoogeographic province (e.g., Kostopoulos and Bernor 2011 and literature therein), although it may have appeared during the Vallesian (e.g., Vislobokova 2005). In Turkey, records of the genus are restricted to the localities of Kayadibi, Eski Bayırköy, and Mahmutgazi (Köhler 1987), as well as Kemiklitepe-A, B and Akkaşdağı (Bouvrain 1994; Kostopoulos 2005). Kostopoulos (2005, 2009a) recognised two species in the Aegean region, *P. pallasi* and *P. majori* Schlosser, 1904, which differ from each other mainly in terms of their cranial and horn core morphology. In addition, a larger species or variety might exist in Maragheh (Iran) and Ukraine (Kostopoulos and Bernor 2011).

The specimens from Şerefköy-2 differ from *P. majori* from Samos and Akkaşdağı in having a relatively (compared to the premolars) and absolutely longer upper molar row (60.7–62.0 mm vs. 64.8–65.4 mm, based on the material from Akkaşdağı), as well as in lacking a central fold (hypoconal spur) on P3 and P4, and an anterior cingulid on the lower molars (Fig. 5; Kostopoulos 2009a). In addition, *P. majori* from Samos differs from the Şerefköy-2 material in the presence of basal pillars on the upper molars and in having a p4 bearing a centrally placed mesolingual conid and a fused posterolingual conid and posterior stylid. By contrast, the Şerefköy-2 specimens resemble *P. pallasi* from Samos and Pikermi in all of these characters, as well as in the presence of a posteriorly curved anterior style on P3, a more centrally placed anterolabial cone on P4 (relative to P3), a strong mesostyle on the upper molars, a weak posterolabial conid on p3 and p4, and a tendency for the mesolingual conid of p4 to be oriented anteroposteriorly. *P. pallasi* from Pikermi differs, however, in having distinct posterolingual and mesolingual conids on p3, as well as distinct anterior and mesolingual

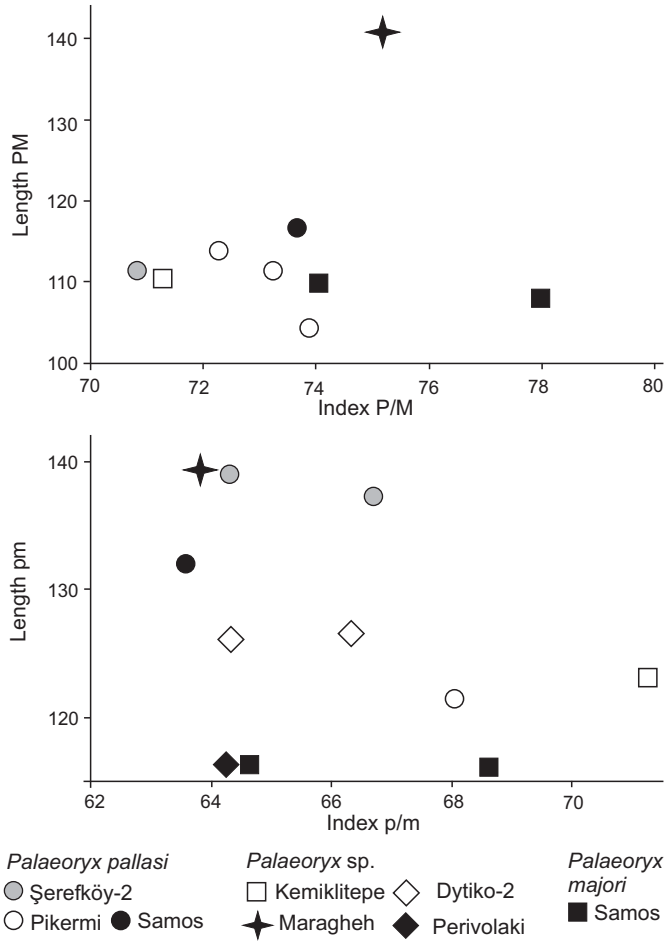

Fig. 5. Scatter plot comparing the upper and lower premolar (P, p) / molar (M, m) ratio against the complete tooth row length of *Palaeoryx* from several localities.

conids on p4, although the degree of variability of these features within *P. pallasi* is not well known.

There is considerable size variation of both the upper and lower tooth rows within *Palaeoryx*. The lower tooth row from Şerefköy-2 (Lpm = 138.9 mm) appears close to that from Maragheh (LPM = 139.3 mm). By contrast, the upper tooth row (LPM = 111.5 mm) is considerably smaller than both that from Maragheh (LPM = 140.8 mm) and a particularly large specimen from Pikermi (MNHN PIK2447; e.g., Kostopoulos and Bernor 2011), but close to *P. pallasi* from Samos and other specimens from Pikermi. The available data are insufficient for statistically sound conclusions; nevertheless, in the absence of marked morphological differences, we suggest that the observed size variation may be intraspecific.

Stratigraphic and geographic range.—Upper Miocene; Balkans to Iran.

Genus *Sporadotragus* Kretzoi, 1968

Type species: *Microtragus schafferi* (Andree, 1926), Samos, Greece; Late Miocene.

Sporadotragus parvidens (Gaudry, 1861)

Fig. 6.

Material.—MYŞE PV-2502, partial skull; MYŞE PV-1573, frontlet preserving the basal part of the horn cores; MYŞE PV-1300, partial left horn core; MYŞE PV-1522, right upper tooth row with P2–M3; MYŞE PV-1412. right M3; MYŞE PV-1423, left M3; MYŞE PV-1533, left M1; MYŞE PV-1511, right mandibular body with p3–m3; MYŞE PV-2561, right mandibular body with p2–m2; MYŞE PV-1429, right mandibular body with p4–m2; MYŞE PV-2556, right mandibular body with m1–m3; MYŞE PV-1630, left mandibular body with p3–m3; MYŞE PV-1407, PV-1574, left mandibular body with p2–m2; MYŞE PV-2569, left mandibular body with p4–m3; MYŞE PV-1406, PV-2559, left mandibular ramus with p2–m3; MYŞE PV-1311, left mandibular ramus with p4–m2. All from Şerefköy-2, Turkey, Late Turolian (Late Miocene).

Description.—This species is represented by at least 7 individuals. The frontals form a 105–115° angle along the sagittal plane and appear moderately pneumatised above the orbits. The supraorbital foramen (doubled on the left side in both MYŞE PV-1573 and PV-2502) is small and round, placed well below the pedicle, and opens directly into the orbit (Fig. 6A). The interfrontal suture is complex in outline and slightly pinched between the horn cores (Fig 6A). The frontoparietal suture is also complex, Y-shaped, and runs very close to the base of the horn core. The postcornual fossa is shallow and round. As preserved, the horn core is long (maximum length: 210 mm along the anterior surface) and gently curved posteriorly. It furthermore bears thin and discontinuous grooves on its surface and shows no evidence of torsion (Fig. 6A). In MYŞE PV-1300, a weak anterior keel runs along its basal portion. The cross section of the horn core is elliptical at the base, with its maximum transverse diameter located posteriorly (TD × 100/APD at the base = 75.3–76.4, n = 3; Table 3). The angle between the greatest anteroposterior diameter of the horn core base and the sagittal plane ranges from 42 to 50°. Towards the tip, the cross section of the horn core remains elliptical, but becomes symmetrical (TD × 100/APD at 7 cm above the base = 72.9–78.3, n = 3; Table 3).

The upper premolars are moderately long compared to the molars, with a premolar/molar ratio 69.7% (n = 1) (Fig. 6C, SOM 3: Table 1). P2 and P3 have a strong anterolabial cone and bear a fossa unequally divided by a central fold (Fig. 6B). The anterior style of P3 and P4 is also strong, but the anterolabial cone of P4 is weak. The upper molars have a strongly developed paracone, parastyle and mesostyle, a weak metacone, and no basal pillars (entostyle) (Fig. 6B). A metaconule fold is present on M2.

The lower premolar row is moderately short compared to the molars, with a premolar/molar ratio of 58.3–62.4%, n = 2

Table 3. Horn core measurements (in mm) at the base and at 7 cm above the base of *Sporadotragus parvidens* from Şerefköy-2 (Turkey). APD, anteroposterior diameter; TD, transverse diameter.

Specimen	TDbase	APDbase	TD7	APD7
MYŞE PV-2502	35.5	44.3	28.1	35.9
MYŞE PV-1573	34.6	46.0	27.8	35.6
MYŞE PV-1300	34.5	45.1	29.0	39.8

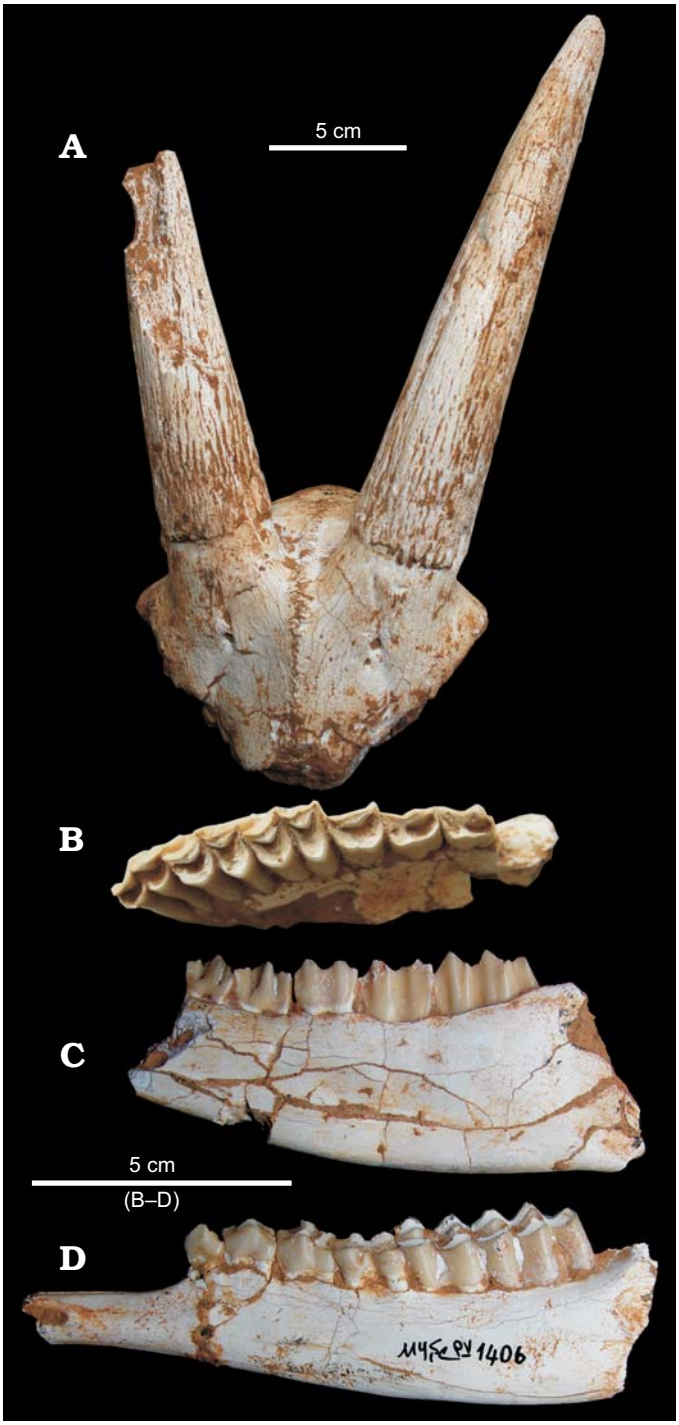

Fig. 6. The bovid artiodactyl *Sporadotragus parvidens* (Gaudry, 1861) from Şerefköy-2 (Turkey), Late Turolian (Late Miocene). **A**. Frontlet (MYŞE PV-2502) in anterior view. **B**. Right P2–M3 (MYŞE PV-1522) in occlusal view. **C**. Right mandibular ramus with p3–m3 (MYŞE PV-1311) in lingual view. **D**. Left mandibular ramus with p2–m3 (MYŞE PV-1406) in labial view.

(Fig. 6C, D, SOM 3: Table 2). The p3 and p4 have a strong anterior stylid and a barely developed anterior conid (Fig. 6C). The mesolingual conid is simple and elongated on p3, but rounded towards the base and slightly curved anteriorly on p4. On both p3 and p4, the posterolingual conid fuses with the posterior stylid during early wear and the posterolabial conid is well developed (Fig. 6C). Both the metastylid and especially the entostylid of the lower molars are well marked during early wear. There is no anterior cingulid. A low ectostylid is present on m1 (Fig. 6D).

Remarks.—Both the size and the overall horn core and dental morphology of the material from Şerefköy-2 match those of *Sporadotragus,* the taxonomic status of which was recently revised by Geraads et al. (2006) and Kostopoulos (2009a). The specimens from Şerefköy-2 have larger horn cores than *Sporadotragus vasili* Geraads, Spassov, and Kovachev, 2006 from the SW Bulgarian localities of Kalimantsi and Strumyani (Geraads et al. 2006, 2011; Fig. 7), which furthermore differs from the present material in having a fused interfrontal suture, as well as a less curved horn core with a flat medial and a wide anterior surface, strong longitudinal grooves, and an anteromedial keel (Geraads et al. 2006). By contrast, the specimens from Şerefköy-2 have several features in common with *Sporadotragus parvidens*, mainly known from Pikermi, Samos (Greece) and Kemiklitepe-D (Turkey) (Bouvrain 1994; Kostopoulos 2009a). These include a small supraorbital foramen not located inside a pit, a complex and slightly raised interfrontal suture, and a Y-shaped frontoparietal suture. In addition, both have a horn core that is long, sub-cylindrical and gently (but markedly) curved posteriorly, bears irregular grooves, and shows no evidence of torsion or keels. The flexion of the frontals along the sagittal plane appears slightly stronger in the material from Şerefköy-2 (105–115°) than in *Sp. parvidens* from Samos (100–105°); however, this, as well as other minor differences (such as somewhat longer

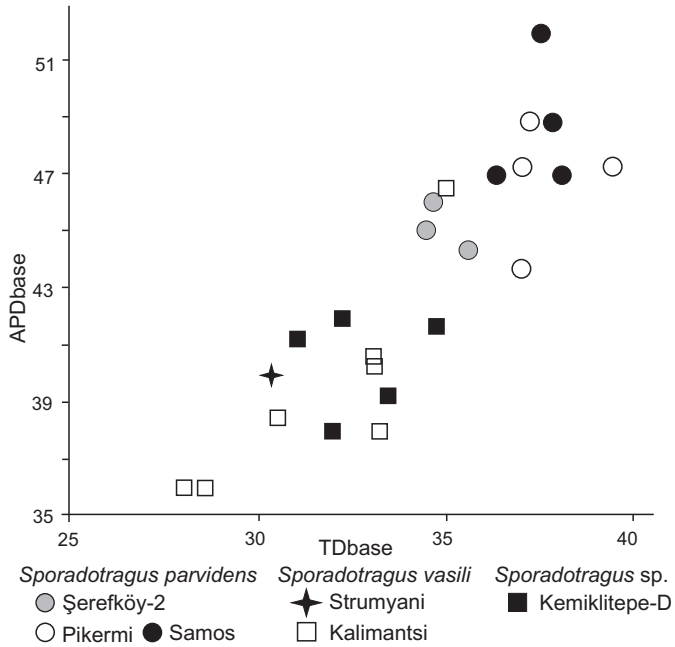

Fig. 7. Scatter plot comparing the basal proportions of the horn cores of *Sporadotragus parvidens* from Şerefköy-2 (Turkey), Samos and Pikermi (Late Miocene, Greece) with *Sporadotragus vasili* from Kalimantsi and Strumyani (Late Miocene, Bulgaria), and *Sporadotragus* from Kemiklitepe D (Late Miocene, Turkey). APDbase, anteroposterior diameter at the base; TDbase, transverse diameter at the base.

horn cores in some specimens from Samos or the degree of p4 molarisation) may well reflect intraspecific variation.

Stratigraphic and geographic range.—Upper Miocene; Aegean region.

Genus *Skoufotragus* Kostopoulos, 2009b

Type species: *Pachytragus schlosseri* (Andree, 1926), Samos, Greece; Late Miocene.

Skoufotragus cf. *Sk. schlosseri* (Andree, 1926)

Figs. 8–10.

Material.—MYŞE PV-547, partial cranium with horn cores; MYŞE PV-1571, 1576, female frontlet; MYŞE PV-1570, left female horn core; MYŞE PV-1575, right horn core; MYŞE PV-1579, partial left female horn core; MYŞE PV-2606, partial female horn core; MYŞE PV-1309, palate; MYŞE PV-1512, PV-1516, PV-2570, right upper tooth row with P2–M3; MYŞE PV-1513, PV-1514, PV-1515, right upper tooth row with P3–M3; MYŞE PV-1622, right upper tooth row with M1–M3; MYŞE PV-1491, right upper tooth row with M2–M3; MYŞE PV-1523, right M3; MYŞE PV-1520, PV-1521, left upper tooth row with M2–M3; MYŞE PV-1519, left upper tooth row with P2–M2; MYŞE PV-1525, left upper tooth row with P4–M1; MYŞE PV-2571, left upper tooth row with P3–M3; MYŞE PV-1410, left upper tooth row with M1–M3; MYŞE PV-1517, left M2–M3; MYŞE PV-1312, left upper tooth row with P2–P4; MYŞE PV-1315, left M3; MYŞE PV-1434, PV-1436, PV-1313, M1 or M2; MYŞE PV-1532, left P2; MYŞE PV-1510, PV-1542, PV-2560, right mandibular body with p2–m3; MYŞE PV-1541, right mandibular body with p3–m3; MYŞE PV-2551, right mandibular body with p4–m2; MYŞE PV-2568, right mandibular body with m1–m3; MYŞE PV-1546, left mandibular body with m2–m3; MYŞE PV-1543, PV-1544, PV-2554, PV-2566, left mandibular ramus with p2–m3; MYŞE PV-1540, left mandibular ramus with p4–m3; MYŞE PV-2001, left mandibular ramus with p3–m1; MYŞE PV-1156, left mandibular ramus with m2–m3. All from Şerefköy-2, Turkey, Late Turolian (Late Miocene).

Description.—This is by far the most abundant bovid found at Şerefköy-2 and represented by at least 10 individuals. The opisthocranium is high, narrow, dolichocephalic (sensu Bosscha-Erdbrink 1978) and has a straight dorsal profile in lateral view (Fig. 8C, Table 4). The temporal lines are moderately developed and run parallel to each other posteriorly. In posterior view, the occiput is triangular and bears a sharp occipital crest (Fig. 8B, C) that ends dorsally in a strong protuberance surrounded by deep scars. The nuchal crest is well developed. The mastoid faces posterolaterally and the paroccipital process is large and flattened. In lateral view, the occipital condyles project posteroventrally, thus forming a very acute angle with the occipital level. The basioccipital is long, relatively narrow and bears a shallow, narrow longitudinal groove (Fig. 8D). The sharp and prominent (crest-like) posterior tuberosities of the basioccipital are oriented perpendicular to the sagittal plane, whereas the weak anterior tuberosities are oriented anteroposteriorly. The oval foramen faces laterally. The preserved outline of the auditory bulla indicates that it was large and bulbous.

The frontal contains large sinuses, one of which occupies the pedicle and even reaches the base of the horn core. There is no postcornual fossa. The horn core, inserted above the orbit, is sabre-like without keels or torsion (Figs. 8A, C, 9A). It is moderately long, moderately curved posteriorly in lateral view and strongly compressed mediolaterally along its entire length (TD × 100/APD at the base: 40–57, n = 5; Table 4). In cross section, the horn core forms an elongated ellipse, which becomes narrower towards the tip. A deep furrow occasionally runs along the upper half of the posterior surface, and, in combination with the strong mediolateral compression, may give the impression of a distal posterior keel.

Two frontlets and three horn core specimens (MYŞE PV-1570, PV-1571, PV-1576, PV-1579, and PV-2606; Fig. 9) likely represent female individuals. The supraorbital foramen is large and round, and placed far anterior to the pedicle. The interfrontal suture is open and simple in outline. The horn core is thin and long (~140 mm) and inserted above the back of the orbit. It is far removed from its counterpart, weakly curved posteriorly and barely twisted homonymously (Fig. 9B). In cross section, the horn core is elliptical at the base but becomes more compressed mediolaterally towards the tip (Table 4). In anterior view, the divergence of the horn cores is weak up to their mid-height, but stronger above.

The premolars are moderately long compared to the molars, with upper and lower premolar/molar ratios of 59.6–65.6% (n = 5) and 60.3–66.6% (n = 4), respectively (Fig. 10,

Table 4. Cranial and horn core measurements (in mm) of *Skoufotragus* cf. *Sk. schlosseri* from Şerefköy-2 (Turkey). APD, anteroposterior diameter at the base and at 10 cm above the base; Lfpo, sagittal length from the frontoparietal suture to the occipital protuberance; TD, transverse diameter at the base and at 10 cm above the base; Watbc, width of the skull at the anterior tuberosities of the basioccipital; Wbrc, maximum width of the braincase; Wptbc, width of the skull at the posterior tuberosities of the basioccipital. sin, left; dex, right.

Specimen	TDbase	APDbase	TD10	APD10	Lfpo	Wbrc	Wptbc	Watbc
MYŞE PV-547 dex	29.29	58.84	20.29	37.22	65.13	61.69	35.85	19.94
MYŞE PV-547 sin	32.2	55.52	22.6	38.3				
MYŞE PV-1571 dex	34	59.5	22.56	43.36				
MYŞE PV-1575 dex	33.36	61.38	22.58	39.84				
MYŞE PV-1570 sin	25.92	64.9	22.65	45.54				
MYŞE PV-1576 dex	22.42	26.64	11.18	14.69				
MYŞE PV-1576 sin	23.16	26.77	9.77	13.95				

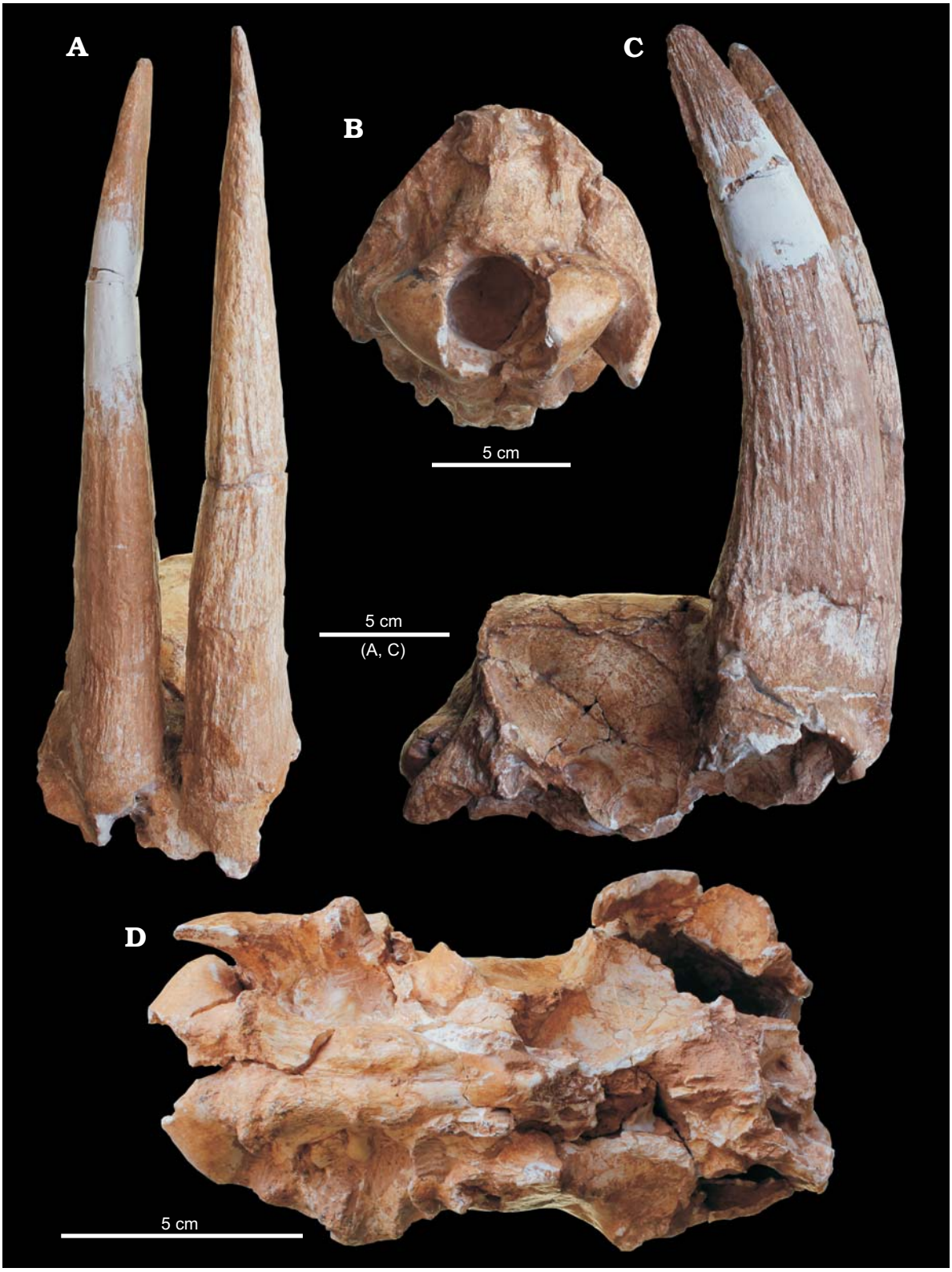

Fig. 8. The bovid artiodactyl *Skoufotragus* cf. *Sk. schlosseri* (Andree, 1926) from Şerefköy-2 (Turkey), Late Turolian (Late Miocene). Partial skull (MYŞE PV-547) in anterior (**A**), posterior (**B**), lateral (**C**), and ventral (**D**) views.

SOM 3: Tables 1, 2). The upper molars have strong styles, bear a fossetta (central islet) and lack entostyles (Fig. 10A, B, D). P2 is bilobed lingually, whereas P3 has a trapezoidal occlusal outline. Both have a strong anterolabial cone (Fig. 10A). The protocone of M1 protrudes lingually. The metastyle of M3 is strong and, in one specimen (MYŞE PV-1622), flares distally (Fig. 10D). The mandibular body is shallow and long (Fig. 10C). On the labial face, a second mental fora-

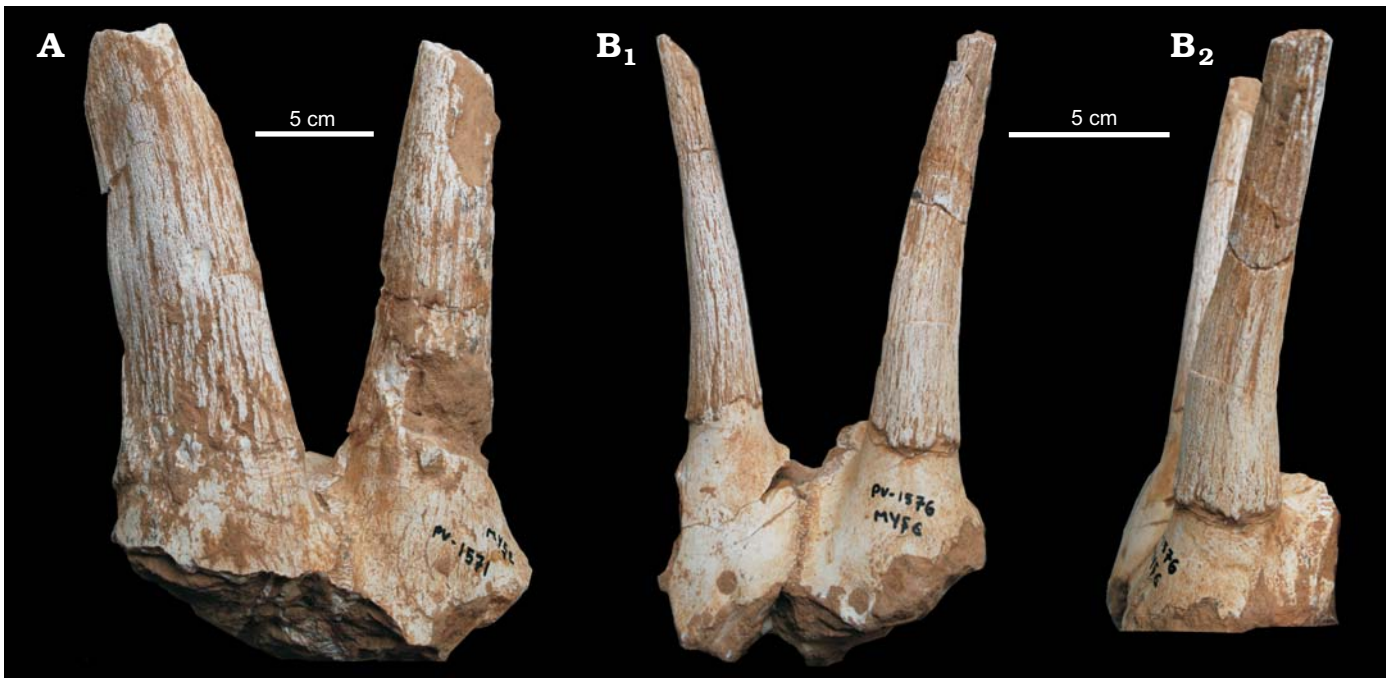

Fig. 9. The bovid artiodactyl *Skoufotragus* cf. *Sk. schlosseri* (Andree, 1926) from Şerefköy-2 (Turkey), Late Turolian (Late Miocene). **A**. Frontlet (MYŞE PV-1571) in anterior view. **B**. Female frontlet (MYŞE PV-1576) in anterior (B_1) and lateral (B_2) views.

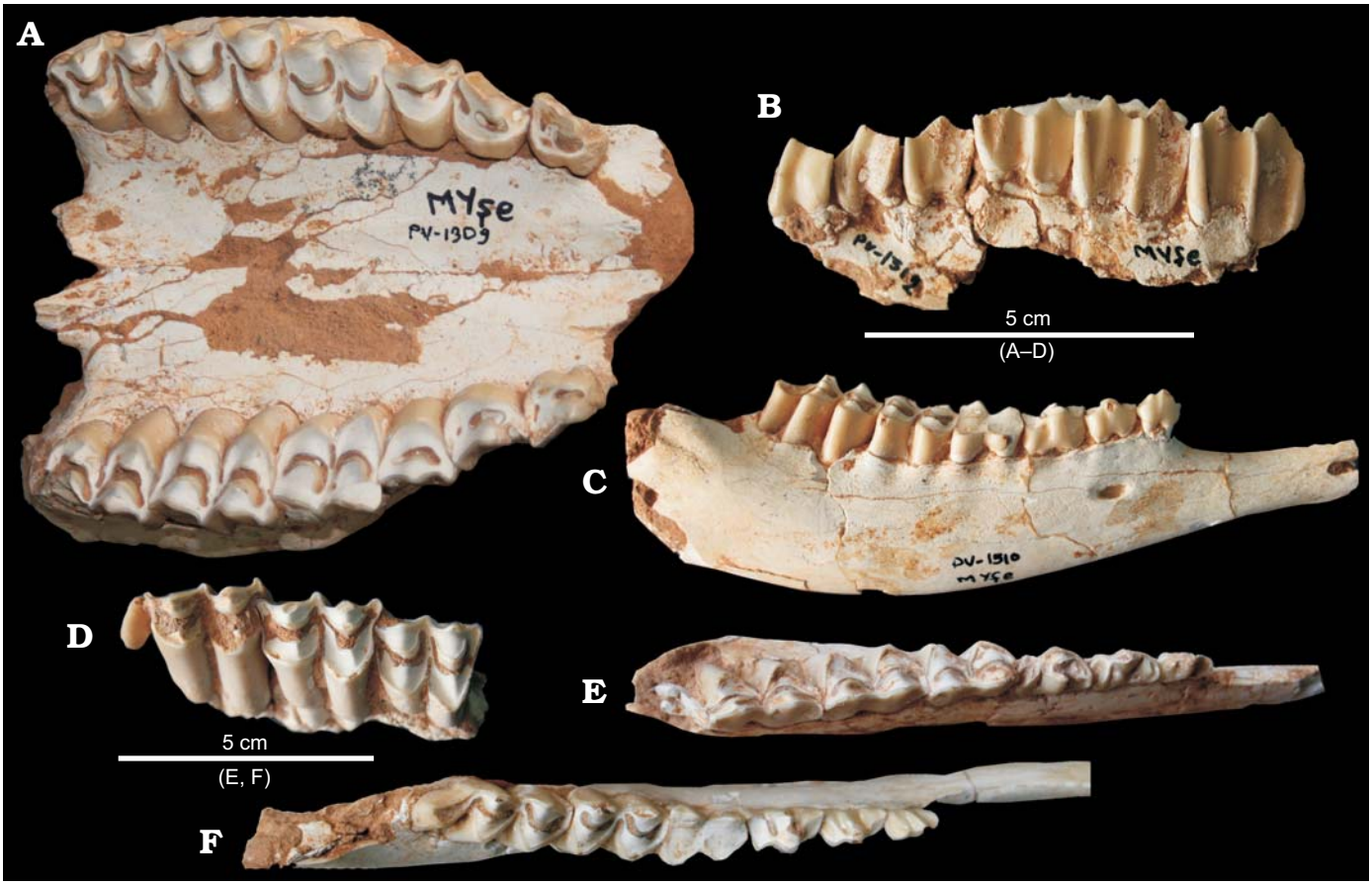

Fig. 10. The bovid artiodactyl *Skoufotragus* cf. *Sk. schlosseri* (Andree, 1926) from Şerefköy-2 (Turkey), Late Turolian (Late Miocene). **A**. Palate (MYŞE PV-1309) in occlusal view. **B**. Left upper tooth row P2–M3 (MYŞE PV-1312) in buccal view. **C**. Right upper tooth row M1–M3 (MYŞE PV-1622) in occlusal view. **D**. Right mandibular ramus with p2–m3 (MYŞE PV-1510) in labial view. **E**. Left mandibular ramus with p2–m3 (MYŞE PV-1544) in occlusal view. **F**. Right mandibular ramus with p2–m3 (MYŞE PV-1510) in occlusal view.

men appears below p3 (Fig. 10C). The p2 is simple without an anterior conid, but with a strong mesolingual conid and anterior stylid (Fig. 10E, F). The p3 has a well-developed anterior conid and stylid, which become fused together with wear. The mesolingual conid of p3 is oriented parallel to the posterolingual conid, which in turn fuses with the weaker and posterolingually directed posterior stylid during early wear (Fig. 10E, F). The p4 resembles p3, but has an anteroposteriorly developed mesolingual conid (Fig. 10E). The lower molars have a strong meta- and mesostylids, but both elements disappear with wear. There is no anterior cingulid. A basal pillar appears on 5 out of 13 m1s, and 3 out of 13 m2s. The third lobe of m3 is labially displaced and has an elongated, semicircular occlusal outline; it bears a strong posterolingual stylid on the upper half of the crown.

Remarks.—Protoryxoid bovids appear in the Eastern Mediterranean area as early as the Late Astaracian (e.g., Gentry 2000). Although they remained rare during the Vallesian, they strongly radiated and dispersed during the Turolian, especially in Anatolia and adjacent territories. They include small to medium-sized antelopes of caprine/hippotragine cranial appearance, but their taxonomy and evolutionary relationships remain debated. Kostopoulos (2009a) partly revised the Turolian protoryxoids from SE Europe assigned to the so-called "*Protoryx/Pachytragus* complex" and recognised two distinct genera: *Protoryx* Major, 1891 and *Skoufotragus* Kostopoulos, 2009 (= partim *Pachytragus* Schlosser, 1904). The Şerefköy-2 specimens resemble *Skoufotragus* in their dental morphology and in having (i) a narrow, long braincase with a straight dorsal profile and parallel sides, (ii) a triangular occiput and (iii) a sabre-like, mediolaterally compressed and uprightly inserted horn core (Kostopoulos 2009a: 364). *Skoufotragus* is known from the Turkish Late Miocene assemblages of Kinik (*Protoryx* sp. of Köhler 1987), Kemiklitepe-A (*Protoryx laticeps* of Bouvrain 1994), and Akkaşdağı (*Pachytragus crassicornis* of Kostopoulos 2005), as well as from Samos, Greece and Maragheh, Iran (Kostopoulos 2009a, Kostopoulos and Bernor 2011).

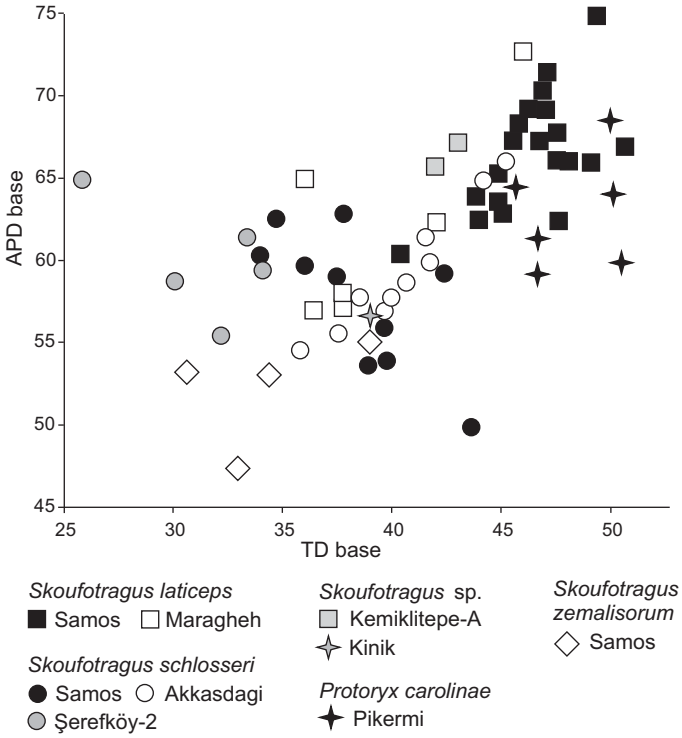

Fig. 11. Scatter plot comparing the basal horn core proportions of *Skoufotragus* from several sites and *Protoryx* from Pikermi (Late Miocene, Greece). APDbase, anteroposterior diameter at the base; TDbase, transverse diameter at the base.

The Şerefköy-2 specimens differ from *Skoufotragus laticeps* from Samos, Kemiklitepe-A and Maragheh in having a narrower braincase, as well as a shorter dorsal parietal sector, less developed anterior tuberosities of the basioccipital, shorter, more slender, and more mediolaterally compressed horn cores, and, on average, smaller tooth rows (but with a similar premolar/molar ratio) (Figs. 11, 12). They are more

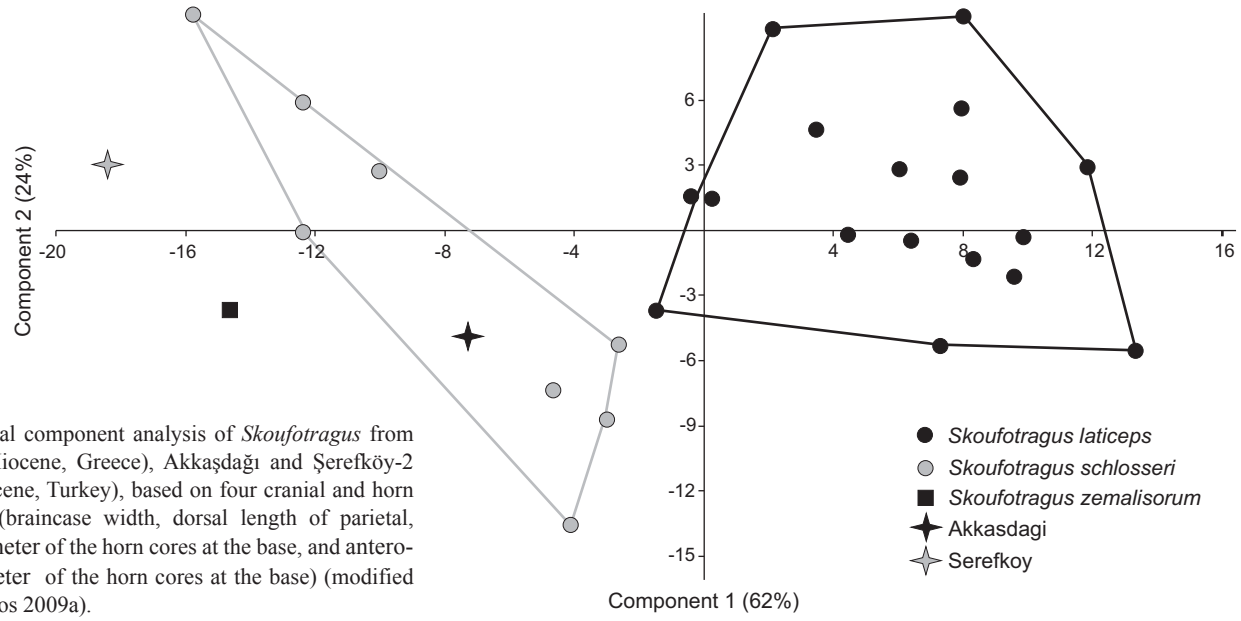

Fig. 12. Principal component analysis of *Skoufotragus* from Samos (Late Miocene, Greece), Akkaşdağı and Şerefköy-2 (both Late Miocene, Turkey), based on four cranial and horn core variables (braincase width, dorsal length of parietal, transverse diameter of the horn cores at the base, and anteroposterior diameter of the horn cores at the base) (modified from Kostopoulos 2009a).

similar to *Sk. zemalisorum* from Samos in terms of their cranial proportions, but differ in having a narrower braincase (61.7 mm vs. 70–78 mm; Kostopoulos 2009a) and a more anteroposteriorly expanded horn core (Figs. 11, 12). Except for a somewhat longer lower premolar row (relative to the molars), the Şerefköy-2 specimens closely resemble *Sk. schlosseri* from Samos and Akkaşdağı in their size and morphology (Figs. 11, 12), although the material from Samos (Q5) is characterised by slightly longer and more divergent horn cores bearing an anterior keel (the latter seems to be more common in short-horned individuals; cf. Kostopoulos 2005: 777).

Female individuals of *Skoufotragus* are rare, but Gentry (1971: 252, pl. 3: 3) interpreted AMNH 20687 as a female individual of *Sk. laticeps*. The frontlet MYŞE PV-1576 from Şerefköy-2 is very similar to this specimen, suggesting that females of *Sk. schlosseri* were likely horned.

Genus *Urmiatherium* Rodler, 1889

Type species: *Urmiatherium polaki* Rodler, 1889, Maragheh, Iran; Late Miocene.

Urmiatherium rugosifrons (Sickenberg, 1932)

Fig. 13.

Material.—MYŞE PV-1182, partial opisthocranium; MYŞE PV-2503, frontlet; MYŞE PV-2504, frontlet of young individual; MYŞE PV-2599, axis+3rd cervical vertebra; MYŞE PV-2506, axis; MYŞE PV-2505, 3rd cervical vertebra (possibly representing the same individual as MYŞE PV-2505). All from Şerefköy-2, Turkey, Late Turolian (Late Miocene).

Description.—This bizarre species is represented by at least two individuals and can unambiguously be identified based on (i) its small size (Table 5); (ii) strong cranio-facial flexion; (iii) strongly elevated, thick and pneumatised frontals; (iv) an extremely shortened opisthocranium; (v) a reduced parietal forming an obtuse angle with the occipital plane; (vi) an enlarged and thickened occipital with large occipital condyles and a dorsally-facing occiput; (vii) a thickened basioccipital with strong and completely fused posterior tuberosities, thus forming an additional, oval facet for the atlas (Fig. 13C); and (viii) thick, short, and moderately homonymously twisted and grooved horn cores, originating very close from each other and—in juveniles—bearing wide and well-defined lateral depressions (Fig. 13A, B).

Remarks.—*Urmiatherium rugosifrons* is the only representative of its genus from Asia Minor. Besides Şerefköy-2, the species is only known from the neighbouring site of Salihpaşalar (Kaya et al. 2012) and the Turolian of Samos (e.g., Solounias 1981; Kostopoulos 2009a, 2014; Jafarzadeh et al. 2011; Table 5). Other possible occurrences of the genus at Garkın, Kınık (Afyon) and Kayadibi (Konya) in mid-western Anatolia (Alan 1997; Saraç 2003) still need to be confirmed.

Stratigraphic and geographic range.—Upper Miocene; Asia Minor.

Genus *Sinotragus* Bohin, 1935

Type species: *Sinotragus wimani* Bohlin, 1935, Locality 30, Shanxi Province, North China.

cf. *Sinotragus* sp.

Fig. 14.

Material.—MYŞE PV-1409, partial left upper tooth row preserving only P2–P3; MYŞE PV-2553, left mandibular body with p2–m3; MYŞE PV-2567, right mandibular body with p2–m3. All from Şerefköy-2, Turkey, Late Turolian (Late Miocene).

Description.—The only maxillary fragment preserves P2 and P3 (Fig. 14C, SOM 3: Table 1). P2 is weekly bilobed lingually and has a trapezoidal occlusal outline, with a weak anterior style, strong anterolabial cone, posterolabially protruding posterior style, and distolingually broadened posterolingual crista. P3 is subrectangular in occlusal view and bears strong labial styles and ribs, as well as a weak lingual groove dividing the distolingually expanded lingual cone (Fig. 14C). A weak notch on the distal wall of the tooth emphasises the posterior style. Traces of enamel on the distal occlusal surface suggest that the tooth originally had an additional distal fossa or a strong central fold.

The lower premolar row is moderately short compared to the molars, with premolar/molar ratios of 56.7% and 57.9% (n = 2) (Fig. 14A, B, SOM 3: Table 2). The lower premolars are narrow and short. The p2 lacks an anterior conid, but bears an anteriorly located mesolingual conid and a week anterior stylid. The mesolingual conid of p3 is elongated and directed posteriorly. The posterolingual conid of p3 is strong. The anterior conid and stylid are equally developed and fuse together during advanced stages of wear. The anterior valley is open. Unlike p3, p4 is distinctly molarised (Fig. 14A, B). On the lingual wall, the anterior valley closes quickly during wear and the mesolingual conid fuses with the posterior conid and stylid. Labially, there is a well-developed posterolabial conid. The lower molars bear a strong ectostylid and have a gently undulating lingual wall covered by cement. The

Table 5. Cranial and horn core measurements (in mm) of *Urmiatherium rugosifrons* from Şerefköy-2 (Turkey) compared to *Urmiatherium rugosifrons* from Samos (Greece) and *Urmiatherium polaki* from Maragheh (Iran). Data are from Kostopoulos (2009a) and Kostopoulos and Bernor (2011). APDbase, anteroposterior diameter at the base; TDbase, transverse diameter at the base; Wbi-co, bicondylar width of the skull; Wbrc, maximum width of the braincase; Wptbc, width of the skull at the posterior tuberosities of the basioccipital.

Specimen	Wbrc	Wbi-co	Wptbc	TDbase	APDbase
MYŞE PV-1182		57.6	28.1		
MYŞE PV-2504	72.6			35.2	48.9
MYŞE PV-2503	92.7			~46.8	~70.8
Urmiatherium rugosifrons, Samos	95–96	50–62	24–30		
Urmiatherium polaki, Maragheh	98	77–83	39	42	78–130

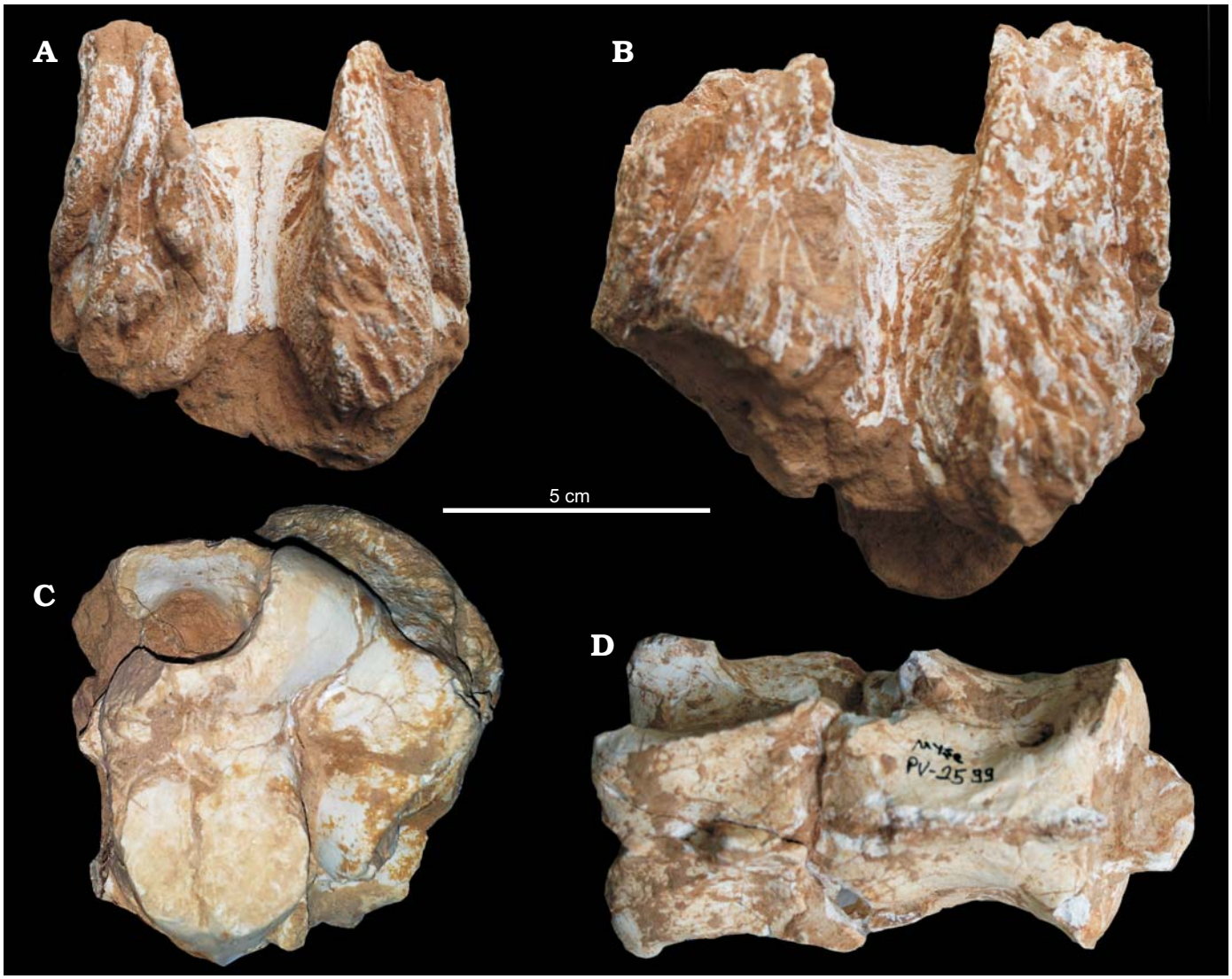

Fig. 13. The bovid artiodactyl *Urmiatherium rugosifrons* (Sickenberg, 1932) from Şerefköy-2 (Turkey), Late Turolian (Late Miocene). **A**. Juvenile frontlet (MYŞE PV-2504) in anterior view. **B**. Frontlet (MYŞE PV-2503) in anterior view. **C**. Opisthocranium (MYŞE PV-1182) in ventral view. **D**. Axis + 3rd cervical vertebra (MYŞE PV-2599) in dorsal view.

third lobe of m3 is relatively high and large, oval in occlusal view, and bears a convex entoconulid.

Remarks.—The finely rippled enamel, advanced p4 morphology, reduced premolars, build-up of cement on the molars, large third lobe of the m3, strong basal pillars, and weak development of the lingual stylids and ribs exclude this taxon from the Late Miocene Antilopini sensu stricto. Together with the inferred additional posterior fossa on P3, the distolingual widening of the lingual cone and the distolabial development of the posterior style on P2 and P3 are reminiscent of the considerably larger *Urmiatherium intermedium* Bohlin, 1935, *U. polaki* Rodler, 1889, and *Plesiaddax depereti* Bohlin, 1935. However, the Şerefköy-2 taxon differs from the large-sized Late Miocene "ovibovines", but resembles the smaller *U. rugosifrons* from Samos (Kostopoulos 2009a: 371), in the development of the third lobe on m3, as well as the weak buccolingual compression of the lower molars and the degree of fusion of their lobes. *U. rugosifrons* and the Şerefköy-2 species furthermore share a comparably reduced premolar row. However, the former species is still about 30–35% larger and characterised by less derived lower premolars.

Although the available data are not sufficient for definite conclusions, it is worth mentioning that a right upper tooth row from Muğla (MNHN TRQ 974) resembles the material from Şerefköy-2 in its size and premolar morphology. The molars of TQR 974 considerably differ from those of *Urmiatherium* and *Plesiaddax*, but resemble those of *Sinotragus wimani* Bohlin, 1935 from China (Bohlin 1935: pl. 16: 8, 9). Unfortunately, the lower dentition of *Si. wimani* is unknown, preventing a direct comparison with Şerefköy-2. TRQ 974 is accompanied by a frontlet from the same region (MNHN TRQ 973), which, based on its morphology and size, likely represents a female *Si. occidentalis* Geraads, Güleç, and Kaya, 2002. This species is well-documented in Muğla by

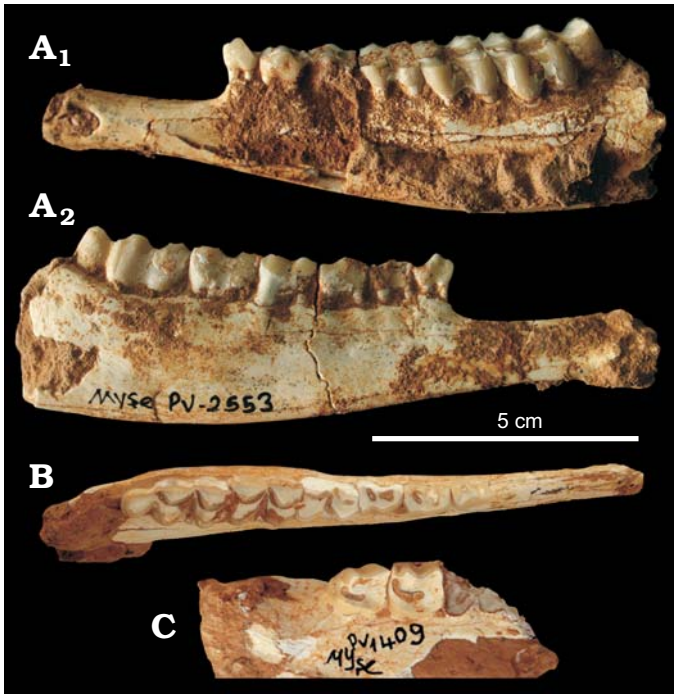

Fig. 14. The bovid artiodactyl cf. *Sinotragus* from Şerefköy-2 (Turkey), Late Turolian (Late Miocene). **A**. Left mandibular ramus (MYŞE PV-2553) in labial (A_1) and lingual (A_2) views. **B**. Right mandibular body (MYŞE PV-2567) in occlusal view. **C**. Left upper P2–P3 (MYŞE PV-1409) in occlusal view.

cranial, but not dental, elements (Geraads et al. 2002). Given the particular dental characters of TRQ 974, the similar size of TQR 974 and TRQ 973, and their common geographic provenance, we speculate that both specimens belong to *Si. occidentalis*. In addition, we tentatively refer the Şerefköy-2 specimens to *Sinotragus* based on their similar dental morphology.

Biochronology of Şerefköy-2

Kaya et al. (2012) suggested a Middle Turolian age for the Şerefköy-2 assemblage and stressed its structural similarity to the mammalian palaeocommunity from Samos. The results of the present study help to refine this biochronological assessment. Among the bovid recovered from Şerefköy-2, *Gazella capricornis* and *Palaeoryx pallasi* are the most widespread, ranging from the Balkans to Iran and the northern coast of the Black Sea. Their co-existence at Şerefköy-2 is strongly indicative of a Middle–Late Turolian age for this faunal assemblage, as is the presence of *Sporadotragus parvidens*. The latter is so far only known from Samos and Pikermi (Greece), although the genus occurs from the southern Balkans all the way to Afghanistan and possibly China and Mongolia (e.g., Geraads et al. 2006). *Urmiatherium rugosifrons* certainly occurs at Mytilinii-1A and most likely also at Q5 of Samos (Kostopoulos 2009a), indicating an age younger than 7.1 Ma (Koufos et al. 2009b). By contrast, *Skoufotragus schlosseri* is present at Akkaşdağı (<7.1 Ma; Karadenizli et al. 2005) and characterises the Final Bovid Assemblage of Samos (~7.0–6.8 Ma; Kostopoulos 2009a; Koufos et al. 2009b). The co-occurrence of *U. rugosifrons* and *Skoufotragus* cf. *Sk. schlosseri* at Şerefköy-2 thus places the latter close to the Middle–Late Turolian boundary (~6.8 Ma; e.g., Steininger 1999; Agusti et al. 2001).

Palaeobiogeographical and palaeoenvironmental analysis

Protoryxoid bovids represent more than 60% (more than 80% together with gazelles) of the Şerefköy-2 bovid community in terms of both the minimum number of individuals (n = 27) and the number of identifiable specimens (n = 102). In sharp contrast, boselaphines and spiral-horned antelopes, both of which are common in contemporaneous faunas of the sub-Paratethyan province, are absent from Şerefköy-2. Even though taphonomic and sampling biases may have exaggerated these results, the absence of these taxa indicates that they were at least rare in the local mammal community. On the other hand, the presence of *Urmiatherium rugosifrons*, so far only known from neighbouring Samos, and of a western Asian representative of *Sinotragus*, known mainly from the surroundings of Şerefköy (i.e., the Muğla-Yatağan Basin; e.g., Geraads et al. 2002), increase the local character of the Şerefköy-2 mammal assemblage.

In our genus-level correspondence analysis, the first three components (out of 15) account for 23.2%, 20.8%, and 14.1% of the inertia, respectively (Fig. 15A). Both in the first (axes 1 and 2; Fig. 15A) and the second (axes 1 and 3; not shown) plane, the continental Greek Turolian bovid associations are sharply distinguished in taxonomic composition and relative abundances from most Anatolian bovid assemblages (including Samos), whereas the Turkish assemblages of Mahmutgazi, Sivas and Akkaşdağı, and the Iranian fauna of Maragheh, occupy an intermediate position, rather close to the Greek bovid faunas (Fig. 15A). The primary polarizing taxa include *Paraoioceros, Plesiaddax, Protragelaphus, Nisidorcas, Majoreas*, and *Urmiatherium*. There is a clear, time-controlled taxonomic shift in the Greek bovid assemblages from Nikiti-2 (Early Turolian) to Dytiko (Late Turolian), with an increase of the magnitude of *Miotragocerus*, *Gazella*, and *Protragelaphus* against *Nisidorcas*, and *Tragoportax* (Fig. 15A).

In the east, the situation seems much more complicated than in continental Greece. The Middle Turolian bovid assemblages of Asia Minor, Mytilinii-1A, B, C, Mytilinii-3, Kemiklitepe-A, B, Kinik, and Şerefköy-2 form a distinct cluster, characterised by *Skoufotragus*, *Sporadotragus*, *Palaeoryx*, *Urmiatherium*, and *Paraoioceros*. The older (Early Turolian) but geographically close assemblages of Kemiklitepe-D and Mahmutgazi are separated from this group mainly because of the high percentages of *Criotherium*, *Majoreas*, *Oioceros*, and *Plesiaddax*. The central-eastern Anatolian bovid faunas

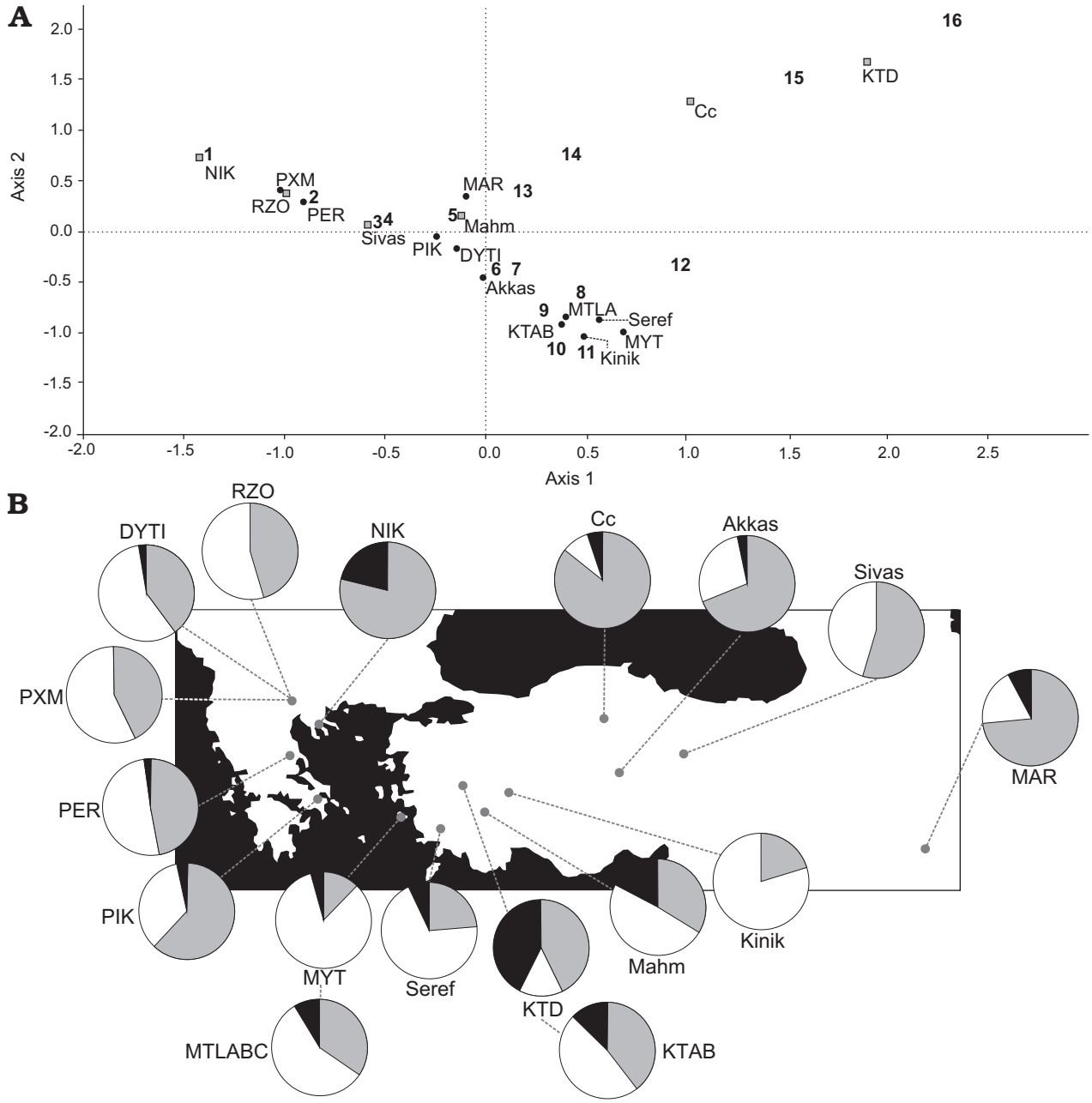

Fig. 15. Correspondence analysis of Turolian (Late Miocene) bovid associations from the sub-Paratethyan zoogeographic province, based on relative taxonomic abundances at the genus level (**A**) and relative size abundances at each site (**B**). See text for explanation, SOM 2 for details of the methodology, and SOM 1: Table 1 for the dataset. Analysed variables: 1, *Nisidorcas*; 2, *Tragoportax*; 3, *Prostrepsiceros*; 4, *Palaeoreas*; 5, *Protragelaphus*; 6, *Miotragocerus*; 7, *Gazella*; 8, *Urmiatherium*; 9, *Palaeoryx*; 10, *Paraoioceros*; 11, *Skoufotragus/Protoryx*; 12, *Sporadotragus*; 13, *Plesiaddax*; 14, *Oioceros*; 15, *Majoreas*; 16, *Criotherium*. Squares represent Early Turolian assemblages; circles represent Middle–Late Turolian assemblages. In the spectra of relative size abundances (pie charts) grey represents small (<50 kg), white medium, and black large-sized bovids (>150 kg). Abbreviations: Akkas, Akkaşdağı; Cc, Çorak-yerler; DYTI, Dytiko-1, 2, 3; KTAB, Kemiklitepe A, B; KTD, Kemiklitepe D; Mahm, Mahmutgazi; MAR, Maragheh (mainly levels MMTT7-13); MTLABC, Mytilinii-1A, B, C; MYT, Mytilinii-3; NIK, Nikiti-2; PER, Perivolaki; PIK, Pikermi; PXM, Prochoma; RZO, Ravin de Zouaves-5; Seref, Şerefköy-2.

exhibit a similar pattern, with the Early Turolian Çorak-yerler assemblage being separated from those of Sivas and Akkaşdağı (late Early and late Middle Turolian, respectively). The bovid assemblages of Çorak-yerler and Kemiklitepe-D are much more alike in their taxonomic structure than are the roughly contemporaneous faunas of continental Greece (Nikiti-2 and Ravin de Zouanes-5) (Fig. 15A). By contrast, Sivas and, to a lesser degree, Akkaşdağı, more closely resemble assemblages from continental Greece to the west and Maragheh to the east than contemporary faunas from Asia Minor.

In the correspondence analysis using broader taxonomic bins, the first two components (out of four) account for 51.8%, and 25.2% of the inertia, respectively (Fig. 16A). The results are similar to those of the genus-level analysis and show no major changes between the Early and mid-Late Tur-

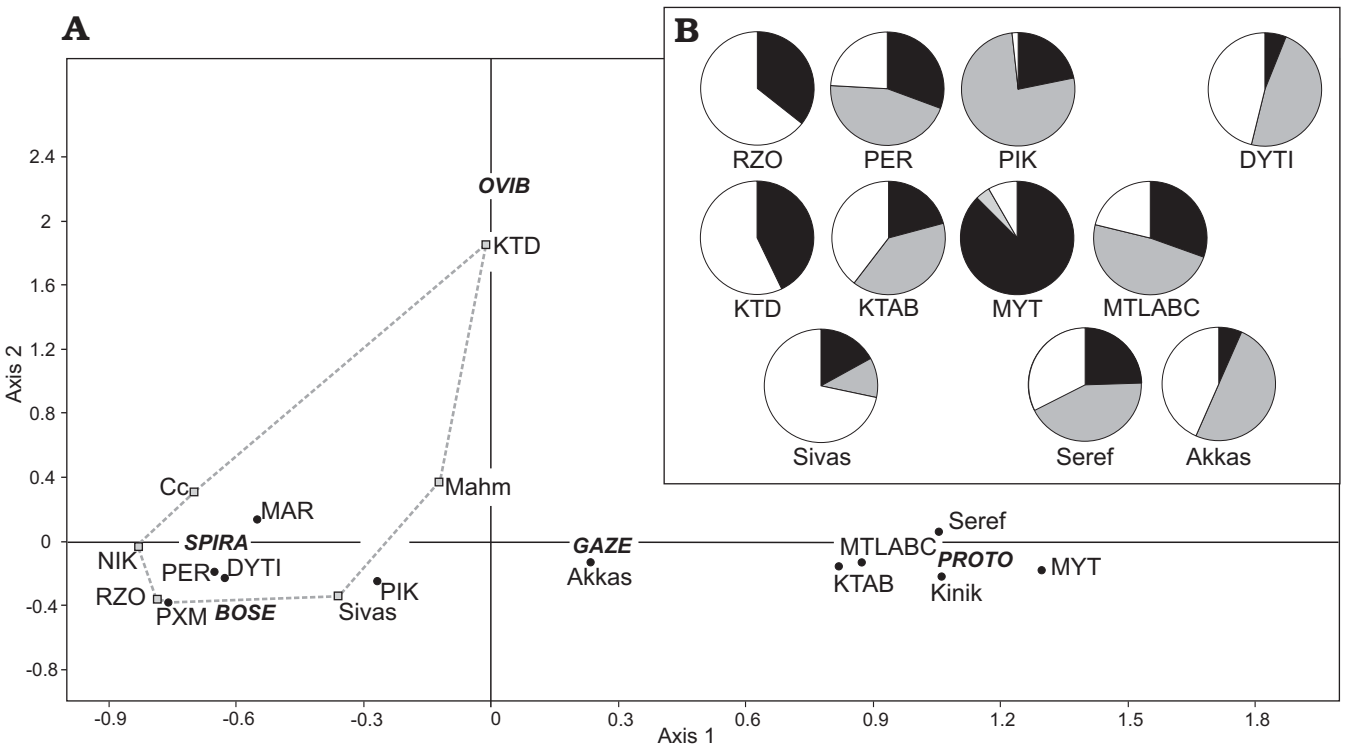

Fig. 16. Correspondence analysis of Turolian (Late Miocene) bovid associations from the sub-Paratethyan zoogeographic province based on taxonomic bins (**A**) and diet spectra of several local bovid associations based on dental wear patterns (**B**). See text for explanation, SOM 2 for details of the methodology, and SOM 1: Table 2 for the dataset. Abbreviations: Akkas, Akkaşdağı; Cc, Çorak-yerler; DYTI, Dytiko-1, 2, 3; KTAB, Kemiklitepe A, B; KTD, Kemiklitepe D; Mahm, Mahmutgazi; MAR, Maragheh (mainly levels MMTT7-13); MTLABC, Mytilinii-1A, B, C; MYT, Mytilinii-3; NIK, Nikiti-2; PER, Perivolaki; PIK, Pikermi; PXM, Prochoma; RZO, Ravin de Zouaves-5; Seref, Şerefköy-2. Dashed-line represents a convex hull of Early Turolian bovid assemblages; BOSE, GAZE, PROTO, OVIB, SPIRA, represent analysed variables (SOM 1: Table 2). Pie charts represent the spectra of feeding preferences: black, browsers; grey, mixed feeders; white, grazers.

olian assemblages from continental Greece, all of which are dominated by spiral-horned antelopes and boselaphines (Fig. 16A). The same taxa fare less well in contemporary Anatolia, where they and "ovibovines" are increasingly replaced by gazelles and protoryxoids. This trend is much sharper in the western part of the region; in central-eastern Anatolia, assemlages instead remain more similar to those of continental Greece and Iran (Fig. 16A).

Although based on a much more limited dataset lacking Turolian faunas from Greece, Bibi, and Güleç (2008: fig. 11) found a similar taxonomic trend in the Anatolian bovid assemblages, including the separation of Çorak-yerler and Kemiklitepe-D from the remaining assemblages. However, they also identified a cluster comprising Kemiklitepe-A, B and Sivas, despite their marked taxonomic differences (*Tragoportax* constitutes 41.5% at Sivas but is absent from KTAB; "*Pachytragus/Protoryx*" constitutes 3.8% at Sivas vs. 39.6% at KTAB; Bibi and Güleç 2008), size distribution and diet spectra (see below). This grouping thus seems rather improbable and probably stems from the inclusion of the Greek Vallesian assemblage of Nikiti-1. This may have resulted in the compression of the remaining faunas within multispace, as in de Bonis et al. (1994: fig. 4).

Faunal body size distributions generally support the results of the CFA (Fig. 15B). Thus, the Turolian faunas of continental Greece contain very few large taxa (<4%) and, with the exception of the mostly small (<50 kg) species constituting the earliest Turolian assemblage of Nikiti-2, show a balance between small and medium-sized forms (Fig. 15B). A similar pattern occurs in central-eastern Anatolia (Fig. 15B), although the dataset is much more restricted here. By contrast, large and small-sized bovids are balanced and predominate at Kemiklitepe-D, whereas from Mahmutgazi to Şerefköy-2 large taxa decline and medium-sized bovids increase considerably, with percentages reaching 80% in some cases (Fig. 15B).

The diet spectra of the assemblages compared here do not follow the regional pattern revealed by the CFA and size distribution analyses. Instead, they point to a general rise of mixed feeders at the expense of grazers in younger associations, as shown by comparisons of, for instance, KTD with KTAB and Şerefköy-2 in western Anatolia, Sivas with Akkaşdağı in eastern Anatolia, and Ravin de Zouaves-5 with Perivolaki, Pikermi, and Dytiko in Greece (Fig. 16B). In addition, several roughly contemporaneous faunas show similar diet spectra despite marked differences in their geographical location, taxonomic composition and size distribution (e.g., Nikiti-2 vs. Çorak-yerler, Dytiko vs. Akkaşdağı, and Pikermi vs. Kemiklitepe-A, B and Mytilinii-1A, B, C; Figs 15A, B, 16B).

Discussion and conclusions

As in the study by Bibi and Güleç (2008: 516), there is no straightforward correlation between the component axes arising from the taxonomy-based CFA and environmental trends, at least at a generalised Greco-Anatolian level. Instead, the age and geographical location of the sites, two parameters not directly involved in the analysis, seem to control much of the distribution of the data. Thus, in line with preliminary suggestions by Kostopoulos and Bernor (2011), our analysis revealed a "Greek" cluster and a "SW Anatolian" cluster, whereas the eastern Anatolian Turolian bovid assemblages possibly form a third group more closely related to Maragheh in Iran.

Like in continental Greece, the general increase of mixed feeders relative to grazers throughout the Turolian in eastern Anatolia is not accompanied by a major reorganization of the structure of the bovid community, with the exception of an increase in the number of protoryxoids. Instead, size ratios generally remain stable, with small taxa always contributing more than 50% (based on the number of identifiable specimens). During approximately the same time period, small taxa slightly decrease in number (by about 10%) in SW Anatolia, whereas medium-sized taxa considerably increase (by about 30%). Protoryxoids at least quadruple at the expense of boselaphines and "ovibovines", while the relative abundances of gazelles and spiral-horned antelopes remain stable at a moderate and low level, respectively.

These results generally agree with ungulate regional endemicity along the Greco-Iranian longitudinal axis, as suggested by Costeur (2009: fig. 4), and are fully compatible with the conclusions of de Bonis et al. (1994). The partial isolation of SW Anatolia from continental Greece was thoroughly discussed by Kostopoulos (2009b, and literature therein) and likely resulted from both the mid-Tortonian/Maeotian transgression into the Aegean domain and the latest Miocene invasion of the Paratethyan Sea. By contrast, the partial faunal isolation of SW Anatolia from adjacent regions to the east may be related to the broad Mio-Pliocene Central Anatolian lake system stretching between the Pontides in the north and the Taurides-Isparta Angle barrier in the south (e.g., Görür et al. 1995; Veen et al. 2009; Alçiçek 2010; Mehmet Cihat Alçiçek personal communication 2012).

Our study demonstrates that similar ecological signals need not necessarily imply identical size distributions or taxonomic content, even for roughly contemporaneous, neighbouring faunas. This implies that the faunal composition of herbivores at various points of a supposedly homogeneous biogeographic province may depend more on historical (i.e., phylogeographic) relationships and limitations than the type of vegetation cover. Assuming that the diet spectrum of a local herbivore assemblage directly reflects vegetational and/or climatic conditions, it therefore seems that local bovid communities adjust to the available habitat, rather than (or prior to) being reorganised by migratory movements and replacements.

Acknowledgements

We thank Tanju Kaya and Serdar Mayda (both Ege University, Izmir, Turkey), Robert Scott (Rutgers University, New Brunswick, New Jersey, USA), and Gildas Merceron (Poitiers University, France) for their help and support in the field and lab, and Mehmet Cihat Alçiçek (Pamukkale University, Denizli, Turkey) for helpful discussions on SW Anatolia geodynamics. Thanks are also due to Kaye Reed (Arizona State University, Tempe, USA), Denis Geraads (CNRS MNHN, Paris, France) and Felix G. Marx (University of Otago, New Zealand) for their fruitful comments and suggestions, as well as to Katerina Vasileiadou (Natural History Museum of the Petrified Forest of Lesvos, Greece) for linguistic improvements. This work was supported by a "Wenner-Gren International Collaborative Research Grant" ("Environmental Dynamics of Western Eurasian Hominids during the Late Miocene"; PI: Robert Scott), as well as grants from Ege University (TTM/001/2008 and TTM/001/2010) and the Scientific and Technological Research Council of Turkey (108Y047).

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