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ARTICLE

LATE MIOCENE 'OVIBOVIN' BOVIDS (MAMMALIA, BOVIDAE) FROM ÇORAKYERLER, TURKEY

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ABSTRACT—Fossil 'ovibovin' bovids are described from the Upper Miocene of Çorakyerler (north-central Anatolia). Two taxa have been recognized: the predominant *Criotherium argalioides*, known by several craniodental remains, and the less common *Hezhengia*? cf. *inundata*, documented by a few dentitions. A review of *C. argalioides* records from Samos and Kemiklitepe D and a thorough comparison with the Çorakyerler sample provides new data on the morphological and metric variability of this taxon, as well as its chronological and geographic range. *Hezhengia*? cf. *inundata* from Çorakyerler reveals important similarities with the Garkin (Turkey) taxon, which, in contrast to previous studies, we find more similar to the Chinese *Hezhengia* than to the Chinese *Plesiaddax* as originally suggested. The same is true for "*Plesiaddax*" *simplex* from Kayadibi (Turkey), which is referred to as *Hezhengia*? *simplex*. The co-occurrence of two 'ovibovin' bovids of similar size in the same assemblage was previously suspected but never before documented.

SUPPLEMENTARY FILES–Supplementary files are available for this article for free at www.tandfonline.com/UJVP.

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INTRODUCTION

The Late Miocene is a period of major bovid (Family Bovidae) diversity in Eurasia (Bibi et al., 2009). Dozens of genera and species have been described from China to Spain, including a great variety of cranial and horn core morphotypes (e.g., Agustí & Antón, 2002; Gentry et al., 1999; Kostopoulos, 2022; Zhang et al., 2002). Among them, there is a group of odd-looking medium- to large-sized taxa of varied horn core morphology, with a thickened basioccipital bearing accessory articular facets for the atlas, and other craniodental features that roughly recall those of extant muskox (*Ovibos moschatus* Zimmermann, 1780), and its Pleistocene relatives, and for which the names Ovibovinae or Ovibovini have been used (Gil, 1872; Simpson 1945; but see Hassanin et al. [2012] for an updated concept of Ovibovina). Late Miocene fossil taxa with similar cranial characteristics continue to be commonly referred to as such ovibovin(e) (Bohlin, 1937; Bouvrain & Bonis, 1984; Gentry, 1996; Shi & Deng, 2020), although their phylogenetic relationships and tribal affiliations are still unresolved (e.g., Bouvrain & Bonis, 1984; Geraads & Spassov, 2008; Hou et al., 2023; Kostopoulos, 2014; Shi & Deng, 2020; Wang et al., 2022), and a complete cladistic analysis is pending. For most scholars they represent a paraphyletic or polyphyletic group of stem Caprini (e.g., Shi & Deng, 2020). Without implying any phylogenetic or systematic meaning to it, we here use the term 'ovibovin' to indicate this artificial ensemble of Late Miocene caprin bovids.

In Turkey, 'ovibovin' bovids are known from several Upper Miocene sites (Fig. 1): a small *Urmiatherium* Rodler, 1889 (= *Parurmiatherium* Sickenberg, 1932 but see also discussion in Shi et al., 2016) is recorded in the middle Turolian faunas of Salihpasalar and Şerefköy-2 (Kaya et al., 2012; Kostopoulos & Karakütük 2015); *Plesiaddax* Schlosser, 1903, is reported from the early Turolian faunas of Kayadibi (*Plesiaddax simplex* Köhler, 1987) and Garkin (*Plesiaddax inundatus* Bosscha Erdbrink, 1978), as well as from Mahmutgazi (Köhler, 1987); *Criotherium* Forsyth Major, 1891, is certainly known from the early Turolian fauna of Kemiklitepe D (Bouvrain, 1994) and possibly from some Vallesian Middle Sinap localities (Gentry, 2003).

The north-central Anatolian primate-bearing Çorakyerler fossil site (Fig. 1) is placed in the Tüğlu Formation of the Çankırı basin (Kaya et al., 2016; Sevim et al., 2001; Sickenberg, 1975). Köhler (1987) ascribed a few isolated teeth from Çorakyerler to *Plesiaddax*, whereas Geraads (2013) referred from the same site two mandibular fragments and a metacarpal to "*Plesiaddax*" *inundatus* and an incomplete horn core to *Criotherium*? sp. Geraads' records from Çorakyerler were based on material collected between 1992 and 2001 (collection numbers up to ÇO 450). Systematic paleontological excavations between 2001–2022 by one of us (ASE) significantly increased the fossil sample. Today, Çorakyerler is extremely rich in bovid remains, including several tens of crania, and hundreds

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FIGURE 1. Upper Miocene fossiliferous sites of Anatolia and surroundings with 'ovibovin' occurrences. **1**, Çorakyerler; **2**, Sinap; **3**, Pinaryaka; **4**, Garkin; **5**, Kemiklitepe D; **6**, Mahmutgazi; **7**, Kayadibi; **8**, Salihpasalar; **9**, Şerefköy-2; **10**, Samos; **11**, Fourka-Kassandra; **12**, Ravin de la Pluie; **13**, Bashibos; **14**, Kalimatsi; **15**, Taraklia. *Criotherium* has been recorded in 1, 2, 3, 5, 10, 13, 14; *Urmiatherium* has been recorded in 8, 9, 10, 11; *Mesembriacerus* has been recorded in 12, 13; "*Plesiaddax*" (here referred to as *Hezhengia*?) has been recorded in 1, 4, 6, 7. Google Earth pro © 2022 Google LLC; map data SIO, NOAA, US Navy, NGA, GEBCO; Image landsat/Copernicus; earth.google.com/web; retrieved 2023.

of toothrows and postcranials (e.g., Kostopoulos et al., 2020, 2021 and unpublished data). Fieldwork and fossil preparation is still ongoing, and although accurate quantitative data are not yet available, it appears that 'ovibovin' bovids make up a significant proportion of the total artiodactyl assemblage at this site. Here we describe available craniodental material recovered up to 2021 and provide a partial review of the contemporaneous Turkish fossil record.

MATERIAL AND METHODS

The local geology and stratigraphy of the Çorakyerler fossil site were described by Sickenberg (1975) and Kaymakçi et al. (2001), and recently reviewed by Kaya et al. (2016). Becker-Platen et al. (1975), Köhler (1987), Ünay et al. (2006), Güleç et al. (2007), Geraads (2013), and Kaya et al. (2016), discussed the age of the Çorakyerler mammal fauna, with estimations ranging from ca. 9 Ma to around 7.5 Ma (late Vallesian to middle Turolian European Mammal Ages; Late Tortonian, Late Miocene; summarized in Kostopoulos et al. [2020:629]; see also Kaya et al. [2016:figs. 1, 3]). We here follow Kostopoulos et al. (2020) in suggesting an earliest Turolian age, about 8.9 Ma, for the Çorakyerler mammal fauna. The material described here is housed in the Çankırı Museum, Turkey, and bears the locality prefix ÇO. We limit our descriptions and comparisons to cranial and dental material. Although bovid postcranials are abundant at Çorakyerler, the presence of several species of similar size and the absence of sufficient comparative information in the published literature means these require an independent, in-depth analysis.

Original comparisons include *Criotherium* cranial and dentognathic material from Samos Island in Greece (Fig. 1), and Kemiklitepe D, Turkey (MTA.Ankara), and part of the "*Plesiaddax*" sample from Garkin and other Turkish sites (BGR.Hannover). The remaining comparative data are from the literature.

Although the Samos sample of *Criotherium* is the richest known so far, its study remains fragmentary as specimens have been dispersed in various museums around the world. More than 12 partial or almost complete crania are currently recorded from Samos (AMNH: 2; NHMUK: 4; MGL: 2; PMM: 1; HLMD: 1; PIM: 1; CCEC.Lyon: 1; BSPG: 1; Fig. S1), while some others are apparently or permanently lost (as for example the three complete crania in BSPG discussed by Schlosser, 1904:23; pl. IV, figs. 1, 3). Complete palates and partial upper and lower dentitions increase considerably the total number of *Criotherium* individuals recovered from Samos (e.g., Pilgrim & Hopwood, 1928; Solounias, 1981). And, although the old Samos collections usually lack precise stratigraphic information, available data on topographic provenance of the *Criotherium* finds within the fossiliferous Mytilinii Basin, and macroscopic examination and the fossils and their matrix show that the majority—if not all—come from the lower fossiliferous horizons, indicating an early Turolian age (8.7–7.5 Ma; Late Tortonian; Late Miocene) (Kostopoulos, 2009:376). Based on the material from Samos and Kemiklitepe D, we provide here a review of the basic cranial and dentognathic features of *C. argalioides* as an addition to the existing body of knowledge (Bohlin, 1935a; Pilgrim & Hopwood, 1928; Schlosser, 1904).

Cranial and horn core terminology used for descriptions and comparisons follow Gentry (1971), Kostopoulos (2009), and Shi et al. (2014:figs. 3, 4). Horncores are considered as heteronymously twisted when the right horncore follows an anticlockwise torsion from the bottom up. Dental terminology follows Gentry et al. (1999: fig. 23.1). Upper case letters (P, M, PM) are for upper teeth and toothrows; lower case letters (p, m, pm) indicate lower teeth and toothrows. A 'd' before premolars indicates deciduous teeth. All linear measurements are in mm; angles are in degrees (°).

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **BGR.Hannover**, Bundesanstalt für Geowisenschaften und Rohstoffe, Hannover, Germany; **BSPG**, Bayerischen Staatssammlung für Paläontologie und Geologie, München, Munich, Germany; **CCEC.Lyon**, Centre de Conservation et d'Etude des Collections, Lyon, France; **HLMD**, Hessishes Landesmuseum Darmstadt, Darmstadt, Germany; **MGL**, Musée Cantonal de Géologie, Lausanne, Switzerland; **MNHN.P**, Musée national d'Histoire naturelle, Paris, France; **MTA.Ankara**, Mineral Research and Exploration Natural History Museum, Ankara, Turkey **NHMUK**, Natural History Museum, London, U.K.; **PIM**, Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität Münster, Münster, Germany.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Family BOVIDAE Gray, 1821
Genus *CRIOTHERIUM* Forsyth Major, 1891

Emended Genus Diagnosis—A bovid of large size. Horncores short and stout, moderately divergent, tightly spiraled with a strong heteronymous torsion, a strong postero-lateral keel, and at least a weaker antero-medial one, inserted behind the orbits, their caudal side not very far from the occipital. Frontal bone extensively hollowed, elevated far above the orbits and much bent, with a post-cornual part in the same plane as the parietal. Ethmoidal fissure closed; maxillary bone in short direct contact with the frontal. Braincase quite short and broad, dorsal part almost in the same plane as the occipital. Occipital low and broad. Occipital condyles with articular surfaces extending far anteriorly onto the posterior tuberosities of the basioccipital, and supplementary articulations medial to the paroccipital processes. Cranial flexure weak (basicranium making a wide angle with the palate). No ethmoidal fissure. Infra-orbital foramen above P2 (modified from Geraads & Spassov, 2008).

Differential Diagnosis—*Criotherium* differs from all similar sized Late Miocene 'ovibovin' taxa in the strongly heteronymously twisted and keeled horn cores. It additionally differs from *Hezhengia* in the slightly longer cranium with relatively narrower and deeper opisthocranium, having relatively larger condyles but equally strong posterior and anterior tuberosities of the basioccipital and relatively shorter nasals and larger toothrow. *Criotherium* differs from *Urmiatherium* in the longer braincase, relatively deeper occiput, larger condyles, significantly longer nasals, and greater premolar row to molar row ratio. It differs from *Plesiaddax* in the longer cranium with larger condyles, relatively shorter nasals, and slightly longer toothrow with longer premolar row compared with the molar row. *Criotherium* differs from *Shaanxispira* in the slightly larger cranium, stronger posterior tuberosities of the basioccipital and larger toothrow.

Type Species—*Criotherium argalioides* Forsyth Major, 1891.

Lectotype— NHMUK M4199, cranium; designated by Pilgrim and Hopwood (1928)

Type Locality—Samos, Mytilinii Basin, unknown level/site.

Type Species Diagnosis—as in Geraads and Spassov (2008).

CRIOTHERIUM ARGALIODES Forsyth Major, 1891

Material—43 cranial and dentognathic specimens. A complete list of the studied material along with basic taphonomic observations is provided in Table S1, Supplementary File 1.

Description

Horn cores—In cranial specimens with at least one fairly complete horn core (ÇO 1045, ÇO 2075, ÇO 2421; Figs. 2, 3) its length maximally reaches the half of the cranium estimated total basal length. The horn cores are robust at the base and gently tapering upwards. They are tightly twisted heteronymously on their axis (1–1.5 coils), rather straight and parallel to weakly divergent each other in their proximal 2/3 but slightly more in their apical 1/3 (Figs. 2B, D, E, 3A, E). They are inserted well behind the orbits on the dorsal surface of the elevated frontals and direct almost vertically upwards (in lateral view; Figs. 2A, 3A). They bear a very strong, flange-like keel descending laterally, just behind the orbits, where it appears as a thick, rough zone (Figs. 2A, D, E, 3A); after completing one coil the keel diminishes rather abruptly. A second much less developed but still sharp keel descending postero-medially is also present, sometimes expressed as a furrow with crest-like edges (Fig. 3A). The basal horn core cross section is fairly rounded to squarish, becoming elongated elliptic (flattened) towards the apexes.

Cranium—In dorsal view the cranium outlines an isosceles triangle with its basal side (occipital) less than half to 1/3 the length of the lateral ones (Figs. 2D, 3C). The craniofacial flexion is relatively weak (145–155°). The frontals are large, highly elevated, strongly flexed (70–90°) above the orbits and hollowed below the horn cores; a large chamber at least is recorded behind the orbits. The pedicles are absent because the horn cores extend onto the frontal bones. The interfrontal suture is open in all the specimens (apart from ÇO 491, see below) and ridge like. The fronto-parietal suture is open 'Y" shaped. The supraorbital foramina are small, placed well in front of the horn cores, not sunken into pits and proceed rostrally into short, shallow furrows.

The orbits are not protruding laterally (Figs. 2D, 3C). The anterior margin of the orbit is placed behind the M3 (from several mm to a couple of cm). The postorbital bar is thick but short (Fig. 2A). The lower orbital border is shallow and continues

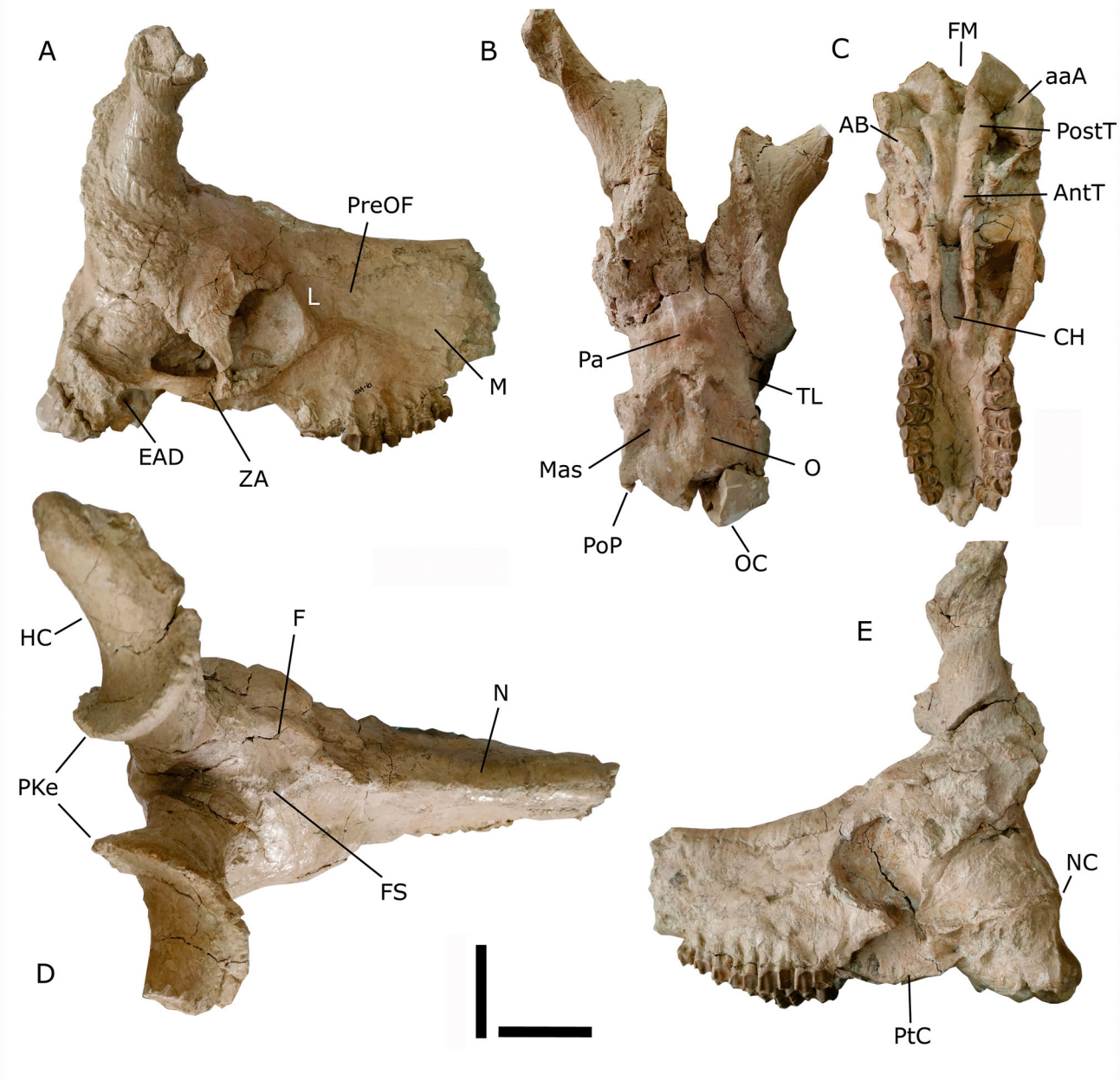


FIGURE 2. The cranium ÇO 1045 of *Criotherium argalioides* from Çorakyerler, Turkey in **A**, right lateral, **B**, posterior, **C**, ventral, **D**, dorsal, and **E**, left lateral views. **Abbreviations**: **aaA**, accessory articulation for atlas; **AB**, auditory bulla; **AntT**, anterior tuberosity of basioccipital (= pharyngeal tuberosity); **CH**, choanae; **EAD**, external auditory duct; **F**, frontal; **FM**, foramen magnum; **FS**, frontal suture; **HC**, horncore; **L**, lachrymal; **M**, maxilla; **Mas**, mastoid exposure; **N**, nasal; **NC**, nuchal crest; **O**, occipital; **OC**, occipital condyle; **Pa**, parietal; **PKe**, posterior keel of the horncore; **PoP**, paroccipital process; **PostT**, posterior tuberosity of basioccipital; **PtC**, pterygoid; **PreOF**, preorbital fossa; **TL**, temporal line; **ZA**, zygomatic arch.- Scale bars equal 5 cm.

rostrally by a well-developed facial crest reaching the level above the middle of M2.

The face is high and narrows significantly toward the rostrum (Fig. 3A, B). The nasals are thick, long (from above the posterior lobe of M3 to well in front of P2) and in lateral view they appear slightly concave caudally to smoothly convex rostrally, running almost parallel to the alveolar level (Fig. 3A, B). They are broader posteriorly and pointed towards the rostrum. Both the lachrymal and jugal extend forwards as far as above the level of the posterior lobe of M2, with the ventral part of the bilobed jugal retracted below the orbit. The lachrymal fossa is clear but shallow (Figs. 2A; 3A, B). The ethmoidal fissure is closed; the maxillary bone has a short direct contact with the frontal (ÇO 1045). The zygomatic arches are short. The choanae opens about 20 mm behind the M3 and more caudally than the lateral indentations (Figs. 2C, 3D). The pterygopalatine crest forms a very open angle (Fig. 2E). The anteriormost part of the snout (premaxillary) is pinched (ÇO 1316, 2075; Fig. 2B, C). The premaxillary does not contact the nasal. The infraorbital foramen is small and close above the P2.

The parietal is placed on the same level with the occipital (180°; apart from ÇO 491, see below) (Figs. 2A, E, 3A, B). The occipital is flattened with a blunt external occipital crest separating two elongated and rather shallow ligament depressions



FIGURE 3. Crania of *Criotherium argalioides* from Çorakyerler, Turkey. Cranium ÇO 2421 in **A**, left lateral view, **B**, cranium ÇO 2075 in right lateral, **C**, dorsal, **E**, ventral views, **D**, partial cranium ÇO 842 in posterodorsal view, and possible female partial cranium ÇO 491 in **F**, ventral, and **G**, dorsal views. Scale bars equal: 5 cm.

(Fig. 2B). The nuchal crest is not thickened or projecting (Figs. 2E, 3B). The overall contour of the occipital face is hexagonal to semi-elliptic. The mastoids are large and face mostly laterally. The occipital condyles are large and not distinguished from the occipital in caudal view.

The basioccipital is oblong with a well-defined furrow running along its length (Figs. 2C, 3D). The posterior tuberosities are strong, slightly diverging from the parasagittal plane. Their posterior surfaces form stop facets for the atlas (Fig. 2C). The anterior tuberosities are large, oval shaped and parallel to the sagittal plane. Additional stop facets for the atlas exist on the medio-ventral surfaces of the large pyramidal paroccipital processes (Fig. 2C). The foramen oval is rounded (6–7 mm), opens in front of the anterior tuberosities of the basioccipital and faces mostly ventrally. The auditory bulla is rather small compared with the size of the cranium. In ventral view it has a subtriangular outline with flattened rostrolateral side; its major axis forms a ~40° angle with the mid-sagittal plane (n = 2). Basic cranial measurements are provided in Table S2, Supplementary File 1.

The partial cranium ÇO 491 (Fig. 3F, G) preserves the braincase, and part of the frontals; it is attached with the palate of a young-adult (M3 just erupting) and possibly the same individual, which is however displaced and twisted, so the molars face rostrally. This cranium shares with the previously described ones a similar basioccipital, though with less developed anterior and less projecting posterior tuberosities and similar occipital condyles that do not distinguish from the occipital level (Fig. 3F). Although severely deformed and damaged, the occipital is not on the same level with the parietal (occipitoparietal angle

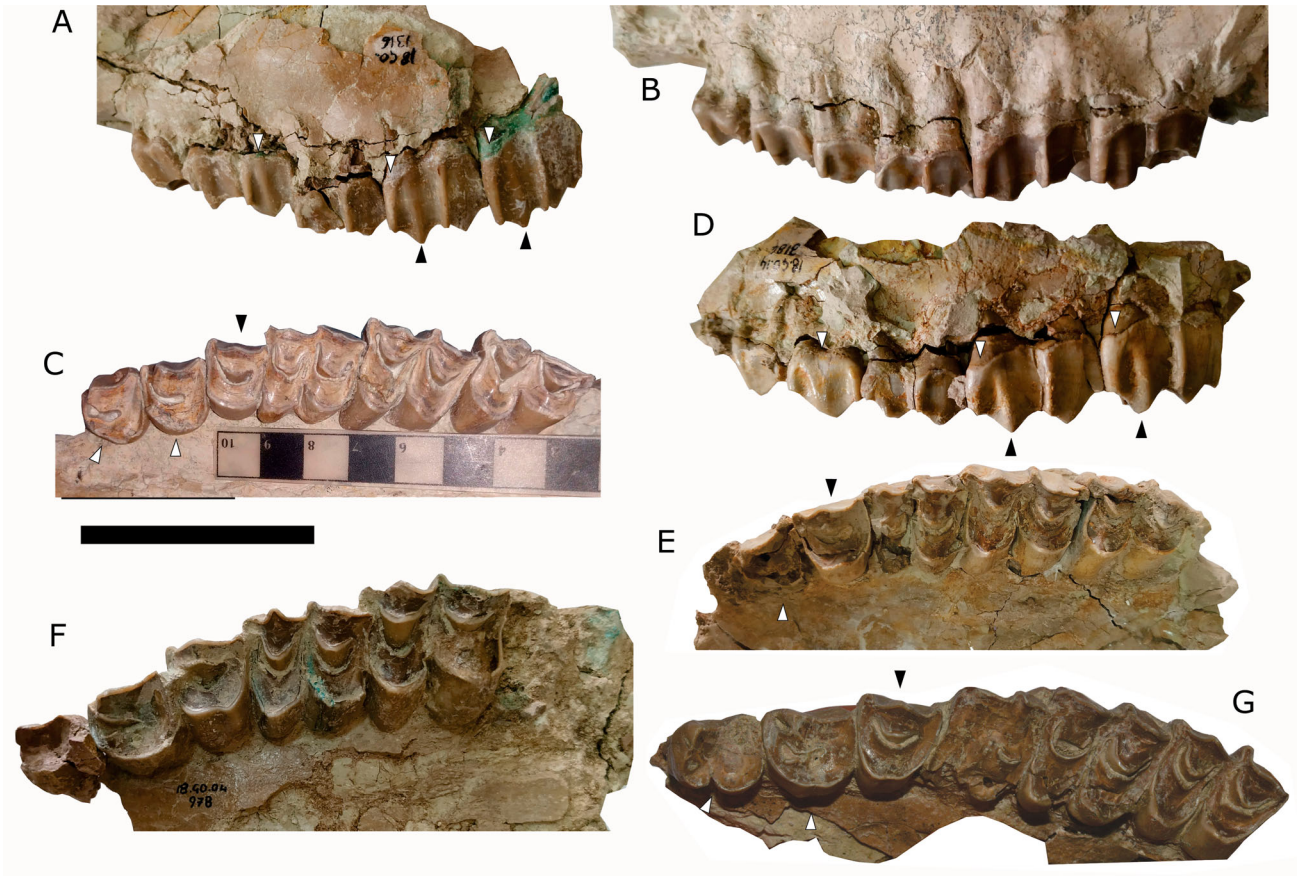


FIGURE 4. Upper toothrows of *Criotherium argalioides* (**A**, **B**, and **C**) and *Hezhengia*? cf. *inundata* (**D**, **E**, **F**, and **G**) from Çorakyerler, Turkey. **A**, upper left toothrow of young-adult ÇO 1316 in lateral view, **B**, upper left toothrow of adult-old ÇO 1045 in lateral and **C**, occlusal views, **D**, upper left toothrow of the palate ÇO 3184 in lateral and **E**, occlusal views, **F**, upper left toothrow of the palate ÇO 978 in occlusal view, and **G**, upper left toothrow ÇO 822 in occlusal view. Arrowheads indicate basic morphological differences between the two taxa discussed in the text. Scale bar equals 5 cm.

~150°) and the craniofacial angle is smoother. The frontals are large again but not elevated nor hollowed and the interfrontal suture is thinner and slightly pinched (Fig. 3G). The frontoparietal suture is of similar shape with that in the remaining crania but the parietals seem to occupy a slightly larger part on the dorsal cranial roof. The left best-preserved side of the orbital roof preserves maximally the basal 2 cm of the caudo-medial side of the horn core, on which there is no evidence of keels or intense torsion. The basal cross-section of the horn core seem to be sub-rounded to oval shaped.

Dentition—The general morphological features of both upper and lower teeth match fairly well those of *C. argalioides* from Samos and Kemiklitepe D (see below) and there is no need to repeat them here again in detail (Figs. 4A–C, 5E–I, L); we focus on some less well-known characters and the frequency of occurrence of some secondary features instead. Basic dental measurements are provided in Tables S3, S4, Supplementary File 1.

Lingually and between the lobes, all but one M1 (n = 10) exhibit a weak cingulum that in two cases forms a very low basal pillar. Half of the M2 (n = 9) and M3 (n = 8) show an even less developed cingulum constricted between the lobes. A central islet is commonly present on M1 (45%) and M2 (55%) in mid-wear stage. Half of the recorded M1 and M3 show a weak hypoconal spur, also present in two out of eight M2. The upper premolar to molar length ratio ranges from 58–65% (n = 5).

No complete mandible is preserved apart from that of the skull ÇO 2075 (Fig. 5I, L). The horizontal ramus is moderately shallow (height below p2: 26.0–27.5 mm, average: 27 mm, n = 3; height below p4–m1: 35.0–40.0 mm, average: 37.0 mm, n = 4; height behind m3: ~52–54 mm, n = 2). The ascending ramus starts rising a couple of centimeters behind the m3 and the angle between its anterior edge and the alveolar level is about 120° (Fig. 5L). The angular process of the mandible is rather strongly projecting caudally.

The lower canine is shorter than i3, which in turn is shorter than i2, which is as long or slightly shorter than i1. The occlusal width of the canine is smaller than that of i3 and significantly smaller than those of i1, i2, having a sub-square occlusal outline (Fig. 5I). Both the p3 and p4 have a strong paraconid well-separated from the parastylid at the upper third of the crown; on p4 it slightly directs distally (Fig. 5E, G). A small knob-like stylid closes the anterior valley (between the paraconid and the metaconid) lingually on 30% of the p4s (n = 10) but only once on p3 (n = 9). On ÇO 2075 a short knob-like ectostylid can be seen only between the last two lobes of m3 (Fig. 5L) and only on m1 of ÇO 2754 but the rest of the dentitions (n = 9) show a clear thin ectostylid on m1 that decreases in size towards the m3 (Fig. 5F). Dentitions with ectostylid on all molars appear slightly longer than the others, though sample size is too low to indicate a clear bimodality. The lower premolar to molar length ratio ranges from 51% to 60% (mean = 57%; n = 5).

Comparison and Remarks

The Samos-west Anatolian *Criotherium* Sample—Schlosser (1904) based on the Munich sample, and later Pilgrim and

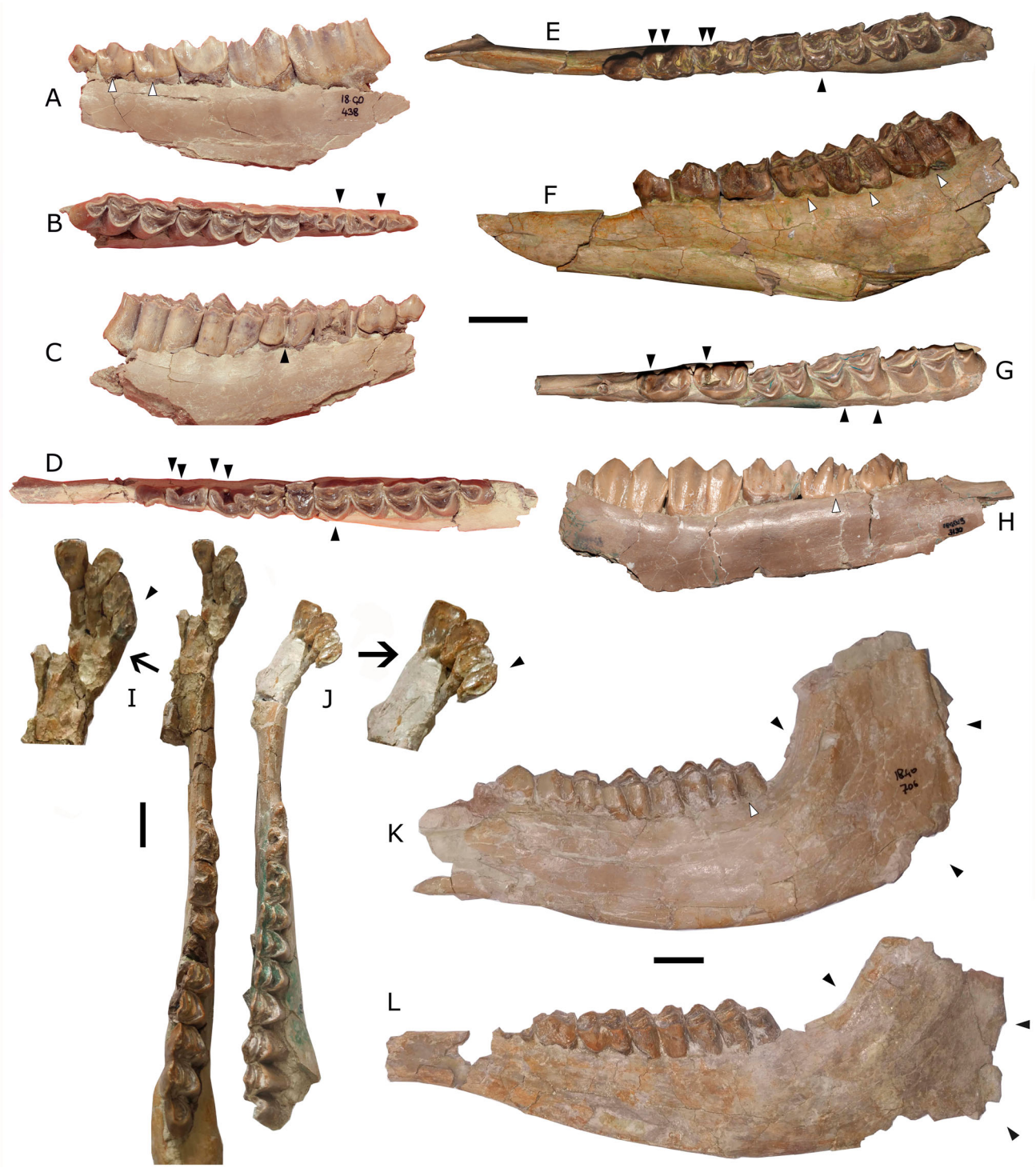


FIGURE 5. Mandibles and lower toothrows of *Hezhengia*? cf. *inundata* (**A**—**D**, **J** and **K**) and *Criotherium argalioides* (**E**—**I**, and **L**) from Çorakyerler, Turkey. Right lower toothrow ÇO 438 in **A**, lingual, **B**, occlusal, **C**, labial views, **D**, partial mandible with left toothrow ÇO 846 in occlusal view, **E**, partial mandible with left toothrow ÇO 3204 in occlusal and **F**, labial views, **G**, left lower toothrow ÇO 3130 in occlusal and **H**, lingual views, **I**, right mandibular ramus ÇO 2075 in occlusal view, **J**, left mandibular ramus ÇO 707 in occlusal view, **K**, left mandibular ramus ÇO 706 in labial view, and **L**, left mandibular ramus ÇO 2075 in labial view. Arrowheads indicate basic morphological differences between the two taxa discussed in the text. Scale bars equal 2 cm.

Hopwood (1928) based on the London collection, provided detailed descriptions of the most important cranial and dental features of *C. argalioides* from Samos. As stated by the latter authors: "Three things distinguish the skull when regarded as a whole. These are the long, straight, high, and narrow muzzle; the almost disproportionately small zygomatic arches and post-orbital bars, both of which are unusually close to the long axis of the skull; and, lastly, the short and strongly twisted horn cores placed right at the back of the head, immediately above the vertical occiput." Bohlin (1935a) provided additional

remarks based on the Lausanne, London and Munich material. Gentry (1971) and Solounias (1981) briefly discussed the Samian species and later Bouvrain (1994) described additional material from the nearby Kemiklitepe D site, western Turkey. Much more recently, Geraads and Spassov (2008) amended the genus and species diagnoses and established a new species from Kalimatsi, Bulgaria (Fig. 1), *Criotherium nikolovi* Geraads and Spassov, 2008.

The structure of the basioccipital is remarkably stable across the different Samos-west Anatolian specimens that preserve this area in good condition (n = 8) and follows descriptions by Schlosser (1904) and Pilgrim and Hopwood (1928) (Fig. S1G, J, Supplementary File 2). In all cases the posterior tuberosities are divided almost symmetrically by a well-developed crest into an anterior and a posterior sector; the latter shaped like caudal (n = 5)/ventrocaudal (n = 3) additional articular facets for the atlas. The crests themselves form a ~50–55° with the mid-sagittal plane (n = 7). Five crania at least (HLMD SS200, AMNH22802, NHMUK M4200, MGL S58, MTA.Ankara KTD-6) show at the base of the paroccipital processes large additional articular facets for the atlas. As already mentioned by previous authors, the paroccipital processes are robust and pyramidal shaped; although often broken and rounded off, it seems that they extend well below the condylar basal level (MTA.Ankara KTD-6, AMNH22802; Fig. S1H, Supplementary File 2). The auditory bullae were described by Schlosser (1904) as bean-shaped and small compared with the basioccipital, whereas Pilgrim and Hopwood (1928) indicated them as moderately inflated wedge-shaped. We assume that the latter description is closer to reality, at least as evidenced by MGL S58 (Fig. S1G), HLMD SS200, CCEC.Lyon PK61, and MNHN.P KTD-6 specimens, where the auditory capsule appears subtriangular in ventral view with a flattened rostrolateral side and a well-curved posterior side and pointed ventrally. The major rostrolateral axis of the auditory bulla forms a ~40° angle with the sagittal plane (n = 3).

The occipital face has a semi-circular overall contour (BSPG 1899VII22, MGL S58, HDML SS200, NHMUK M4201; Fig. S1A, D, F, Supplementary File 2) but is rather more compressed laterally (semi-oval) in MNHN.P KTD-6 and AMNH22802. The occipital condyles are large, 1.3 times broader than the transverse diameter of the foramen magnum (n = 4).

The nasals are almost never preserved entirely, apart from AMNH22802 (Fig. S1H, Supplementary File 2) and NHMUK M4200. As described by Pilgrim and Hopwood (1928) they are bluntly pointed anteriorly and broaden significantly at the level of the anterior margins of the lachrymal. Their length is about 1.4 longer than the toothrow itself (n = 2), and about 60–65% of the frontal length (along the mid-sagittal plane; n = 2). The lateral profile of the cranium becomes from flat rostrally to slightly concave in front of the orbits, to weakly convex toward the horn bases (Fig. S1C, E, H, Supplementary File 2). As shown by several specimens partially crushed below the horns, the frontals are heavily pneumatized with large sinuses occupying the lateral area above the orbits, but without extending into the horn core itself. As observed by Pilgrim and Hopwood (1928), Bohlin (1935a), and Bouvrain (1994) in all crania the interfrontal suture is open and raised as a ridge between the horn cores (Fig. S1B, H, Supplementary File 2); in front of them it widens significantly and complicates forming a wide blunt bulge above the orbits (best seen in AMNH22802); the depressions created on either side communicate directly with the shallow lachrymal fossae (Fig. S1B, H, Supplementary File 2). Further back the interfrontal suture continues as a ridge.

The lachrymal fossa occupies the whole facial part of the lachrymal bone and the upper lobe of the bilobed jugal (NHMUK M4199, NHMUK M4201, AMNH22802). It is delimited ventrally by a smooth facial crest not extending farther forward than the M1/M2 boundary. The lachrymal bone is quadrangular in shape, with its anteriormost margin above the back lobe of M2. The ethmoidal fissure is closed as evidenced by all the crania preserving this part of the face (n = 8). In fact, three of the crania (NHMUK M4199, NHMUK 4201, AMNH22802) show that the maxillary bone comes to a short direct contact with the frontal separating completely the nasal from the lachrymal (Fig. S1I, Supplementary File 2). Bouvrain (1994) observed the same feature in the MTA.Ankara KTD-6 cranium. In lateral view the premaxillary bones are elongated teardrop shaped and do not contact the nasals (AMNH22802, NHMUK M4200; Fig. S1H, Supplementary File 2).

Most basic features of the horn cores and their insertion on the cranium are already provided by previous authors (Schlosser, 1904; Pilgrim & Hopwood, 1928; Bohlin, 1935a). However, it should be stressed that although generally horn cores are reported as very short, in most crania (PIM 15, NHMUK M4200, MGL S71, AMNH22802, CCEC.Lyon PK61, MTA.Ankara KTD-6) they lack their upper part and often their surface is eroded, losing or reducing many morphological features (Fig. S1, Supplementary File 2). Although all crania (except NHMUK M4200) show an upstanding horn core position well behind the orbit, the horn cores appear straight in the cranium illustrated by Schosser (1904:pl. IV, fig. 3), CCEC.Lyon PIK61, HLMD SS200, and AMNH 10743 (Fig. S1A, C, D, Supplementary File 2), but with a clear forward curvature in NHMUK M4201, AMNH22802, and possibly PIM15 and MGL S71 (Fig. S1E, H, Supplementary File 2). In the specimen HLMD SS200 in which the horn core is best preserved, its length is almost double the distance from occipital protuberance to the anterior edge of the orbit (Fig. S1A–C, Supplementary File 2). In the same specimen the horn core twisting covers almost two complete coils (Fig. S1A–C, Supplementary File 2). Apart from the sharp posterior keel descending posterolaterally to laterally recognized more or less in all specimens (see also Bohlin, 1935a for details; Fig. S1A, C, D, F, Supplementary File 2), 1–3 secondary and much less intense keels descending posteriorly, posteromedially, and anteromedially, respectively may occur. Basic cranial measurements are provided in Table S2, Supplementary File 1.

The dental characters of *C. argalioides* have been discussed by Schlosser (1904), and then briefly by Pilgrim and Hopwood (1928) and Bouvrain (1994), each of them, however, limited to a sub-sample of the available set. Bohlin (1935a) also gave some interesting remarks about size variability mentioned by Schlosser (1904). Here we provide an overview of dental morphology based on all Samos plus Kemiklitepe D specimens known to us.

The cheekteeth are mesodont with finely rippled enamel and occasional traces of cement. The upper premolar to molar length ratio (%) ranges from 60–67 (n = 16). P2 has a square occlusal outline, slightly wider distally than mesially. The strong paracone pillar is in a very mesial position, while the thin parastyle marginally reaches the labial wall. The P3 also has a subsquare occlusal outline, certainly wider distally than mesially with a strong, acute paracone pillar placed anteriorly and well developed parastyle. The P4 has a symmetric semi-oval to quadrangular occlusal outline, the parastyle is more projected labially than the wider paracone pillar; the metastyle is less developed but quite clear. Five out of 13 (40%) of the P4 show a weak distal fold on the central fossete. The parastyle is strong and thick on all upper molars, the mesostyle is thinner but well projected labially, the paracone pillar is always well developed, the metacone pillar is weak and traced mostly on the upper half of the crown, the metastyle is weak on M1 and M2 but strong on M3 with a disto-labial (less worn) to distal (advanced wear) orientation. A tiny basal pillar is occasionally present on M1, much less often on M2. A central islet is present on four out of nine M3 (44%), on five out of 10 M2 (50%) and on five out of

eight M1 (63%); the character is present on molars on mid-wear wear stage. On both M1 and M2 the mesio-lingual crescent is narrower and more angular than the distolingual one but almost equally broad on M3. A weak hypoconal fold, stronger on M2 than on M1 or M3 is present in 50% of the molars (out of 11 M1s, 13 M2s, and 12 M3s).

Complete lower toothrows are much less known; two specimens from Kemiklitepe D provide a premolar to molar length ratio index of 52–60%, whereas the specimen illustrated by Schlosser (1904:pl. V, fig. 3) gives an index of ~65% and the skull in Lausanne (MGL S71) an index of ~56%. The rostral edge of the ascending ramus of the mandible forms with the alveolar level an obtuse angle (~120° in MGL S71). The p2 is simple with well developed parastylid, metaconid, and entoconid, all directed distolingually and with the latter two fused quickly with wear. The p3 is weakly bilobed labially; a strong paraconid is distinguished from the thin parastylid only in initial wear stage; the short metaconid strongly directs disto-lingually towards the crown base fused with the entoconid-entostylid complex. On the p4 the labial bilobation is clearer; the robust paraconid is distinct from the thin parastylid only on initial wear stage; the metaconid is distally placed but directs strongly forward, quickly fuses with the entoconid-entostylid complex and in advanced stage of wear may touch (but not fuse with) the paraconid, closing the anterior valley. As opposed to the upper toothrow, the mesiolabial crescent of the molars is wider and less protruding labially than the distolabial one. A basal pillar is frequently seen on m2, rarely on m1, and never on m3. A weak goat fold may also be seen on m1 and less often on m2. The lingual wall of the molars is gently undulated with a weak parastylid being almost always discernible. On m3 the third lobe consists of a single cuspid and the entostylid quite strong. Basic dental measurements are provided in Tables S3, S4, Supplementary File 1.

The Çorakyerler *Criotherium* Sample—The moderately long and strongly heteronymously twisted and keeled horn cores of the Çorakyerler taxon differentiate it from most Late Miocene 'ovibovin' taxa of similar size such as the Chinese *Hezhengia* Qiu, Wang, and Xie, 2000, *Shaanxispira* Liu, Li, and Zhai, 1978, and *Plesiaddax* or the Asian *Urmiatherium* Rodler, 1889. *Hezhengia* has a slightly shorter cranium but with relatively wider and shallower opisthocranium, bearing relatively smaller condyles but equally strong posterior and anterior tuberosities of the basioccipital and relatively longer nasals and smaller toothrow (Fig. 6). The cranium of *Urmiatherium* is shorter but with equally wide braincase, relatively shallower occiput and smaller condyles, and significantly shorter nasals but equally long upper toothrow (Fig. 6). *Plesiaddax* has again a shorter but equally wide cranium with smaller condyles, relatively longer nasals and slightly shorter toothrow (Fig. 6). *Shaanxispira* has a slightly smaller cranium (both shorter and narrower), relatively less developed posterior tuberosities of the basioccipital and smaller upper toothrow.

The overall craniodental morphological features and the horn core of the Çorakyerler sample unquestionably indicate the genus *Criotherium*. By its longer, less backward and more uprightly inserted and less tightly twisted horn cores with stronger keels and ridges, shorter braincase and longer face, much more backward shifted choanae opening, more robust basioccipital, more triangular shaped and less rostrocaudally oriented auditory bullae, and overall larger cranial size the Çorakyerler taxon differs from *C. nikolovi* from Bulgaria (Geraads & Spassov, 2008) and approaches *C. argalioides* from Samos and Kemiklitepe D. Çorakyerler and Samos-Kemiklitepe D samples are also metrically fully compatible (Fig. 6; Table S2, Supplementary File 1) except for the width of the opisthocranium, which appears narrower in Çorakyerler probably because of an intense taphonomic effect caused by mediolateral compression known for most cranial specimens from this site.

As in Samos and Kemiklitepe D, *Criotherium* from Çorakyerler is characterized by a closed ethmoidal fissure with the maxillary bones shortly projecting dorso-caudally above the lachrymals, coming into direct narrow contact with the frontals, and thus, separating fully the nasals from the lachrymals (Fig. 1I). The same pattern occurs in the Kalimantsi cranium of *C. nikolovi*, though much more difficult to be traced due to the preservation status of the specimen. Although such a configuration cannot be fully assessed at present, it is quite different from that seen on *Shaanxispira*, *Hezhengia*, *Plesiaddax*, *Urmiatherium*, the Late Miocene Chinese *Tsaidamotherium* Bohlin, 1935b and the Turkish Garkin taxon (see below), in which a closed ethmoidal fissure is associated by a direct contact of the lacrymals with the nasals as is usually the case in several extant caprins (Bohlin, 1935c; Shi & Deng, 2020; Shi et al., 2014; DSK, personal data).

The cranial differences of ÇO 491 from the remaining *Criotherium* crania at Çorakyerler are difficult to interpret because of the poor preservation of the specimen. If indeed the attached toothrows belong to the same individual, then ÇO 491 must represent a subadult of about 2 years old. Usually, crania of extant male bovids of similar age and weight (i.e., ~200 kg and 24 months) are close to sexual maturity and have already reached the main cranial shape seen in adulthood (e.g., Brakora, 2012; Calamari, 2016). This would indicate that the stronger parieto-occipital flexion, the less elevated frontals, and the overall weaker anterior and posterior basioccipital tuberosities of ÇO 491 compared with the other *Criotherium* crania could not be attributed to ontogenetic age (alone) and possibly express sexual dimorphism. Similar differences between males and either horned or hornless females of other Late Miocene 'ovibovin' bovids of comparable body mass (Bohlin, 1935c) support this view. If this interpretation is correct, then *Criotherium* will be proved to have horned females.

A metrical comparison of the upper dentition (Fig. 7) shows that the Çorakyerler sample along with *C. argalioides* from Samos and Kemiklitepe D are characterized by relatively large toothrows with moderately short premolar row compared with the molars. The Chinese *Hezhengia* has similarly short premolars compared with molars but also smaller toothrow (Fig. 7), whereas *Plesiaddax*, *Shaanxispira*, and *Urmiatherium* exhibit smaller premolar to molar ratio overall (Fig. 7). The Garkin sample is placed on the upper range of *Criotherium* (Fig. 7). As for the lower dentition, both *Plesiaddax depereti* Schlosser, 1903 from China and *Urmiatherium* are characterized by shorter premolars compared with the molars than *Hezhengia*, *Criotherium*, and the Garkin taxon (Fig. 8). *Hezhengia* further differs in its overall smaller dentition. The mandible ÇO 2075 along with ÇO 2754 and ÇO 3149 plot close to the few specimens of *Criotherium* known from Kemiklitepe D (Fig. 8), whereas the *Criotherium* lower toothrow sample from ÇO strongly overlaps with the Garkin range (Fig. 8).

Genus *HEZHENGIA*? Qiu, Wang, and Xie, 2000

Genus Diagnosis—as in Shi and Deng (2020).

Type Species—*Hezhengia bohlini* Qiu, Wang, and Xie, 2000.

Holotype—HMV 0922, cranium lacking the muzzle (Hezheng Paleozoological Museum, Gansu Province, China).

Type Locality— Linxia Basin, Gansu Province, China; Dashengou fauna, Bahean (Late Miocene).

Type Species Diagnosis—as in Shi and Deng (2020).

HEZHENGIA? cf. *INUNDATA* (Bosscha Erdbrink, 1978)

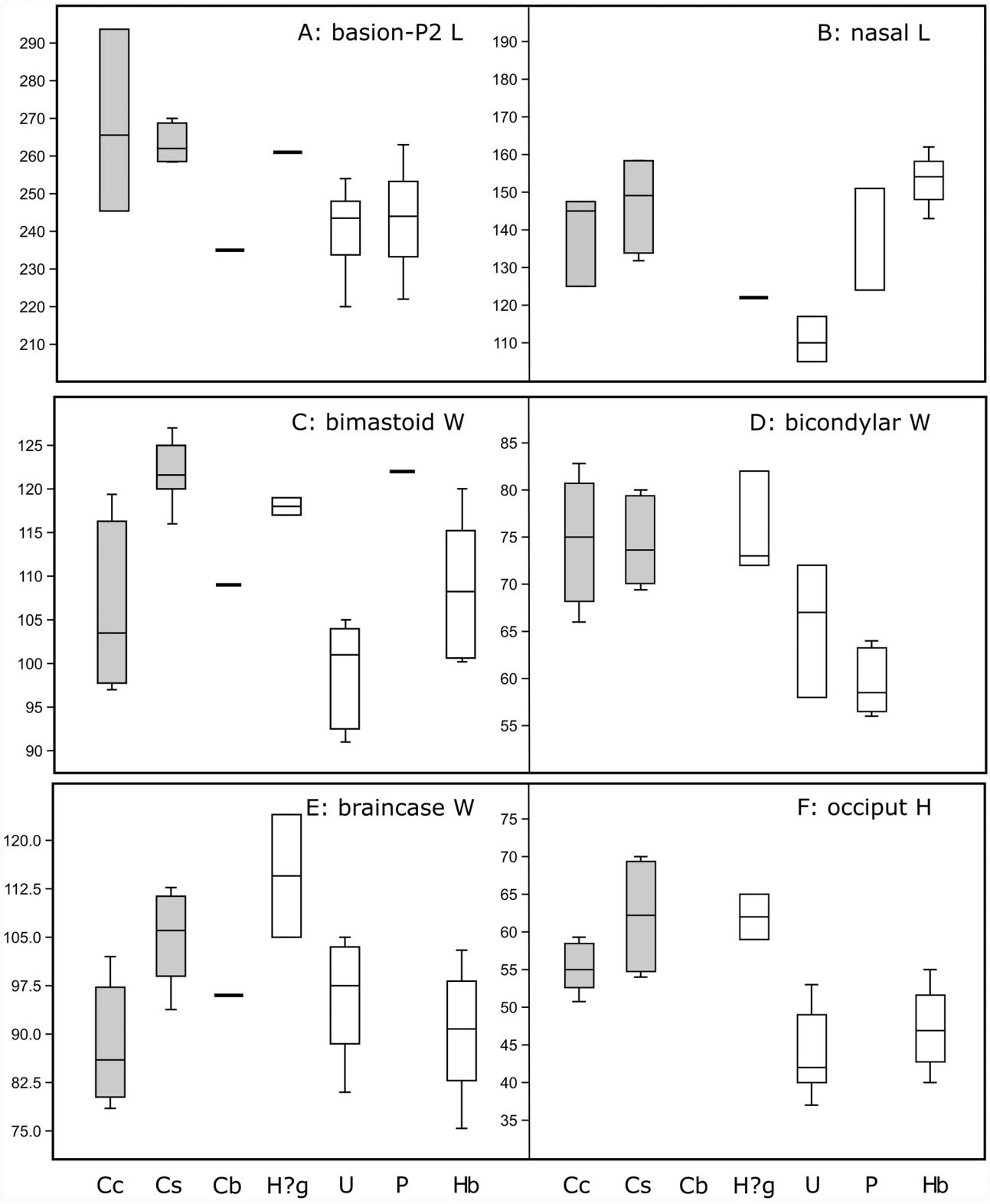


FIGURE 6. Box plots of basic cranial linear measurements in several late Miocene Eurasian 'ovibovins.' **A**, length from basion to the anterior edge of P2; **B**, nasal length; **C**, bimastoid width; **D**, bicondylar width; **E**, braincase width (maximum); **F**, occiput height (from opisthion to top of occipital protuberance). Data from Bohlin (1935c), Geraads and Spassov (2008), Shi et al. (2021), and DSK (personal data). All measurements are in mm. **Abbreviations**: **Cb**, *Criotherium nikolovi* from southern Bulgaria; **Cc**, *Criotherium argalioides* from Çorakyerler; **Cs**, *Criotherium argalioides* from Samos and Kemiklitepe D; **H**, height; **Hb**, *Hezhengia bohlini* from China; **H?g**, *Hezhengia*? *inundata* from Garkin; **L**, length; **P**, *Plesiaddax depereti* from China; **U**, *Urmiatherium intermedium* from China; **W**, width.

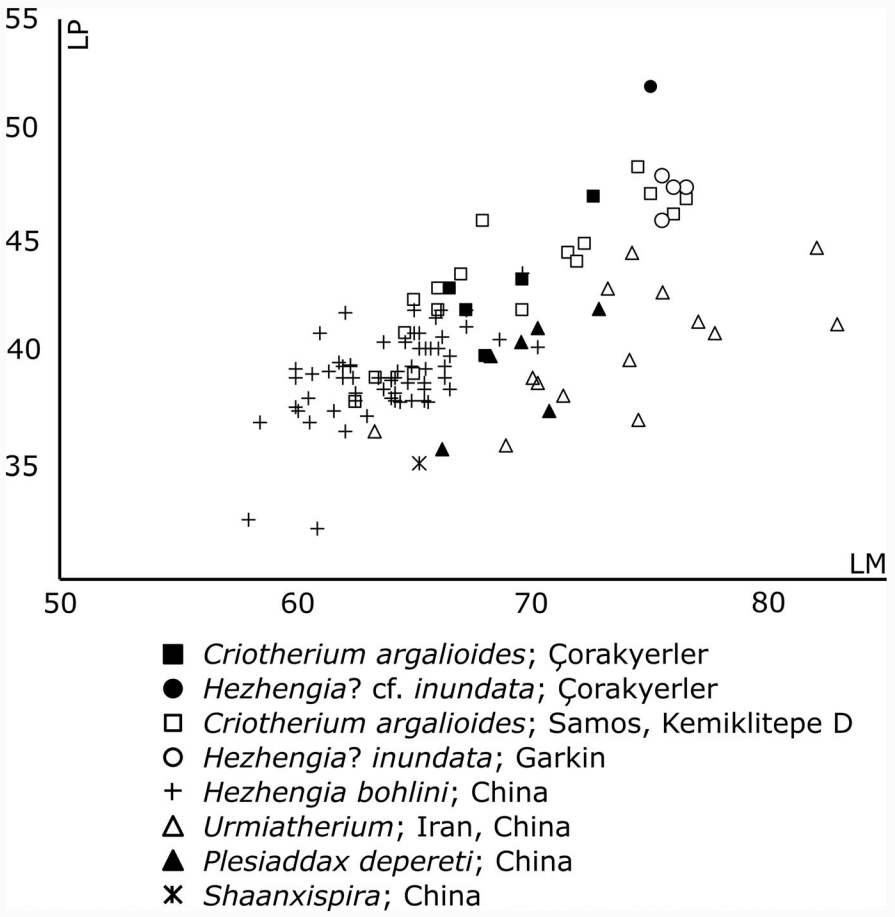


FIGURE 7. Scatter plot of upper molar row length (LM) against upper premolar row length (LP) in several Late Miocene Eurasian 'ovibovins.' Data from Bohlin (1935c), Bosscha Erdbrink (1978), Bouvrain (1994), and DSK (personal data); raw data of *Hezhengia* were provided by Q.Q. Shi. All measurements are in mm.

Material—The list of the studied material is provided in Table S1, Supplementary File 1. Basic dental measurements are provided in Tables S3 and S4, Supplementary File 1.

Description

A few upper and several lower toothrows and two partial mandibles (Figs. 4D–G, 5A–D, J, K) from Çorakyerler are allocated to a second 'ovibovin' bovid. The teeth are slightly more hypsodont than those of *Criotherium* and with finely rugose enamel. The upper toothrow is slightly larger (122–125 mm) than that of *Criotherium* from the same site but with comparable premolar to molar length ratio. Only two specimens preserve the second upper premolar. In ÇO 822 it is short with a strong paracone pillar occupying the mesio-labial corner of the tooth, a very weak and mesially placed parastyle reaching the paracone pillar only at the base of the crown, and a deep lingual notch, separating the shorter mesial from the longer and wider distal part of the tooth (Fig. 4G). The overall morphology is quite peculiar, so we cannot exclude the possibility that this tooth represents a persistent dP2. Both second upper premolars of the palate ÇO 978 (Fig. 4F) are badly preserved, so little can be said. The occlusal outline of the tooth is roughly triangular (wider distally than mesially), with a clear but not as deep as in ÇO 822 lingual groove separating the two parts, and a strong paracone pillar placed far mesially. The more triangular (instead of square) occlusal outline of the tooth and the presence of a lingual furrow are the most striking differences from the P2 of *Criotherium* (compare Fig. 4C and F, G). The P3 has a semi-circular occlusal outline in distinction from the squarish to trapezoid outline of *Criotherium* P3 and bears a hint of a weak lingual furrow (compare Fig. 4C with E–G). The P4 has again a more semi-oval than squarish occlusal outline and in difference from *Criotherium* the metastyle is thicker and the paracone pillar has a more central position on the labial wall expanding mesiodistally towards the base of the crown (compare Fig. 4A with D and 4C with E, F). A weak lingual furrow is evident on ÇO 978 (Fig. 4F) but hardly traceable on ÇO 822 (Fig. 4G). The lingual lobes of the upper molars and especially the distal one, have a more round and bulbous outline than in *Criotherium*, the parastyle and the paracone pillar are stronger and the former inflates significantly towards the crown base and takes a more mesial direction in occlusal view (compare Fig. 4A with D). On the M3 the metastyle is moderate to strong and in three of the four specimens directs distally (Fig. 4E–G). Although all dentitions are in a moderate to advanced wear stage and several in a bad preservation status, an interlobar cingulum is always present on M2 but absent on M1 or M3; a hypoconal spur is seen on one M2 and one M3 (out of four, respectively); a central islet is commonly present on M2 and M3 (three out of four specimens).

The partial mandibles ÇO 706 and ÇO 707 differ from the mandible ÇO 2075 of *Criotherium* in the shorter diastema (about 15%), shallower mandibular body (15–20%), and more vertically placed ascending ramus (compare Fig. 5I, L with J, K). The first two lower incisors of ÇO 707 appear slightly wider and certainly longer than those of ÇO 2075 (compare Fig. 5I with J). In lateral view the top level of the incisor-canine arcade is placed at the alveolar level of the cheekteeth,

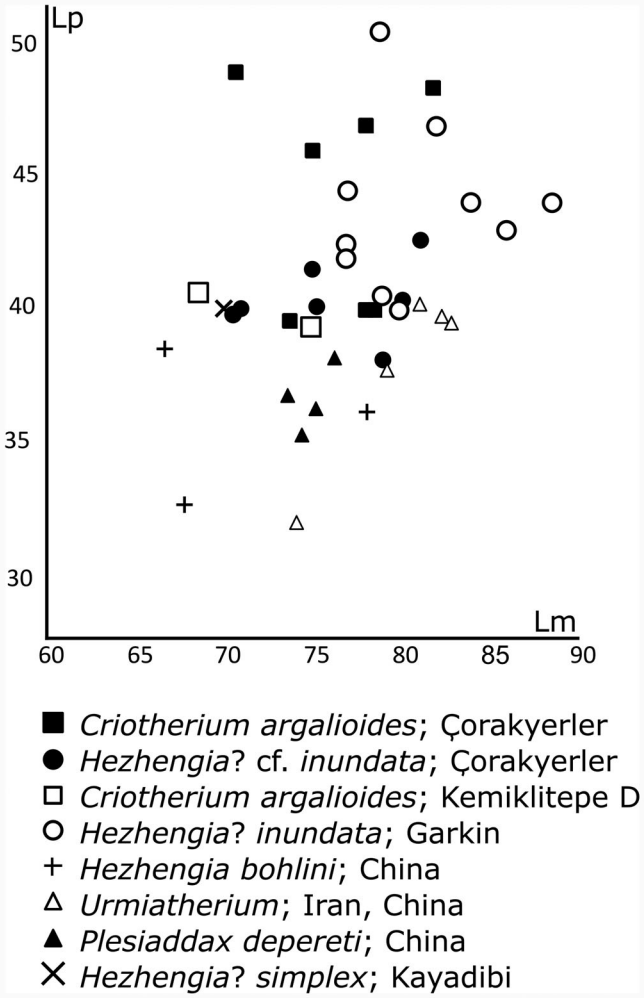


FIGURE 8. Scatter plot of lower molar row length (Lm) against lower premolar row length (Lp) in several Late Miocene Eurasian 'ovibovins.' Data from Bohlin (1935c), Bosscha Erdbrink (1978), Bouvrain (1994), Shi et al. (2021), and DSK (personal data). All measurements are in mm.

i.e., in a lower plane than in ÇO 2075 but distortion may easily affect this feature. Although of a comparable p2–m3 length to *Criotherium* (117 mm versus 120 mm on average), the lower premolar to molar ratio length ranges from 48–56% (mean = 53%; n = 7), indicating a slightly shorter premolar row. The overall morphology of the lower cheekteeth is again quite similar to that of *Criotherium* from the same site but the paraconid on both the p3 and the p4 is much weaker trending in parallel to the parastylid with which it fuses quickly (so in four out of 11 p3s and three out of 11 p4s the paraconid cannot be traced at all) (compare Fig. 5B, D with E, G), the lingual anterior valley (between the paraconid-metaconid) is commonly blocked by a basal enamel knob on p3 (35%) and on p4 (45%) (Fig. 5B, D), the lingual wall of the molars is flatter and their labial crescents wider and narrower (compare Fig. 5B, D with E, G), and a very short knob-like ectostylid appears always on m1 but never on m2 or m3 (Fig. 5C, K).

Comparison

Although mandibular, upper, and lower dentition morphology of the second Çorakyerler 'ovibovin' taxon are well-distinct from those of *Criotherium* from the same site and Kemiklitepe D–Samos sample, metric data are highly overlapping (e.g., Fig. 8). The wider and more squarish upper molars with strong central islets, and quadrangular outlined lower molars lacking basal pillars, and the shorter premolars compared with the molars (Figs. 7, 8) differentiate *Urmiatherium* from the studied taxon. The lingual bilobation of P2 and P3 and their occlusal outlines, the bulbous paracone and parastyle of the upper molars, the vertically ascending ramus of the mandible, the long i1, i2, and canine, and the weak paraconid on p3 and p4 recall in general *P. depereti* from China, which however has significantly shorter premolars compared with the molars (Fig. 8). *Hezhengia bohlini* from Linxia Basin, China has smaller toothrow but of comparable premolar to molar length ratio (Figs. 7, 8), the P3 lacks a lingual furrow and has a stronger parastyle, the P4 fossette has a distal spur, the paracone pillar of the upper molars is weaker and the protocone more rounded lingually, and the metaconid of p4 is independent from the endoconid. By most of its morphological characters, as well as absolute size and relative proportions the second Çorakyerler 'ovibovin' bovid matches illustrated specimens and metric data of the Garkin taxon (Figs. 7, 8) originally referred to as *Plesiaddax inundatus* by Bosscha Erdbrink (1978). The generic attribution of the latter is, however, highly disputable.

We have not been able to locate the rich material from Garkin for a full review, except for the partial cranium SaG 69 (Bosscha Erdbrink, 1978:pl. I, figs. C, G, H, I) stored in BGR.Hannover, on which we base our remarks along with observations on other specimens figured by Borsccha Erdbrink (1978). By most metric aspects and proportions, the Garkin crania match *Criotherium* better than any other Late Miocene 'ovibovin' bovid in comparison (Fig. 6). Bouvrain et al. (1995) already stressed these similarities in cranial proportions and challenged both main morphological arguments on which Bosscha Erdbrink (1978) based his generic attribution (i.e., the thickening of the basioccipital and the less derived dental features). According to the same authors, and Geraads and Spassov (2008), the long and narrow cranium (a), the short distance of the horn cores between them and the nuchal crest (b), the thickened but not extremely specialized basioccipital with less developed extra facets for the atlas on the posterior tuberosities (c), the more rostral opening of the choanae (d), and the not much reduced premolars (e) prevent an attribution of the Garkin taxon to the same genus as the Chinese *P. depereti*, resembling instead *Criotherium*. Both known species of *Criotherium* differ, however, considerably from the Garkin taxon and *Plesiaddax* in the placement and morphology of the horn cores (extremely enlarged anteroposteriorly and rather flattened mediolaterally, possibly short and with a hint of homonymous torsion in the latter versus moderately long, with much less expanded, subrounded bases and strongly heteronymously torsioned and keeled in the former). The very same features (a–e) shared by the Garkin taxon and *Criotherium* are also recorded, however, in *Hezhengia bohlini* (Qiu et al., 2000; Shi & Deng, 2020). Additionally, the horn cores of *H. bohlini* are quite anteroposteriorly expanded and short, with a weak homonymous torsion, inserted slightly laterally and close to each other frontally, characters shared with the Garkin taxon; *Plesiaddax* horn cores are also similar but more expanded rostrally by supraorbital buttresses. The basicranial morphology of the Garkin taxon and *H. bohlini* is also quite comparable (compare Bosscha Erdbrink, 1978:pl. I, figs. F, I with Shi & Deng, 2020:figs. 2B, 4A). Therefore, we suggest that *Hezhengia* might be a better match for affiliating the Garkin species, which is therefore referred to as *Hezhengia*? *inundata.*

As for *Criotherium* and *H. bohlini*, the Garkin taxon shows a wide size variation concerning dental dimensions. Given the metric overlap and morphological similarity between the two taxa recognized in Çorakyerler (especially on the lower toothrows), we wonder, however, whether the Garkin material

might also include specimens of a second species of similar size, namely *Criotherium*, misinterpreting minor size and morphological differences as intraspecific variation. For instance, the shape of the mandible SaG 7-5 described and illustrated by Bosscha Erdbrink (1978:155; pl. 3E, F) as probably of the same individual as the type cranium, is much more similar to that of *Criotherium* than to *Plesiaddax* (Bohlin 1935c:pl. VIII, fig. 5), *Hezhengia* (Shi & Deng, 2020:fig. 6) or ÇO 706 from Çorakyerler in the more gradual way the ascending ramus rises compared with the corpus and the right-angled configuration of the mandibular angle. In any case, a re-examination of the Garkin material is necessary before final conclusions. The absence of cranial material from Çorakyerler prevents a full comparison with *H.*? *inundata* from Garkin. Based on the morphological and metric similarity of the few available dentitions with those of the crania and mandibles that can be safely attributed to the taxon of Bosscha Erdbrink, we refer to the second 'ovibovin' bovid from Çorakyerler as *Hezhengia*? cf. *inundata*.

Köhler (1987) reported two more occurrences of *Plesiaddax* in Turkey: *Plesiaddax simplex* Köhler, 1987 from Kayadibi and "*Plesiaddax*" cf. *inundatus* from Mahmutgazi. We located the material attributed to both taxa in BGR.Hannover. We agree with Köhler (1987) that the Mahmutgazi isolated teeth resemble closely in size and morphology those of *H.*? *inundata* from Garkin, with which it should be conspecific. As for the validity of the Kayadibi taxon, most authors agree that is too incomplete, though Geraads and Spassov (2008) suggest that it is likely correctly attributed to *Plesiaddax*. According to Köhler (1987) both the frontal profile and the (rounded-) triangular horn core cross section of the holotype skull fragment KBS 7/1 (BGR.Hannover Ma 13649) of the Kayadibi taxon are similar to those of *Plesiaddax*; the frontoparietal angle is not as vertical as in *P. depereti* though. We have to add, that also in difference from *P. depereti* the nasal level is quite lower than the frontals between the horn cores in KBS 7/1, and the horn bases are not expanded anteriorly by buttresses. In these features the Kayadibi holotype cranium resembles again more closely *H.*? *inundata* from Garkin. The less abrupt frontoparietal angle, the less laterally inserted horn cores and more localized horn bases resting wider apart on the frontals, and the wide and complicated interfrontal suture raised as a ridge in between them, meet characters reported for the specimen SaG7-1/142 from Garkin, which is indicated by Bosscha Erdbrink (1978) as a presumably female of *H.*? *inundata*. The few dental specimens ascribed by Köhler (1987:figs. 65–70) to *P. simplex*, appear smaller than those from Garkin but they also show some degree of morphological mismatch between them (e.g., the lower toothrows KBS 7/99 and KB 7, the former [Köhler 1987:fig. 62] having slightly longer premolar row and p3 and p4 with strong paraconid, whereas the latter [Köhler 1987:pl. VI, fig. 4] having a fully molarized p4 and a paraconid trending in parallel with the parastylid on p3). Although still inadequate for definite conclusions, we think Köhler's taxon much more closely related to *H.*? *inundata* from Garkin than either of them is to the Chinese *P. depereti* and therefore we refer to it as *Hezhengia*? *simplex* awaiting more material to confirm the validity of the species.

DISCUSSION AND CONCLUSION

The rich fossil record of 'ovibovins' at Çorakyerler emphasizes their great contribution to the composition of the local bovid and mammal fauna. Two unequally represented taxa have been recognized: the predominant *Criotherium argalioides* and the less common *Hezhengia*? cf. *inundata*. Although time-range distributions from both China and Anatolia support the possible co-occurrence of similar-sized 'ovibovin' bovids with highly specialized cranial features, the Çorakyerler record is in fact the first confirmed evidence of such a joint presence in the same assemblage (see also Shi et al., 2016). Their co-occurrence might have been possible due to distinct feeding preferences and ethology, as deduced from indirect evidence for *C. argalioides* from Samos and Kemiklitepe D and *H.*? *inundata* from Garkin, based on differences in relative hypsodonty, masticatory morphology, horn shape, and limb proportions (Bouvrain, 1994; Köhler, 1993; Solounias & Dawson-Saunders, 1988; Solounias et al., 2010). According to those data, *C. argalioides* might have been a herd-living mixed feeder to grazer, with moderate running abilities and a complex fighting behavior (possibly combining pushing/ramming with stabbing/wrestling). *Hezhengia*? *inundata* on the other hand, was likely a more dedicated grazer, living in herds, having good running abilities and ramming fighting behavior.

The review of the Samos-Kemiklitepe D and the newly described, rich Çorakyerler record of *C. argalioides* provide important data on both morphological and metric variation within the species but also stress the stability of the most diagnostic features of the taxon, already known from previous studies (e.g., Bohlin, 1935a; Bouvrain 1994; Geraads & Spassov, 2008; Pilgrim & Hopwood, 1928; Schlosser, 1904; Solounias, 1981). Contra Bohlin (1935a) and in agreement with Schlosser (1904) the present study also reveals great dental size variation in *C. argalioides.* A possible bimodal distribution, perhaps representing sexual dimorphism, occurs in both the Samos and Çorakyerler samples (Figs. 7, 8), though the recorded ranges do not exceed those of better-known related taxa (see for instance *Hezhengia*'s rich upper toothrow record in Fig. 7) and definitive conclusions seem premature in the absence of adequate evidence.

To our knowledge, available crania of *C. argalioides* from both Samos and Kemiklitepe D all belong to young-adult to old individuals (with an M3 from an initial to a quite advanced wear stage) without hints of any bimodality in skull or horn core morphology and size. This could mean that the females of this species were horned and sexual differentiation was little to non-existent, or that all the available specimens belong to males. The study of the Çorakyerler material feeds this discussion with some interesting new evidence. Our interpretation of the horned cranium ÇO 491 as most likely female allows recognizing *C. argalioides* as having horned females and the small cranial differences of ÇO 491 from the remaining Çorakyerler *Criotherium* crania might be indicative of some degree of sexual dimorphism. In this case, the almost exclusive presence of male skulls of *C. argalioides* in the thanatocoenoses of Samos and Çorakyerler should be considered in the light of some selective taphonomic or ethological bias.

As currently understood, *Criotherium* shows a quite restricted chronological and geographic distribution. Most likely, the genus is first known from the late Vallesian of Middle Sinap (Gentry, 2003), though its origin and phylogenetic relationships are still debatable (e.g., Gentry, 2003; Geraads & Spassov; 2008; Kostopoulos & Soubise, 2018). During the early Turolian, *C. argalioides* dominated Anatolia with the best evidence coming from Samos, Kemiklitepe D, and Çorakyerler. Although more primitive, *C. nikolovi* from southern Bulgaria also occurred during the early Turolian, allowing Geraads and Spassov (2008) to suggest the presence of two contemporaneous lineages in the eastern Mediterranean. As Kalimantsi-1 is the only attested reference of *Criotherium* outside Anatolia, its phylogeographic connections with the rest of the genus distribution are difficult to trace at present. The most parsimonious scenario would probably be that both lineages split from an (early?) Vallesian anticlockwise-spiraled antilopine but an in-depth analysis is needed. The genus certainly becomes increasingly rare during the middle Turolian as implied by its characteristic absence from most rich Balkano–Anatolian mammal assemblages of this period. An unpublished partial cranium from Pinaryaka (Saraç et al., 2002) stored in MTA, Ankara (D. Geraads, personal

communication, 2023) is so far the best available evidence of *Criotherium* in the middle Turolian of Turkey; however, we find it possible that dental material of *Criotherium* from some other Anatolian sites might have been wrongly attributed to other taxa. *Criotherium* is also tentatively reported from the middle Turolian of Samos (upper levels), localities 26, 50, and 88 of Middle Sinap, as well as from Thermopigi (N. Greece) and Taraklia (Moldova) (Gentry, 2003; Geraads et al., 2007; Khomenko, 1913; Solounias, 1981). Although we doubt the Thermopigi record (the referenced material is most likely to be *Palaeoreas* Gaudry, 1861, well known from this site), the Taraklia dental remains are probably correctly attributed to this genus by Khomenko (1913). In any case, more material is needed to confirm the presence of the taxon on the northern shores of the Black Sea. Previous reports of the species from Maragheh, Iran (Günther, 1896; Pilgrim & Hopwood, 1928) have long been disputed (Bohlin, 1935a) and part of the referable material has been proved to belong to *Urmiatherium* (Bohlin, 1935a; Kostopoulos & Bernor, 2011). We know of no reports of the genus further east of Maragheh.

Confirming previous doubts (Bouvrain et al., 1995; Geraads & Spassov, 2008) the present review suggests that there is no indisputable evidence for *Plesiaddax* in Turkey so far. The second Çorakyerler 'ovibovin,' along with that from Mahmutgazi, are most likely conspecific with the much better known Garkin species, here referred to as *Hezhengia*? *inundata* awaiting a formal and complete review of the original material. Among known Eurasian 'ovibovin' genera, we find more resemblance between Bosscha Erdbrink's species and *Hezhengia* than to *Plesiaddax* itself, and we think it quite possible that both Chinese *Plesiaddax* and Anatolian *Hezhengia*? might derive from Vallesian *Hezhengia* in China. The Kayadibi "*Plesiaddax*" *simplex* is also seen here as more closely related to *H.*? *inundata* from Garkin than to Chinese *Plesiaddax* and is therefore referred to as *H.*? *simplex*. In any case, we agree with previous authors (Bosscha Erdbrink, 1978; Köhler, 1987) that this group of Turkish taxa appears tightly linked to the Chinese bovid group of *Hezhengia–Plesiaddax–Urmiatherium* (Urmiatheriini sensu Shi & Deng, 2020), strengthening the hypothesis by Geraads et al. (2002) of a Late Miocene Middle Asiatic Province across the 35°N latitude.

As far we know, 'ovibovin' bovids are entirely missing from West European Late Miocene mammal faunas and they are probably only occasionally present on the northern shores of the Black Sea. In contrast, this group appears to have thrived in China and Anatolia and its surroundings during this period (Bohlin, 1935c; Bouvrain & Bonis, 1984; Bouvrain et al., 1995; Jafarzade et al., 2012; Köhler, 1987; Kostopoulos & Bernor, 2011; Schlosser, 1904; Shi & Deng, 2020; Shi et al., 2014, 2016; Zhang, 2003). Although relationships among known genera are still unresolved (see discussions in Geraads & Spassov, 2008; Kostopoulos, 2014; Shi & Deng, 2020), the shared cranial features they exhibit suggest similar ecological adaptations that must be related to some common extrinsic factors (e.g., climate, vegetation). What is perhaps even more interesting, and worthy of further investigation as to its causes, is the fact that the diversity trends observed at the two sectors of Asia (e.g., China versus Balkano–Iranian region) appear opposite in the transition from the Vallesian to Turolian (or during the Bahean Chinese Neogene Land Mammal Age; Tortonian, Late Miocene). Hence, in China 'ovibovin' bovid diversity declines remarkably from ≥ 5 (*Tsaidamotherium*, *Shaanxispira*, *Lantiantragus*, *Hezhengia*, *Urmiatherium*) to two genera (*Urmiatherium*, *Plesiaddax*), whereas in the Balkano–Iranian region it increases from two genera (*Mesembriacerus*, *Urmiatherium*) in the Vallesian to up to four (*Urmiatherium*/*Parurmiatherium*, *Criotherium*, *Hezhengia*?), in the early–middle Turolian.

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AUTHOR CONTRIBUTIONS

ASE conceived and planned the study, SM gathered field data, measurements, and photographic material, DSK contributed to systematics, data analysis and drafted the manuscript. All authors edited the manuscript.

LIST OF SUPPLEMENTARY FILES

Supplementary File 1. List of studied material and craniodental measurements of *Criotherium argalioides* and *Hezhengia*? cf. *inundata* from Çorakyerler, Turkey and comparative material: Table S1, List of studied material; Table S2, Cranial measurements; Table S3, Upper toothrow measurements; Table S4, Lower toothrow measurements.

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