Middle Miocene Bovids from Mae Moh Basin, Northern Thailand: The First Record of the Genus Eotragus from Southeast Asia

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Middle Miocene bovids from Mae Moh Basin, Northern Thailand: The first record of the genus *Eotragus* from Southeast Asia

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We describe the first bovid fossils from the late middle Miocene (13.4–13.2 Ma) of the Mae Moh Basin of Northern Thailand, and assign the material to the new species *Eotragus lampangensis* sp. nov., *Eotragus* cf. *lampangensis*, and an indeterminate bovid. Our material represents the first report of *Eotragus* from Southeast Asia, thus greatly extending the geographic distribution of this genus across the Old World continents. While comparisons of the Southeast Asian specimens with abundant material of *E. clavatus* from Sansan (France) and *E.* aff. *clavatus* from Tarazona de Aragón (Spain) indicate a high degree of intraspecific variation within single species of *Eotragus*, the existence of two distinct taxa at Mae Moh remains a possibility. Based on previous carbon isotope studies of Mae Moh herbivore tooth enamel, *Eotragus lampangensis* sp. nov. foraged predominantly in an ecotone between grassland and forest.

Key words: Mammalia, Bovidae, *Eotragus*, Miocene, Southeast Asia, Thailand, Mae Moh Basin.

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Introduction

Eotragus is the oldest bovid possessing true horn cores, and first appears in the fossil record around 18 Ma (Gentry 2000; Solounias 2007). Some *Eotragus* species, such as *Eotragus clavatus* (Gervais, 1850) (= *Eotragus sansaniensis* [Larlet, 1851]) and *Eotragus noyei* Solounias, Barry, Bernor, Lindsay, and Raza, 1995, are considered to form the stem group of Bovinae (Bibi et al. 2009). These earliest known true bovids were initially recorded from Europe and Pakistan (Barry and Flynn 1989; Gentry 1994; Solounias et al. 1995; Gentry et al. 1999). Nowadays their fossils are widely reported across the Old World continents (Europe, Asia, and probably Africa), with the ages ranging from the early Miocene to the early Pliocene (Gentry 1994; Solounias et al. 1995; Solounias 2007; Khan et al. 2009).

Relatively little is known about bovids from the Miocene of Southeast Asia, with fossils of *Eotragus* in particular never having been reported from this region. Here, we describe four horn cores, jaw fragments, and numerous teeth of late middle Miocene bovids collected from the K and Q coal layers (13.4–13.2 Ma) of the Nakhaem Formation, Mae Moh coal mine, northern Thailand (Fig. 1), and assign them to the new species *Eotragus lampangensis*, *Eotragus* cf. *lampangensis*, and Bovidae gen. et sp. indet. In addition, we discuss the morphological differences between our new specimens in light of the high degree of intraspecific variation shown by the abundant material of *Eotragus clavatus* from the French locality of Sansan and elaborate on the paleoecological and paleoenvironmental implications of our findings.

Institutional abbreviations.—KNM, Kenya National Museum, Nairobi, Kenya; MNHN Sa, Sansan collection, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, Natural History Museum, London, United Kingdom; IPS BN, Buñol collection, Instituto de Paleontología, Sabadell, Spain; UPP MM, Mae Moh Paleontological collection, Institut In-

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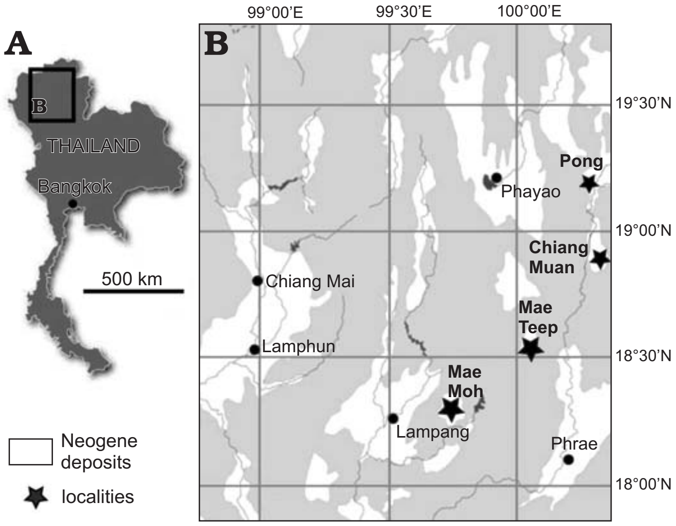

Fig. 1. Map of Thailand showing the location of the Mae Moh Basin (**A**). Map of intermontane basins showing the location of mammal-bearing fossil localities (**B**).

ternational de Paléoprimatologie, Paléontologie Humaine: Évolution et Paléoenvironnements, University of Poitiers, France; UPV T, Tarazona collection, Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco, Bilbao, Spain.

Other abbreviations.—DAP, anteroposterior diameter of the horn core; DML, mediolateral diameter of the horn core; DTa, transverse diameter of the anterior lobe of the teeth; DTp; transverse diameter of the posterior lobe of the teeth; EH, full height of the horn core; H, height of the teeth; L, length of the teeth.

Material and methods

All specimens were measured using a vernier caliper. The height of the horn cores was measured from the central base (in lateral view) to the preserved tip, and their full height (EH) was estimated by reconstructing any broken portions. Anteroposterior and mediolateral diameters (DAP and DML) of the horn cores were recorded at the base and at the several distances (1, 2, 3, and 4 cm) from the base. The degree of the inclination of the horn core was determined based on the orientation of the frontal plane. We calculated EH/DAP and EH/DML to quantify the relative height of the horn core, as well as the compression index (100DML/DAP) in order to compare their basal outlines. The length (L) of the teeth was measured along the labial side of the upper molars and at the lingual side of the lower molars, whereas their height (H) was measured at the mesolabial crista of the upper premolars, the mesostyle of the upper molars, the protoconid of the lower premolars, and the metastylid of the lower molars. The transverse diameters of the anterior (DTa) and posterior lobes (DTp) of the teeth were recorded at the base of the tooth crown. Finally, the degree of hypsodonty of the teeth was calculated as H/L. Dental terminology follows Bärmann and Rössner (2011: figs. 1, 2). Upper case letters denote upper teeth, whereas lower case letters indicate lower teeth.

Table 1. Mammalian fauna of the Mae Moh Basin, Thailand.

I coal layer (12.0–11.6 Ma)	Rodentia
	Castoridae
	Steneofiber siamensis
J coal layer (12.8–12.2 Ma)	Proboscidea
	Stegodontidae
	Stegolophodon praelatidens
	Carnivora
	Mustelidae
	Siamogale sp.
Q and K coal layers (13.4–13.2 Ma)	Primates
	Tarsiidae
	Tarsius sirindhornae
	Sivaladapidae
	Siamoadapis maemohensis
	Insectivora
	Erinaceidae indet.
	Rodentia
	Platacanthomyidae
	Neocometes cf. *orientalis*
	Rhizomyidae
	Prokanisamys benjavuni
	Carnivora
	Mustelidae
	Siamogale thailandica
	Vishuonyx sp.
	Viverridae
	cf. *Viverra* sp.
	Amphicyonidae
	Maemohcyon potisati
	cf. *Pseudarctos* sp.
	Proboscidea
	Gomphotheriidae
	Gomphotherium cf. *browni*
	Stegodontidae
	Stegolophodon praelatidens
	Perissodactyla
	Rhinocerotidae
	Gaindatherium sp.
	Artiodactyla
	Cervidae
	Lagomeryx manai
	Stephanocemas rucha
	Tragulidae
	Dorcatherium sp.
	Bovidae (this study)
	Eotragus lampangensis sp. nov.
	Eotragus cf. *lampangensis*
	Suidae
	Tetraconodontinae
	Conohyus thailandicus
R coal layer (14.2–14.1 Ma)	Proboscidea
	Gomphotheriidae
	Gomphotherium cf. *browni*
	Carnivora
	Mustelidae
	Vishuonyx sp.

Geological setting

The Nakhaem Formation of the Mae Moh Basin consists of fluvio-lacustrine sediments indicating swamp environments (Chaodumrong 1985) (for more details of sedimentology and stratigraphy, see Benammi et al. 2002; Coster et al. 2010). The unit is composed of five mammal-bearing fossiliferous coal layers (I, J, K, Q, and R, from the top to the bottom) (Corsiri and Crouch 1985), which have yielded one of the richest middle Miocene mammalian faunas of Southeast Asia (Table 1) (Koenigswald 1959; Ginsburg et al. 1983; Ducrocq et al. 1994, 1995; Peigné et al. 2006; Chaimanee et al. 2008; Chavasseau et al. 2009; Coster et al. 2010; Grohé et al. 2010; Grohé 2011; Suraprasit et al. 2011, 2014). The age of the fossil-bearing deposits ranges between 14.2 and 12.0 Ma according to magnetochronological data (Coster et al. 2010), with the age of layers which yielded the material described here (K and Q) in particular having been estimated at 13.4–13.2 Ma.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1848

Family Bovidae Gray, 1821

Genus *Eotragus* Pilgrim, 1939

Type species: *Eotragus clavatus* (Gervais, 1850) (= *Eotragus sansaniensis* [Larlet, 1851]); middle Miocene (MN6), Sansan, France.

Emended diagnosis (modified from Solounias et al. 1995).—Small-sized bovids characterized by a horn core with an asymmetrical and triangular outline in lateral view. The anterior portion of the horn core base is thickened, making the latter appear relatively wide compared to its total height. In lateral view, the horn core is inclined posteriorly at about 40°. The posterior edge is generally convex and the anterior edge concave, resulting in a slightly anteriorly curved longitudinal axis of the horn core. The cross section of the horn core is slightly oval, often associated with a weak anterior keel. The horn core inserts on a short pedicle located above the orbit, with the orbital rim protruding laterally beyond the position of the pedicle.

Geographic and stratigraphic range.—Old World continents, including Europe (Central Europe, France, and Spain), Africa? (Kenya), and Asia (Israel, Pakistan, Mongolia, China, and Thailand); early Miocene to early Pliocene.

Eotragus lampangensis sp. nov.

Figs. 2A, 3A–H, 4A; Tables 2, 3.

Etymology: From the geographic location of the Mae Moh coal mine in the Lampang Province of Northern Thailand.

Holotype: UPP MM-68, a left horn core with preserving part of the frontal bone.

Type locality: Mae Moh coal mine, Northern Thailand.

Table 2. Horn core measurements (in mm) of the bovid mammals, *Eotragus lampangensis* sp. nov. (UPP MM-68, holotype) and *Eotragus* cf. *lampangensis* (UPP MM-29, UPP MM-55, and UPP MM-56) from the locality of Mae Moh, Thailand.

	UPP MM-68	UPP MM-29	UPP MM-55	UPP MM-56
Maximum preserved height	55.1	40.7	16.1	28.3
Estimated full height	65.0	45.0	50.0	50.0
Anteroposterior diameter (DAP)				
At base	18.4	15.9	17.8	16.3
1 cm above base	14.8	13.0	12.8	13.8
2 cm above base	12.8	10.3	–	12.1
3 cm above base	10.7	7.2	–	–
4 cm above base	9.4	5.5	–	–
Mediolateral diameter (DML)				
At base	15.8	13.6	14.0	13.6
1 cm above base	11.8	10.6	10.5	11.0
2 cm above base	9.1	8.4	–	10.2
3 cm above base	7.4	5.7	–	–
4 cm above base	6.3	4.3	–	–
Basal horn core compression index (100DML/DAP)	85.9	85.5	78.7	83.4
Horn core compression index 2 cm above the base	71.1	81.6	–	84.3

Type horizon: Nakhaem Formation, coal layer Q, late middle Miocene (13.4–13.2 Ma).

Referred material: From coal layer Q: UPP MM-69, right P2; UPP MM-70, right P3; UPP MM-57, left DP3; UPP MM-58 and UPP MM-71, left M3; UPP MM-59, right p2; UPP MM-60, left p2; UPP MM-61, right p4; UPP MM-62, fragmentary left mandible with p4 and m1; UPP MM-67, fragmentary right fragmentary mandible with m3; UPP MM-63 and UPP MM-66, right m1; UPP MM-64 and UPP MM-65, left m1; and from coal layer K: UPP MM-72, right p2; UPP MM-73, left m2; UPP MM-74, right m3; UPP MM-75, right astragalus.

Diagnosis.—Species of *Eotragus* similar in size to *E. artenensis* Ginsburg and Heintz, 1968, with a long, slender, and scimitar-shaped horn core. The horn core is inserted slightly posterior to the orbit, and inclined posteriorly at about 45° (relative to the frontal plane) and laterally at about 15° (relative to the sagittal plane). The lateral outline of the horn core corresponds to an asymmetrical triangle. In cross section, the horn core is subcircular at its base, becoming elliptical and transversely compressed halfway along its length. A distinct anterior keel originates 1 cm above the base of the anterior face of the horn core, which also bears a faint posterior keel on its posterolateral surface. In lateral view, the anterior surface of the horn core is relatively concave, whereas the posterior surface is slightly convex or flattened.

Differential diagnosis.—Differs from most species of *Eotragus*, including *E. clavatus*, *E. artenensis*, *E. noyei*, and *E. minus* Ginsburg, Morales, and Soria, 2001, in having a more vertically inserted and more laterally inclined horn core, as well as in the slender shape and comparatively great height of the horn core (compared to the size of its base) and the presence of a more distinct and sharper anterior keel; differs from *E. artenensis* in having a faint posterior keel of the horn

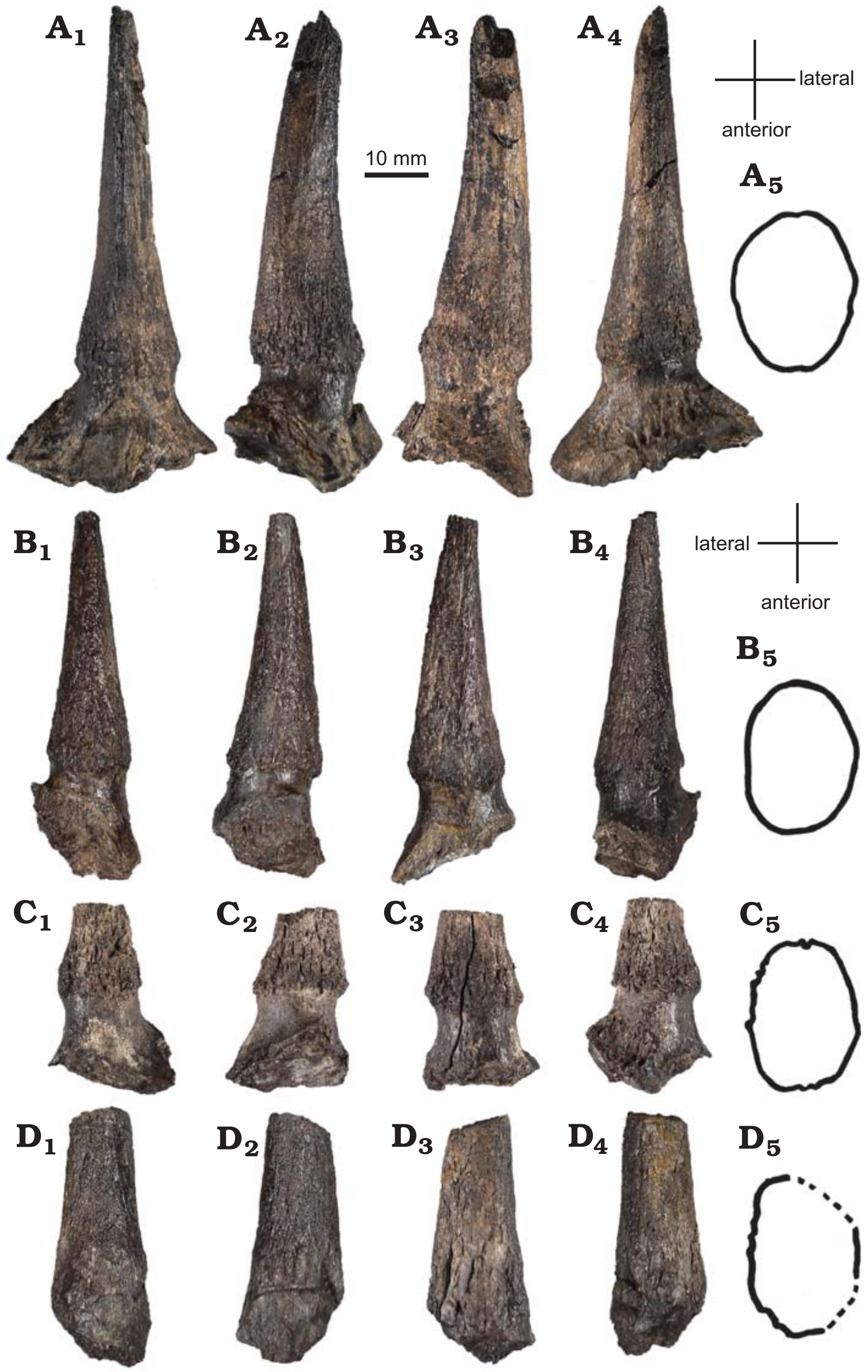

Fig. 2. Cranial appendage remains of the bovid mammal *Eotragus* from the middle Miocene of Mae Moh Basin, Thailand, in anterior (A_1–D_1), medial (A_2–D_2), lateral (A_3–D_3), and posterior (A_4–D_4) views, and basal cross sections (A_5–D_5, dashed lines indicate broken areas). **A**. *Eotragus lampangensis* sp. nov., holotype, UPP MM-68, left horn core. **B**–**D**. *Eotragus* cf. *lampangensis*. **B**. UPP MM-29, right horn core. **C**. UPP MM-55, partial fragment of right horn core with pedicle. **D**. UPP MM-56, fragmentary right horn core. The basal cross sections (B_5, C_5, and D_5) are oriented in the same direction.

core, more hypsodont tooth crowns, and relatively longer molars; differs from *E. clavatus* in its smaller size, as well as in having a faint posterior keel, more rugose tooth enamel, and a weaker lingual cingulum on M3; differs from *E. halamagaiensis* Ye, 1989 in its smaller size and less vertical insertion of the horn core, as well as the presence of a posterior keel and more distinct anterior keel.

Description.—A left horn core (UPP MM-68; Fig. 2A) from the Q coal layer is completely preserved and attached to a portion of the frontal including the dorsal orbital rims. The preserved part of the frontal is thick and slightly elevated in the region of the inter-frontal suture. The long, slender, and scimitar-shaped horn core is inserted slightly posterior to the orbit, and inclined more posteriorly (45° relative to the frontal plane) and more laterally (about 15° relative to the sagittal plane) than in other species of *Eotragus*. In lateral view, the horn core is slightly curved anteriorly owing to its relatively concave anterior and slightly convex posterior surfaces (Fig. $2A_2$, A_3), however, neither spiral nor anticlockwise torsion can be detected. In cross section, the horn core is subcircular

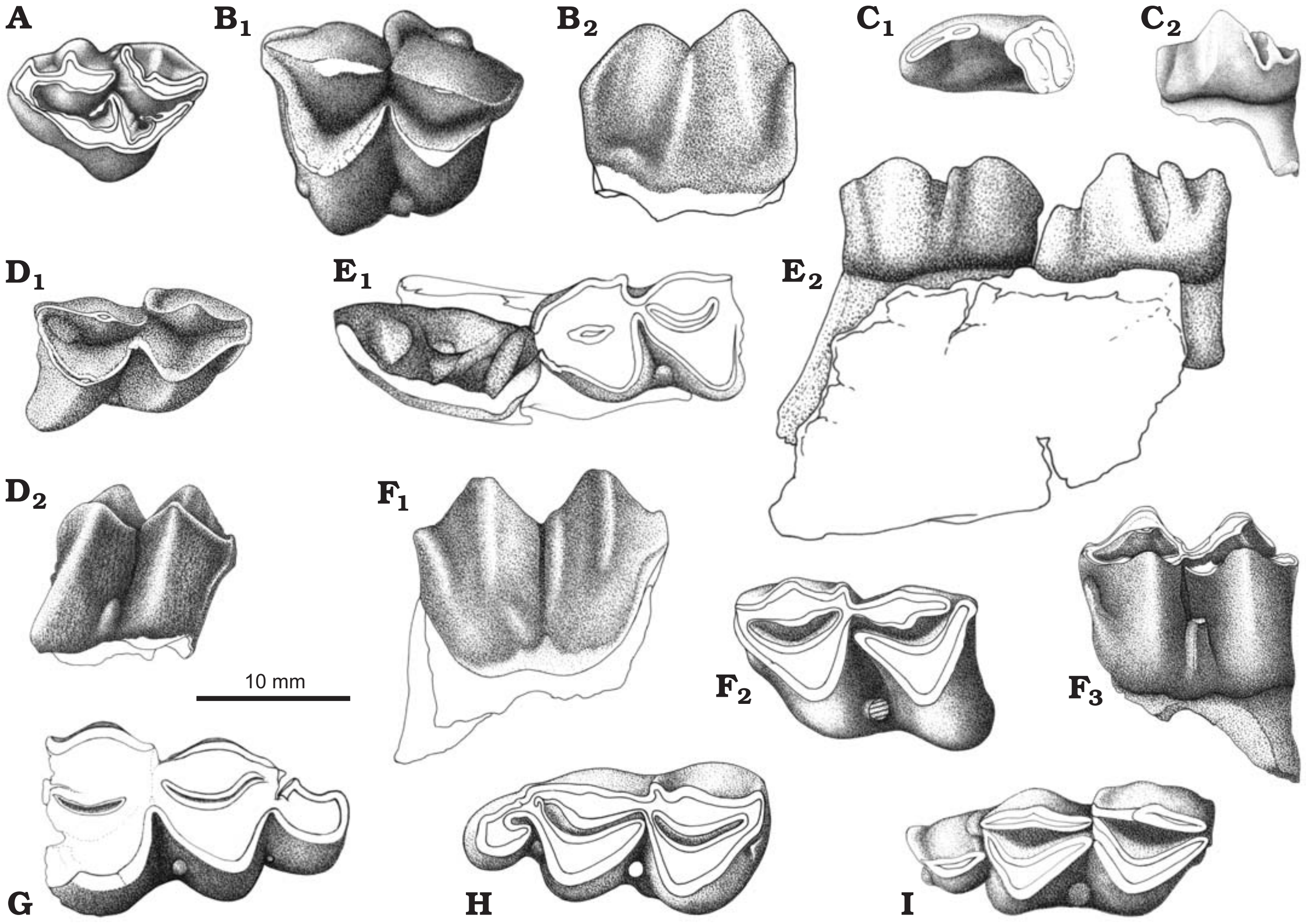

Fig. 3. Dental remains of the bovid mammals, *Eotragus lampangensis* sp. nov. (**A**–**F**, **H**, **I**) and Bovidae gen. et sp. indet. (**G**) from the the middle Miocene of Mae Moh Basin, Thailand. **A**. UPP MM-57, left DP3 in occlusal view. **B**. UPP MM-71, left M3 in occlusal (B_1) and labial (B_2) views. **C**. UPP MM-72, right p2 in occlusal (C_1) and lingual (C_2) views. **D**. UPP MM-66, right m1 in occlusal (D_1) and labial (D_2) views. **E**. UPP MM-62, fragmentary left mandible with p4 and m1 in occlusal (E_1) and lingual (E_2) views. **F**. UPP MM-73, left m2 in lingual (F_1), occlusal (F_2), and labial (F_3) views. **G**. UPP MM-76, left m3 in occlusal view. **H**. UPP MM-67, right m3 in occlusal view. **I**. UPP MM-74, right m3 in occlusal view.

at its base (Fig. $2A_5$), but turns elliptical (i.e., transversely compressed) halfway along its length, as indicated by the horn core compression index at 2 cm above the base (Table 2). A distinct anterior keel originates 1 cm above the base of the horn core and runs along its anterior surface. The posterior side of the horn core is flatter than the anterior one, owing to the weak development of the posterior keel on its posterolateral surface (Fig. $2A_4$). The surface of the horn core becomes smooth near its base, with the surface of the pedicle being even smoother. The anterior portion of the pedicle is slightly higher than its posterior one.

All of the premolars and molars share a selenodont morphology with brachyodont crowns, although they are rather more hypsodont than those of cervids and tragulids from the same locality. The enamel is finely rugose. The upper molars lack lingual cingula. The anterior and labial cingulids of the lower molars are usually weak. In terms of the upper dentition, DP3 (Fig. 3A) has a triangular occlusal outline and relatively flattened lingual and posterior borders. The parastyle, mesostyle and metastyle are well developed as paracone and metacone ribs. The posterior lobe is more developed and much wider than the anterior one. Compared with the molars, the DP3 is relatively brachyodont.

P2 is characterized by a triangular occlusal outline and the lack of obvious cingula. This tooth is relatively wide posteriorly owing to a wide posterior style and a well-developed mesolabial crista and anterior style. The mesolabial crista is the highest cusp and situated close to the anterior style. P3 generally resembles P2 in its morphology, but is marked by a much wider posterior portion and more flattened posterior surface.

The flattened labial wall of M3 (Fig. 3B) appears oblique in occlusal view, and slightly inclined towards the lingual side. The postparacrista is attached to the premetacrista, corresponding to a straight labial wall in occlusal view (Fig. $3B_1$). The parastyle, paracone rib, and metastyle are less developed than the mesostyle. The protocone and paracone are situated higher than the metacone and metaconule. The anterior and posterior fossettes are rather narrow. Both the anterior and lingual cingula are either weak or absent. A small entostyle is present in UPP MM-71.

In the lower dentition, p2 (Fig. 3C), is distinctly smaller than p4. The highest part of p2 lies on the mesolabial conid. There is no anterior conid. By contrast, the anterior stylid, posterolingual conid, and posterior stylid are all well developed and extend to the lingual side of the tooth. The posterolingual conid is higher than the posterior stylid, but the latter does not fuse with the posterolingual cristid at the middle wear stage. In lingual view, the base of the crown is slightly concave ventral to the mesolingual conid (Fig. $3C_2$).

The p4 (Fig. 3E) is characterized by the presence of an anterior conid, a small posterolabial conid, an anterolingual cristid, and a posterolingual cristid, with the anterolingual cristid being more elevated than the posterolingual one. The anterior stylid is lower than the anterior conid. The posterolingual cristid is not attached to the posterior stylid. The posterior valley, which is smaller than the anterior valley, is open (Fig. $3E_1$).

The m1 (Fig. 3D, E) is smaller than the m2 and marked by a relatively smooth wall with two distinct metaconid ribs and a metastylid. The mesostylid, entostylid, and entoconid rib are weak. The metaconid is higher than the entoconid. The hypoconid is slightly lower and protrudes more labially than the well-developed protoconid. In lateral view, all of the major cuspids (protoconid, metaconid, entoconid, and hypoconid) are inclined anteriorly (Fig. $3D_2$). The internal postprotocristid does not fuse with the prehypocristid at the early wear stage. In the unworn UPP MM-66, the internal preprotocristid is fused with the pre-entocristid (Fig. $3D_1$). At the middle wear stage, the internal postmetacristid, internal postprotocristid, pre-entocristid, and prehypocristid are fused together and the preprotocristid joins the premetacristid (Fig. $3E_1$). The anterior and posterior fossettes are extremely narrow. The ectostylid is present labially, close to the prehypocristid. The anterior cingulum is weak.

Table 3. Dental measurements (in mm) of *Eotragus lampangensis* sp. nov. and an indeterminate bovid from Mae Moh, Thailand.

Specimen number	Type	L	DTa	DTp	H	H/L	Wear stage
Eotragus lampangensis sp. nov.							
UPP MM-57	left DP3	9.72	6.57	9.24	5.71	0.59	moderate wear
UPP MM-69	right P2	9.65	6.16	8.52	6.27	0.65	heavy wear
UPP MM-70	right P3	9.77	6.83	9.06	6.51	0.67	heavy wear
UPP MM-71	left M3	13.37	12.65	10.57	11.16	0.83	unworn
UPP MM-58	left M3	–	12.35	10.01	6.87	–	heavy wear
UPP MM-59	right p2	9.96	4.65	5.73	6.59	0.66	slight wear
UPP MM-60	left p2	9.86	5.33	5.98	6.16	0.62	moderate wear
UPP MM-72	right p2	9.85	4.74	4.85	7.82	0.79	slight wear
UPP MM-61	right p4	11.24	4.75	6.31	6.56	0.58	moderate wear
UPP MM-62	left p4	11.74	4.85	6.87	9.13	0.78	slight wear
UPP MM-62	left m1	11.51	6.98	7.61	6.67	0.58	moderate wear
UPP MM-63	right m1	11.49	7.05	8.07	5.89	0.51	heavy wear
UPP MM-64	left m1	11.58	6.83	7.32	8.60	0.74	slight wear
UPP MM-65	left m1	–	6.27	–	4.66	–	heavy wear
UPP MM-66	right m1	12.11	6.65	7.74	10.67	0.88	unworn
UPP MM-73	left m2	12.57	8.32	9.21	10.89	0.87	slight wear
UPP MM-74	right m3	17.25	8.24	7.21	12.83	0.74	slight wear
UPP MM-67	right m3	17.11	8.45	7.73	9.02	0.53	middle wear
Bovidae gen. et sp. indet.							
UPP MM-76	left m3	18.64	11.43	8.61	7.52	0.40	heavy wear

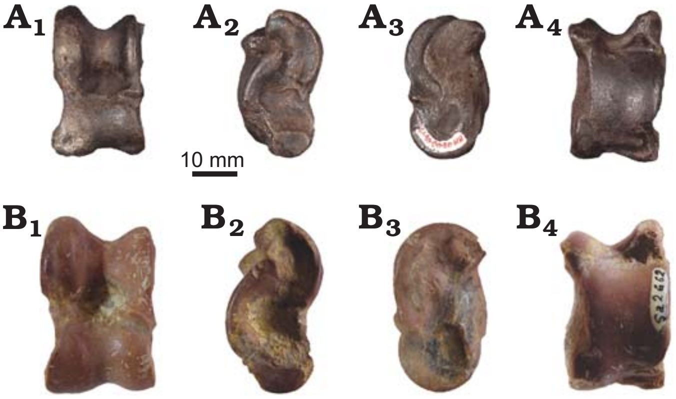

Fig. 4. Right astragalus of the bovid mammals, *Eotragus lampangensis* sp. nov., UPP MM-75 (**A**) and *Eotragus clavatus* (Gervais, 1850), MNHN Sa 2662 (**B**) middle Miocene of Sansan (France), in dorsal (A_1, B_1), lateral (A_2, B_2), medial (A_3, B_3), and plantar (A_4, B_4) views.

The m2 (UPP MM-73; Fig. 3F) closely resembles that of m1, but is distinctly larger (Table 3).

The m3 is represented by an isolated and unworn specimen (UPP MM-74; Fig. 3I), as well as a fragmentary mandible preserving a moderately worn m3 (UPP MM-67; Fig. 3H). UPP MM-74 is rather elongated and bears a poorly developed hypoconulid. The ectostylid is present labially, but the posterior ectostylid is absent. By contrast, UPP MM-67 shows a well-developed hypoconulid and fusion of the posthypocristid and posthypoconulidcristid (Fig. 3H), as well as the well-developed ectostylid and posterior ectostylid. In addition, the anterior and posterior lobes are slightly more robust in UPP MM-67 than in UPP MM-74. Both specimens bear a weakly developed anterior cingulum and are characterized by a moderately flattened lingual wall with weak stylids and lingual ribs. The hypoconulid is low compared to other main conids. The metaconid is more elevated than the entoconid. The internal postprotocristid is attached to pre-entocristid without fusion. The prehypocristid is longer and more developed than the posthypocristid (Fig. 3H). The fossettes are extremely narrow and their labial faces are slightly steeper than their lingual ones.

The single and isolated right astragalus (UPP MM-75; Fig. 4A) is characterized by a strong process on the proximal medial condyle, as well as an asymmetrical distal trochlea bearing a relatively shallow valley. The width of the distal trochlea is equal to its anteroposterior length. The stop facets of the posterior surface are relatively smooth. The astragalus of *Eotragus lampangensis* sp. nov. morphologically resembles that of *E. clavatus* from Sansan, France (Fig. 4B), *E. artenensis* from Corcoles, Guadalajara, Spain (Alférez et al. 1981), and *E. minus* from Dera Bugti, Pakistan, but is larger than the latter two and slightly smaller than in *E. clavatus*.

Geographic and stratigraphic range.—Mae Moh coal mine, Northern Thailand; Nakhaem Formation, coal layers of K and Q, late middle Miocene (13.4–13.2 Ma).

Eotragus cf. *lampangensis*

Fig. 2B–D, Table 2.

Material: Mae Moh coal mine, Northern Thailand; late middle Miocene (13.4–13.2 Ma), Nakhaem Formation, coal layer Q—UPP MM-29, right horn core attached to a portion of the dorsal orbital roof; UPP MM-55, partial right horn core with pedicle; UPP MM-56, fragmentary right horn core.

Description.—UPP MM-29 (Fig. 2B) represents a virtually complete horn core missing only a small part of its apex. In lateral view, the horn core is situated slightly posterior to the orbit and is inclined posteriorly at an angle of about 55° degrees relative to the frontal plane. The horn core is short, conical, and entirely oval in cross section (i.e., transversely compressed) along its entire length (Fig. 2B$_5$, Table 2). The longitudinal axis of the horn core is rather straight, without any torsion. Overall, the surface of the horn core is relatively rough. In lateral view, the anterior surface is moderately concave, whereas posterior one is slightly convex (Fig. 2B$_2$, B$_3$). The lateral surface of the horn core is slightly flatter than the medial one. There is no anterior keel, whereas the posterior keel, originating about 1 cm above the base of the posterior surface and terminating at the apex, is faint. The anterior portion of the pedicle is slightly higher than the posterior one, and its surface is relatively smooth.

UPP MM-55 (Fig. 2C) preserves only the lower part of the horn core with the pedicle and some parts of the orbital roof. The cross section of the horn core is suboval at the base (Fig. 2C$_5$). Both the anterior and posterior surfaces of the preserved basal horn core are relatively flattened and bear no obvious keels. The lateral surface is flatter than the medial one. The surface of the horn core is rough.

The fragmentary horn core represented by UPP MM-56 (Fig. 2D) is also suboval in cross section (Fig. 2D$_5$), with its base being more massive anteriorly than posteriorly. There is no keel on its flattened anterior surface, but a moderately distinct keel is present on its posterior side. The lateral surface of the horn core is more flattened than the medial one. The surface of the horn core is rough.

Remarks.—Both UPP MM-55 and UPP MM-56 are slightly larger than UPP MM-29, probably as a result of size variation within the population. These three horn cores differ from those assigned to *Eotragus lampangensis* sp. nov. in being shorter relative to their basal diameter and oval in cross section, as well as in their more conical shape, straight longitudinal axis, and less concave anterior surface. They further differ in the position of the posterior keel on the posterior surface, the absence of a distinct anterior keel, and their comparatively small size. However, it should be noted that the size difference between these specimens and *E. lampangensis* sp. nov. falls within the range of intraspecific variation shown by *E. clavatus* (Fig. 5), while the morphological differences resemble those between *E. clavatus* from Sansan, France, and *E.* aff. *clavatus* from Tarazona de Aragón, Spain (Table 4). Rather than erecting a new species, we therefore decided to assign the material described here to *E.* cf. *lampangensis*.

Bovidae gen. et sp. indet.

Fig. 3I.

Material: UPP MM-76, left m3, Mae Moh Basin, Northern Thailand; late middle Miocene (13.4–13.2 Ma), Nakhaem Formation, coal layer K.

Description and remarks.—UPP MM-76 (Fig. 3G) is heavily worn, making impossible to assign it to any particular genus. However, the specimen shares several morphological features, such as a selenodont tooth morphology and hypsodont crown, with *Eotragus*. While resembling *E. lampangensis* sp. nov. in the presence of a well-developed ectostylid and posterior ectostylid, UPP MM-76 differs from the other material described here in the extreme width of its anterior portion (transverse diameter of the anterior lobe measured at the base of the tooth crown) and in its poorly developed hypoconulid (Fig. 3G). Taken together, these features may indicate the existence of another bovid taxon in the Mae Moh Basin.

Biogeographic records and comparisons with other *Eotragus* species

European records of *Eotragus*.—*Eotragus clavatus* is one of the oldest known bovids (Ginsburg 1963; Gentry et al. 1999; Solounias and Moelleken 1992a) and is widely distributed among the early to middle Miocene (MN5–MN6) faunas of Serbia (Made et al. 2007; Alaburić and Marković 2010), France (Solounias and Moelleken 1992a; Made et al. 2007; Made 2012), Germany (Rössner 2006; Seehuber 2008), Austria (Ye 1989), and Spain (Mazo et al. 1998, Badiola et al. 2001). The teeth of *E. clavatus* are characterized by their pronounced selenodonty, the presence of an ectostyle on M1, poorly developed or absent lingual cingula, and straight labial walls of the upper molars (Supplementary Online Material, SOM available at http://app.pan.pl/SOM/app60-Suraprasit_etal.SOM.pdf), and differ from those of *E. lampangensis* sp. nov., in the presence of a stronger lingual cingulum on M3 and their smooth enamel surface (SOM). In addition, the horn core of *E. clavatus* (e.g., MNHN Sa 2493; Solounias and Moelleken 1992a) differs from that of *E. lampangensis* sp. nov. in its less distinct anterior keel and the absence of a posterior keel, as well as its larger size (Fig. 5) and oval cross section. Similarly, it differs from *E.* cf. *lampangensis* in its larger size and the absence of a posterior keel, as well as the presence of an anterior keel, and its slightly more concave anterior surface.

Eotragus haplodon (Meyer, 1846) was previously described from the middle Miocene (MN5–MN6, 13.5–15 Ma) localities of Neudorf Sandberg in Slovakia, Göriach and Gamlitz in Austria, and Sansan in France (Thenius 1952; Astibia 1985; Mein 1989; Ye 1989). *E. haplodon* (sensu Ye

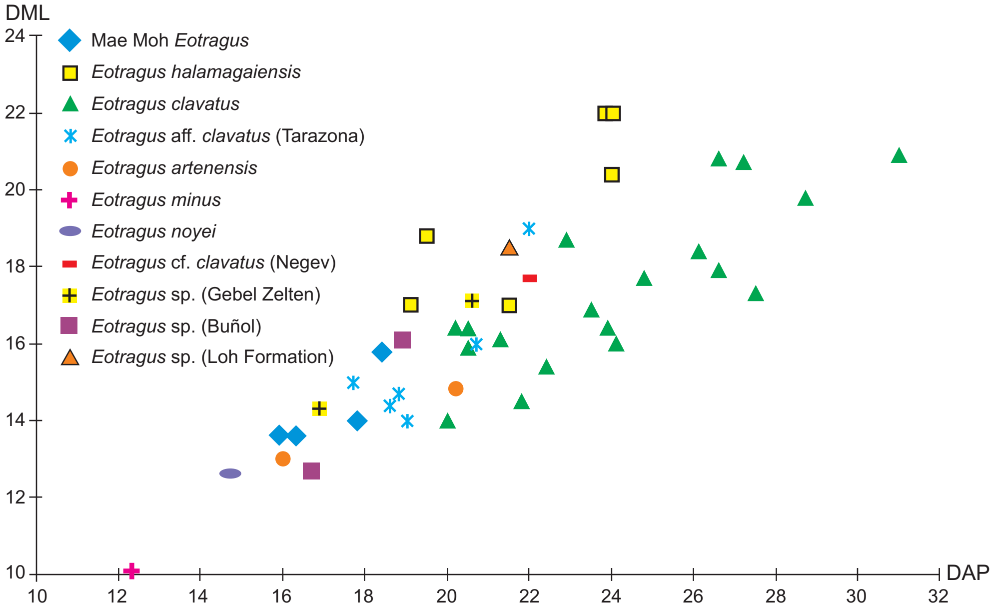

Fig. 5. Scatter diagrams of the basal horn core diameters (DAP, anteroposterior diameter of the horn core and DML, mediolateral diameter of the horn core) of different species of *Eotragus*.

1989) from Göriach, Gamlitz, and Sansan is defined by a large, transversely compressed, and relatively short horn core, larger than that of *E. lampangensis* sp. nov. and approximately equal in size to that of *E. clavatus* (Fig. 5; SOM). *E. haplodon* is further characterized by elongated lower premolars, and rather brachyodont molars with basal pillars (ectostylids) (Ye 1989). Although previously considered to differ from *E. clavatus* in the presence of a more distinct anterior keel and its slightly larger size (Ye 1989), several authors have regarded the two species as being synonymous (Moyà-Solà 1983; Made 1989; Solounias et al. 1995; this paper) or closely related (Made 2012). Furthermore, Made (2012) even cast doubt on the inclusion of the material from Neudorf Sandberg described by Meyer (1846: 471) and Thenius (1952: figs. 55–58) in Bovidae.

Horn cores referred to *Eotragus* aff. *clavatus* (UPV T5.10) from the middle Miocene locality of Tarazona de Aragón, Ebro Basin, Spain (Badiola et al. 2001) resemble *E. lampangensis* sp. nov. in having an anterior keel, a subcircular basal cross section and relatively concave anterior and slightly convex posterior surfaces, as well as in being transversely compressed halfway along their length. However, the specimens of *E. lampangensis* sp. nov. are more slender and longer (compared to their basal diameters) than those from Tarazona de Aragón (Table 4; SOM). By contrast, the horn cores of *E.* cf. *lampangensis* are equal in size to most of the Tarazona specimens (although UPV T5.10 and UPV TE.420 are slightly larger; Fig. 5), but differ from the Spanish material in their lack of an anterior keel and in their more conical shape, as well as their less concave anterior surface (relatively straight in UPV TE.420).

Mazo et al. (1998) described the upper molars (M1–M3) of *E.* cf. *clavatus* from Segovia (MN5), Spain. These teeth are characterized by their rather brachyodont crowns and relatively large size, as well as the apparent absence of an ectostyle. Another isolated M2 was reported from Visnijica, Slanci Formation (15.1–13.25 Ma) of Serbia (Made et al. 2007). This M2 displays a distinct mesostyle and a relatively flat labial wall, thus resembling the M3 of *E. lampangensis* sp. nov. (UPP MM-71), but differs from the latter in having a lower crown.

Eotragus artenensis is one of the oldest known European species reported from the locality of Artenay, France (approximately 18 Ma; MN4), as well as contemporary deposits from the locality of Corcoles, Guadalajara, Spain and the locality of Quinta Do Narigao, Portugal (Ginsburg and Heintz 1968; Alférez et al. 1981; Moyà-Solà 1983; Gentry et al. 1999; Badiola et al. 2001; Made et al. 2007). The teeth of this species are characterized by having a low crown (lower than in *E. clavatus*), a distinct parastyle and mesostyle, a paracone rib, and a metaconule fold in the upper molars, as well as in the presence of relatively wide upper molars (compared to their length), and the lack of both an external postprotocrista in the upper molars and a *Palaeomeryx* fold (external postprotocristid) in the lower molars. *E. lampangensis* sp. nov. differs from *E. artenensis* in having a larger m2 and more hypsodont lower molars, but resembles the latter in the morphology of the M3, except for its more inclined labial walls (in occlusal view) and the absence of a metaconule fold. In addition, the horn core of *E. lampangensis* sp. nov. differs from *E. artenensis* in having a more distinct anterior keel and the presence of a faint posterior keel.

Two complete upper tooth rows of *Eotragus* sp. from MN4 deposits exposed at Can Canals and Sant Mamet, Barcelona (Spain), as well as two fragmentary horn cores from the contemporary locality of Buñol, Valencia (Spain) were reported by Moyà-Solà (1983). The horn cores are poorly preserved, but one of them (IPS BN 20592) is clearly larger than those of *E. lampangensis* sp. nov., and seems to have a more completely circular cross section. Both horn cores are transversely compressed halfway along their length, and display distinct anterior keels.

Table 4. Morphological comparisons of the horn cores of different species of *Eotragus* within the same localities, including *Eotragus clavatus* from Sansan, France (morphotype A: MNHN Sa 1113, Sa 1115, Sa 1183, Sa 1195, and Sa 2514; morphotype B: MNHN Sa 2524, Sa 10780, and Sa 10788), *Eotragus* aff. *clavatus* from Tarazona de Aragón, Spain (UPV T5.10 and UPV TE.420), and *Eotragus lampangensis* sp. nov. (UPP MM-68) and *Eotragus* cf. *lampangensis* (UPP MM-29) from the Mae Moh Basin, Thailand. The full height of the horn core compared to its basal (anteroposterior and mediolateral) diameters was calculated as EH/DAP (< 2.5 = short, 2.5-3 = medium, > 3 = long) and EH/DML (< 3 = short, 3-4 = medium, > 4 = long). See SOM for further details. Abbreviations: DAP, anteroposterior diameter of the horn core; DML, mediolateral diameter of the horn core; EH, full height of the horn core.

	Eotragus clavatus from Sansan		*Eotragus* aff. *clavatus* from Tarazona de Aragón		*Eotragus* from Mae Moh	
	Morphotype A	Morphotype B	UPV T5.10	UPV TE.420	UPP MM-68	UPP MM-29
EH/DAP	medium	short	medium	medium	long	medium
EH/DML	medium to long	short	medium	medium	long	medium
Cross section	oval	circular	subcircular	circular	subcircular	oval
Presence of keels	moderately distinct anterior keel	faint anterior keel	moderately distinct anterior keel	faint anterior keel	distinct anterior keel and faint posterior keel	faint posterior keel
Position of keels	anterior side starting at the base	anterior side starting at the base	anterior side starting at the base	anterior side starting at 1 cm above the base?	anterior side starting at 1 cm above the base and posterolateral side starting at the base	posterior side starting at 1 cm above the base
Horn core axis	slightly curved anteriorly	straight	straight	straight	slightly curved anteriorly	straight
Horn core shape	scimitar-shaped	conical	scimitar-shaped	relatively conical	scimitar-shaped	conical
Anterior and posterior margins in lateral view	relatively concave and slightly convex	straight and slightly convex	relatively concave and slightly convex	slightly concave and slightly convex	relatively concave and slightly convex	moderately concave and slightly convex

African records of *Eotragus*.—In Africa, the occurrence of *Eotragus* is still ambiguous. A horn core (KNM 63.340) (Gentry 1970: pl. 15: 7) from Fort Ternan (13.7 Ma; Pickford et al. 2006) and two partial bovid crania (NHMUK M 15543 and M 15544) from Maboko (15 Ma) (Morales et al. 2003) in Kenya were previously referred to *Eotragus* sp. However, the Fort Ternan specimen, while resembling *E. clavatus* except for its relatively short and broad shaft of the pedicle, is fragmentary and still covered in matrix (Solounias et al. 1995). In terms of its size, the Fort Ternan horn core is approximately equal to that of *E. clavatus* (Gentry 1970) but is larger than the specimens from Mae Moh. Concerning the material from Maboko, NHMUK M 15543, previously considered as belonging to a climacoceratid by Thomas (1984), was referred to the bovid subfamily Hypsodontinae by Morales et al. (2003) in agreement with Gentry (2010), whereas the horn core attached to NHMUK M 15544 is morphologically close to *Homoiodorcas tugenium* (Thomas 1981).

Another *Eotragus* sp. (two horn cores, NHMUK M 26688 and NHMUK M 26689) was reported from the locality of Gebel Zelten, Libya (16.5 Ma) (Hamilton 1973: pl. 13: 1; Mein 1989), but likely does not belong to the genus owing to its medially convergent horn cores and the presence of a slight twist along the horn core axis (Solounias et al. 1995). Moreover, Morales et al. (2003) argued that the horn cores from Gebel Zelten could belong to a hypsodontine based its high pedicle, vertical insertion, and almost circular cross section without any compression. *Eotragus* from Mae Moh differs from those of Gebel Zelten specimens in lacking an anterior keel terminating medial to the supraorbital foramen, in the absence of twisted and medially converging horn cores, and in the anterior widening of the horn core at its base.

Asian records of *Eotragus*.—In Asia, *Eotragus* is represented by the small-sized *E. noyei* from the early Miocene Kamlial Formation (18.3–18.0 Ma) and the early middle Miocene Vihowa Formation (17 Ma), both exposed in Pakistan (Solounias et al. 1995; Raza et al. 2002). *E. lampangensi*s sp. nov. differs from *E. noyei* in having a larger, longer, and more slender horn core with a subcircular cross section and a more concave anterior edge (Fig. 5). In addition, *E.* cf. *lampangensis*. differs from *E. noyei* in having a more conical and slightly more anteriorly concave horn core with no anterior keel.

Eotragus minus, the smallest species, was described from the early Miocene (MN3) of Dera Bugti in Pakistan, and considered to be possibly both older and more archaic than *E. noyei* (Ginsburg et al. 2001; Bibi et al. 2009). *E. lampangensis* sp. nov. differs from this species in having a larger horn core (Fig. 5) with a subcircular cross section, a more distinct anterior keel, and relatively more concave anterior and less convex posterior edges. Similarly, *E.* cf. *lampangensis* differs from *E. minus* in its larger size, conical shape, more concave anterior and less convex posterior edges, and the absence of an anterior keel.

Several teeth, referred to *Eotragus* sp. from the Middle Siwaliks (7–5 Ma) of Hasnot, Punjab, Pakistan (Pilbeam et al. 1977; Barry et al. 2002; Khan et al. 2009), share several features, such as selenodonty, the presence of an ectostylid and an inclined labial wall of the metacone with *E. lampangensis* sp. nov., but are generally smaller than the latter. Additional specimens of *Eotragus* sp. from Pakistan have been reported from the early Miocene deposits of Dhok Bin Mir Khatoon (Khan et al. 2008), the early to middle Miocene Gaj Formation of Sindh (Thomas 1984), and the late Miocene Dhok Bun Ameer Khatoon Formation of Chakwal (Samiullah et al. 2012), indicating a total chronological range of 18.3–5.0 Ma (Lower to Middle Siwaliks; Khan et al. 2009).

Eotragus halamagaiensis was described based on horn cores and teeth from the middle Miocene Halamagai Formation, Xinjiang, China (Ye 1989). Except for its more completely circular cross section, the horn core of *E. halamagaiensis* generally resembles that of *E. clavatus*, but differs from that of *E. lampangensis* sp. nov. in its larger size (Fig. 5), more upright insertion, less distinct anterior keel, and the absence of a posterior keel. It likewise differs from *E.* cf. *lampangensis* in its larger size, more upright insertion, and the lack of a posterior keel.

Eotragus sp. has also been reported from the late early Miocene to early middle Miocene Loh Formation of Central Mongolia, based on a fragmentary skull with an incomplete horn core (Vislobokova and Daxner-Höck 2002), and differs from the Mae Moh material in having a larger pedicle and horn core base (Fig. 5).

Finally, the most convincing evidence of an African species of *Eotragus* is represented by a horn core and two lower premolars (p2 and p4) referred to *E.* cf. *clavatus* from the early middle Miocene deposits (MN5) of Rotem Basin, Negev, in Israel (Tchernov et al. 1987; Gentry 2010; Made 2012). The horn core is similar to *E. clavatus*, but has relatively flattened anterior and posterior surfaces, thus also resembling *E. noyei* (Solounias et al. 1995). In terms of their size, the specimens from Israel are larger than those from Mae Moh.

Discussion

Intraspecific variation.—Numerous specimens (partial skulls, lower jaws, teeth and postcranial elements) of *Eotragus* are known from Sansan in France (see SOM). Solounias and Moelleken (1992a) noticed that some of the horn cores from this locality (MNHN Sa 1183, Sa 1187, and Sa 2535) are shorter and more massive than the others, and that female specimen (MNHN Sa 1034) is apparently hornless (Made 2012), but considered all of the Sansan material as belonging to the single species *E. clavatus*.

Our examination of the horn cores from Sansan revealed a high degree of morphological variation. We thus reflect on the presence of two distinct morphotypes (Table 4). The first (morphotype A) is characterized by being relatively long, transversely compressed (narrower anteriorly and oval in cross section), and either straight or slightly curved anteriorly in lateral view, with a faint anterior keel and no posterior keel. Most of the specimens described by Solounias and Moelleken (1992a) clearly fall into this category (e.g., MNHN Sa 1113, Sa 1115, Sa 1183, Sa 1195, and Sa 2514). By contrast, morphotype B corresponding to some specimens (MNHN Sa 1184, Sa 2524, Sa 10775, Sa 10780, Sa 10787, and Sa 10788 [SOM]) comprises relatively short, straight, and conical horn cores with no anterior or posterior keels, and a symmetrical and triangular outline in lateral view. It is possible that these two morphotypes may reflect different ontogenetic stages, with morphotype B possibly representing a subadult (sensu Made 2012).

In addition to the horn cores, the teeth of *E. clavatus* from Sansan also show a wide range of variation, for example in the presence or absence of cingula on the upper molars, the development of the hypoconulid on m3, or the size differences previously pointed out by Sahnouni et al. (2004), Made et al. (2007), and Made (2012). A similar degree of the horn core (Table 4) and dental variability occurs among the material of *E.* aff. *clavatus* from Tarazona de Aragón (Spain), as well as the specimens from Mae Moh. Thus, although it is relatively easy to distinguish *E.* cf. *lampangensis* from *E. lampangensis* sp. nov. and other members of the genus, the question of whether two distinct species of *Eotragus* may exist at Mae Moh remains open.

Paleoecological and paleoenvironmental adaptations of *Eotragus*.—Dental mesowear and microwear analyses of *Eotragus clavatus* from Sansan (France) and Göriach (Austria), as well as *E.* aff. *clavatus* from the Calatayud-Daroca Basin (Toril 3A) of Spain showed both taxa to be generalized browsers, similar to *Tragelaphus strepsiceros* (Solounias and Moelleken 1992b; DeMiguel et al. 2011; Merceron et al. 2012). Carbon and oxygen isotopes extracted from the tooth enamel of Mae Moh herbivores (including two bovid samples here identified as *E. lampangensis* sp. nov.) indicate that they inhabited a variety of habitats ranging from grasslands to woodlands, characterized by low-seasonal climate related to swamp deposits (Chaodumrong 1985; Suraprasit et al. 2014). Specifically, the stable carbon isotope values of *E. lampangensis* sp. nov. (-11.5‰ and -10.7‰) (Suraprasit et al. 2014: fig. 7) suggest that this species lived in an ecotone between grassland and forest, and occupied more closed habitats than the contemporary cervid *Lagomeryx manai*, which displays slightly more brachyodont crowns. This interpretation is rather consistent with *E. lampangensis* sp. nov. being a browser, as having been suggested for the European *E. clavatus* (Solounias and Moelleken 1994; DeMiguel et al. 2011; Merceron et al. 2012), but may also indicate a degree of ecological differentiation. The latter may have resulted from, or have given rise to, the high degree of diversity (more than 11 known species) of the Mae Moh herbivore assemblage.

Conclusions

A hitherto unknown archaic bovid, *Eotragus lampangensis* sp. nov., was present in Northern Thailand between 13.4–13.2 Ma. The discovery of *Eotragus* at Mae Moh considerably extends the geographic range of this genus during the late middle Miocene. As is the case in Europe and Pakistan (Gentry et al. 1999), *Eotragus* represents the earliest record of bovids with true horn cores in Southeast Asia. Carbon isotope analysis of tooth enamel indicates that *Eotragus lampangensis* sp. nov. inhabited an ecotone between open grassland and closed forest habitats. The occurrence of *Eotragus* in Thailand raises questions regarding the role of Southeast Asia in the adaptive radiation of bovids during the Late Neogene.

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