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A new genus of tragulid ruminant from the early Miocene of Kenya

ISRAEL M. SÁNCHEZ, VICTORIA QUIRALTE, JORGE MORALES, and MARTIN PICKFORD



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We re-describe the type material of the tiny African tragulid "*Dorcatherium*" *moruorotensis* from the early Miocene of Kenya, and erect the new genus *Afrotragulus*, the first African Miocene tragulid that does not belong to *Dorcatherium*. This new taxon is characterized by its elongated and stretched lower molars with a unique morphological dental pattern that strongly contrasts with that of *Dorcatherium*. We additionally include the former "*Dorcatherium*" *parvum*, also a small species from the early Miocene of Kenya, into the new genus *Afrotragulus* as *Afrotragulus parvus*, figuring it for the first time. We discuss the usefulness of body size as the main taxonomical criterion for studying the Tragulidae. And finally we comment on the taxonomical and morphological diversity of tragulids in the moment of their sudden early Miocene re-apparition and expansion in the Old World.

Key words: Mammalia, Ruminantia, Tragulidae, *Afrotragulus*, *Dorcatherium*, Miocene, Moruorot Hill, Rusinga Island, Kenya, Africa.

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Introduction

The Tragulidae comprise small non-pecoran ruminants that include the smallest living cetartiodactyls (see e.g., Janis 1984; Scott and Janis 1993; Hassanin and Douzery 2003; Marcot 2007; Agnarsson and May-Collado 2008). As the most primitive representatives of the extant Ruminantia, tragulids are less advanced than living pecorans in almost all of their morphological and physiological features (Dubost 1965; Kay 1987; Métais et al. 2001; Rössner 2007). They survive as relics in the Old World tropical belt: the Asian spotted and yellow-striped chevrotains of the genus *Moschiola* live in India and Sri Lanka, the mouse-deer *Tragulus* inhabits Southeast Asia and the Philippines, and the monotypic water chevrotain *Hyemoschus* ranges in Africa from Sierra Leona to Uganda (Grubb 1993; Nowak 1999; Meijard and Groves 2004; Groves and Meijard 2005; Rössner 2007). As noted by Gentry et al. (1999) the disjunct distribution of the extant Tragulidae probably reflects the fragmentation of the Miocene range of the group, previously extending throughout Eurasia and Africa.

Tragulids belong to an ancient radiation of basal ruminants often known as the paraphyletic "Traguloidea" (or "Tragulina" sensu Webb and Taylor 1980), which were quite common during the Paleogene (see Métais and Vislobokova 2007). All "traguloids" except the tragulids became extinct before the Neogene. The early evolutionary history of tragulids is extremely poorly known. The late Eocene taxon *Archaeotragulus krabiensis* from Thailand is usually regarded as the most ancient record of the Tragulidae (Métais et al. 2001; Tsubamoto et al. 2003; Métais and Vislobokova 2007), but apart from *Archaeotragulus*, no tragulid remains have been recovered from Paleogene deposits. We consider that the assignation of the primitive ruminant *Krabitherium waileki* Métais, Chaimanee, Jaeger, and Ducrocq, 2007, from the late Eocene of Thailand, to the Tragulidae needs to be better substantiated, since the purported tragulid characters presented by the authors are not clear, and, as it is actually implied in the paper (see Métais et al. 2007: 493), the tragulid affinities of *K. waileki* are only tentatively suggested. The Tragulidae became abundant and diverse in the early Miocene, when they re-appeared documented by a good fossil record from Africa (Whitworth 1958; Hamilton 1973; Pickford 2001, 2002; Quiralte et al. 2008), South Asia (Mein and Ginsburg 1997; Ginsburg et al. 2001), and Europe (Mein 1989; Gentry et al. 1999) that reveals a surprisingly sudden and widespread distribution of the group (Gentry et al. 1999; Rössner 2007). From this moment on, tragulids extended throughout the Old World.

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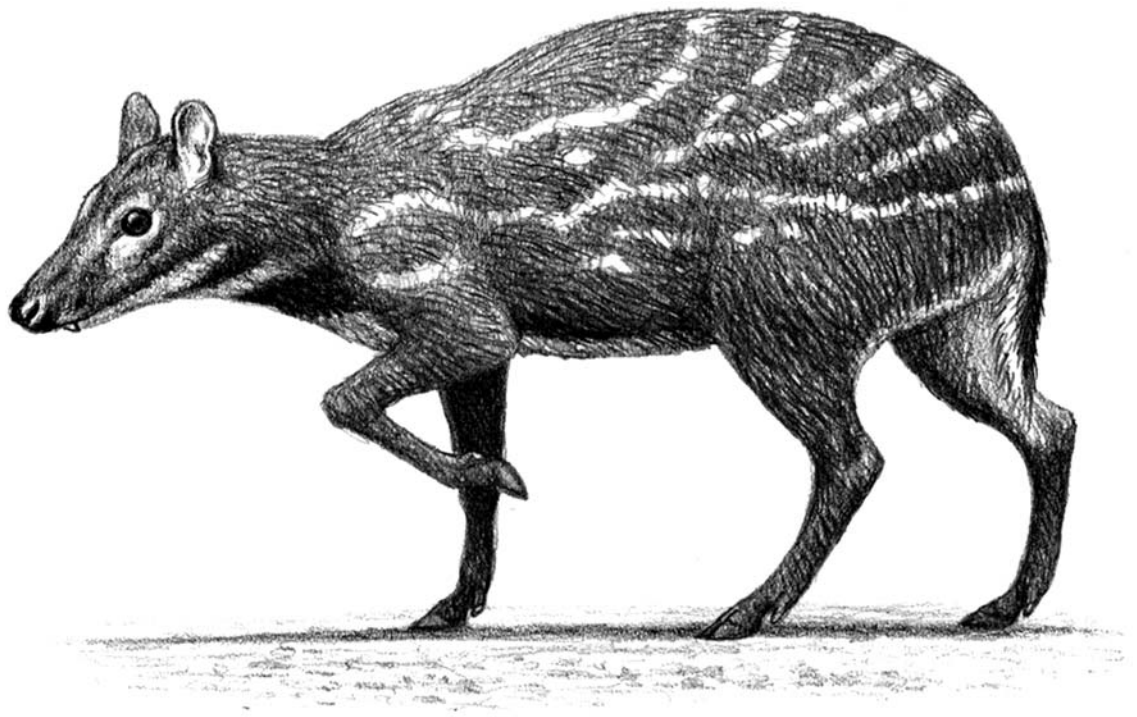


Fig. 1. Life reconstruction of an adult male *Dorcatherium*. Illustration by Mauricio Antón.

As pointed out by Rössner (2007), the majority of fossil tragulids and the totality of fossil African species have been included in the extinct genus *Dorcatherium* (Fig. 1), which was first described from the late Miocene of Europe with the type species *Dorcatherium naui* Kaup and Scholl, 1834. This genus embraces the major part of the Miocene–Pliocene diversity of the Tragulidae, with 22 recognized species (see Rössner 2007: table 16.1), exceeding other genera such as *Siamotragulus* Thomas, Ginsburg, Hintong, and Suteethorn, 1990, *Dorcabune* Pilgrim, 1910, and *Yunnanotherium* Han, 1986 by far in specific diversity. *Dorcatherium* has a widespread biogeographic distribution that covers Africa and Eurasia, ranging in Africa from the early Miocene to (probably) the early Pliocene (Arambourg 1933; Whitworth 1958; Janis 1984; Fahlbusch 1985; Gaur 1992; Gentry et al. 1999; Pickford 2001; Morales et al. 2003; Pickford et al. 2004; Rössner 2007; Quiralte et al. 2008). As noted by Rössner (2007), *Dorcatherium*, as it is defined so far, includes a varied array of buno-selenodont and selenodont tragulids that show a great degree of variation in both body size and dental morphology. Specifically, this body size variability has been classically over-used to diagnose and assign *Dorcatherium* species (see Arambourg and Piveteau 1929; Colbert 1935; Withworth 1958; West 1980; Gaur 1992; Pickford 2001, 2002; Morales et al. 2003; Quiralte et al. 2008 among others), with much less emphasis put on the description of morphologically diagnostic characters (although some dental and postcranial characters were discussed by Morales et al. 2003; Geraads et al. 2005; Hillenbrand et al. 2009). Although body size is one of the biological factors that defines a species, its use as the only (or main) taxonomic criterion presents some critical drawbacks. For example, this practice can lead to the expansion of the morphological variability of a given species to non-real limits; also, it can obscure phenomena such as the existence of equally sized but morphologically divergent related species, casting uncertainty over our knowledge of the evolutionary history of a given lineage (see Sánchez et al. 2009 for a good example regarding moschid pecorans). The inclusion of a number of species in *Dorcatherium* that depart morphologically in a broad manner from the type species *D. naui* and that, in some cases, embrace a morphological variability nearly equivalent to that observed between extant *Hyemoschus* and *Tragulus*/*Moschiola* is becoming highly untenable. In the context of comparative morphology within Tragulidae the morphological diversity seen in *Dorcatherium* strongly suggests that this genus, as defined so far, is really a paraphyletic assemblage of diverse species that includes true *Dorcatherium* along with several other non-*Dorcatherium* forms. It is very clear that, as noted by Rössner (2007) among other authors, the genus *Dorcatherium* is in need of a deep morphological revision, to diagnose and extract all those taxa that are morphologically divergent in a significant way from the type species *D. naui*.

Although a complete revision of *Dorcatherium* lies beyond the scope of this paper, the aim of this work is to present our first steps of such a revision regarding the early Miocene African *Dorcatherium*. Fossils of a minuscule tragulid from Moruorot Hill (Northern Kenya) found during the year 2000 field campaign of the Kenya Palaeontology Expedition were described by Pickford (2001) and assigned to the new species

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"*Dorcatherium*" *moruorotensis*. In this paper we re-describe the remains of this ruminant, making special emphasis on the comparative morphology of its lower cheek teeth, and reconsider its taxonomic assignment, including it in the new genus *Afrotragulus*. We also re-describe, discuss and figure the type material of "*Dorcatherium*" *parvum* Withworth, 1958, including previously unpublished specimens, and re-assess its taxonomic adscription, assigning it to *Afrotragulus* as *A. parvus*.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BMNH and NHM, Natural History Museum, London, UK; CMK, Community Museums of Kenya, Nairobi, Kenya; MNCN-CSIC, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; UM, Uganda Museum, Uganda; UMZC, University Museum of Zoology, University of Cambridge, Cambridge, UK.

Materials and methods

The type materials of *Afrotragulus moruorotensis* (Pickford, 2001) and *A. parvus* (Withworth, 1958) have been compared with *Siamotragulus sanyathanai* Thomas, Ginsburg, Hintong, and Suteethorn, 1990, the type species of *Dorcatherium* (*D. naui* from Eppelsheim, MN 9) as well as the Miocene African *Dorcatherium* species from Namibia described by Morales et al. (2003) and Quiralte et al. (2008). The type series of *A. moruorotensis* is curated by the CMK and the NHM (the paratype specimens BMNH M82380l and BMNH M82382). All the studied fossils of *A. parvus*, including the type series and additional previously undescribed material, are curated by the NHM. The material of *D. naui* studied in this paper comprises a complete skull and mandible (BNHM M40432), originally studied and figured by Kaup (1839: pl. 23a and pl. 23b: 3). This specimen belongs to the type series from Eppelsheim and it is stored in the NHM. The holotype of *D. naui* (a right hemimandible figured by Kaup (1839: pl. 23: 1) is lost and only a cast is available at the NHM, but it is nearly useless for comparison purposes.

Regarding the extant tragulid collections, we examined the following material pertaining to *Hyemoschus, Moschiola* and *Tragulus* stored in the MNCN-CSIC, the UMZC, and the AMNH: *Hyemoschus aquaticus* MNCN-CSIC 18947 (young female), *Moschiola meminna* private collection Jan Van der Made (Madrid) (adult female), *Tragulus javanicus* UMZC H15071 (adult male), *Hyemoschus aquaticus* AMNH 53646 (adult male), *Moschiola meminna* AMNH 240826 (adult female), *Moschiola meminna* AMNH 163184 (adult female), *Moschiola meminna* AMNH 32652 (adult male), *Moschiola meminna* AMNH 200098 (adult male), *Tragulus napu* AMNH 103694 (adult male), *Tragulus napu* AMNH 103977 (adult male), *Tragulus napu* AMNH 106292 (young female), *Tragulus javanicus* AMNH 102078 (adult male).

Anatomical definitions.—We use the terminology of Azanza (2000: 47, figs. 14, 15) for nomenclature of the dentition (English version in Sánchez and Morales 2008: fig. 3). We follow the nomenclature of Janis (1987) and Geraads et al. (1987) to designate some key lower molar structures of tragulids. The *Dorcatherium*-fold is the fold that occurs on the linguo-distal side of the metaconid. The *Tragulus*-fold is the fold situated on the distal side of the protoconid, basally related to the pre-hypocristid and linked to the post-protocristid (probably not homologous with the pecoran *Palaeomeryx*-fold; see Métais et al. 2001). Both the *Dorcatherium*-fold and the *Tragulus*-fold form the "M"-structure, which characterizes the Tragulidae.

Systematic paleontology

Mammalia Linnaeus, 1758

Cetartiodactyla Montgelard, Catzeflis and Douzery, 1997

Ruminantia Scopoli, 1777

Tragulidae Milne-Edwards, 1864

Genus *Afrotragulus* nov.

Type species: Afrotragulus moruorotensis (Pickford, 2001). Moruorot, Turkana District, Kenya; early Miocene.

Etymology: After its home continent Africa and the family name Tragulidae.

Diagnosis.—Tragulids with narrow and elongated selenodont lower molars with well developed and vertically expanded cristids, except post-entocristid, and flat lingual cusps. Differing from other tragulids in having enlarged and wide central valley; loss of contact between the pre-hypocristid and the distal part of the anterior lobe with presence of interlobular bridge; contact between pre-hypocristid and pre-entocristid; presence of a reduced and round-shaped *Dorcatherium*-fold; and upper molars with heavy protoconal cingulum and absent metaconule cingulum. Differing also from *Dorcatherium*, *Dorcabune*, and *Hyemoschus* in having mesially closed trigonid due to the anterior expansion of both the pre-protocristid and the pre-metacristid, that contact in an anterior acute angle. From *Dorcatherium*, *Dorcabune*, *Hyemoschus*, *Yunnanotherium*, and *Siamotragulus* in having a strong reduction of the "M"-structure due to the complete absence of *Tragulus*-fold (this structure is present sometimes in *Moschiola* and *Tragulus*). And from *Yunnanotherium*, *Moschiola*, and *Tragulus* in having a elongated posterior wing of the p4, with a bifurcation that spreads out from the central conid, instead of being very short and starting beneath the central conid.

Referred species.—*Afrotragulus parvus* (Withworth, 1958).

Stratigraphic and geographic range.—Late early Miocene (16.8–17.5 Mya) of Kenya. It was probably already present in the basal early Miocene of Namibia (19 Mya, Faunal Set I) and in the late early Miocene of Uganda (see Discussion).

Afrotragulus moruorotensis (Pickford, 2001)

Fig. 2.

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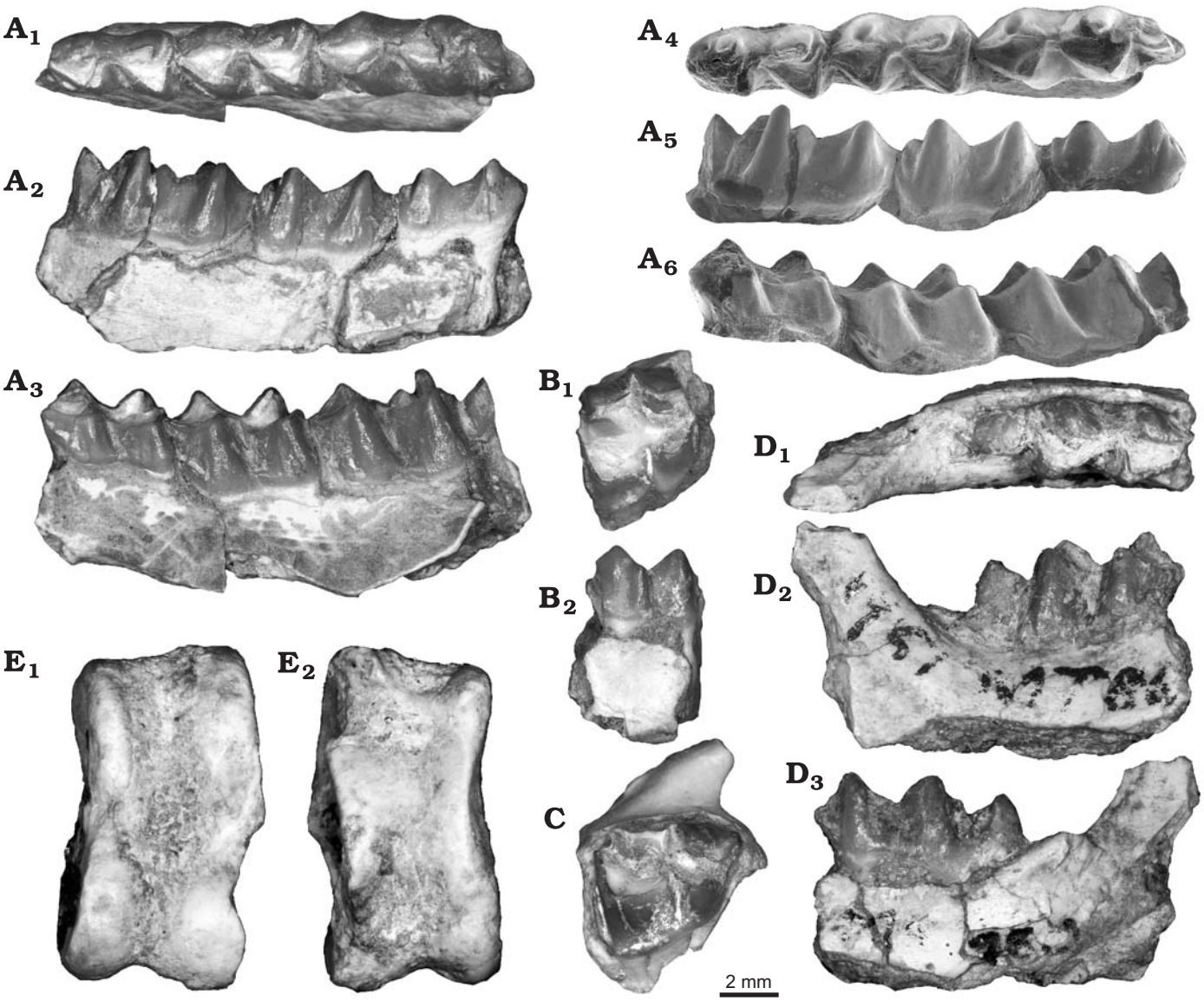


Fig. 2. Tragulid ruminant *Afrotragulus moruorotensis* (Pickford, 2001), Moruorot, late early Miocene of Kenya. **A**. Multi-focus photographs (A_1–A_3) and SEM (A_4–A_6) micrographs of the holotype Mor1'2000, left hemimandible with m1–m3, in occlusal (A_1, A_4), lingual (A_2, A_5) and buccal (A_3, A_6) views; **B**. Multi-focus photographs of the paratype CMK Mor 1'2000, fragment of left maxilla with M2 in occlusal (B_1) and buccal (B_2) views. **C**. Multi-focus photograph of the paratype CMK Mor 1'2000, fragment of left maxilla with M3, in occlusal view. **D**. BMNH M82380, right hemimandibular fragment with m3 in occlusal (D_1), buccal (D_2) and lingual (D_3) views. **E**. BMNH M82382, left astragalus, in dorsal (E_1) and plantar (E_2) views.

2001 *Dorcatherium moruorotensis* Pickford, 2001: 438, fig. 1.

Type material: Holotype: CMK Mor 1'2000, left hemimandible with m1–m3 (Pickford 2001: fig. 1, table 1). Paratypes: Fragment of left maxilla with M2 and fragment of left maxilla with M3, both pertaining possibly to the same individual as the holotype (Pickford 2001: fig. 1, table 1) and with the same catalogue number CMK Mor 1'2000; BMNH M82380 (right hemimandibular fragment with m3) and BMNH M82382 (left astragalus), both from same locality as the holotype (Pickford 2001: table 1).

Type locality: Moruorot, Turkana District, Kenya (Pickford 2001).

Type horizon: The Moruorot localities lie within the lower part of the Kalodirr Member of the Lothidok Formation, early Miocene ca. 16.8–17.5 Mya (Boschetto et al. 1992).

Emended diagnosis.—*Afrotragulus* with very elongated and narrow lower molars that show very mesio-distally enlarged and shallow central valley; almost continuous lingual wall due to both the great vertical development of the cristids and the alignment of the cusps; very flat lingual wall of the metaconid; very developed cristids that unite all cusps, with the exception of the distal part of the entoconid; developed post-hypocristid in the m1–2, which almost reach the linguo-distal corner of the teeth.

Description

Mandible and lower molars.—The mandible fragment of the holotype lacks the ventral border, nevertheless the mandible seems to be low as is typical in tragulids. The lower molars of *Afrotragulus moruorotensis* (Fig. 2A, D) are elongated and narrow. The distal lobe of both m1 and m2 is broader than the

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anterior lobe. The buccal cusps are crescent shaped. The metaconid is very flat and the cristids are high. The elongation of the lower molars enlarges the triangular central valley mesio-distally, making it markedly broad. This elongation cuts the contact between the pre-hypocristid and the anterior lobe. Moreover, the pre-hypocristid in *Afrotragulus* contacts the inner wall of the pre-entocristid. The cristids are very developed for a tragulid except the post-entocristid, which is absent, and unite all the main cusps at a medium degree of molar wear. Both the height and the extension of the cristids make the lower molars of *Afrotragulus moruorotensis* very selenodont for a tragulid. The *Dorcatherium*-fold is short and rounded, and the *Tragulus*-fold is absent; consequently, the "M"-structure is poorly developed. The entoconid is placed slightly forward with respect to the hypoconid. The post-hypocristid extends lingually but does not completely reach the disto-lingual corner of the tooth. There is no ectostylid. The anterior cingulid is strongly developed. The posterior cingulid is also robust in both the m1 and m2. Although part of the buccal and distal surfaces of the third lobe of the m3 are missing, this lobe is well developed, being typically tragulid in morphology: the hypoconulid has a strongly pointed tip and the lobe is linguo-distally open.

Upper molars.—The upper molars of *Afrotragulus moruorotensis* (Fig. 2B, C) have broad and low cusps with strongly developed mesostyle and buccal ribs. However, the cristae are somewhat longer than in *Dorcatherium*. The post-protocrista is short, but the pre-metaconulecrista is well developed. As occurs in *A. parvus* (as noted by Withworth 1958) *A. moruorotensis* has a strong lingual cingulum in the base of the protocone, and lacks an entostyle.

Astragalus.—The postcranial skeleton of *Afrotragulus* is poorly known. The astragalus (BMNH M82382, Fig. 2E) looks rather narrow and slender, with a markedly inclined and triangular proximo-plantar facet for the calcaneum.

Stratigraphic and geographic range.—"*Dorcatherium*" *moruorotensis* has been cited from Rusinga, Karungu, Arongo Uyoma and Mfwangano (Kenya, lower Miocene; Pickford 2001). A form assigned to "*Dorcatherium*" sp. cf. "*Dorcatherium*" *moruorotensis* has been cited from the lower Miocene of the Sperrgebiet, Namibia (Quiralte et al. 2008; see Discussion).

Afrotragulus parvus (Withworth, 1958)

Fig. 3.

1958 *Dorcatherium parvum* Withworth, 1958: 11–14.
2002 *Dorcatherium parvum* Pickford, 2002: 88: pl. 1: 2–4.

Type material: Holotype: BMNH M29514, left hemimandible with m1–m3 (Withworth 1958). Paratypes: Withworth (1958) does not specify paratypes, and some of the original specimens are not currently located. We consider the specimens from Rusinga localities listed and described by Withworth (1958: tables 5, 6) as the paratypes of the species. We exclude the specimens BMNH 1171.50 (Kathwanga locality) and BMNH R.846.48 (Rusinga locality; see Discussion).

Referred specimens: BMNH M82689, left hemimandibular fragment with m1–m2; BMNH M82690, hemimandibular fragment with m2; BMNH M82686, left maxillar fragment with P4–M3; BMNH M82687 and BMNH M82688, right astragali (measurements in Tables 1, 2; all from Rusinga localities; see Discussion).

Table 1. *Afrotragulus parvus*, Rusinga Island, late early Miocene of Kenya. Dental measurements of the new specimens described in this paper (the measurements of the type series appear in Whitworth 1958). Measurements in millimeters.

Specimen	Dental piece	Length	Width
BMNH M82689	m1	4.9	2.59
	m2	6.01	3.15
BMNH M82690	m2	6.49	3.24
BMNH M82686	M1	5.05	4.45
	M2	5.61	5.63

Table 2. *Afrotragulus parvus*, Rusinga Island, late early Miocene of Kenya. Measurements of the new astragali described in this paper. Measurements in millimeters.

Specimen	Length	Proximal width	Middle width	Anteroposterior width
BMNH M82687	12.65	6.29	6.25	6.44
BMNH M82688	11.5	5.65	6.25	6.13

Type locality: Rusinga localities (Kathwanga series, Hiwegi beds, Kiahera series), Rusinga, Western Kenya (Withworth 1958).

Type horizon: Early Miocene ca. 17.5 Mya (Withworth 1958; Pickford and Senut 2003). Withworth (1958) does not specify a horizon for the holotype specimen.

Emended diagnosis.—*Afrotragulus* differing from the type species in its larger size and in some morphological characters of the lower molars: shorter post-hypocristid in the m2; weaker posterior cingulid; less vertically developed cristids; less aligned lingual cusps; and entoconid located almost in front of the hypoconid.

Description

Mandible and lower molars.—As noted by Withworth (1958) the mandible of *A. parvus* is low and narrow as is typical of tragulids. The elongated and narrow lower molars of *A. parvus*, with their well-marked selenodonty and high cristids are very similar to those of the type species (Fig. 3A–C, E, F). Both the separation between the pre-hypocristid and the anterior lobe and the contact of the pre-hypocristid with the pre-entocristid are very clear. The post-hypocristid in the m2 is not as developed as in *A. moruorotensis*. The *Dorcatherium*-fold is rounded and poorly developed, and the *Tragulus*-fold is absent. The entoconid is located almost in front of the hypoconid, whereas is displaced in the type species. The lingual cusps are not aligned, at least not at the level of *A. moruorotensis*. The posterior cingulid is less developed than that of the type species. The anterior cingulid is strong and there are no ectostylids.

Upper molars.—The upper molars of *A. parvus* are very similar to that of the type species (Fig. 3D). The molars are more selenodont than those of *Dorcatherium*. The lingual ribs are strong and the mesostyle is well developed. The post-proto-

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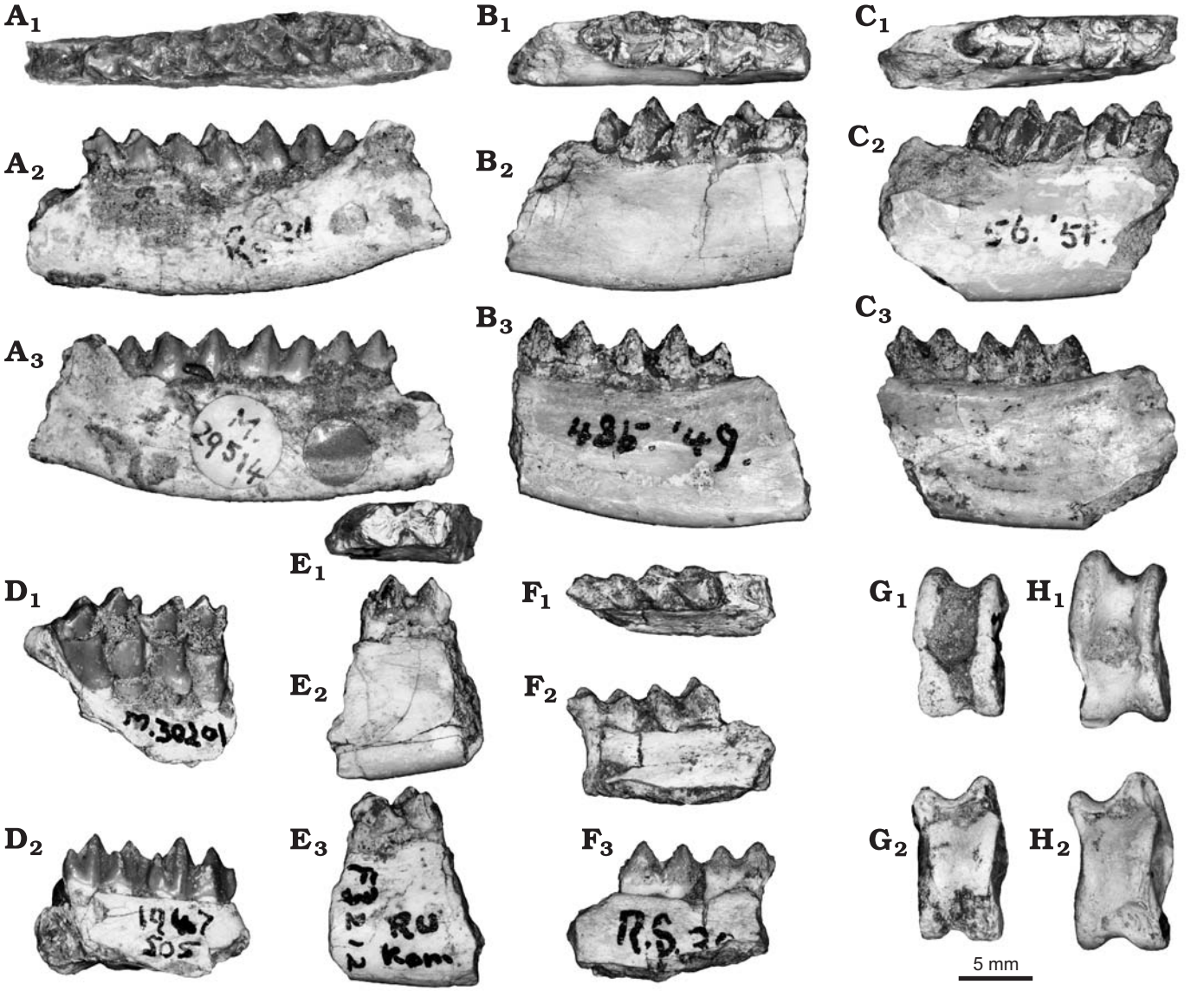


Fig. 3. Selected specimens of tragulid ruminant *Afrotragulus parvus* (Withworth, 1958), Rusinga Island, late early Miocene of Kenya. **A**. Holotype BMNH M29514, left hemimandible with m1–m3, in occlusal (A_1), buccal (A_2) and lingual (A_3) views. **B**. Paratype BMNH 485.49, right hemimandibular fragment with m2–m3, in occlusal (B_1), buccal (B_2) and lingual (B_3) views. **C**. Paratype BMNH 56.51, right hemimandibular fragment with m2–m3, in occlusal (C_1), buccal (C_2) and lingual (C_3) views. **D**. Paratype BMNH M30201 (BMNH 505.47 in Withworth 1958: table 6), right maxillary fragment with M2–M3, in linguo-occlusal (D_1) and buccal (D_2) views. **E**. BMNH M82690, left hemimandibular fragment with m2, in occlusal (E_1), lingual (E_2) and buccal (E_3) views. **F**. BMNH M82689, left hemimandibular fragment with m1–m2, in occlusal (F_1), buccal (F_2) and lingual (F_3) views. **G**. BMNH M82688, right astragalus, in dorsal (G_1) and plantar (G_2) views. **H**. BMNH M82687, right astragalus, in dorsal (H_1) and plantar (H_2) views.

crista is short, but the pre-metaconulecrista is well elongated, almost reaching the internal side of the buccal wall. The protoconal cingulum is strong, but it is lost in the metaconule. There is no entostyle.

Astragalus.—The astragali BMNH M82687 and BMNH M82688 are extraordinarily similar to the specimen BMNH M82382 from Moruorot; they are narrow and tall, with a triangular shaped proximo-plantar facet for the calcaneum (Fig. 3G, H).

Stratigraphic and geographic range.—"*Dorcatherium*" *parvum* has been cited from the late early Miocene of the Napak Member in Uganda (Pickford 2002). Also a form described as "*Dorcatherium*" sp. cf. "*D*." *parvum* has been cited in the basal early Miocene of Langental, Namibia (Quiralte et al. 2008). See Discussion.

Discussion

In his description of "*Dorcatherium*" *parvum*, Withworth (1958) already noted that this species seemed "to be a somewhat advanced form" (Withworth 1958: 13). The characters of the lower dentition of *Afrotragulus* make it, in fact, truly remarkable and clearly different from any other described

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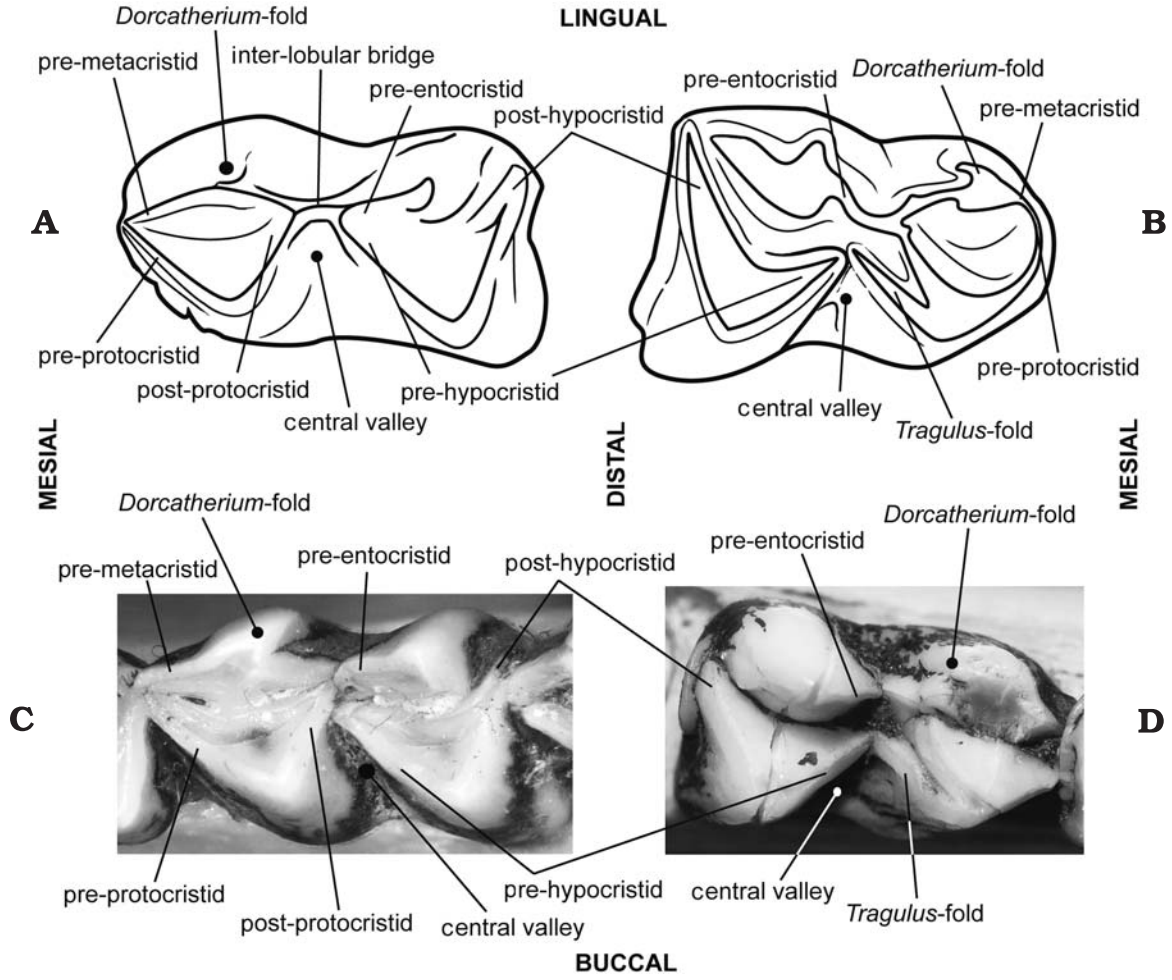


Fig. 4. *Afrotragulus moruorotensis* (Pickford, 2001) and *Dorcatherium naui* Kaup and Scholl, 1834, type species of each respective genus, late early Miocene of Kenya and Eppelsheim (Germany), respectively. Also below *Moschiola meminna* Erxleben, 1777 and *Hyemoschus aquaticus* Ogilby, 1841 (extant tragulids). **A**. Drawing of *A. moruorotensis*, m2 of the holotype CMK Mor 1'2000, showing the main characters discussed in the text. **B**. Drawing of *D. naui*, m2 of the right mandible of the specimen BMNH M40432 (Eppelsheim; the holotype is lost, see Hillenbrand et al. 2009), showing the main characters discussed in the text. **C**. *Moschiola meminna*, left m2 (private collection Jan van der Made, Madrid). **D**. *Hyemoschus aquaticus*, right m1 of the specimen MNCN-CSIC 18947. Note the main morphological features that characterize the lower molars of *Afrotragulus* in occlusal view (**A**), differentiating it from *Dorcatherium* (**B**) and the extant selenodont (**C**) and bunoselenodont (**D**) tragulids: enlarged cristids, main cusps with flat internal walls, enlarged and triangular central valley, separated mesial and distal lobes, presence of interlobular bridge that extends between the post-metacristid and the pre-entocristid (note that the lobes in *Moschiola* are connected though there is no *Tragulus*-fold present), incomplete "M"-structure, short *Dorcatherium*-fold. Note also the clear differences in the mesial closing of the trigonid: whereas in *Afrotragulus* (**A**) the pre-metacristid and the pre-protocristid extend forward contacting in a marked angle, *Dorcatherium* (**B**) presents a hyper-developed and curved pre-protocristid that contacts with a very short pre-metacristid, forming a well developed mesial platform. Drawings not to scale.

tragulid. We summarize in the Fig. 4 the key morphological characters of the lower molars that clearly distinguish between *Afrotragulus* and *Dorcatherium*.

It has been stated that the presence of the "M"-structure might be the most reliable dental feature for recognizing a tragulid, at least the most primitive representatives of the group (Métais and Vislobokova 2007). This structure is very clear in genera such as *Dorcatherium*, *Hyemoschus*, *Dorcabune*, and *Siamotragulus*, but it becomes diffused in *Yunnanotherium*, *Tragulus*, and *Moschiola*, and totally breaks down in *Afrotragulus*. The loosening of the "M"-structure in *Afrotragulus* derives from the shortening of the *Dorcatherium*-fold and the loss of the *Tragulus*-fold. All the studied specimens of both *Afrotragulus moruorotensis* and *A. parvus* totally lack the *Tragulus*-fold, showing a clean posterior wall of the protoconid. Withworth (1958) claimed that this structure appeared in some specimens of "*Dorcatherium*" *parvum*. However, the examination of specimens such as the mandibular fragments BMNH 1171.50 from Kathwanga and BMNH R.846.48 from Rusinga (Withworth 1958: table 5), that still have a *Tragulus*-fold, a complete "M"-structure, bunoid cusps, short pre-metacristid and a well developed anterior trigonid "platform", demonstrates that they belong in fact to a *Dorcatherium* species larger than *A. parvus* and morphologically different. Thus, *Afrotragulus* seems to be the only tragulid that totally lost the *Tragulus*-fold, since both *Tragulus* and *Moschiola* can sometimes show a weak fold behind the protoconid that connects with the pre-hypocristid (typical of tragulids). The *Dorcathe-*

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rium-fold in *Afrotragulus* is much shorter and more rounded than that of *Dorcatherium* (although it can be somewhat rounded in some *Dorcatherium* species), *Siamotragulus*, *Dorcabune*, *Yunnanotherium*, *Hyemoschus*, *Moschiola*, and *Tragulus*. In all these genera, the *Dorcatherium*-fold is flatter and runs parallel to the lingual wall of the metaconid, generating a marked furrow. However, although morphologically unique, the *Dorcatherium*-fold of *Afrotragulus* still can be recognized as such, since its bucco-distal side still faces the lingual wall of the metaconid, contrary to the condition observed in the metaconid rib of pecorans. Although the "M"-structure can still be considered the most reliable feature for recognizing tragulid lower molars, advanced forms such as *Afrotragulus* and the Asian extant genera demonstrate that it has been secondarily reduced and/or lost several times in the course of the evolutionary history of the group.

Tragulids comprise bunoselenodont and selenodont forms, with a distinct group of general features characterizing both types of dentition. We focus here on the lower molars, since they are the basis of our systematic discussion on *Afrotragulus*. Bunoselenodont tragulids have rounded cusps with more or less developed cristids, whereas selenodont forms have, in addition to enlarged cristids, non-rounded cusps with flat internal walls. Thus, selenodonty in tragulids (as in all ruminants) is determined by the longitudinal extension and vertical development of the cristids, and also by the flattening of the main cusps. The cristids of the bunoselenodont taxa (*Dorcatherium, Dorcabune*, and *Hyemoschus*) are variable in their vertical and longitudinal extension within certain limits. As a result, the lower molars of these forms have very pointed main cusps. Specifically, *Dorcatherium* can show a variable amount of well-developed "selenodonty" (i.e., extension of the cristids, as in *D. naui* and *D. guntianum*) but does not show the characters of fully selenodont forms as *Afrotragulus*. The type species *D. naui* from Eppelsheim (Germany) shows clearly bunoselenodont lower molars (despite its somewhat expanded cristids), with a well-developed "M"-structure. The *Dorcatherium*-fold is somewhat short but flat. The *Tragulus*-fold is well developed. Although the cristids are more developed than in several other *Dorcatherium* forms, the cusps are clearly bunoid with curved internal walls. Also the pre-protocristid is very well developed; it turns lingually and connects with the very short pre-metacristid, mesially closing the trigonid and developing an anterior round "platform" (Fig. 4). The Miocene African *Dorcatherium* (*D. songhorensis*, *D. pigotti*, *D. iririensis*, and *D. chappuisi*; see Arambourg 1933; Withworth 1958; Pickford 2002; Morales et al. 2003; Quiralte et al. 2008), albeit showing less-developed cristids than *D. naui*, consistently show the general lower molar plan of the type species from Eppelsheim: bunoselenodont lower molars with bunoid main cusps and mesial closing of the trigonid conducted by the hyper-elongation of the pre-protocristid. This suggests that true *Dorcatherium* can develop a variable degree of "selenodonty" while maintaining its general lower molar features. The general lower molar plan of *Dorcatherium* persists through a wide range of body sizes, from large (e.g., the European *D. crassum* and *D. naui*) to small species (as *D. songhorensis* or *D. nagrii*). Additionally, the existence of large to tiny-sized selenodont tragulids (e.g., from "*Dorcatherium*" *majus* to *Afrotragulus*, *Yunnanotherium* and the extant Asian forms) that overlap with most of the size range of *Dorcatherium*, suggests that the enhanced selenodonty in tragulids evolved independently of body size and is not an allometric by-product. The lower molars of the selenodont tragulids such as *Afrotragulus*, *Siamotragulus*, *Yunnanotherium*, *Moschiola*, and *Tragulus* are characterized by the presence of flat main cusps with cristids that are not only elongated but also very vertically developed. Those flat cusps are not encountered in *Dorcatherium*, *Dorcabune*, or *Hyemoschus*. Also, the mesial closing of the trigonid is conducted through the longitudinal development of both the pre-protocristid and the pre-metacristid, resulting in a characteristic triangular anterior shape (Fig. 4). This feature is very obvious in the extant Asian species, *Yunnanotherium* and *Afrotragulus*, while *Siamotragulus* has a less developed pre-metacristid and the mesial closing of the trigonid is less conspicuous. The feature that makes *Afrotragulus* unique among both selenodont and bunoselenodont tragulids is the marked elongation and the extremely high crown of the lower molars, which is accompanied by a set of associated traits (Fig. 4). The central buccal valley is very wide and triangular-shaped, instead of the narrow valley present in both the selenodont and the bunoselenodont forms. This feature is still more exaggerated in *A. moruorotensis* than in *A. parvus*. Also, the elongation of the lower molars results in the interruption of the contact between the pre-hypocritstid and the mesial lobe. In all known tragulids except *Afrotragulus*, the pre-hypocristid is always connected (or related) with the mesial lobe, independent of the degree of development of the *Tragulus*-fold. When the *Tragulus*-fold is present, the pre-hypocristid connects with it, and when it is under-developed, as in *Tragulus* and *Moschiola*, the pre-hypocristid still maintains the connection with the distal wall of the protoconid. In *Afrotragulus* this contact is lost, and the pre-hypocristid connects with the pre-entocristid instead; also, a narrow interlobular bridge of enamel connects the mesial and the distal lobes (Fig. 4). We find all these characters important enough to justify the separation of *Afrotragulus* from *Dorcatherium*.

Apart from the Kenyan type localities, certain fossil materials from the late early Miocene of Uganda and the early Miocene of Namibia have been described as belonging to "*Dorcatherium*" *parvum* and "*D.*" *moruorotensis*. Scarce and small-sized tragulid postcranial material from the Napak Member in Uganda (see Pickford 1986, for a correlation between Napak and Western Kenya localities) was assigned to "*Dorcatherium*" *parvum* (Pickford 2002: pl. 1: 2–4). The lack of dental remains makes this assignment ambiguous, since such small remains could belong either to *Afrotragulus parvus* or a small-sized *Dorcatherium*. However, the morphology of the astragalus UM Nap V 2'95, narrow and slender, recalls the morphology of the specimen BMNH M82382

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(*A. moruorotensis*) from Moruorot. Also, Pickford (2001) assigned a certain number of small-sized tragulid astragali from several Western Kenya localities (see Pickford 2001: table 10, for a complete list of localities and measurements) to "*Dorcatherium*" *moruorotensis*. Again, the lack of dentition from these localities makes the assignment of this material ambiguous. Lower molar remains are needed to confirm the presence of *A. parvus* in the Napak Member of Uganda and of *A. moruorotensis* in more Western Kenyan localities other than Moruorot. On the other hand, Quiralte et al. (2008) identified "*Dorcatherium*" sp. cf. "*D.*" *moruorotensis* and "*Dorcatherium*" sp. cf. "*D.*" *parvum* in the early Miocene of the Sperrgebiet (Namibia). The single astragalus pertaining to the former, smaller tragulid, which would correspond to *A. moruorotensis*, is narrow and elongated with a markedly inclined proximo-plantar facet for the calcaneum (see Quiralte et al. 2008: pl. 1: 10). As with the Napak astragalus, this specimen is very similar in size and morphology to the paratype astragalus BMNH M82382 from Moruorot. However, a single astragalus is insufficient to unambiguously refer the smaller Namibian species to *A. moruorotensis*. The M3 assigned to "*Dorcatherium*" sp. cf. "*D.*" *parvum* shows a very strong protoconal cingulum but an absent metaconule cingulum (Quiralte et al. 2008: pl. 1: 5), a typical feature of the upper molars of *Afrotragulus*, so it probably belongs to *A. parvus* indeed. Nevertheless, the lack of lower molars also makes the *Afrotragulus* status of these Namibian fossils ambiguous (especially those referred to "*Dorcatherium*" sp. cf. "*D.*" *moruorotensis*), so the presence of this genus in the early Miocene of Namibia still has to be fully confirmed with future discoveries. If it finally were the case, the paleobiogeographical and biochronological range of *Afrotragulus* would extend into Southern Africa and to 19 Mya, respectively.

The fossil record indicates that the specific diversity of the Tragulidae increased by the end of the early Miocene not only in Africa, but also in the entire Old World (Gentry et al. 1999; Pickford, 2001, 2002; Rössner 2007). The presence of *Afrotragulus* in the late early Miocene of Kenya expands both the taxonomical and morphological diversity of early Miocene tragulids, and demonstrates that the early radiation and diversification of the group involved at least two types of distinct selenodont advanced forms that were, apparently, endemic to Asia (*Siamotragulus*) and Africa (*Afrotragulus*) respectively. Rössner (2007: 219) pointed out that the Miocene distribution of the Tragulidae "testify to an early geographic division between Eurasian and African family branches". It is difficult to discuss this assertion without a reliable genus-level phylogenetic analysis of the Tragulidae. However, it seems that a stronger relationship exists between Africa and Europe regarding the early Miocene Tragulidae (as already pointed out by Janis 1984), than between Europe and Asia, and thus it would be better to refer to an early geographic division between the "Euro-African" and "Asian" branches of the Tragulidae. In strict biogeographic terms *Afrotragulus* and *Dorcatherium* could be considered the "African" branch of the Tragulidae, since both are first recorded in the African early Miocene, whereas *Dorcabune* and *Siamotragulus* could be considered the "Asian" branch, first recorded in Asia almost synchronically (Withworth 1958; Ginsburg et al. 2001; Pickford 2001, 2002; Quiralte et al. 2008). *Dorcatherium* appeared only a bit later in Europe (see Gentry et al. 1999; Rössner 2007) as part of the taxa that entered Eurasia from Africa through the "*Gomphotherium*"-landbridge in the latest early Miocene (Agustí et al. 2001; Koufos et al. 2005) revealing a complex pattern of sympatric lineages that were spreading throughout Africa and Europe. Asian tragulids, on the other hand, appear to have remained more or less isolated since their early Miocene first appearance. Interestingly, a *Dorcatherium* sp. nearly as small as *Afrotragulus moruorotensis* has been cited from the basal middle Miocene of Antonios (Greece), but its morphology has not been described yet (Koufos and Syrides 1997; Koufos et al. 2005). As commented, we do not have a genus-level phylogeny of tragulids to discuss the lineages of the group; however, the presence of *Afrotragulus* in the early Miocene of Africa and the increasingly high diversity of the Tragulidae during the course of the early Miocene, strongly suggests that these ruminants underwent a strong radiation event or events prior to the early Miocene. This evolutionary pulse led to the appearance of a highly varied array of tragulids, from primitive bunoselenodont taxa to derived selenodont forms, which spread out throughout the Old World during the Miocene.

Conclusions

Body size alone is not a trustworthy tool to study the taxonomy and systematics of the Tragulidae. The analysis of comparative morphology of the early Miocene African forms shows that *Afrotragulus*, which possessed a unique array of lower molar characters, was a type of selenodont tragulid clearly different from *Dorcatherium*, and demonstrates that the latter was not the only tragulid genus present in the African Miocene, as previously thought. Although unambiguously identified in the late early Miocene of East Africa, it is very possible that *Afrotragulus* was present earlier in the early Miocene of Southern Africa. The establishment of the genus *Afrotragulus* updates and expands the previously described taxonomic and morphological diversity of the early Miocene tragulids in the moment of their sudden appearance and expansion throughout the Old World. When tragulids are first recorded in the late early Miocene of Africa and Asia, two apparently endemic advanced selenodont forms (the African *Afrotragulus* and the Asian *Siamotragulus*) existed along with two more primitive bunoselenodont genera (*Dorcabune* in Asia and *Dorcatherium* in Africa), suggesting that tragulids underwent a very important and still unknown radiation event or events prior to their first Miocene record. A deep revision of *Dorcatherium* tragulids and a genus-level phylogenetic analysis of the Tragulidae are still needed to fully understand the evolutionary history of this ancient ruminant family.

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