First African record of the Miocene Asian mouse-deer *Siamotragulus* (Mammalia, Ruminantia, Tragulidae): implications for the phylogeny and evolutionary history of the advanced selenodont tragulids

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New remains of the small tragulid *Dorcatherium songhorensis* Whitworth, 1958 from the Early Miocene fossil site of Napak XXI (Uganda) include the first significant sample of postcranial bones from this species ever described. The limb bones of this tragulid are very similar to that described in the Miocene Asian long-legged tragulids of the genus *Siamotragulus* Thomas \textit{et al}., 1990, a type previously unknown in the African Miocene. A cladistic analysis links *D. songhorensis* to a *Siamotragulus* clade as its basal offshoot, so we propose the name *Siamotragulus songhorensis* (Whitworth, 1958) for this species. Also, the *Siamotragulus* clade belongs to a monophyletic group that includes *Afrotragulus* Sánchez \textit{et al}., 2010 and the extant Asian genera *Moschiola* and *Tragulus*. This inclusive clade is characterized by both a derived selenodont dentition and an advanced postcranial skeleton. Additionally *Siamotragulus* shows some cursorial refinements reflected in its postcranial skeleton including the pecoran-like metatarsals III–IV. *Siamotragulus songhorensis* shows that the genus *Siamotragulus* was not endemic to Asia as previously thought, and that a highly diverse guild of tragulids, including different members of the advanced selenodont clade, inhabited Africa as early as the Early Miocene (19–20 Ma).

**Keywords**: Africa; Asia; phylogeny; Ruminantia; Tragulidae

**Introduction**

The Tragulidae (chevrotains and mouse-deer) are the most basal of extant Ruminantia, and the only living remnant of an ancient radiation of ruminants that produced successive sister groups to the Pecora (Rössner \textit{et al}., 2010). They include the smallest living cetartiodactyls and survive today as Old World tropical relics: *Moschiola* in India and Sri Lanka, *Tragulus* in South-East Asia and the Philippines, and *Hyemoschus* in Africa from Sierra Leona to Uganda (Grubb 1993; Nowak 1999; Meijard & Groves 2004; Groves & Meijard 2005; Rössner 2007). The fossil record of Palaeogene tragulids is extremely poor (Métais \textit{et al}., 2001; Tsukamoto \textit{et al}., 2003; Métais & Vislobokova 2007). The Late Eocene Asian ruminant *Archaeotragulus krabensis* Métais \textit{et al}., 2001 is considered the most basal of tragulids, and also constitutes the only Palaeogene record of the family. This lack of Palaeogene remains opens a gap in the fossil record that extends up to the Early Miocene, when tragulids suddenly reappear with a high diversity in Africa, Asia and Europe (Whitworth 1958; Hamilton 1973; Mein 1989; Mein & Ginsburg 1997; Gentry \textit{et al}., 1999; Ginsburg \textit{et al}., 2001; Pickford 2001, 2002; Rössner 2007; Quiralte \textit{et al}., 2008; Sánchez \textit{et al}., 2010). Tragulids experienced a great evolutionary success during the Miocene, and where their habitat preferences were met they even successfully competed with pecoran ruminants (Rössner 2004).

Classically it has been thought that only the genus *Dorcatherium* inhabited Africa during the Miocene, but this scenario is in need of urgent revision (see e.g. Rössner 2007; Sánchez \textit{et al}., 2010). The description of the highly derived and tiny *Afrotragulus* Sánchez \textit{et al}., 2010 from the late Early Miocene of Kenya (probably present also in Southern Africa) showed the presence in Africa of a new type of tragulid different from *Dorcatherium* and increased the morphological diversity of African tragulids. Moreover, *Afrotragulus* demonstrated that the classical use of size as the main taxonomic criterion for the Tragulidae (see e.g. Arambourg & Piveteau 1929; Colbert 1935; Whitworth 1958; West 1980; Gaur 1992; Ginsburg \textit{et al}., 2001; Pickford 2001, 2002; Morales \textit{et al}., 2003; Quiralte \textit{et al}., 2008) was critically flawed, and that morphology is of the upmost importance for understanding tragulid systematics. In this work we present another step towards the systematic revision of the Miocene African tragulids.
During the field campaigns of 2008–2013, fossils of a small tragulid were discovered in the Napak XXI fossil site (Uganda; Fig. 1). The lower molars of this form are virtually indistinguishable from those of Dorcatherium songhorensis Whitworth, 1958, a species previously cited from other Napak fossil sites (Pickford 2002). The type material of D. songhorensis from Songhor lacked any postcranial bones (Whitworth 1958), and although some postcranial fossil material from other sites in Napak and from the Sperrgebiet (Namibia) were previously described (Pickford 2002; Quiralte et al. 2008), it was fragmentary and lacked significantly different features from what was then known about the African forms. Contrary to this, the majority of fossils from Napak XXI are postcranial remains in a fairly good state of preservation, and some of them shed significant light on the nature of the appendicular skeleton of D. songhorensis: surprisingly, the limb bone morphology of this species corresponded to a type never described before in any African tragulid, but already known in the Asian Miocene long-legged genus Siamotragulus Thomas et al., 1990 (see Thomas et al. 1990; Ginsburg et al. 2001). The aim of this work is to describe these new findings of Dorcatherium songhorensis from Napak XXI and test the phylogenetic relationships of this species within the Tragulidae, reassess the diagnosis and definition of the genus Siamotragulus, and finally offer new information on the phylogeny and evolutionary history of the clade of selenodont derived tragulids in which Siamotragulus is included, with special remarks on the African Miocene.

The Napak XXI fossil sites

The locality of Napak XXI (Fig. 1) was discovered in 2008 in the southern slopes of Akisim Mountain, a remnant of the Early Miocene Napak carbonatite-nephelinite volcano (Bishop 1958, 1962, 1964, 1967, 1968, 1972; Bishop & Whyte 1962; Bishop & Trendall 1967). The sediments, exposed at the top of a hillock, comprise red pedogenic clays with calcareous nodules developed on volcanic ash of the Napak Member. The associated fauna and flora is typical of the Napak area, with taxa such as the rodent Diamantomys luederitzi, the primate Micropithecus clarki and the ruminant Dorcatherium songhorensis (Pickford et al. 2010). The locality is exceptional, however, in yielding an abundance of extremely well-preserved gastropods and plant seeds (Celtis rusingensis) which indicate a tropical woodland to forest environment. Among the gastropods the first shells of Koruella magnifica and Edentulina rusingensis from the Napak area were collected in association with specimens of Gulella, Haplonepion naggasi, Maizania, subulinids, achatinids (Tholachatina leakeyi, Burtoa nilotica), Trochozonites, and other lineages characteristic of tropical forest to woodland (Pickford 2009). It also yielded the first beetle fossil from Napak preserved in three dimensions. Vertebrates are rare at the site, but enough are present to establish the age as Early Miocene, older than Rusinga and approximately equivalent to Songhor, Kenya (Faunal Set I of Pickford 1981; Musalizi et al. 2009). Radio-isotopic analyses indicate an age for the deposits of between 19 and 20 Ma (Bishop et al. 1969; Werdelin 2010).
Material and methods

The tragulid fossils from Napak XXI described in this paper are curated by the Uganda Museum in Kampala (Uganda). This material probably belongs to a single individual since the fossils were found scattered over an area of 3 metres by 5 metres, there is no duplication of skeletal parts, and the preservation characteristics of all the bones are similar, with parts of the skeleton still connected to each other. It has been compared with some extant and extinct tragulid taxa (listed in Supplemental Table 1).

Anatomical definitions

We use the terminology of Azanza (2000) for nomenclature of the dentition (English version in Sánchez & Morales 2008). The Dorcatherium-fold is the fold that occurs on the linguodistal side of the metaconid. The Tragulus-fold is the fold situated on the distal side of the protoconid, usually linked to the post-protocristid (sometimes to the conid itself). Combined, both the Dorcatherium-fold and the Tragulus-fold form the so-called M-structure (see e.g. Janis 1987; Geraads et al. 1987). The inter-lobular bridge is the rectilinear bridge of enamel that connects the anterior and posterior lobes in an Afrotragulus-type lower molar (Fig. 2; Sánchez et al. 2010). The Zhailimeryx-fold is a fold of enamel that originates from the anterior part of the entoconid, the development of which is highly variable amongst tragulids (from well developed to absent). We define the Dorcatherium-platform as the mesial semicircular structure of the lower molars formed by a hyper-developed pre-protocristid that turns lingually to contact a very small pre-metacristid (Fig. 2; see also Sánchez et al. 2010; Morales et al. 2012). For nomenclature of the postcranial skeleton we follow Barone (1999).

Measurement abbreviations

The measurements taken on postcranial remains are defined in Sánchez & Morales (2008). The detailed measurements of dental and postcranial material of the fossil traguld from Napak XXI are presented in Supplemental Appendix 1.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; NHMUK: Natural History Museum, London, UK; GSN: Geological Survey of Namibia, Windhoek, Namibia; MNCN-CSIC: Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; MAUV: Museo Anatómico de la Universidad de Valladolid, Valladolid, Spain; MNHN: Muséum National d’Histoire Naturelle, Paris, France; UM: Uganda Museum, Kampala, Uganda; UMZC: University Museum of Zoology, University of Cambridge, Cambridge, UK.

Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order Cetartiodactyla Montgelard et al., 1997
Suborder Ruminantia Scopoli, 1777
Family Tragulidae Milne-Edwards, 1864
Genus Siamotragulus Thomas et al., 1990

Type species. Siamotragulus sanyathanai Thomas et al., 1990.

Emended diagnosis. Tragulids with selenodont lower cheek teeth and postcranial skeleton characterized by the presence of fused, long and narrow metatarsals III–IV that form a true, pecoran-like, cannon bone; presence of a dorsoconstrict in the acetabular cavity that conforms to it a ‘three-lobed’ morphology; elliptic and wide cavity located caudal to the acetabular notch in the pelvis; and short, deep and triangular distolateral furrow for the tendon of the fibularis longus muscle in the navicular-cuboid. Differing from Dorcatherium, Hyemoschus and Dorcacbune in: presence of selenodont molars; weaker buccal rib on the metacone; presence of a well-developed pre-metacristid smaller than the pre-protocristid and absence of Dorcatherium-platform; fused metacarpals III–IV; presence of a slight convexity over the palmar distal articular area in the humerus; presence of curved dorsal border of the medial epicondyle in the humerus. Differing from Tragulus, Moschiola and Afrotragulus in: lack of well-extended, Tragulus-like cristids; and lesser development of the pre-metacristid. Differing from Afrotragulus in: the lack in the lower molars of the interlobular bridge linking the lobes. Differing from Tragulus and Moschiola in: lingual and buccal distal cristids of the p4 originating from the central conid.

Siamotragulus sanyathanai Thomas et al., 1990

Emended diagnosis. Siamotragulus with poorly developed mesial cingulid; fused, long and narrow pecoran-like metatarsal III–IV with square cross-section at mid-shaft; and metatarsals II and IV fused with the metatarsals III–IV.

Siamotragulus bugtiensis Ginsburg et al., 2001

Emended diagnosis. Siamotragulus with relatively low cristids in lower dentition and navicular-cuboid not fused with the ectomesocuneiform.

Siamotragulus songhorensis (Whitworth, 1958) (Figs 3–6)

1958 Dorcatherium songhorensis Whitworth: 14, figs 7, 8, tables 7, 8.
Figure 2. Occlusal anatomical elements of tragulid lower molars, showing the differences discussed in the text. A, *Afrotragulus morurotensis*, m2 of the holotype CMK Mor 1’2000. B, *Dorcatatherium nauui*, m2, right hemimandible of the specimen NHMUK M40432 from the type locality Eppelsheim. C, *Moschiola muminna*, left m2 (private collection Jan van der Made, Madrid). D, *Dorcatatherium crassum*, left m2 of neotype hemimandible Sa 9950 from Sansan (Morales et al. 2012), mirrored for comparison purposes. Modified from Sánchez et al. (2010) and Morales et al. (2012). E, schematic depiction of the three types of mesial morphology in tragulid molars; from left to right: very large pre-protocristid which turns lingually and contacts a very small pre-metacristid, forming the *Dorcatatherium*-platform; large rectilinear pre-protocristid that meets a smaller pre-metacristid, with no *Dorcatatherium*-platform; straight pre-protocristid and pre-metacristid which are subequal in length, meeting parasagitally and forming a triangular mesial outline of the teeth; the centre morphology corresponds with *Siamotragulus*. 

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**A**
- Dorcatatherium-fold
- Pre-metacristid
- Inter-lobular bridge
- Pre-entocristid
- Post-hypocristid
- Central valley

**B**
- Dorcatatherium-fold
- Pre-entocristid
- Dorcatatherium-platform
- Distal
- Pre-metacristid
- Post-entocristid
- Pre-entocristid
- Tragulus-fold
- Post-hypocristid
- Pre-metacristid
- Central valley

**C**
- Pre-metacristid
- Pre-entocristid
- Post-hypocristid
- Central valley

**D**
- Pre-metacristid
- Pre-entocristid
- Post-hypocristid
- Central valley

**E**
- Metacristid
- Dorcatatherium-platform
- Pre-metacristid
- Pre-protocristid
- Protocristid
Figure 3. Dentition of *Siamotragulus songhorensis* from Napak XXI. A–C, left m1 UM NAP XXI 10j’08 in: A, buccal, B, lingual and C, occlusal views. D–F, right m1 UM NAP XXI 10k’08 in: D, buccal, E, lingual and F, occlusal views. G–I, left m3 UM NAP XXI 10i’08 fragment in: G, buccal, H, lingual and I, occlusal views.

Figure 4. Postcranial skeleton of *Siamotragulus songhorensis* from Napak XXI. A, B, proximal fragment of left scapula UM NAP XXI 10d’08 in: A, lateral and B, distal views. C, right pelvic fragment UM NAP XXI 10g’08-1 in lateral view. D, E, left pelvic fragment UM NAP XXI 10g’08-2 in: D, lateral and E, caudal views. Abbreviation: For, foramen caudal to the acetabular cavity showing the elliptical morphology.
**Emended diagnosis.** Basal *Siamotragulus* with a well-developed post-protocrista in the upper molars.

**Material.** Napak: UM NAP XXI 10j’08, left m1; UM NAP XXI 10k’08, right m1; UM NAP XXI 10i’08, fragment of left m3; UM NAP XXI 10l’08, lower molar fragment; UM NAP XXI 10d’08, proximal fragment of left scapula; UM NAP XXI 10h’08, right fragmented humerus; UM NAP XXI 10f’08, left humerus; UM NAP XXI 4’12, right radius; UM NAP XXI 10b’11, right scaphoid; UM NAP XXI 10g’08-1, right pelvis fragment; UM NAP XXI 10g’08-2, left pelvis fragment; UM NAP XXI 10e’08, proximal fragment of right femur; UM NAP XXI 10c’08, articulated left hind limb elements comprising the distal part of the tibia, complete tarsus and metatarsal III–IV lacking the distal epiphysis; UM NAP XXI 10n’08, right calcaneum; UM NAP XXI 10a’08-1, fragmented metatarsal III–IV; UM NAP XXI 10m’08, distal fragment of metatarsal III–IV; UM NAP XXI 10a’08-2, distal fragment of lateral metatarsal; UM NAP XXI 10c’11, distal fragment of lateral metatarsal; UM NAP XXI 40a’10, first phalanx; UM NAP XXI 40c’10, first phalanx; UM NAP XXI 40b’10, proximal fragment of first phalanx; UM NAP XXI 10a’08-3, proximal fragment of second phalanx; UM NAP XXI 40d’10, fragment of third phalanx. Songhor, Kenya: type material of *Dorcattherium songhorensis*, Whitworth, 1958 (see Whitworth 1958).

**Figure 5.** Postcranial skeleton of *Siamotragulus songhorensis* from Napak XXI. A, B, right radius UM NAP XXI 4’12 in: A, dorsal and B, palmar views. C–E, left humerus UM NAP XXI 10f’08 in: C, medial, D, lateral and E, dorsal views. F, G, proximal fragment of right femur UM NAP XXI 10e’08 in: F, plantar and G, dorsal views. H, I, first phalanx UM NAP XXI 40a’10 in: H, interdigital and I, external views. J, K, first phalanx UM NAP XXI 40c’10 in: J, interdigital and K, external views. L, M, proximal fragment of second phalanx UM NAP XXI 10a’08-3 in: L, interdigital and M, external views. N, O, proximal fragment of third phalanx UM NAP XXI 40d’10 in: N, interdigital and O, external views.
Occurrence. Late Early Miocene of Kenya and Uganda (Whitworth 1958; Pickford 2002; Musalizi et al. 2009); Faunal Set I of Pickford (1981).

Description. The lower molars of *Siamotragulus songhorensis* are very similar to those of *Siamotragulus sanyathanai*, with flat cuspids and well-developed cristids. The mesial closure of the trigonid is achieved by a long rectilinear pre-protocristid that meets a smaller pre-metacristid (with no *Dorcatherium*-platform present; see Fig. 2E, centre, and Fig. 3). This contrasts with the mesial closure in *Dorcatherium* and *Dorcabune*, which show a clear *Dorcatherium*-platform (Sánchez et al. 2010; Morales et al. 2012). However, contrary to *Afrotragulus* or *Tragulus*, the pre-protocristid is shorter than the pre-metacristid, not sub-equal in length. The M-structure is
well developed. Both the Dorcatherium-fold and the Tragulus-fold are robust, and the latter contacts the pre-hypocristid. Siamotragulus songhorensis lacks an inter-lobular bridge (see Fig. 2). The post-entocristid is virtually nonexistent. The post-hypocristid does not reach the lingual border of the tooth. The mesial cingulid is moderately developed, the buccal cingulids are weak, and the ectostyloid is moderately well developed. The posterior cingulid is strongly developed, especially at the post-hypocristid level. The only m3 recovered has only the distal part preserved. The pre-hypoconulidcristid is long and contacts the post-hypocristid. The post-hypoconulidcristid, albeit shorter, is still well developed. However it does not close the third lobe distally. There is a well-developed distolingual cingulid.

In the postcranial skeleton the scapula (Fig. 4A, B) has a subcircular and not very deep glenoid cavity. The supra-glenoid tubercle and the coracoid process form a high and well-developed structure that attains an inverted ‘L’ shape, forming a strong canal for the supraspinatus muscle. A similar canal is present in the African chevrotain but not in Tragulus.

There is a single, almost complete, humerus (Fig. 5C–E). The tricipital line is very narrow and well marked. It contacts the distal border of the convexity of the major tubercle, reaching the area for the infraspinaus muscle. Both the deltoide tuberosity and the tuberosity for the teres minor muscle are poorly developed. Overall, the entire bone is as slender as in Tragulus. In Siamotragulus sanyathanai the tuberosity for the teres minor is marked by a superficial rounded concavity, so the condition in the smaller sized S. songhorensis and Tragulus is probably due to allometry. The palmar border of the medial epicondyle shows a slight convexity over the distal articular area, very similar to the condition in Tragulus. However, Dorcatherium and Hyemoschus have a straight border. On the other hand, the dorsal border is clearly curved in S. songhorensis and also in Tragulus, and straight or almost straight in Hyemoschus and Dorcatherium. The coronoid pit is triangular and deep, comparatively wider than that of Tragulus. Also, the capitulum and the trochlea have more similar proximodistal lengths than in Tragulus, resulting in a more rectangular shape of the distal articulation of the humerus.

The radius (Fig. 5A, B) is long and slender, very similar to that of Tragulus and Siamotragulus sanyathanai, contrasting with the short and wider radius of Hyemoschus. As in S. sanyathanai and Hyemoschus the medial proximal facet for the humeral trochlea is dorsopalmarly wide, with divergent proximal and palmar borders, different from the rectangular facet of Tragulus. The attachment area for the biceps brachii muscle is more developed than in Tragulus. The palmar surface is distinctively flattish, as in S. sanyathanai. The distal articular area is not well preserved.

The scaphoid has a dorsally wide proximal facet, with a very clear lateral projection similar to that of Hyemoschus. The dorsomedial border is rectilinear, contrasting with the more bulging border present in Hyemoschus and Tragulus. As in Hyemoschus the centromedial apophysis is weak, differing from the well-developed apophysis present in Tragulus.

Two right coxal fragments preserve the acetabular cavity and its surroundings (Fig. 4C–E). The acetabular cavity is subcircular with a dorsal constriction. Together with the caudal acetabular notch the constriction breaks the subcircular profile into a three-lobed profile. This is also the case with Siamotragulus sanyathanai, but not with Tragulus and Hyemoschus, in which the acetabular cavity lacks the dorsal constriction and is perfectly circular in shape. The acetabular notch is wide and triangular. The major sciatic notch is triangular and weak, very similar to that of S. sanyathanai and Tragulus. The cavity located caudal to the acetabular notch is elliptic and relatively wider (Fig. 4E) than that of Tragulus and Hyemoschus, which show a narrow and slit-like cavity. As observed in Tragulus, the crest for the psoas minor in the inner surface of the ilium is very weak.

The femur of Siamotragulus songhorensis (Fig. 5F, G) is nearly morphologically identical to that of S. sanyathanai. The crest of the greater trochanter is well marked, and runs almost vertically. The caput femoris is transversely elongated, with a triangular and upwards-oriented fovea capitis, corresponding to Köhler’s type-A (see Köhler 1993). The trochanteric pit is wide and triangular. Hyemoschus shows a similar morphology, but apparently Tragulus has a narrower pit. The distal part of the femur is not preserved.

The only tibia (Fig. 6A, B) lacks the proximal region above the mid-part of the tibial crest. The tibia of Siamotragulus songhorensis is long and slender, very similar to that of S. sanyathanai. The medial malleolus is short but surpasses the border of the distal articulation. In Siamotragulus sanyathanai it is quadrangular and shorter, and does not surpass the border of the articulation. The fibular notch is wide with well-marked ridges. The notch of origin of the long collateral medial ligament is also well marked and delimited by sharp ridges. Contrary to the case of Siamotragulus sanyathanai and S. bugtiensis the malleolar bone is fused to the tibia.

The calcaneum (Fig. 6A, B, H) has pentagonal-shaped tuber calcanei, with two well-developed plantar tubercles for the insertion of the gastrocnemius tendon. The two plantar ridges of the corpus are proximally well marked, forming a distinct canal that runs down to the middle of the shaft. The dorsal and plantar borders of the corpus are not parallel. The sustentaculum tali is dorsally less developed than in Siamotragulus sanyathanai. Also, the plantar border of the sustentaculum is concave whereas it is straight in S. sanyathanai. The dorsal surface of the
sustentaculum is also concave, contrasting with the flatish and dorsally inclined surface in *S. sanyathanai*.

The astragalus (Fig. 6A, B) is narrow and slender, with an elliptical proximoplantar facet for the calcaneum. The only recovered navicular-cuboid is fully articulated with the metatarsals III–IV and the rest of the tarsus (Fig. 6A, B). The navicular-cuboid is fused with the ectomesocuneiform. As in *Siamotragulus sanyathanai* the laterodistal furrow for the tendon of the fibularis longus muscle is narrow and triangular and does not contact the lateral articular facet for the calcaneum. Contrary to this condition, the narrow and triangular and does not contact the lateral articular facet for the calcaneum. Dewey et al. (2001) pointed out that the lower cheek teeth of this species were ‘less bunoid’ than those of *D. chapussi* and *D. pigottii*. Actually not only are the cusps of *Siamotragulus songhorensis* flat instead of rounded, especially in their inner wall, but also the teeth are mesially closed by means of an enlarged and straight pre-meta-

cristid that meets a non-curved pre-protocristid as in selenodont trigulids such as *Afrotragulus*, *Tragulus*, *Moschiola* and the other two species of *Siamotragulus*, lacking the plesiomorphic *Dorcathe-rium*-platform typical of such forms as *Dorcathe-rium*, *Dorcabune* and *Archaeotragulus*. These features are present both in the type series from Songhor (Western Kenya; Whitworth 1958) and in the material from Napak (Pickford 2002; this paper). Quiralte et al. (2008) assigned to *Dorcathe-rium songhorensis* some small trigulid material from the sites of Langental and Grillental (Early Miocene, Sperrgebiet, Namibia). Some features of this form (e.g. lack of *Dorcathe-rium*-platform and a proximal metatarsal III–IV fragment that could be of the derived type) are *Siamotra-gulus*-like. Thus the material from the Sperrgebiet should be re-examined keeping in mind its possible *Siamotragulus* nature. Also, a further re-analysis of the *D. songhorensis* material (both the type from Songhor and the new material from Uganda) allowed us to reject a previous characterization of the species as a bunoselonodont trigulid (see Sánchez et al. 2010). This material highlights the difficulties in dealing with the waste-basket taxon that the genus *Dorcathe-rium* has become, the correct characterization of which only will be achieved through the re-
description of the tremendous variability of forms that have been included into it.

**Remarks.** In his description of *Dorcathe-rium songhorensis* Whitworth (1958) pointed out that the lower cheek teeth of this species were ‘less bunoid’ than those of *D. chapussi* and *D. pigottii*. Actually not only are the cusps of *Siamotragulus songhorensis* flat instead of rounded, especially in their inner wall, but also the teeth are mesially closed by means of an enlarged and straight pre-meta-
cristid that meets a non-curved pre-protocristid as in selenodont trigulids such as *Afrotragulus*, *Tragulus*, *Moschiola* and the other two species of *Siamotragulus*, lacking the plesiomorphic *Dorcathe-rium*-platform typical of such forms as *Dorcathe-rium*, *Dorcabune* and *Archaeotragulus*. These features are present both in the type series from Songhor (Western Kenya; Whitworth 1958) and in the material from Napak (Pickford 2002; this paper). Quiralte et al. (2008) assigned to *Dorcathe-rium songhorensis* some small trigulid material from the sites of Langental and Grillental (Early Miocene, Sperrgebiet, Namibia). Some features of this form (e.g. lack of *Dorcathe-rium*-platform and a proximal metatarsal III–IV fragment that could be of the derived type) are *Siamotra-gulus*-like. Thus the material from the Sperrgebiet should be re-examined keeping in mind its possible *Siamotragulus* nature. Also, a further re-analysis of the *D. songhorensis* material (both the type from Songhor and the new material from Uganda) allowed us to reject a previous characterization of the species as a bunoselonodont trigulid (see Sánchez et al. 2010). This material highlights the difficulties in dealing with the waste-basket taxon that the genus *Dorcathe-rium* has become, the correct characterization of which only will be achieved through the re-
description of the tremendous variability of forms that have been included into it.

**Cladistic analysis**

We performed a cladistic analysis at the species-level to explore the phylogenetic relationships of *Dorcathe-rium songhorensis* using the TNT software (Goloboff et al. 2008). We chose *Zaihlimeryx jingweni* as the outgroup since this taxon was previously used successfully to root a tragulid cladistic analysis (Métais et al. 2001). The morphological characters found in the trigulid from Napak XXI indicated that this form does not belong to *Dorcathe-rium* (see further discussion). As we intended test the hypothesis that ‘*Dorcathe-rium’ songhorensis* falls outside of the genus *Dorcathe-rium* we accordingly selected as the ingroup several taxa useful for performing that test: primitive trigulid forms such as *Archaeotragulus kraibiensis* (Métais et al. 2001) and *Dorcabune anthracotheiroides* Pilgrim, 1910, the bunodont *Dorcathe-rium crassum* and the buno-selenodont *Dorcathe-rium nau* (thus covering the dental morphological extremes included within *Dorcathe-rium* and also including postcranial data), the extant *Hyemoschus aquaticus*, *Moschiola memminia* and *Tragulus javanicus*, the two described species of *Siamotragulus* (Thomas et al. 1990; Ginsburg et al. 2001)
and the two described species of *Afrotragulus* (Sánchez et al. 2010). For this analysis we combined the morphological data from the type series of *Dorcatherium songhorensis* (upper and lower molars) and the new material from Napak XXI *D. songhorensis* (lower molars and postcranial skeleton) into a single operational taxonomic unit (OTU). We did this after running a test-analysis with the two datasets of *D. songhorensis* (type and Napak XXI) as separate OTUs and checking that both terminals grouped together (see Fig. 7). The data matrix included 53 characters picked from the skull (six), upper dentition (seven), lower dentition (22) and postcranial skeleton (18), thus resulting in the largest morphological dataset used in a tragulid cladistic analysis so far. The data matrix and the list of characters and their descriptions are included as Supplemental Appendices 2 and 3 respectively. We performed a run using a traditional search with 1000 replicates with TBR that recovered one most parsimonious tree (MPT) of 88 steps (CI = 0.795; RI = .798) in which *Dorcatherium songhorensis* (*Siamotragulus songhorensis* hereafter) appears as the most basal of a *Siamotragulus* clade, which is part of a more inclusive clade of derived tragulids that contains the extant Asian forms (Fig. 7). The character/state distribution for the discussed internal nodes as well as the autapomorphies for each *Siamotragulus* species are presented in Supplemental Table 2.

**Discussion**

We do not intend to reconstruct a complete phylogeny for Tragulidae, so we are going to discuss the region of our MPT that is important for describing the phylogenetic

![Figure 7. A, MPT showing the phylogenetic position of *Siamotragulus songhorensis*. Clades A, B and C are the ones discussed in the text. Numbers above the branches represent the bootstrap support values. Numbers below the branches represent the absolute (left) and relative (right) Bremer support values. B, simplified test MPT showing the type ‘*Dorcatherium* songhorensis’ from Kenya and the new material from Napak XXI clustering together as sister groups.](image-url)
relationships of the Siamotragulus clade amongst tragulids and also the character/state distribution within that clade. In past works we linked the presence of flat cuspids in the Tragulidae with the acquisition of the derived mesial closure of the lower molars, describing these two states as the combined morphological signature of the selenodont forms (Sánchez et al. 2010). However, we did not discuss in detail the case of the extant African chevrotain Hyemoschus due to the lack of a proper phylogeny. The African chevrotain is a particular case in which the presence of a derived mesial closure of the lower cheek teeth is linked with bunodont cuspids. This mixture of features could reflect two phylogenetic scenarios. First, a single origin of the derived mesial closing of the teeth, and therefore this state would exist previous to the development of full selenodonty and flat cuspids, or alternatively, the appearance of the derived mesial closing of the teeth was achieved in parallel at least twice during the evolutionary history of the Tragulidae. Our present MPT clearly supports the former hypothesis. Therefore, if the derived mesial closure of the lower cheek teeth was achieved once (Hyemoschus + Node A), then the acquisition of the full set of features that characterize the selenodont tragulids (Node A) was a two-step evolutionary scenario. More taxa have to be added to the analysis to fully confirm this hypothesis (work in progress by the authors).

The node A (Siamotragulus plus the clade composed by Afrotragulus and the extant Asian species) is characterized by the presence of derived cheek teeth with reduced buccal structures in the upper molars and the presence of flat cusps in the lower molars, morphological innovations that become extreme in the case of Afrotragulus. Also this clade features the acquisition of a new type of appendicular skeleton characterized by its slenderness and the fusion of the central metapodials. The central metatarsals in particular are fused together forming a true metatarsal III—IV cannon bone, contrary to Hyemoschus and Dorcatherium in which the metatarsals III and IV are fused but still individualized. Of all the taxa belonging to this clade only the appendicular skeleton of Afrotragulus remains unknown, so future discoveries will test the evolutionary scenario proposed here. Both the longer legs and the fusion of metapodials into a single cannon-bone are characteristics usually linked with enhanced cursorial abilities (see e.g. Kardong 2009). Apart from that, whether or not these important morphological novelties are linked to changes in the common ancestor of clade-A with respect to habitat exploitation (e.g. extant Asian species are known to enter and live in drier and more open areas than the humid tropical deep-forest African chevrotain; Wilson & Mittermeier 2011) or maybe modifications in the aquatic escape behaviour typical of some tragulids still has to be explored.

We define Siamotragulus as the clade comprising S. songhorensis, S. bugtiensis and S. sanyathanai, their more recent common ancestor and all of its descendants. The Siamotragulus clade (node B) is entirely diagnosed by postcranial characters. The morphology and orientation of the furrow for the terminal tendon of the fibularis longus muscle, short and with a divergent outwards angle relative to the lateral plane of the navicular-cuboid, is notable. This configuration probably indicates that the origin area of this muscle is relatively more laterally placed than in the other tragulid forms, in which the tendon runs very close to the lateral side of the navicular-cuboid and hence the orientation of the muscle crossing over the tibia is more medial. One of the functions of the fibularis longus muscle is the rotation of the foot (Barone 1999), so if the entire muscle is more laterally placed its foot rotational capabilities would become restricted without affecting its main function as a tarsal extensor. This synapomorphic modification of Siamotragulus could be interpreted as a running improvement achieved by this genus by restricting the movement of the autopodium to a (mainly) fore-and-aft (parasagittal) action.

The type species Siamotragulus sanyathanai is the most autapomorphic of the Siamotragulus clade. This species is also the most recent member of the clade (Middle Miocene; Thomas et al. 1990; Chavasseau et al. 2009; Coster et al. 2010). Its main morphological innovations lie in the acquisition of still more pecoran-like, very long metatarsals III—IV with a square cross section at mid-shaft and fused lateral metatarsals. As Thomas et al. (1990) pointed out, this type of highly derived metatarsal III—IV is not found in any other Neogene or recent tragulid. It is worth noting that the branch support for the node C (S. bugtiensis + S. sanyathanai) is low. However, we decided against collapsing it until more taxa are added in a future work, and so we can show the synapomorphies that link Siamotragulus sanyathanai and S. bugtiensis in this hypothesis of relationship: presence of derived cheek teeth with extended post-hypocristid and weak upper buccal ribs and sustentaculum tali in the calcaneum with rectilinear plantar border.

The genus Siamotragulus was previously recorded only in Asia; however, S. songhorensis extends the palaeobiogeographical distribution of the genus to Africa. The existence of an African Siamotragulus rejects the previous hypothesis about the Asian endemism of this genus (see e.g. Rüssner 2007; Sánchez et al. 2010) and also shows that both lineages of clade-A tragulids (represented by Siamotragulus and Afrotragulus respectively) were already present in the African Early Miocene (Fig. 8). Moreover, S. songhorensis is the most ancient of the three Siamotragulus species, recorded at the 19–20 Ma mark (a bit older than S. bugtiensis; see Ginsburg et al. 2000), thus adding complexity to the already complex Miocene biogeographical distribution of the Tragulidae. As far as we know, clade-A tragulids were not present in Europe; however, we must confirm this in future studies. As we pointed out in the case of Afrotragulus (Sánchez et al. 2010) the fact that
some of the earliest records of the Miocene Tragulidae comprise such a diversity of members of such a derived clade strongly supports the idea of an unknown large-scale radiation event prior to the Early Miocene. This radiation of tragulids led to the situation we know from the late Early Miocene deposits, with a high diversity of tragulids that was poised to spread throughout the Old World.

Conclusions

Significant remains of the African tragulid *Dorcatherium* songhorensis Whitworth, 1958 were discovered in the Early Miocene fossil site of Napak XXI (Uganda), including the first-known postcranial skeleton of the species. The derived limb bones (mainly the long cannon-bone metatarsals III–IV) belong to a type that had never been described before in any African tragulid. Our phylogenetic analysis links *Dorcatherium* songhorensis with the Asian long-legged genus *Siamotragulus*, hence we rename this form as *Siamotragulus songhorensis* (Whitworth 1958). The postcranial fossils from Napak XXI allow us to re-diagnose the genus *Siamotragulus* adding some interesting characters to the original diagnosis. *Siamotragulus* is defined as the clade comprising *S. songhorensis*, *S. sanyathanai* and *S. hugtiensis*, their more recent common ancestor and all of its descendants. *Siamotragulus songhorensis* branches off as the most basal of the *Siamotragulus* clade, and helps to root and diagnose a large clade of tragulids (in which the extant Asian tragulids *Tragulus* and *Moschiola* are included) characterized by their advanced long slender limbs and derived selenodont dentition. Additionally to the long limbs, the genus *Siamotragulus* probably developed cursorial refinements such as the loss of rotational capabilities in the hind leg autopodium. The existence of an African *Siamotragulus* allows us to reject the hypothesis that regarded the genus as an Asian endemic taxon. The clade of derived tragulids that includes *Siamotragulus*, *Afrotragulus*, *Moschiola* and *Tragulus* contains some of the oldest known forms that are recorded from the Early Miocene African deposits (19–20 Ma).

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Supplemental material

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References

Arambourg, C. & Piveteau, J. 1929. Les Vertébrés du Pontien de Salonique. Annales de Paléontologie, 18, 57–140.
Azanza, B. 2000. Los Cervidae (Artiodactyla, Mammalia) del Mioceno de las cuencas del Duero, Tajo, Calatayud-Teruel y Levante. Memorias del Museo Paleontológico de la Universidad de Zaragoza, 8, 1–376.
Barone, R. 1999. Anatomie comparée des Mammifères domestiques, Tome 2. Archéologie et Myologie. 4th edition. Vigot, Paris, 984 pp.
Bishop, W. W. 1958. Miocene Mammalia from the Napak volcanics, Karamoja, Uganda. Nature, 182, 1480–1482.
Bishop, W. W. 1962. The mammalian fauna and geomorphological relations of the Napak volcanics, Karamoja. Records of the Geological Survey of Uganda, 1957–1958, 1–18.
Bishop, W. W. 1964. Mammalia from the Miocene volcanic rocks of Karamoja, East Africa. Proceedings of the Geological Society of London, 1617, 91–94.
Bishop, W. W. 1967. The later Tertiary. Pp. 31–56 in W. W. Bishop & J. D. Clark (eds) East Africa — Volcanics, Sediments and Faunal inventory, Chicago Press, Chicago.
Bishop, W. W. 1968. The evolution of fossil environments in East Africa. Transactions of the Geological Society of Canada, 62, 22–44.
Bishop, W. W. 1972. Stratigraphic succession ‘versus’ calibration in East Africa. Pp. 219–246 in W. W. Bishop & J. A. Miller (eds) Calibration of Hominoid Evolution. Scottish Academic Press, Edinburgh.
Bishop, W. W. & Trendall, A. F. 1967. Erosion-surfaces, tectonics and volcanic activity in Uganda. Quarterly Journal of the Geological Society, 122, 385–420.
Bishop, W. W. & Whyte, F. 1962. Tertiary mammalian faunas and sediments in Karamoja and Kavirondo, East Africa. Nature, 196, 1283–1287.
Bishop, W. W., Miller, J. A. & Fitch, F. J. 1969. New Potassium-Argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. American Journal of Science, 267, 669–699.
Boschetto, H.-B., Brown, F.-H. & McDougall, I. 1992. Stratigraphy of the Lothidok Range, Northern Kenya, and k-Ar ages of its Miocene primate. Journal of Human Evolution, 30, 47–71.
Chaimanee, Y., Yamee, CH., Marandat, B. & Jaeger, J.-J. 2007. First Middle Miocene rodents from the Mae Moh Basin (Thailand): biochronological and paleoenvironmental implications. Bulletin of Carnegie Museum of Natural History, 39, 157–163.
Chavasseau, O., Chaimanee, Y., Yamee, CH., Tian, P., Rugbunrungr, M., Marandat, B. & Jaeger, J.-J. 2009. New proboscidians (Mammalia) from the middle Miocene of Thailand. Zoological Journal of the Linnean Society, 155, 703–721.
Colbert, E. H. 1935. Siwalik mammals in the American Museum of Natural History. Transactions of the American Philosophical Society, New Series, 26, 1401.
Coster, P., Benammi, M., Chaimanee, Y., Yamee, CH., Chavasseau, O., Emonet, E.-G. & Jaeger J.-J. 2010. A complete magnetic-polarity stratigraphy of the Miocene continental deposits of Mae Moh Basin, northern Thailand, and a reassessment of the age of hominoid-bearing localities in northern Thailand. Geological Society of America Bulletin, 122, 1180–1191.
Gaur, R. 1992. On Dorcatherium nagrii (Tragulidae, Mammalia): with a review of Siwalik tragulids. Rivista Italiana di Paleontologia e Stratigrafia, 98, 353–370.
Gentry, A. W., Rössner, G. E. & Heizmann, E. J. 1999. Suborder Ruminantia. Pp. 225–253 in G. E. Rössner & K. Heissig (eds) The Miocene Land Mammals of Europe. Dr. Friedrich Pfeil Verlag, Munich.
Geraads, D., Bouvrain, G. & Sudre, J. 1987. Relations phylétiques de Bachitherium Filhol, ruminant de l’Oligocene d’Europe occidentale. Palaeovertebrata, 17(2), 43–73.
Ginsburg, L., Morales, J. & Soria, D. 2001. Las Ruminantia (Artiodactyla, Mammalia) del Mioceno de los Bugí (Balochistan, Pakistan). Estudios Geologicos, 57, 155–170.
Goloboff, P., Farris, S. & Nixon, K. 2008. TNT, a free program for phylogenetic analysis. Cladistics, 24, 774–786.
Groves, C. P. & Meijaard, E. 2005. Interspecific variation in Moschiola, the Indian chevrotain. Raffles Bulletin of Zoology, 12, 413–421.
Grubb, P. 1993. Order Artiodactyla. Pp. 377–414 in C. M. Wenmer (ed.) Mammal species of the world: A taxonomic and geographic reference. 2nd edition. Smithsonian Institution Press, Washington DC.
Hamilton, W. R. 1973. The lower Miocene ruminants of Gebel Zelten, Libya. Bulletin of the British Museum (Natural History), Geology, 21, 75–150.
Janis, C. M. 1987. Grades and classes in hornless ruminant evolution: the reality of the Gelocidae and the systematic position of Lophiomeryx and Bachitherium. Journal of Vertebrate Paleontology, 7, 200–216.
Kardong, K. V. 2009. Vertebrates: Comparative anatomy, function and evolution. McGraw-Hill International Edition, 5th edition, Boston, 779 pp.
Köhler, M. 1993. Skeleton and habitat of fossil and Recent ruminants. Münchner Geowissenschaftliche Abhandlungen (A), 25, 1–88.
Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. 10th edition, reformata. Laurenti Salvii, Holmiae, 824 pp.
Meijaard, E. & Groves, C. P. 2004. A taxonomic revision of the Tragulus mouse-deer (Artiodactyla). Zoological Journal of the Linnean Society, 140, 63–102.
Mein, P. 1989. Updating of MN zones. Pp. 73–90 in E. H. Lindsay, V. Falbusch & P. Mein (eds) European Neogene Mammal Chronology. NATO ASI Series 180. Plenum Press, New York.
Mein, P. & Ginsburg, L. 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironnement. Geodiversitas, 19, 783–844.
Métais, G. & Vişlobokova, I. 2007. Basal ruminants. Pp. 189–212 in D. R. Prothero & S. E. Foss (eds) The Evolution of Artiodactyls. The Johns Hopkins University Press, Baltimore.
Métais, G., Chaimanee, Y., Jaeger, J. J. & Ducrocq, S. 2001. New remains of primitive ruminants from Thailand: evidence of the early evolution of the Ruminantia in Asia. Zoologica Scripta, 30, 231–248.

Milne-Edwards, A. 1864. Recherches anatomiques, zoologiques et paléontologiques sur la famille des chevrotains. Annales de Science Naturelle, Paris, 5, 1–167.

Montgelard, C., Catzeflis F. M. & Douzery E. 1997. Phylogenetic relationships of artiodactyls and cetaceans as deduced from the comparison of cytochrome b and 12S rRNA mitochondrial sequences. Molecular Biology and Evolution, 14, 550–559.

Morales, J., Soria, D., Sánchez, I. M., Quiralte, V. & Pickford, M. 2003. Tragulidae from Arrisdrift, basal Middle Miocene, Southern Namibia. Memoir of the Geological Survey of Namibia, 19, 359–369.

Musalizi, S., Senut, B., Pickford, M. & Musiime, E. 2009. Geological and palaeontological archives relating to Early Miocene localities of Uganda, 1957–1969. Geo-Pal Uganda, 1, 2–96.

Nowak, R. M. 1999. Walker’s Mammals of the World. Sixth Edition. The Johns Hopkins University Press, Baltimore, 1629 pp.

Pickford, M. 1981. Preliminary Miocene mammalian biostratigraphy for western Kenya. Journal of Human Evolution, 10, 73–97.

Pickford, M. 2001. Africa’s smallest ruminant: a new tragulid from the Miocene of Kenya and the biostratigraphy of East African Tragulidae. Geobios, 34, 437–447.

Pickford, M. 2002. Ruminants from the early Miocene of Napak, Uganda. Annales de Paléontologie, 88, 85–113.

Pickford, M. 2009. Land snails from the Early Miocene Legetet Formation, Koru, Kenya. Geo-Pal Kenya, 2, 1–88.

Pickford, M. & Senut, B. 2003. Miocene palaeobiology of the Orange River Valley, Namibia. Memoir of the Geological Survey of Namibia, 19, 1–22.

Pickford, M.,Musilizi, S., Senut, B., Gommery, D. & Musiime, E. 2010. Small apes from the Early Miocene of Napak, Uganda. Geo-Pal Uganda, 3, 1–111.

Pilgrim, G. E. 1910. Notice of new mammalian genera and species from territories of India. Records of the Geological Survey of India, 40, 63–71.

Quiralte, V., Sanchez I. M., Morales, J. & Pickford, M. 2008. Tragulidae (Artiodactyla, Ruminantia) from the Lower Miocene of the Sperrgebiet, Southern Namibia. Memoir of the Geological Survey of Namibia, 20, 387–396.

Rössner, G. E. 2004. Community structure and regional patterns in late Early to Middle Miocene Ruminantia of Central Europe. Pp. 91–100 in F. F. Steininger, J. Kovar-Eder & M. Fortelius (eds) The Middle Miocene Environments and Ecosystem Dynamics of the Eurasian Neogene (EEDEN). Courier Forschungsinstitut Senckenberg, 249.

Rössner, G. E. 2007. Family Tragulidae. Pp. 213–220 in D. R. Prothero & S. E. Foss (eds) The Evolution of Artiodactyls. The Johns Hopkins University Press, Baltimore.

Sanchez, I. M. & Morales, J. 2008. Micromeryx azanzae sp. nov. (Ruminantia: Moschidae) from the middle–upper Miocene of Spain, and the first description of the cranium of Micromeryx. Journal of Vertebrate Paleontology, 28, 873–885.

Sanchez, I. M., Quiralte, V., Morales, J. & Pickford, M. 2010. A new genus of tragulid ruminant from the early Miocene of Kenya. Acta Palaeontologica Polonica, 55, 177–187.

Scopoli, J. A. 1777. Introductio ad historiam natvralem sistens genera lapidvm, plantarvm, et animalivm hactenvs detecta, caracteribvs essentialibvs donata, in trivbs divisa, svbinde ad leges natvrae. Gerle, Pragae, 506 pp.

Thomas, H., Ginsburg, L., Hintong, C. & Suteethorn, V. 1990. A new tragulid, Siamotragulus sanyathani ng. n. sp. (Artiodactyla, Mammalia) from the Miocene of Thailand (Amphoe Pong, Phayao Province). Comptes Rendus de l’Académie des Sciences. Série II, 310, 989–995.

Tsubamoto, T., Tun, S. T., Egi, N., Takai, M., Shigebara, N., Soe, A. N., Aung, A. K. & Thein, T. 2003. Reevaluation of some ungulate mammals from the Eocene Pondagung Formation, Myanmar. Palaeontological Research, 7, 219–243.

Werdelin, L. 2010. Chronology of Neogene mammal localities. Pp. 27–43 in L. Werdelin & W. J. Sanders (eds) Cenozoic Mammals of Africa, University of California Press.

West, R. M. 1980. A minute new species of Dorcatherium (Tragulidae: Mammalia) from the Chinji Formation near Daud Khel, Mianwali district, Pakistan. Contributions in Biology and Geology, 33, 1–6.

Whitworth, T. 1958. Miocene ruminants of East Africa. Fossil Mammals of Africa, 15, 1–50.

Wilson, D. E. & Mittermeier, R. A. 2011. Handbook of the mammals of the world. Volume 2. Hoofed mammals. Lynx Edicions, Barcelona.