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## Tragulidae (Artiodactyla, Ruminantia) from the Early Miocene of the Sperrgebiet, Southern Namibia

<sup>1</sup>Victoria Quiralte, <sup>1</sup>Israel M. Sánchez, <sup>1</sup>Jorge Morales and <sup>2</sup>Martin Pickford

<sup>1</sup>Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, C/ José Gutiérrez Abascal 2, 28006-Madrid, Spain.  
(e-mail : vickyq@mncn.csic.es)

<sup>2</sup>Collège de France, and Département Histoire de la Terre, UMR 5143 du CNRS, 8 Rue Buffon, F-75005, Paris  
(e-mail : pickford@mnhn.fr)

The Early Miocene fluvio-paludal deposits of the Northern Sperrgebiet, Namibia, have yielded a varied artiodactyl assemblage comprising anthracotheres, suids, sanitheres, pecorans and traguloids. Prior to the activities of the Namibia Palaeontology Expedition, a single species of tragulid was reported from the area on the basis of an extremely limited sample in a generally poor state of preservation. The new collections contain a dozen fossils attributable to three species of tragulid, all of small dimensions. Similar species occur in the Early Miocene deposits of East Africa where they are associated with well wooded to forested palaeoenvironments, and it is possible that patches of dense woodland or forest may have existed in the Sperrgebiet during the period of deposition 20-19 million years ago.

### Introduction

The Namibian expeditions carried out by the Geological Survey of Namibia and the Muséum National d'Histoire Naturelle of Paris have yielded many fossil mammal remains of Early and Middle Miocene age (Morales *et al.*, 1999; Pickford and Senut, 2003) extending our knowledge of the faunas that inhabited Southern Africa during Miocene times. Among the fossils from the Early Miocene sites of Langental and Grillental, there are remains of Tragulidae.

Tragulids (Fig. 1) are non-pecoran ruminants that were widespread in Africa during the Early and Middle Miocene (Arambourg, 1933; Whitworth, 1958; Pickford, 2001, 2002; Morales *et al.*, 2003) but at present, the only species in the African continent is *Hyemoschus aquaticus*, the water or African chevrotin,



**Figure 1:** Anatomical reconstruction of the tragulid *Dorcatherium*; the individual depicted is a male, showing the elongated upper canines. Illustration by Mauricio Antón.

whereas in tropical Asia the genera *Moschiola* and *Tragulus* are the extant representatives of the group (Grubb, 1993; Meijaard and Groves, 2004).

In this paper we study the tragulid remains from the Early Miocene deposits at Langental and Grillental, in the Sperrgebiet (Southern Namibia).

### Materials and methods

**Material.** *Langental* - SAM-PQ.N.21, left hemimandible with m/3 and m/2, the roots of m/1 and p/4, and broken p/3; LT 164'06, right M3; LT 82'03, left distal tibia; LT 132'03, left distal tibia; LT 75'99, left navicular-cuboid; LT 398'96, right astragalus; LT 400'96, right astragalus; LT 58'06, right astragalus; LT 173'06, right astragalus; LT 56'04, right proximal metatarsal III-IV. *Grillental* - GT 82'06, left distal tibia; GT 37'04, left astragalus.

All fossils studied in this paper are housed in the collections at the Geological Survey of Namibia, Windhoek except for SAM PQ.N.21 which is stored in the Iziko South African Museum in Cape Town.

**Measurements.** All measurements of bones were taken with digital calipers following the method of Pickford (2001, 2002).

**Nomenclature.** For the postcranial skeleton, anatomical terms are based on Barone (1999). Azanza (2000) has been followed for nomenclature of the dentition.

**Abbreviations.** The abbreviations used are as follows:- LT, Langental; GT, Grillental. For the measurements, abbreviations are explained in each figure.

**Data analysis.** Morphometric analysis of dentition and postcranial material has been performed using scatter-plot comparisons of the measurements.

**Systematic descriptions**

**Suborder Ruminantia Scopoli, 1777**  
**Family Tragulidae Milne-Edwards, 1864**  
**Genus *Dorcatherium* Kaup, 1833**  
**Species *Dorcatherium songhorensis* Whitworth, 1958**

**Type Locality:** Songhor, Western Kenya.

**Material from the Sperrgebiet (Langental and Grillental):** Cranial and dental. SAM-PQ.N.21, left hemimandible with m/3 and m/2, the roots of m/1 and p/4, and broken p/3. (Pl. 1, Fig. 1; Fig. 2); LT 120'07, left m/2 (Fig. 2).

**Postcranial skeleton.** LT 82'03, left distal tibia; LT 132'03, left distal tibia; GT 82'06, left distal tibia; LT 75'99, left navicular-cuboid; LT 398'96, right astragalus; LT 400'96, right astragalus; LT 58'06, right astragalus; LT 173'06, right astragalus; LT

56'04, right proximal metatarsal III-IV. (Pl. 1, Figs. 2-4, 6-9, 11-12).

**Description:** *Dentition.* The lingual cusps of m/3 (Fig. 2.1; Pl. 1, Fig. 1) are strongly conical in shape. The buccal cusps have a half-moon shape. The pre-protocristid is longer than the pre-metacristid and the two structures are well separated from each other. The post-protocristid and post-metacristid are bifurcate, thus forming a well-developed *Dorcatherium*-fold; the two cristids join the pre-entocristid in the central area of the tooth (Fig. 2.1). The pre-hypocristid joins the buccal bifurcation of the post-protocristid (the likely equivalent of the *Palaeomeryx*-fold). The hypoconulid is located buccally and the pre-hypoconulid cristid joins the post-hypocristid. The post-hypoconulid cristid is very small and divided, and it ends far from the post-entocristid, thus forming a strong lingual opening between the two structures (Fig. 2.1).

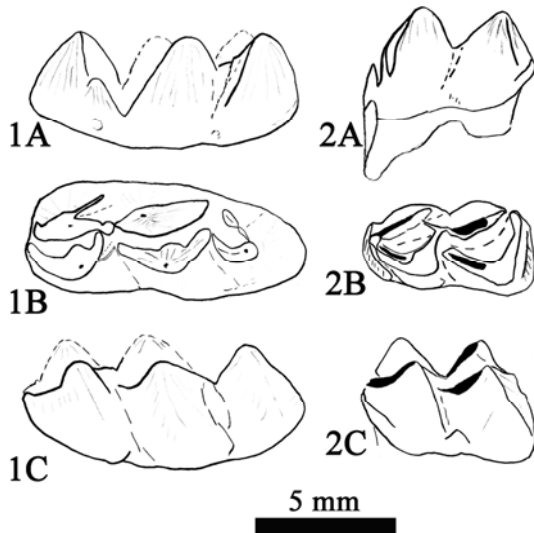
The m/2 in the mandible is broken, lacking most of the buccal wall. The basic characters are the same as in the m/3. The only remarkable difference is the presence of what appears to be a small entoconulid, which is not present in the m/3.

LT 120'07, a left m/2 (Fig. 2.2) is basically similar in morphology to the two front lobes of the m/3 described above. The tooth is in a slightly more advanced stage of wear which reveals the blade-like outline of the lingual cusps and the more selenodont outline of the buccal ones. The *Dorcatherium* fold is well developed as is the opening between the post-entocristid and the post-hypocristid. There is a low entoconulid at the buccal end of the valley between the protoconid and hypoconid.

Measurements of the dentition of *Dorcatherium* species from the Northern Sperrgebiet are presented in Table 1.

*Postcranial skeleton:* the postcranial sample is scarce and all the remains belong to the hind limb (Pl. 1, Figs. 2-4, 6-9, 11-12). Measurements of the postcranial skeleton are given in Tables 2 to 4.

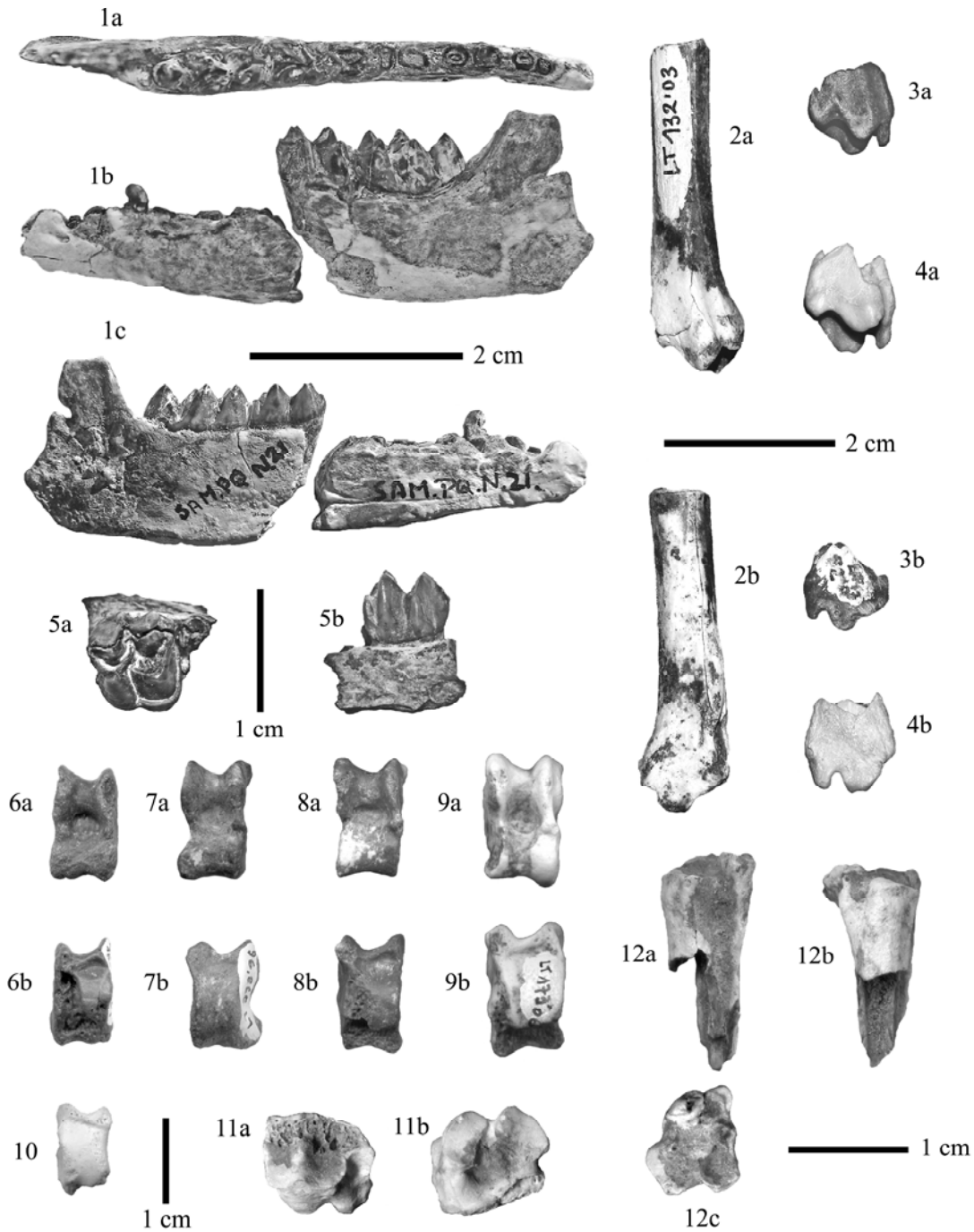
*Tibia.* (Table 2; Pl. 1, Figs. 2-4). LT 82'03, GT 82'06 and LT 132'03 are all left distal tibial frag-



**Figure 2:** *Dorcatherium songhorensis*, 1) m/3 in left hemimandible SAM-PQ.N.21, a) lingual view, b) occlusal view; notice the *Dorcatherium*-fold and the postero-lingual opening located behind the entoconid, c) buccal view; 2) left m/2, LT 120'07 a) lingual view, b) occlusal view, c) buccal view.

**Table 1 :** Measurements (in mm) of the dentition of *Dorcatherium songhorensis* (SAM-PQ.N.21) and *Dorcatherium* sp. cf. *D. parvum* (LT 164'06) from Langental, Early Miocene, Namibia. The asterisk represents an approximate measurement due to poor preservation.

Specimen	Locality	Taxon	Tooth	Mesio-distal length	Bucco-lingual breadth
LT 120'07	Langental	<i>D. songhorensis</i>	m/1	6.7	3.6
SAM-PQ.N.21	Langental	<i>D. songhorensis</i>	m/2	10.9	4.6
SAM-PQ.N.21	Langental	<i>D. songhorensis</i>	m/3	7.2	4*
LT 164'06	Langental	<i>D. cf. parvum</i>	M3/	6.6	7.6



**Plate 1:**

- Figure 1: SAM-PQ.N.21, left hemimandible of *D. songhorensis*, a) occlusal view; b) buccal view; c) lingual view.  
 Figure 2: LT 132'03, left distal tibia of *D. songhorensis*, a) ventral view; b) dorsal view.  
 Figure 3: LT 82'03, left distal tibia of *D. songhorensis*, a) ventral view; b) dorsal view.  
 Figure 4: GT 82'06, left distal tibia of *D. songhorensis*, a) ventral view; b) dorsal view.  
 Figure 5: LT 164'06, right M3/ of *Dorcatherium* sp. cf. *D. parvum*, a) occlusal view; b) buccal view.  
 Figure 6: LT 400'96, right astragalus of *Dorcatherium songhorensis*, a) dorsal view; b) plantar view.  
 Figure 7: LT 398'96, right astragalus of *Dorcatherium songhorensis*, a) dorsal view; b) plantar view.  
 Figure 8: LT 58'06, right astragalus of *Dorcatherium songhorensis*, a) dorsal view; b) plantar view.  
 Figure 9: LT 173'06, right astragalus of *Dorcatherium songhorensis*, a) dorsal view; b) plantar view.  
 Figure 10: GT 37'04, left astragalus of *Dorcatherium* sp. cf. *D. moruorotensis*, plantar view.  
 Figure 11: LT 75'99, left navicular-cuboid of *D. songhorensis*. a) proximal view; b) distal view.  
 Figure 12: LT 56'04, proximal fragment of right metatarsal III-IV of *Dorcatherium songhorensis*, a) dorsal view; b) lateral view; c) proximal view.

**Table 2:** Measurements of the tibia of *Dorcatherium songhorensis* from Langental and Grillental, Early Miocene, Namibia. Abbreviations : distDT : distal transverse diameter; distDAP, distal antero-posterior diameter. Measurements are in mm.

Specimen	Locality	distDT	distDAP
LT 132'03	Langental	10.8	9.1
LT 82'03	Langental	10.1	7.9
GT 82'06	Grillental	10.7	8.8

ments but only LT 132'03 retains a significant portion of the diaphysis.

The fibular fissure is not preserved in LT 132'03, but it is well marked in LT 82'03 and GT 82'06; it is delimited by two crests and its morphology is similar to that of *Hyemoschus*. The tubercle located ventrally to the fibular fissure is more rounded in the fossils than in the extant African chevrotain.

The malleolar facet is elongated and shallow, with lesser lateral development than in *Hyemoschus*, and its overall morphology is simpler than that of the malleolar facet of the Pecora. The medial groove of the distal articular facet is narrower than the lateral groove, as in the extant African chevrotain.

The antero-distal tibial process is wide with convergent sides (Pl. 1, Figs. 2b-3b-4b). It differs from that of *Hyemoschus* by its lesser relative distal breadth, the more convergent sides and its more pronounced overall gracility. The medial malleolus is missing in LT 132'03, but it is present in LT 82'03 and GT 82'06. It is slightly shorter than the antero-distal process, subtriangular in shape with a rounded apex, and it is relatively longer than that of *Hyemoschus* (Pl. 1, Figs. 3b-4b).

The groove for the medial digital flexor muscle is highly developed, relatively more than in *Hyemoschus*, and is delimited by two well-marked crests (Pl. 1, Fig. 2a).

**Astragalus** (Table 3; Pl. 1, Figs. 6-9). The poor preservation of the specimens and the aspect of the

bone surface, polished by aeolian erosion, do not allow us to provide a detailed morphological description. The fossils are also incomplete. The best-preserved specimen is LT 173'06 (Pl. 1, Fig. 9) although part of the plantar surface for articulation with the calcaneum is lacking. Even so, the typical tragulid condition, with the edges of the proximal trochlea tilted with respect to the distal one, not parallel as in the Pecora, can be clearly observed in LT 398'96 and LT 58'06 (Pl. 1, Figs. 7-8). Both lateral and medial condyles of the proximal trochlea seem to be subequal, contrary to the greater development of the lateral one noted in *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al.*, 2003) and in extant *Hyemoschus*.

**Navicular-cuboid** (Table 4; Pl. 1, Fig. 11). The specimen LT 75'99 shows the posterior half of the proximal articular facet damaged, this area being totally missing.

The calcaneal facet is morphologically different from that of *Hyemoschus* because there is a pronounced step that is absent in the extant species, and the anterior half of the facet forms a deep quadrangular pit, that is lacking in navicular-cuboids of *Hyemoschus*. This lateral facet does not reach the distal border of the bone (the opposite of the case in *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift; Morales *et al.*, 2003). Contrary to the condition found in extant *Hyemoschus*, the lateral groove does not contact the calcaneal facet nor does it limit it distally.

The posterior surface is almost flat, very similar to that of *Hyemoschus*. It is not possible to describe the distal extension of the latero-distal process because this part is broken.

The ectomesocuneiform tarsal is fused with the navicular-cuboid bone. The distal facet of the ectomesocuneiform is kidney-shaped and less triangular than that of the extant African chevrotain (Pl. 1, Fig. 11b). The anterior metatarsal facet has a deep step located halfway, a structure which is not present in *Hyemoschus*. The posterior medial metatarsal facet is less well preserved than the anterior one, and has an overall morphology similar to that of *Hyemoschus*; it

**Table 3:** Measurements of the astragali of *Dorcatherium songhorensis* from Langental and *D. sp. cf. D. moruorotensis* from Grillental, Early Miocene, Namibia. Asterisks represent approximate measurements due to poor preservation. Abbreviations : medLt, medial length; latLt, lateral length; latDAP, lateral antero-posterior diameter; medDAP, medial antero-posterior diameter; proxDT, proximal transverse diameter; distDT, distal transverse diameter. Measurements are in mm.

Specimen	Locality	medLt	latLt	latDAP	medDAP	proxDT	distDT
LT 400'96	Langental	13.6*	-	-	-	8.4*	7.8*
LT 398'96	Langental	14*	14.1*	-	-	-	7.8*
LT 58'06	Langental	14	14.4	7.5	-	7.9*	7.5*
LT 173'06	Langental	15.4	15*	8.9	9.1	9.2	8.7*
GT 37'04	Grillental	11.2*	11.5*	-	-	6.4	6.2*

**Table 4:** Measurements of the navicular-cuboid of *Dorcatherium songhorensis* from Langental, Early Miocene, Namibia. Abbreviations : maxDAP, maximum antero-posterior diameter; maxDT, maximum transverse diameter; antH, anterior height. Measurements are in mm.

Specimen	Locality	maxDAP	maxDT	antH
LT 75'99	Langental	9.0	10.3	7.6

is large and subtriangular in shape and extends forwards. There is a vascular foramen located behind the distal facet of the ectomesocuneiform, in front of which extends a well-developed groove (Pl. 1, Fig. 11b). This groove is deeper in the extant African chevrotain than in the Sperrgebiet tragulid; furthermore, in *Hyemoschus* the groove is separated from the vascular foramen by a marked crest that does not exist in the fossil species.

**Metatarsal III-IV** (Pl. 1, Fig. 12). There is only a small proximal fragment, LT 56'04, which shows a broken metatarsal III. Therefore it is not possible to observe the complete proximal aspect of the bone. Nevertheless the fusion of the two metatarsals can be seen, each one preserving its respective medullary cavity independently, the same condition that occurs in *Hyemoschus* and other fossil tragulids such as *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al.*, 2003). In dorsal view the metatarsals are placed at different levels, the medial one, or Mt III, being elevated with respect to the lateral one, or Mt IV (Pl. 1, Fig. 12a). The difference in height between the two metatarsals seems to be more accentuated in the species from the Sperrgebiet than in *Hyemoschus* or *Dorcatherium* species from Arrisdrift. The dorsal metatarsal *sulcus* is quite wide in the proximal end, and not as narrow as that of *Dorcatherium* sp. aff. *D. pigotti*, resembling more the *sulcus* in *Hyemoschus* (Pl. 1, Fig. 12a).

In the proximal surface only the anterior lateral facet for articulation with the navicular-cuboid, with its typical kidney-shape, is complete. It is proportionally shorter than in *Hyemoschus*, which shows a facet that is more projected towards the plantar border/surface. The anterior medial facet is incomplete. Dorsally the edges of these two anterior facets are projected and make an angular border which extends along the diaphysis, forming a keel, as occurs in *Hyemoschus* (Pl. 1, Fig. 12c). However in *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al.*, 2003) the anterior border is rounded.

In proximal view of the two plantar facets, only the medial one for articulation with the entocuneiform seems to be complete and well developed. The lateral one, where the distal process of the navicular-cuboid rests, is incomplete and poorly preserved. Even so, it seems to be shorter and more rounded than in *Hyemoschus*, which has a well developed facet with an elongated shape that occupies almost

half of the plantar surface.

The fossette for articulation with metatarsal II is not discernible due to the poor preservation of the specimen. The fossette for metatarsal V is present (Pl. 1, Fig. 12b) but the facet where this lateral metatarsal is attached is not visible because the surface is polished.

The proximal antero-posterior diameter is 9.0 mm.

**Genus *Dorcatherium* Kaup, 1833**

**Species *Dorcatherium* sp. cf. *D. moruorotensis* Pickford, 2001**

**Type Locality:** Moruorot, Turkana district, Kenya.

**Material from the Sperrgebiet (Grillental):** Postcranial skeleton. GT 37'04, left astragalus (Pl. 1, Fig. 10).

**Description:** *Postcranial skeleton:* only a small, incomplete and polished astragalus of small tragulid has been attributed to this species. Measurements of GT 37'04, most of them approximate due to the erosion, are given in Table 3.

**Astragalus** (Pl. 1, Fig. 10). The poor preservation of the specimen only allows us to observe the shape of the plantar surface for articulation with the calcaneum, which is narrow and concave in its central area. The same morphology is present in other tragulids such as *Hyemoschus* and *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al.*, 2003).

**Genus *Dorcatherium* Kaup, 1833**

**Species *Dorcatherium* sp. cf. *D. parvum* Whitworth, 1958**

**Type Locality:** Rusinga Island, Western Kenya.

**Material from the Sperrgebiet (Langental):** Dentition. LT 164'06, right M3/ (Pl. 1, Fig. 5).

**Description:** *Dentition.* Only an isolated M3/ has been attributed to this small *Dorcatherium* species. The measurements of this specimen are shown in Table 1.

**M3/** (Pl. 1, Fig. 5). The cusps of this tooth are typically bunoselenodont in the tragulid fashion, with broad bases and pointed tips. The buccal cusps are not aligned and show a pyramidal profile, with the base far broader than the tip. Buccal structures are well developed, especially the paraconal rib and the mesostyle, which are both strong (Pl. 1, Fig. 5b). The pre-protocrista joins the pre-paracrista, and the same occurs with the post-metacrista and the post-metacrista (Pl. 1, Fig. 5a). The post-protocrista is short, the opposite of the situation in the pre-metacrista, which is long and extends as far as the centre of the occlusal surface. There is a well developed cingulum around the antero-lingual area,

which is particularly strong at the base of the protocone (Pl. 1, Fig. 5a).

### Discussion

Tragulids are rare in the fossil sites of the Northern Sperrgebiet. Hopwood (1929) listed Tragulidae indet. cf. *Dorcatherium* and Tragulidae indet. cf. *Bachitherium* based on three mandibles with poorly preserved dentitions. Hamilton and Van Couvering (1977) doubted Hopwood's (1929) taxonomic attributions, and suggested that the mandible identified by him as *Dorcatherium* sp. pertained instead to the genus *Propalaeoryx*, and the ones identified as *Bachitherium* sp. were the mandibles of a small-sized ruminant of ambiguous taxonomic affinities. Nevertheless Hamilton and Van Couvering (1977) confirmed the presence of *Dorcatherium* in the Miocene of the Northern Sperrgebiet on the basis of a new mandibular specimen, which is, with all probability, the hemimandible SAM-PQ.N.21 described in this paper. Also, the mandible AM No. 22525 classified by Hopwood (1929) as *Bachitherium* sp. has a dentition of similar size to that of *Dorcatherium songhorensis*, showing only minor differences in the bucco-lingual breadth that can be easily attributed to the strong enamel wear of that specimen's teeth. In any case, the existence of the species *D. songhorensis* in Langental is confirmed by the mandible SAM-PQ.N.21 and the postcranial bones described in this paper.

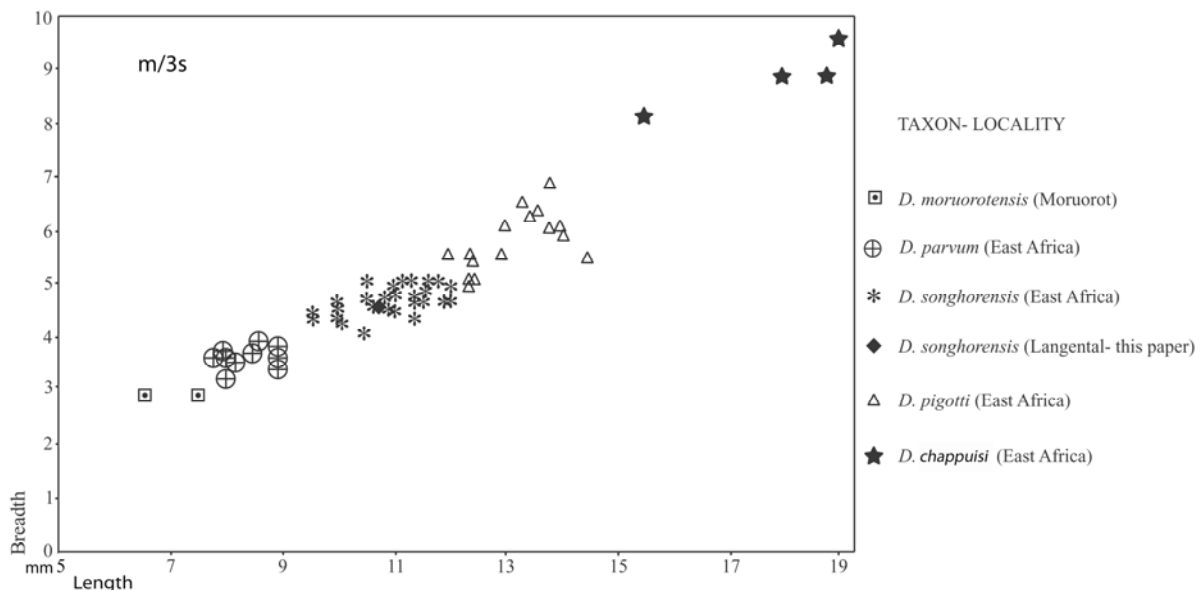
The morphology of the upper dentition and the presence of a *Dorcatherium*-fold in the lower dentition, along with the presence of a navicular-cuboid fused with the ectomesocuneiform, the morphology of the metatarsal and the non-parallel sides of the

astragalar trochleae (a feature especially visible in LT 398'96) provide conclusive evidence as to the tragulid affinities of the fossil remains.

The fossil sample is scarce and in general terms the preservation is not good. The hemimandible SAM-PQ.N.21 is broken although both m/2 and m/3 are preserved. Also, there is not a single complete long bone and the majority of specimens are eroded and polished. Even so, three tragulid species have been identified in the Northern Sperrgebiet. Specific attributions have been made on the basis on both size and morphology. When the preservation is not good enough for a morphological discussion, identifications are based on size.

The majority of fossil remains (hemimandibular fragment, four astragali, three distal fragments of tibia, a navicular-cuboid and a proximal end of metatarsal III-IV) belong to a small to medium sized tragulid, smaller than *Dorcatherium pigotti*. It is likely that they correspond to *Dorcatherium songhorensis* Whitworth, 1958. *D. songhorensis* was already reported from the fossil site of Langental by Pickford (2001) but it was not known from the slightly older site of Grillental. Among the postcranial material studied in this work there is a fragment of tibia from Grillental (GT 82'06) that confirms the presence of *D. songhorensis* in this locality.

Dimensions of the dentition in SAM-PQ.N.21 fall into the range of metric variation of *D. songhorensis* (Fig. 3) located in a position intermediate between *D. parvum* and *D. pigotti* (Whitworth, 1958; Pickford, 2001). All these species share a similar morphological pattern, with slight variation, and are mainly recognized by the presence of low-crowned molars with clearly bunodont cusps and a strongly



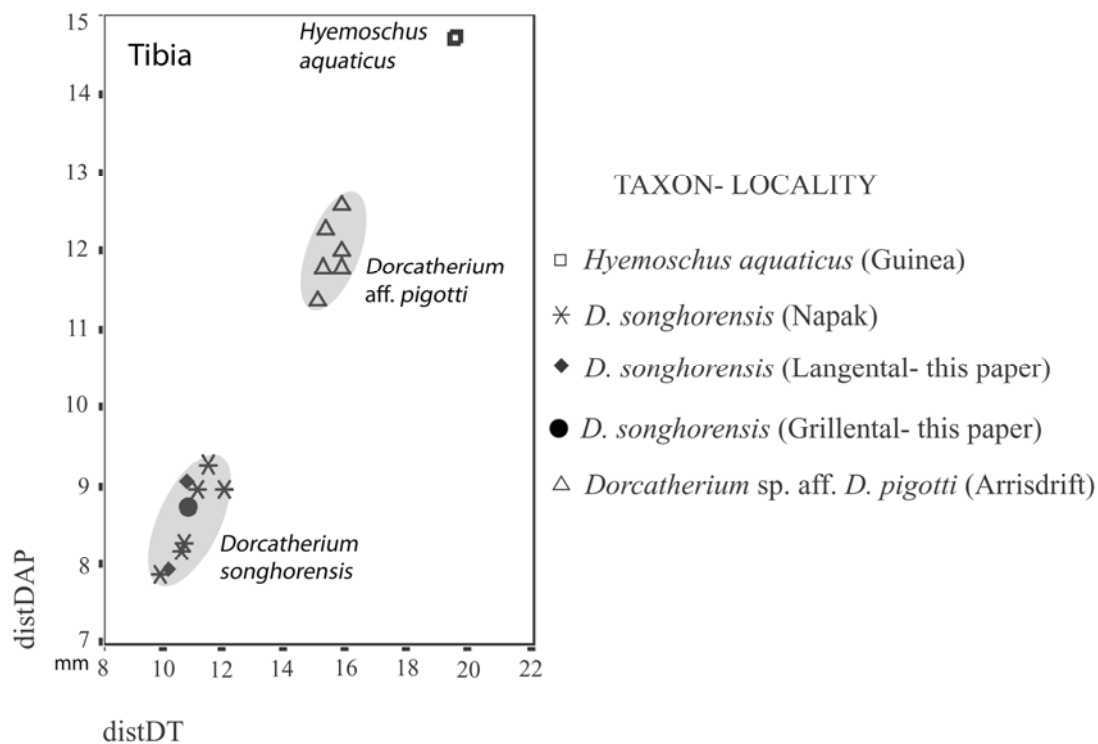
**Figure 3:** Bivariate (length/breadth) plot of lower third molars of several African tragulids. Notice the position of the Langental m/3 within the *Dorcatherium songhorensis* group. Measurements are in mm.

developed *Dorcatherium*-fold. The morphometric comparisons of postcranial remains also support the identification of *Dorcatherium songhorensis* in the Sperrgebiet. The tragulid tibiae from Langental and Grillental are much smaller than those of *Dorcatherium* sp. aff. *D. pigotti* from Arrisdraft (Morales *et al.*, 2003) (Fig. 4) and the extant African chevrotain (*Hyemoschus aquaticus*) the Sperrgebiet specimens being almost identical in size to those of *D. songhorensis* from Napak, Uganda (Pickford, 2002). The minimum dimensions of the astragali from Langental are also close to the size of *D. songhorensis* from Napak (Pickford, 2002) but the specimens are somewhat shorter than the aforementioned species (Fig. 5). This small difference in proportions might be explained by the poor preservation of astragali in the sample, polished by aeolian abrasion. The metatarsal LT 56'04 is not complete, but the proximal antero-posterior dimension is comparable to that of *D. songhorensis* form Napak (Pickford, 2002). Also, the only navicular-cuboid from Langental is clearly smaller than Arrisdraft specimens (Fig. 6) thus excluding *D. pigotti* from the former fossil site.

There is also clear evidence of the presence of two more species of tragulids among the Sperrgebiet fossil sample. Firstly, there is a very small astragalus (GT 37'04) from the locality of Grillental. The measurements place this specimen within the distribution of the tiny *Dorcatherium moruorotensis* (Pickford,

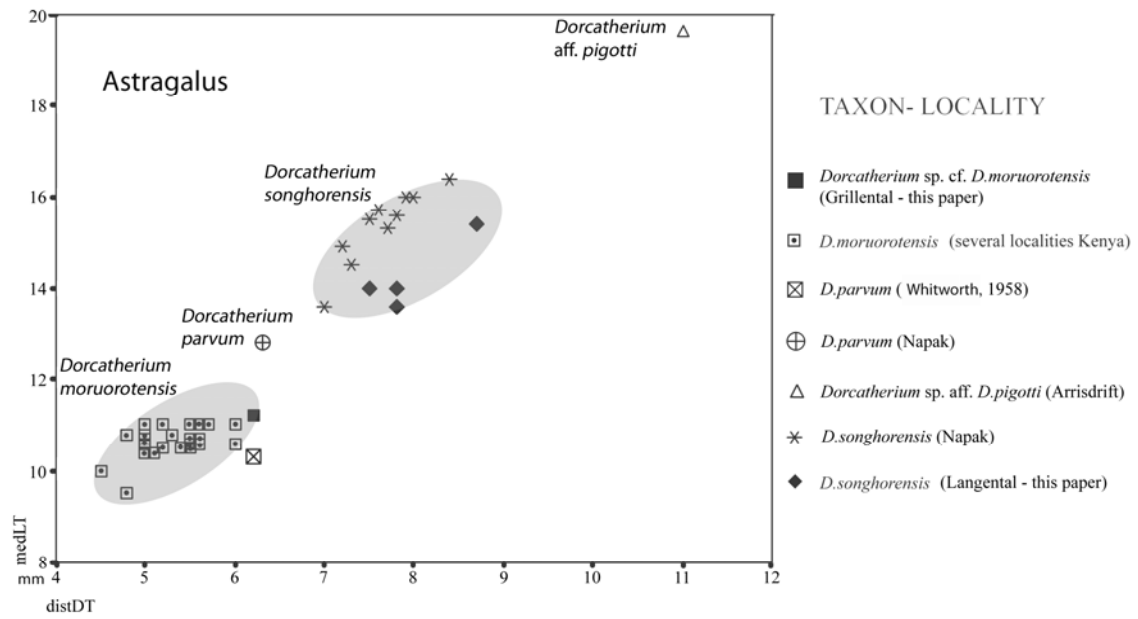
2001) being among the larger values (Fig. 5). It is also located below the dimensions provided by Pickford (2002) for *D. parvum*. However, as can be seen in the bivariate plot distribution (Fig. 5) the astragalus attributed by Whitworth (1958) to *D. parvum* is also placed together with the distribution of *D. moruorotensis*. Pickford (2001) pointed out that Whitworth (1958) himself made comments on the appreciable variation in size among the material assigned to *D. parvum*, and concluded that some of the material studied by Whitworth (1958) actually corresponds to two distinct species : *D. parvum* and the smaller *D. moruorotensis*. Thus, the small astragalus figured by Whitworth as *D. parvum* (1958, pg. 38, fig. 17g) probably belongs to *D. moruorotensis*, just the same as the small astragalus studied in this paper. However, because of the poor preservation of this specimen we classify this small species from Grillental as *Dorcatherium* sp. cf. *D. moruorotensis*.

In contrast, the M3/, LT 164'06, falls into the upper end of the size range of *Dorcatherium parvum* (Fig. 7). *D. parvum* is somewhat smaller than *D. songhorensis*, but its dentition shows great variability in size, as was noted by Whitworth (1958). However it appears that two specimens in the bivariate-plot comparison may have been "transposed" (see Fig. 7). One of them pertains to *D. parvum* and the other to *D. songhorensis*. Both measurements come from Whitworth (1958) and we cannot exclude the possi-

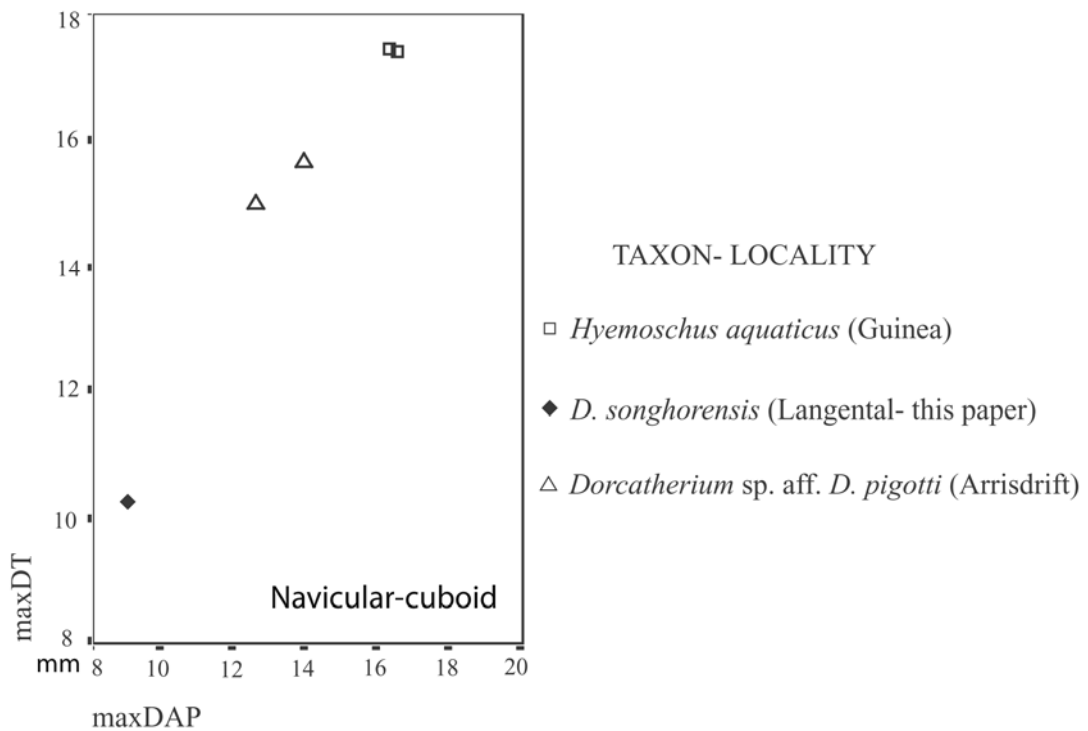


**Figure 4:** Bivariate plot of several African tragulid tibiae, including extant *Hyemoschus*, *Dorcatherium* sp. aff. *D. pigotti* from Arrisdraft and the fossils studied in this paper. Abbreviations : distDT, distal transverse diameter; distDAP, distal antero-posterior diameter. Measurements are in mm.

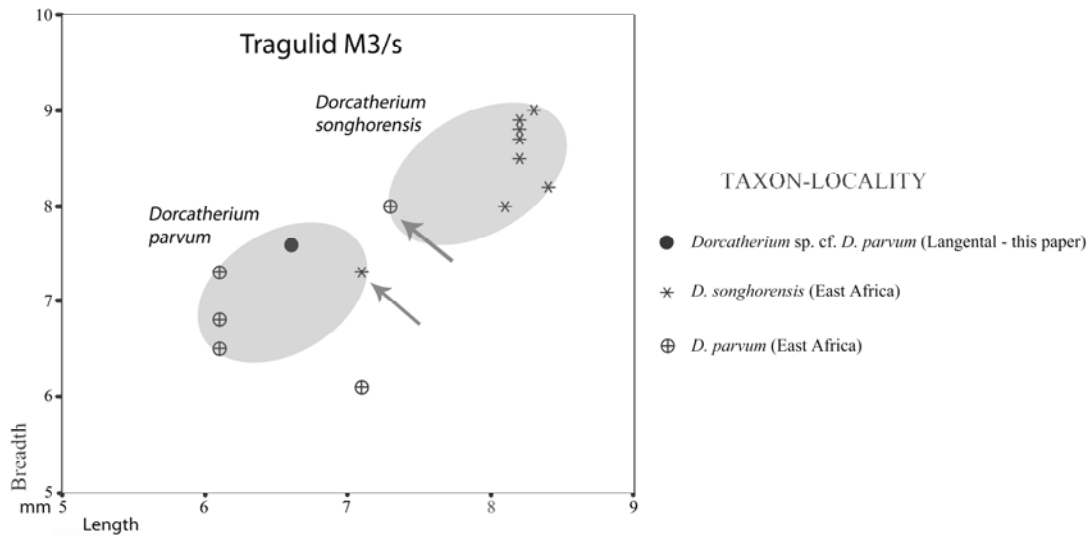




**Figure 5:** Bivariate plot of the astragalus of several African *Dorcatherium* species, including the two species studied in this paper. Abbreviations : distDT, distal transverse diameter; medLT, medial length. Measurements are in mm.



**Figure 6:** Bivariate plot of several African tragulid navicular-cuboids, including the extant *Hyemoschus*, *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift and the fossils studied in this paper. Abbreviations : maxDAP, maximum antero-posterior diameter; maxDT, maximum transverse diameter. Measurements are in mm.



**Figure 7:** Bivariate plot of upper third molars of *Dorcatherium parvum* and *D. songhorensis*. Notice the “interchanged” position of a pair of measurements (arrows) (Whitworth’s 1958 data). The Langental M3/ falls into the *Dorcatherium parvum* group. Measurements are in mm.

bility of a misidentification or mislabelling of Whitworth’s two specimens, the smaller one corresponding to *D. parvum* instead of *D. songhorensis* and the larger one to *D. songhorensis* instead of *D. parvum*. The morphology of LT 164’06 is, as is usually the case in African tragulids, highly conservative and primitive, and nearly identical to that of other *Dorcatherium* species. We finally classify this species from Langental as *Dorcatherium* sp. cf. *D. parvum* because of the aforementioned situation and the possible overlap in the size range between *D. parvum* and *D. songhorensis* for this particular specimen.

Although Sperrgebiet tragulid material is scarce and not very well preserved, the probable presence of *Dorcatherium moruorotensis* and *Dorcatherium parvum* in the area extends the known geographic distribution of these species, which now includes Southern Africa. This study also adds new information about chronological ranges in the two taxa. Previously the oldest known record of *D. parvum* was from the upper levels of the Napak Member (Uganda) probably with an age of 18–18.5 Ma (Pickford, 2002). Thus, the presence of *D. parvum* in the site of Langental (19 Ma) expands the chronologic range of this species, being now registered in older deposits of Early Miocene age. In the case of *Dorcatherium moruorotensis* the extension of its chronological range is even more notable. Pickford (2001) described *D. moruorotensis* from the basal middle Miocene locality of Moruorot, in Kenya, but also recognizes its presence in older localities in East Africa, covering a time interval from 18 to 17.2 Ma. Thus the record of *D. moruorotensis* at Grillental, a locality slightly older than Langental, indicates the presence of this small tragulid species in deposits aged about 20 Ma.

The fact that these two species occur earlier in southern Africa than in East Africa possibly supports

the idea proposed by Pickford and Senut (2003) about the South African origin of several mammal lineages (in this case tragulids) which later occupied equatorial or northern regions of Africa.

Up to now only the species *Dorcatherium songhorensis* was reported from the basal Early Miocene or Faunal Set I in Africa (Pickford, 2001). Nevertheless this study shows the possible coexistence of at least three *Dorcatherium* species in southern Africa at that time.

Finally, if Miocene *Dorcatherium* were as tied to warm and humid environments as modern chevrotains are, it is suggested that similar ecological conditions were present, at least locally, in Southern Africa during Early Miocene times.

## Conclusions

The tragulid fossil remains from the Early Miocene sites of Langental and Grillental (Sperrgebiet, Southern Namibia) are scarce and not well preserved due to strong aeolian erosion. Despite the poor preservation, we have identified three taxa of tragulids. The majority of specimens corresponds to the species *Dorcatherium songhorensis* Whitworth, 1958, previously reported from the fossil site of Langental (Pickford, 2001) but never cited before from the locality of Grillental. It is a medium to small tragulid clearly inferior in size to *Dorcatherium* sp. cf. *D. pigotti* from the younger Namibian site of Arrisdrift (Morales *et al.*, 2003). The other two taxa are *Dorcatherium* sp. cf. *D. moruorotensis* Pickford, 2001 and *Dorcatherium* sp. cf. *D. parvum* Whitworth, 1958, represented in our fossil sample by an astragalus and an M3/ respectively. The former is a very small tragulid originally described from the basal middle Miocene deposits of Moruorot, Kenya

(Pickford, 2001) and identified in this paper for the first time in older localities in the Sperrgebiet, Namibia. The latter is a species previously described by Whitworth (1958) from Rusinga Island, Western Kenya, and also reported from Napak sites, Uganda (Pickford, 2002) in deposits younger than Langental. Despite the scarcity of the material, the geographical and chronological ranges of these two tragulid species would therefore be expanded, now including Southern Africa and extending the record of *Dorcatherium moruorotensis* and *Dorcatherium parvum* to earlier times (20-19 Ma).

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