Preliminary phylogenetic analysis of the Tragulidae (Mammalia, Cetartiodactyla, Ruminantia) from Arrisdrift: implications for the African Miocene tragulids

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Abstract: We perform a phylogenetic analysis to test the affinities of '*Dorcatherium*' from Arrisdrift (early middle Miocene, Sperrgebiet, Namibia). Our results show Arrisdrift '*Dorcatherium*' included in a clade of Miocene African forms that also contains '*D.*' *pigotti* and '*D.*' *iririensis*. This clade is not related to the true *Dorcatherium*-clade which includes the type species *D. naui*. Although we are not taking taxonomic decisions at the genus level until more data are used in future analyses, it is clear that the Arrisdrift form is a distinct new species that we name '*Dorcatherium*' *namaquensis*.

Key Words: Ruminants; Basal Middle Miocene; Namibia; Sperrgebiet; Evolution; Phylogeny.

Introduction

The Tragulidae (mouse-deer and chevrotains; Fig. 1) comprise the most basal extant Ruminantia, the only living members of an ancient Eocene radiation of ruminants (Rössner, 2007; Sánchez *et al*. 2010, 2015a; and references therein), and the only non-pecoran group that survived the Palaeogene-Neogene transition. Tragulids include the smallest living cetartiodactyls, surviving as relics in the Old World tropical belt: *Tragulus* (6 species) in South-East Asia and the Philippines, *Moschiola* (3 species) in India and Sri Lanka, and *Hyemoschus* (monotypic, *H. aquaticus*) in Africa from Sierra Leona to Uganda (Meijaard, 2011). They are associated with water and with more-or-less forested areas, with some of them (mostly the African and Asian chevrotains, *Hyemoschus* and *Moschiola*) using a peculiar diving behavior that consists of walking on the river bed in order to escape predators and other suspected menaces (Meijaard, 2011). Interestingly, it appears that the link with humid areas was also present in the Miocene forms (Rössner, 2004). As the most primitive living ruminants, tragulids are less advanced than pecorans in many physiological and morphological features (Dubost, 1965; Kay, 1987; Métais *et al*. 2001; Rössner, 2007).
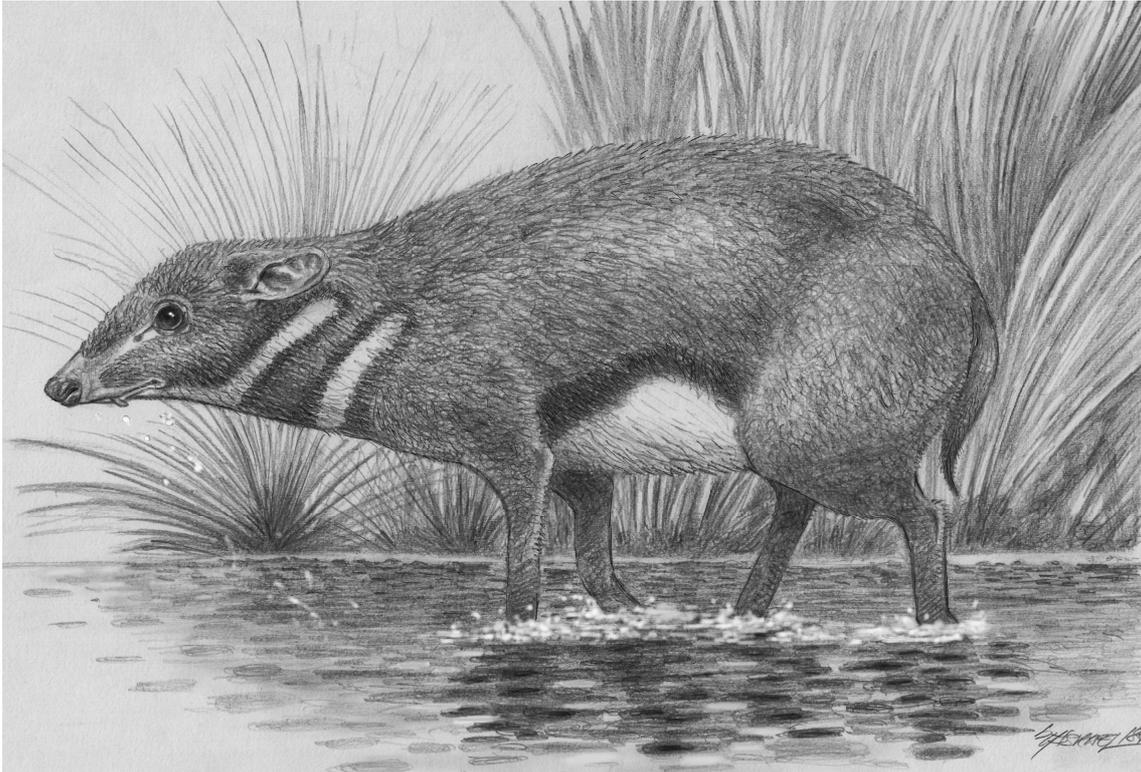
Figure 1. Reconstruction of an adult male '*Dorcatherium' namaquensis*. The head is based on the '*D.*' *chappuisi* skull figured in Geraads (2010) and the mandible and postcranial anatomy is based on Arrisdrift fossils and, when no fossil information was available, on extant *Hyemoschus*. Illustration by Israel M. Sánchez.

The early evolutionary history of the group is poorly known, with the late Eocene *Archaeotragulus krabiensis* being the only undisputed Palaeogene member of the Tragulidae (Métais *et al*. 2001; Tsubamoto *et al*. 2003; Métais & Vislobokova, 2007). *Archaeotragulus* was also recovered recently as the most basal tragulid (Sánchez *et al*. 2015a). The gap in the fossil record of the Tragulidae extends through time to the early Miocene, when tragulids suddenly reappear with a great diversity in fossil sites in Africa, Asia and Europe (Rössner, 2007; Geraads, 2010; Sánchez *et al*. 2010, 2015a and references therein). Members of both the derived 'Selenodont-clade' (the clade that includes the extant *Tragulus* and *Moschiola*) together with more basal forms were distributed through Asia and Africa during the final part of the early Miocene (Sánchez *et al*. 2015a). Tragulids entered Europe somewhat later (Rössner, 2007; Sánchez *et al*. 2010, 2015a) and experienced a great evolutionary success during the Miocene throughout their palaeobiogeographical range, even successfully competing with pecoran ruminants where their habitat preferences were met (Rössner, 2004).

Tragulid fossils are found in Namibia at several sites in the Sperrgebiet, comprising two main time frames. On the one hand, Lower Miocene sites possess the highest diversity of the group, including three small-sized representatives of the 'selenodont-clade', *Siamotragulus songhorensis*, *Afrotragulus* sp. cf. *A. parvus*, and *Afrotragulus* sp. cf. *A. moruorotensis* (see Quiralte *et al*. 2008, although all of them were still included in *Dorcatherium* in that work). On the other hand, in the early Middle Miocene site of Arrisdrift, relatively abundant tragulid fossils were described by Hendey (1978) and Morales *et al*. (2003) which were attributed to *Dorcatherium* sp. cf. *D. pigotti* and *Dorcatherium* sp. aff. *D. pigotti* respectively. As was pointed out by Rössner (2007) and Sánchez *et al*. (2010), *Dorcatherium* is a paraphyletic assemblage of diverse unrelated tragulid forms (both buno-selenodont and selenodont) that is in urgent need of a systematic and taxonomic

revision. Also, tragulids are phylogentically poorly known, with only one published paper to date regarding this subject, focused to the characterization of the 'selenodont-clade' (Sánchez *et al*. 2015a). In this work we attempt a preliminary phylogenetic analysis of the genus *Dorcatherium* with special emphasis on the African forms, with the specific aim of checking the phylogenetic position of *Dorcatherium* from Arrisdrift and its link to the 'true' *Dorcatherium* represented by the type species *D. naui* and its closest relatives.

Material and Methods

Material. We have used the *Afrotragulus* material described in Sánchez *et al*. (2010), the type material of *D. naui* from Eppelsheim (NHM-London), *D. guntianum* (SMN- Stuttgart), *D. iririensis* (UM) and *D. pigotti* (NHM-London), including the cranial material figured by Geraads (2010). Regarding the extant forms we examined specimens of *Hyemoschus, Moschiola* and *Tragulus* stored in the MNCN-CSIC (Madrid), the Museum of Zoology of the University of Cambridge (Cambridge) and the AMNH (New York) (as pointed out in Sánchez *et al*. 2010): *Hyemoschus aquaticus* MNCN-CSIC 18947 (young female), *Moschiola meminna* private collection J. 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 javanicus* AMNH 102078 (adult male).

Nomenclature. For the postcranial skeleton anatomical terms are based on Barone (1999). Azanza (2000) - English version in Sánchez & Morales (2008) - has been followed for nomenclature of the dentition. The anatomical definitions specific to tragulids follow Sánchez *et al*. (2015a) and references therein.

Abbreviations. AMNH, American Museum of Natural History (New York, USA); GSN, Geological Survey of Namibia (Windhoek); MNCN-CSIC, Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain); NHMUK, Natural History Museum (London, UK); OCO, Orrorin Community Organisation (Kipsaraman, Kenya); SMN, Staatliches Museum für Naturkunde (Stuttgart, Germany); UM, Uganda Museum (Kampala, Uganda); UMZC, Museum of Zoology of the University of Cambridge (Cambridge, UK).

Cladistic analysis. We performed a cladistic analysis at the species-level to make a preliminary exploration of the phylogenetic affinities of the Arrisdrift tragulid with some other tragulid species. We used *Zhailimeryx jingweni* as the outgroup following Métais *et al*. (2001) and Sánchez *et al*. (2015a). Apart from the Arrisdrift tragulid the ingroup is composed by *Dorcabune anthracotherioides*, *Dorcabune welcommi*, *Dorcatherium crassum*, *Dorcatherium iririensis*, *Dorcatherium pigotti*, *Dorcatherium guntianum*, *Dorcatherium naui*, the type species of *Siamotragulus*, the two species of *Afrotragulus* and the extant tragulids *Hyemoschus aquaticus*, *Tragulus javanicus* and *Moschiola memmina*. The morphological data matrix used here is a development of the dataset published by Sánchez *et al*. (2015a), comprising 62 characters (cranial, dental and postcranial) and 16 terminals (Annex 1). The data matrix was compiled in MacClade 4.05 and run in TNT v1.5 (Goloboff & Catalano, 2008). Also, we used MacClade 4.05 to reconstruct the character-state distributions for the internal node.

Systematic Palaeontology

Ruminantia Scopoli, 1777

Tragulidae Milne-Edwards, 1864

Species '*Dorcatherium*' *namaquensis* sp. nov.

Synonymy:
Dorcatherium aff. *pigotti* (Morales *et al*. 2003)
Dorcatherium cf. *pigotti* (Hendey, 1978)

Etymology: From the area known as Namaqualand that comprises a desert coastal area that extends North and South of the Orange River, including Arrisdrift.

Holotype: GSN AD 424'97, left mandible with p/3-m/3 (Morales *et al*. 2003; plate 1.5)

Paratypes: The other material from Arrisdrift referred to the species and figured by Morales *et al*. (2003, plates 1-4), with the exception of GSN AD 95'95, left maxilla with P3/-P4/ and M2/-M3/ (Morales *et al*. 2003; plate 1.1), plus GSN AD 694'94 (second phalanx) and GSN AD 695'94 (third phalanx) that were not described by Morales *et al*. (2003).

Locality and age: Basal Middle Miocene (ca 17 Ma) so far known only from the type locality, Arrisdrift, Namibia.
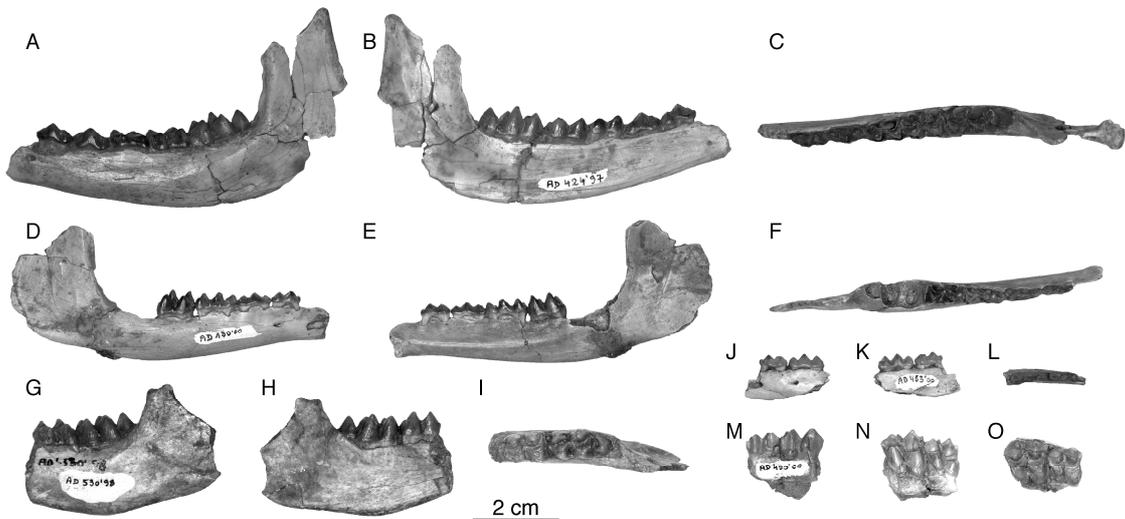
Figure 2. '*Dorcatherium*' *namaquensis* sp. nov., dentition. A) GSN AD 424'97, holotype, left hemi-mandible with p/3-m/3 in buccal view; B) GSN AD 424'97, holotype, left hemi-mandible with p/3-m/3 in lingual view; C) GSN AD 424'97, holotype, left hemi-mandible with p/3-m/3 in occlusal view; D) GSN AD 180'00, right hemi-mandible with dp/2-m/1, in buccal view; E) GSN AD 180'00, right hemi-mandible with dp/2-m/1, in lingual view; F) GSN AD 180'00, right hemi-mandible with dp/2-m/1, in occlusal view; G) GSN AD 550'98, fragment of right hemi-mandible with m/2-m/3, in buccal view; H) GSN AD 550'98, fragment of right hemi-mandible with m/2-m/3, in lingual view; I) GSN AD 550'98, fragment of right hemi-mandible with m/2-m/3, in occlusal view; J) GSN AD 463'00, fragment of left hemi-mandible with dp/2-dp/3, in buccal view; K) GSN AD 463'00, fragment of left hemi-mandible with dp/2-dp/3, in lingual view; L) GSN AD 463'00, fragment of left hemi-mandible with dp/2-dp/3, in occlusal view; M) GSN AD 400'00, fragment of right maxilla with M1/-M2/, in buccal view; N) GSN AD 400'00, fragment of right maxilla with M1/-M2/, in linguo-occlusal view; O) GSN AD 400'00, fragment of right maxilla with M1/-M2/, in occlusal view (scale : 2 cm).

Material: The same fossils described by Morales *et al*. (2003) with the exception of GSN AD 95'95, left maxilla with P3/-P4/ and M2/-M3/ (Morales *et al*. 2003; plate 1.1), plus GSN AD 694'94 (second phalanx) and GSN AD 695'94 (third phalanx) that were not described by Morales *et al*. (2003).

Diagnosis: Medium-sized buno-selenodont tragulid with poorly developed protoconal cingulum; short post-hypocristid that does not extend between the third lobe and the post-entocristid; *Dorcatherium*-fold not reaching the mid-length of the post-metacristid; and rounded proximo-medial facet for metacarpal IV in metacarpal III.

Differential diagnosis: '*Dorcatherium*' *namaquensis* sp. nov. differs from *Archaeotragulus* and *Dorcabune* by its more developed selenodonty and associated dental characters. From '*Dorcatherium*' *crassum* by the lack of *Zhailimeryx*-fold and post-entoconid groove; by having less-developed *Dorcatherium*-fold; metaconule cingulum; a poorly developed protoconal cingulum; short hypocristid; malleolar unfused with the tibia; a complex inter-metacarpal locking system; and a latero-plantar groove in the navicular-cuboid. Differs from '*Dorcatherium*' *pigotti* and '*D*.' *iririensis* by the lack of a light *Zhailimeryx*-fold, and differs from the clade comprising the crown-Tragulidae by the lack of relatively developed cristae and cristids; presence of *Dorcatherium*-platform in the lower molars; and medial tibial cochlea remaining at the same level as the plantar border of the distal articulation of the tibia.
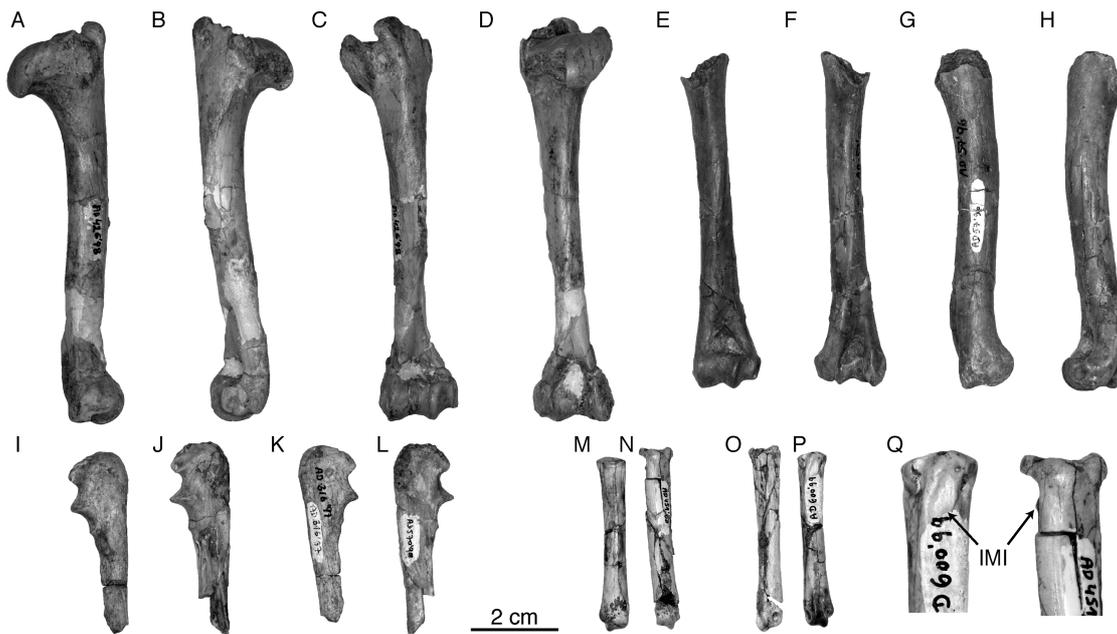
Figure 3. '*Dorcatherium*' *namaquensis* sp. nov., postcranial skeleton, forelimb. A) GSN AD 426'98, left humerus, in medial view; B) GSN AD 426'98, left humerus, in lateral view; C) GSN AD 426'98, left humerus, in cranial view; D) GSN AD 426'98, left humerus, in caudal view; E) GSN AD 57'96, fragment of left humerus, in cranial view; F) GSN AD 57'96, fragment of left humerus, in caudal view; G) GSN AD 57'96, fragment of left humerus, in medial view; H) GSN AD 57'96, fragment of left humerus, in lateral view; I) GSN AD 316'97, proximal fragment of left ulna, in lateral view; J) GSN AD 570'99, proximal fragment of left ulna, in lateral view; K) GSN AD 316'97, proximal fragment of left ulna, in medial view; L) GSN AD 570'99, proximal fragment of left ulna, in medial view; M) GSN AD 600'99, right metacarpal IV, in cranial view; N) GSN AD 451'00, right metacarpal III, in cranial view; O) GSN AD 600'99, right metacarpal IV, in caudal view; P) GSN AD 451'00, right metacarpal III, in caudal view; Q) detail of the inter-metacarpal locking mechanism, not to scale with the remaining images. *Abbreviation*: IMI, Inter-metacarpal locking mechanism (scale : 2 cm).

Description

Here we describe some postcranial elements (phalanges) that were not available in previous descriptions of the Arrisdrift tragulid material.

Second phalanx. The second phalanx of '*Dorcatherium*' *namaquensis* is of primitive aspect, short and robust, more similar to the phalanges of *Hyemoschus* than to those of *Tragulus* or *Siamotragulus* (see Sánchez *et al.* 2015a). As in *Hyemoschus*, the areas of plantar/palmar ligamentary insertion are well marked. The inter-digital condyle of the distal articulation is clearly smaller than the external one.

Third phalanx. The third phalanx has the typical tragulid morphology. It is long, lacking both an extensor process and a plantar platform. The articular surface occupies the entire proximal surface.
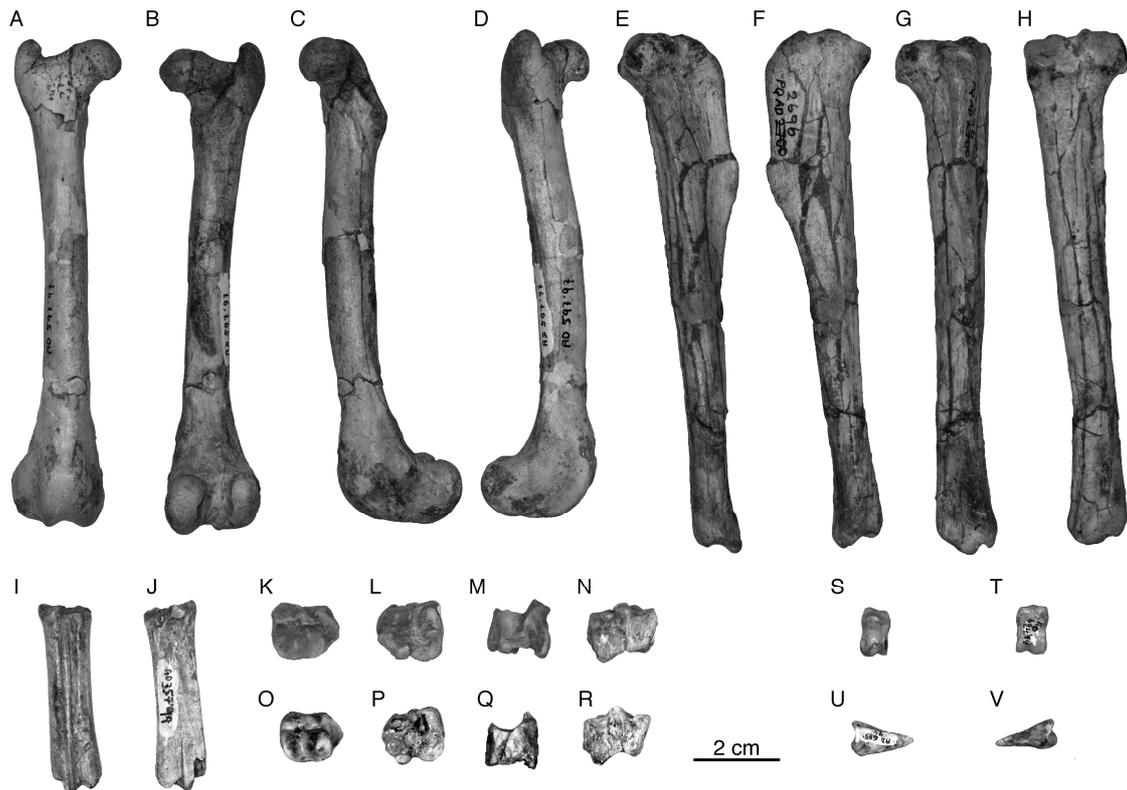
Figure 4. '*Dorcatherium*' *namaquensis* sp. nov., postcranial skeleton, hind limb. A) GSN AD 597'97, right femur, in cranial view; B) GSN AD 597'97, right femur, in caudal view; C) GSN AD 597'97, right femur, in medial view; D) GSN AD 597'97, right femur, in lateral view; E) GSN PQAD 2696, right tibia, in medial view; F) GSN PQAD 2696, right tibia, in lateral view; G) GSN PQAD 2696, right tibia, in cranial view; H) GSN PQAD 2696, right tibia, in caudal view; I) GSN AD 357'99, left metatarsal III-IV, in cranial view; J) GSN AD 357'99, left metatarsal III-IV, in caudal view; K) GSN AD 189'97, left navicular-cuboid, in proximal view; L) GSN AD 189'97, left navicular-cuboid, in distal view; M) GSN AD 189'97, left navicular-cuboid, in lateral view; N) GSN AD 189'97, left navicular-cuboid, in plantar view; O) GSN AD 707'94, left navicular-cuboid, in proximal view; P) GSN AD 707'94, left navicular-cuboid, in distal view; Q) GSN AD 707'94, left navicular-cuboid, in lateral view; R) GSN AD 707'94, left navicular-cuboid, in plantar view; S) GSN AD 694'94, second phalanx, in dorsal view; T) GSN AD 694'94, second phalanx, in plantar / palmar view; U) GSN AD 695'94, third phalanx, in external view; V) GSN AD 695'94, third phalanx, in inter-digital view (scale : 2 cm).

Results of the phylogenetic analysis

We performed a Maximum Parsimony run using a traditional search with 1000 replicates and TBR that recovered two most parsimonious trees (MPT) of 103 steps (CI = 0.738; RI = 0.733). We calculated the strict consensus of these four MPTs (Fig. 5)

and its Bremer support values. The character / state distribution of the discussed internal nodes are presented in Table 1 (Annex 1). The strict consensus shows '*Dorcatherium*' *namaquensis* nested as the basal offshoot of a clade of Miocene African forms that also includes '*Dorcatherium*' *pigotti* (early-middle Miocene, Kenya) and '*Dorcatherium*' *iririensis* (early Miocene, Uganda, Pickford, 2002)). This clade of African '*Dorcatherium*' is recovered separated from the crown-tragulids, which in this MPT comprise the true *Dorcatherium*-clade (also containing the extant African water chevrotain) plus the 'Selenodont-clade' as recovered by Sánchez *et al.* (2015a).

Table 1. Distribution of character / states for the discussed internal nodes of the MPT (clades A and B) and autapomorphies of the African '*Dorcatherium*' terminals included in this work.

NODE/TAXON	CHARACTER: STATE
Node A	9:1; 27:1
Node B	37:2
'D.' namaquensis	25:1; *40:1*; *44:0*; *58:1*; *61:0*
'*D.*' *pigotti*	*7:0*; 13:1; 16:1
'*D.*' *iririensis*	38:1
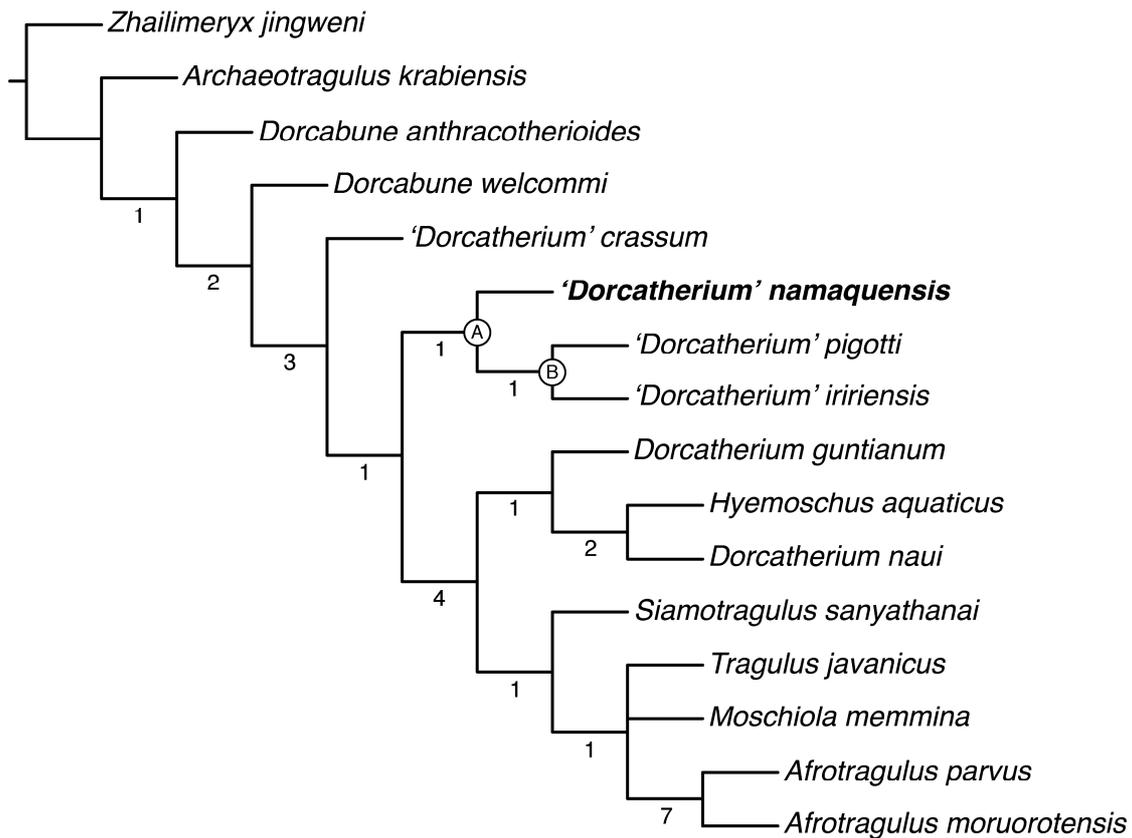
Figure 5. MPT showing the phylogenetic position of '*Dorcatherium*' *namaquensis* sp. nov. from Arrisdrift.

Discussion

Although this analysis is preliminary and is not intended to be a full phylogeny of the Tragulidae (more terminals and characters are needed; Sánchez *et al.* in prep.), its results yield hints as to the phylogenetic affinities and systematics of three Miocene African tragulids, including '*Dorcatherium*' *namaquensis*.

'*Dorcatherium*' *pigotti*, '*D.*' *iririensis* and '*Dorcatherium*' *namaquensis* are bunoselenodont forms (see Sánchez *et al*. 2010, 2015a; Fig. 6) characterized by possessing an m3 with a short post-hypocristid that does not extend between the third lobe and the post-entocristid and poorly developed protoconal cingulum. In all the other forms, the post-hypocristid runs between the third lobe and the post-entocristid, sometimes reaching the latter. This is consistent among both bunoselenodont and true selenodont species. The clade '*D.*' *pigotti* – '*D.*' *iririensis* is characterized in this MPT by the presence of a lightly marked form of post-entoconid groove and a rudimentary

Zhailimeryx-fold, which results in an apparent parallelism with European '*Dorcatherium*' *crassum*. This is something to be re-examined in future works, because if confirmed it will mean that there are several variations of these structures, just as with the different *Palaeomeryx*-folds in pecorans, not a unique structure but several different ones amongst the diverse lineages (Sánchez *et al*. 2015a). '*Dorcatherium*' *namaquensis* possesses a *Dorcatherium*-fold not reaching the mid-length of the post-metacristid and a rounded proximo-medial facet for the metacarpal IV in the metacarpal III.
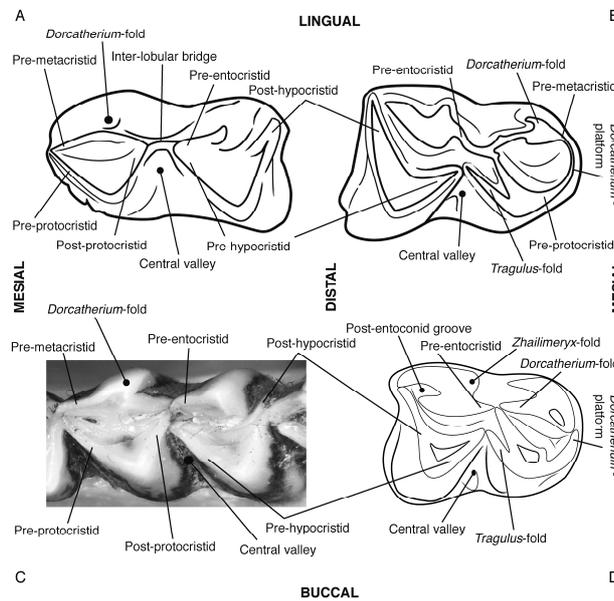
Figure 6. Occlusal anatomical elements of tragulid lower molars, showing the differences between selenodont (A and C) and buno-selenodont (B and D) forms. A, *Afrotragulus moruorotensis*, m/2 of OCO Mor 1'2000 (holotype); B, *Dorcatherium naui*, m/2 of NHMUK M40432 (type locality, Eppelsheim, Germany); C, *Moschiola meminna*, m/2 (private collection Jan van der Made, Madrid); D, '*Dorcatherium*' *crassum*, m/2 of MNHN Sa 9950 (neotype, Sansan, France). Modified from Sánchez *et al*. (2015a).

We have extracted the maxilla AD 95'95, originally included in the material of *Dorcatherium* sp. aff. *D. pigotti* from Arrisdrift (Morales *et al*. 2003), from the type series of '*D.*' *namaquensis*. This maxilla corresponds to a tragulid of similar dimensions to '*D.*' *namaquensis*, but it shows a dentition with characters that differ from those seen in the latter species. The lack of both protocone and metaconule cingula and the presence of a fully developed post-protocrista in the M3 are amongst the most important of them. These

are derived traits that do not correspond to a relatively primitive form such as '*D.*' *namaquensis*. Since the presence of derived non-*Dorcatherium* crown-tragulids in the African Miocene is now well-established (Sánchez *et al*. 2010, 2015b), we need to make further comparisons of this isolated maxilla in order to arrive at more accurate conclusions.

The classic notion of *Dorcatherium* as the only tragulid genus of the African Miocene (see e.g. Geraads, 2010) has been recently disputed with the description of the

new genus *Afrotragulus* (two species) and the species *Siamotragulus songhorensis*, both from the latest early Miocene of Uganda and Kenya, with *Afrotragulus* also possibly present in the lower Miocene of the Sperrgebiet as previously commented (Sánchez *et al*. 2010, 2015a). All these new forms that belong to the 'Selenodont-clade', in which the extant Asian forms are also included, were originally attributed to *Dorcatherium* (Whitworth, 1958; Pickford, 2001). This fact perfectly characterizes the problems that surround this genus, which was first described from the late Miocene of Europe with the type species *Dorcatherium naui* Kaup & Scholl, 1834. *Dorcatherium* still encompasses the major part of the Miocene-Pliocene diversity of the Tragulidae (Rössner, 2007) and it has a widespread recognized palaeobiogeographic distribution that includes Africa and Eurasia, ranging in Africa from the early Miocene to the early Pliocene (see e.g., Arambourg, 1933; Whitworth, 1958; Fahlbusch, 1985; Gaur, 1992; Gentry *et al*. 1999; Pickford *et al*. 2004; Morales *et al*. 2003; Rössner, 2007; Quiralte *et al*. 2008). However, some authors (e.g. Rössner, 2007; Sánchez *et al*. 2010, 2015a) challenged the classical conception of *Dorcatherium*, largely affected by the use of size as the almost exclusive systematic tool (see Sánchez *et al*. 2010 for a discussion of this point). They stated that, as defined so far, this genus is a paraphyletic bag of bones grouping together diverse species that include many different buno-selenodont and bunodont forms, an artificial grouping of tragulids that embraces a range of morphological variability similar to that which exists between the extant genera *Hyemoschus*,

Tragulus and *Moschiola*. The hypothesis of the paraphyly of *Dorcatherium* was already put to test, and so far has been confirmed (Sánchez *et al*. 2015a). Moreover, the results of the present MPT, showing a clade of African stem-tragulids which is not related to the clade of true *Dorcatherium*, definitively challenges the very presence of this genus in the African Miocene. Hence, the paradigm of *Dorcatherium* as the only Miocene African tragulid can be possibly modified and substituted by the recognition of a diverse array of stem and crown-tragulids comprising at least three genera (none of them *Dorcatherium*) which lived in Africa during the early and middle Miocene.

Due to the preliminary nature of this phylogenetic work we prefer not to take taxonomic decisions at the genus level based on its results. Thus, we name the studied African species '*Dorcatherium*' (in parentheses) (as '*D.*' *pigotti*, '*D.*' *iririensis* and '*Dorcatherium*' *namaquensis*). However we can confirm that the Arrisdrift form is different from the type material of '*D.*' *pigotti* and can be considered to represent a distinct species. If our results are further confirmed in future analyses using more taxa and more characters, including DNA sequences from the extant species in a combined analysis (Sánchez *et al*. in prep), '*Dorcatherium*' *pigotti*, '*Dorcatherium*' *iririensis* and '*Dorcatherium*' *namaquensis* will be subjected to a change in genus name. The position of extant *Hyemoschus* within the true *Dorcatherium*-clade will also be tested again, and if the results confirm it, it will mean that the only true African *Dorcatherium* that has probably existed lives today in the African tropical forests.

Conclusions

The tragulid from Arrisdrift (Sperrgebiet, Namibia, early middle Miocene), previously identified as *Dorcatherium* sp. aff. *D. pigotti* is a new species that we name '*Dorcatherium*' *namaquensis*. The genus *Dorcatherium* is clearly a paraphyletic assemblage of different tragulid types and is in need of a deep revision. The phylogenetic position of an African clade of Miocene stem-tragulids including

'*Dorcatherium*' *iririensis*, '*Dorcatherium*' *pigotti* and '*Dorcatherium*' *namaquensis* that are not linked with the *Dorcatherium*-clade, together with the last published discoveries on Miocene African tragulids, overturn the paradigm of the genus *Dorcatherium* in Africa during the Miocene. For a long time considered to be the only genus of tragulid in the Miocene of Africa, the hypothesis of the very existence

of true *Dorcatherium* in the continent is seriously challenged. However, additional analyses with more data (both morphological and molecular) and more taxa are needed to fully confirm these results.

Acknowledgements

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Annex 1. Character list. Character / taxon matrix (62 characters / 16 terminals).

SKULL
1. Styloid process: slightly nasally oriented (0); strongly nasal orientation (1)
2. Styloid process: contacts with the paroccipital process (0); does not contact with the paroccipital process due to the intrusion of the tympanic bulla (1).
3. Paroccipital process: nuchally oriented (0); dorso-ventrally oriented (1).
4. Tympanic bulla: hollow (0); cancellous (1).
5. Sagittal crest: nuchal end well-developed, with triangular profile (0); nuchal end slightly developed with rounded profile (1).
6. Occipital profile in lateral view: straight (0); curved (1).
7. Location of the anterior lower corner of the orbit: M1/-M2/ (0); P4/-M1/ (1).

UPPER DENTITION
8. Metaconule cingulum: absent (0); present (1).
9. Development of the protoconal cingulum: well developed (0); poorly developed (1); absent (2).
10. Development of the cristae: poorly developed in extension and height (0); developed in extension and height (1).
11. Development of the post-protocrista: poorly developed (0); well developed, making a well-marked half-moon profile in the protocone (1); absent (2).
12. Morphology of the buccal ribs: short and with a broad base (0); elongated and more column-like (1).

LOWER DENTITION
13. Position of the third lobe of the m/3: more buccal (0); more central (1).
14. Orientation of the long axis of the m/3 third lobe: antero-lingual (0); without orientation, rounded lobe (1).
15. Opening of the m/3 third lobe: open (0); closed (1).
16. p/1: present (0); absent (1).
17. Morphology of cuspids: bunoid with rounded base (0); flattish base and walls, more trenchant cuspids (1).
18. Development of cristids: low and poorly extended (0); moderately high and extended (1); well extended, *Tragulus*-like (2).
19. Premetacristid: absent (0); present (1).
20. Interlobular bridge: absent (0); present (1).
21. Morphology of the central valley: narrow (0); enlarged and wide (1).
22. Mesial closing of the lower molars: almost non-existent pre-metacristid, with long pre-protocristid that turns lingually and contacts with the pre-metacristid forming a rounded *Dorcatherium* platform (0); presence of a developed pre-metacristid, smaller than the pre-protocristid and absence of true *Dorcatherium* platform (1); well developed and straight pre-metacristid and pre-protocristid that contact parasagitally and form a mesial triangular shape (2).
23. Post-entoconid groove: marked (0); poorly marked (1); absent (2).
24. 'M-structure': present (0); absent (1); extremely reduced (2).
25. Development of *Dorcatherium*-fold: as long or almost as long as the post-metacristid (0); not reaching the mid-length of the post-metacristid (1); very poorly developed, almost non-existent (2).
26. *Tragulus*-fold: present (0); absent (1).
27. Relationship of the post-hypocristid with the m/3 third lobe: long, extending between the third lobe and the post-entocristid, touching it or not (0); short, not extending between the third lobe and the post-entocristid (1).
28. Hypoconulid in m/1-m/2: present (0); absent (1).
29. Relative position of lobes: mesial and distal lobes contact in the centre of the teeth (0); mesial and distal lobes separated due to the elongation of the molars (1).
30. Opening of the distal lobe: lingually open (0); lingually closed (1).
31. Mesial cingulid: present (0); poorly developed or absent (1).
32. Number of cuspids in the p/2: bi-cuspid p/2 (0); tri-cuspid p/2 (1).
33. Occlusal morphology of the p/4: lingual and buccal distal cristids originate from the central conid (0); lingual and buccal distal cristids originate from a single cristid that departs from the central conid (1).
34. Development of the post-entocristid: short post-entocristid (0); long post-entocristid (1).
35. Paraconid: well developed (0); rudimentary (1); absent (2).
36. Trigonid: lingually open (0); closed (1).
37. *Zhailimeryx*-fold: present (0); absent (1); rudimentary (2).

38. Morphology of the p/4: main cuspid in a buccal position with no accessory structures (0); presence of buccal rib, main cuspid in a more central position and presence of elongated bucco-distal fossette (1); main cuspid in a more central position, presence of accessory crests and rounded bucco-distal fossette (2).

POSTCRANIAL SKELETON

39. Morphology of the metatarsal(s) III-IV: fused, long, narrow, conforming to a true, pecoran-like, metatarsal III-IV (0); fused but short and flat, with clearly distinguishable metatarsal III and metatarsal IV not united into a true, pecoran-like, cannon bone (1).
40. Malleolar bone: fused with the tibia (0); free from the tibia (1).
41. Morphology of the palmar border of the medial epicondyle in the humerus: presence of a slight convexity over the articular area (0); non-convex straight border (1).
42. Morphology of the dorsal border of the medial epicondyle in the humerus: curved (0); straight (1).
43. Morphology of the acetabular cavity in the pelvis: presence of dorsal constriction ('three-lobed' morphology) (0); absence of dorsal constriction (circular morphology) (1).
44. Morphology of the cavity located caudal to the acetabular notch in the pelvis: elliptic and wide (0); narrow and slit-like (1).
45. Trochanteric pit in the femur: wide (0); narrow (1).
46. Plantar border of the sustentaculum in the calcaneum: concave (0); straight (1).
47. Dorsal border of the sustentaculum in the calcaneum: concave and perpendicular to the corpus (0); straight and perpendicular to the corpus (1); straight and oblique to the corpus (2).
48. Inter-metacarpal locking mechanism: non-existent, inter-metacarpal articulation mainly ligamentous with the exception of the proximal facets (0); complex locking system comprising (from proximal to distal) the proximal facets, a pit-and-process locking structure and a distal ligamentous articulation (1).
49. Navicular-cuboid and ectomesocuneiform: fused together (0); not fused (1).
50. Fusion of metacarpals III and IV: fused, forming a cannon bone (0); unfused (1).
51. Morphology of the plantar surface of the metatarsal III-IV: presence of two individualized flattish plantar surfaces (0); presence of a single narrow V-shaped groove (1); presence of a single flattish surface (2).
52. Condition of metatarsals II and V: unfused to the central metatarsals (0); fused to the central metatarsals (1).
53. Morphology of the disto-lateral furrow in the navicular-cuboid for the tendon of the long fibular muscle: short, deep, and triangular, not reaching the lateral facet for the calcaneum (0); forming a parallel-sided canal that contacts with the lateral side of the lateral facet for the calcaneum (1); forming a parallel-sided canal that contacts with the dorsal end of the lateral facet for the calcaneum, opening in front of it (2).
54. Morphology of the planto-distal lateral process in the navicular-cuboid: short and blunt, not surpassing the distal border of the bone (0); long and pointed, clearly surpassing the border of the bone (1); long and blunt (2).
55. Morphology of the planto-medial surface of the navicular-cuboid: presence of a strong Y-shaped structure for ligament attachment (0); absence of such strong structure (1); presence of two parallel ridges as a ligamentary attachment (2).
56. Morphology of the articulation surface for the malleolar in the calcaneum: sub-triangular and concave (0); elongated and convex (1); triangular and flat (2); elongated and concave-convex (3).
57. Triangular notch dorsal to the calcaneum facet in the navicular-cuboid: absent (0); short (not surpassing the distal border of the calcaneum facet) with faint borders (1); short with marked borders (2); long (surpassing the distal border of the calcaneum facet) with marked borders (3).
58. Latero-plantar groove in the navicular-cuboid: absent (0); present (1).
59. Well-marked and circular proximal planto-lateral pit in the navicular-cuboid: absent (0); present (1).
60. Deep slit-like groove in the middle of the plantar surface of the navicular-cuboid: absent (0); present (1).
61. Morphology of the proximo-medial facet for the metacarpal IV in the metacarpal III: rounded (0); wedge-like (1).
62. Plantar extension of the medial tibial cochlea: clearly surpasses the plantar border of the articulation (0); the cochlea remains at the same level as the plantar border of the articulation (1).