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Denis Geraads

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1 **A reassessment of the Bovidae (Mammalia) from the Nawata Formation of**  
2 **Lothagam, Kenya, and the late Miocene diversification of the family in**  
3 **Africa**  
4

5 Denis Geraads <sup>a, b</sup>

Mis en forme : Français (France)

6  
7 <sup>a</sup> Sorbonne Universités - CR2P-MNHN, CNRS, UPMC-Paris 6 - CP 38, Muséum National  
8 d'Histoire Naturelle, 8 rue Buffon, F-75231 Paris Cedex 05, France; denis.geraads@mnhn.fr

9 <sup>b</sup> Max Planck Institute for Evolutionary Anthropology, Department of Human Evolution,  
10 Deutscher Platz 6 - D-04103 Leipzig - Germany

11  
12 **Abstract.** The late Miocene Bovidae from the Nawata Formation of Lothagam were all  
13 assigned to modern tribes by Harris (2003), with the majority of specimens being referred to a  
14 species of *Aepyceros*, a genus that includes the modern impala. However, an alternative  
15 interpretation of the collection lessens the modern character of the faunal composition. Many  
16 of the identifications are revised; there might be a single species of Boselaphini, there is no  
17 evidence of Hippotragini, and *Aepyceros* is less common than previously thought. Two new  
18 genera, *Afrotragus* and *Turkanatragus*, are erected; together with an unnamed species and  
19 '*Kobus*' *laticornis* Harris, 2003, they cannot easily be allocated to any existing tribe. These  
20 two new genera share long, slender, spiralled horn-cores, and it is conceivable that they  
21 belong to the same group, which might also include the '*Prostrepsiceros*' from Sahabi, Libya,  
22 but does not seem closely related to Eurasian *Prostrepsiceros*. Along with sparser evidence  
23 from elsewhere in Africa, this strongly suggests that by the Late Miocene, African Bovidae  
24 underwent a wider radiation than reflected in the tribes that survived into the Pliocene,  
25 showing that the crown groups very incompletely document the relatively recent past  
26 diversity of the family.

27  
28 **Keywords.** Africa, Kenya, Mammalia, Bovidae, Late Miocene, diversity

29  
30 **Introduction**

31  
32 The Lothagam area in North-Western Kenya, which yielded over 100 mammalian  
33 taxa, is one of the richest late Neogene sites in Africa (Leakey & Harris 2003). It spans a long

1 time period, from the Late Miocene to the Late Pliocene, and is thus critical for deciphering  
2 the evolution of many African mammalian groups that diversified in the Late Neogene. The  
3 most fossiliferous part of the sequence is the Nawata Formation, with two members, the  
4 Lower Nawata dated to 7.44 to 6.54 Ma, and the Upper Nawata dated to less than 6.54 Ma.  
5 The Nawata Formation is overlain by the Apak Member of the Nachukui Formation, which  
6 includes a tephra unit dated at 4.22 Ma and is overlain by the Lothagam Basalt. The  
7 Kaiyumung Member overlays the lacustrine sediments of the Muonogori Member but its age  
8 is poorly constrained (Feibel 2003; McDougall & Feibel 2003). The site was first surveyed by  
9 B. Patterson from 1967 onwards, and from 1989 onwards by M. Leakey and colleagues; the  
10 fossils discussed here were collected by both parties. A detailed history of the research at  
11 Lothagam can be found in Leakey (2003).

12 In the monograph devoted to the site, Harris (2003) described 16 species of Bovidae in  
13 the Nawata Formation, which he all assigned to tribes still existing today, although one of  
14 them, the Boselaphini, is now restricted to Asia. These species were (with their original  
15 spelling and tribal attribution): *Tragelaphus kyaloae* (Tragelaphini), an unidentified Bovini,  
16 *Tragoportax* aff. *cyrenaicus*, *Tragoportax* sp. A, *Tragoportax* sp. B (Boselaphini), *Kobus*  
17 *presigmoidalis*, *K. laticornis*, *Menelikia leakeyi* (Reduncini), *Praedamalis* ? sp., *Hippotragus*  
18 sp. (Hippotragini), *Damalacra* sp. A, *Damalacra* sp. B (Alcelaphini), *Aepyceros*  
19 *premelampus* (Aepycerotini), *Gazella* sp., *Raphiceras* sp., *Madoqua* sp. (Antilopini). To this  
20 list he added *Tragelaphus* cf. *scriptus* from the Kaiyumung Member, *Simatherium* aff.  
21 *kohllarseni* (Bovini) from the Kaiyumung and Apak Members, and *Tragelaphus nakuae*,  
22 represented by a single specimen of unknown stratigraphic provenance. Some comments on  
23 the Bovidae from these members are provided in Supplemental material A, but the present  
24 work focuses on those from the Nawata Formation.

25 According to Harris (2003:531–532), they 'seemingly represent some of the first  
26 representatives of the tribes characteristic of Africa today'. Indeed, in spite of some turnover  
27 at the generic level, with the extinction of the genera *Tragoportax*, *Simatherium*, *Menelikia*  
28 and *Damalacra* since those times, this assemblage would suggest a relative stability of the  
29 tribal composition, after the early diversification of the African endemic tribes (Bibi *et al.*  
30 2009).

31 The present revision partly confirms Harris' conclusions, but also reassesses the  
32 identifications and affinities of many specimens and their relationships to modern taxa,  
33 leading to a reevaluation of the supposed modern character of the bovid fauna, and

1 emphasizing instead the occurrence in the Nawata Formation of several taxa that cannot be  
2 assigned to any of the crown groups.

3

#### 4 **Materials and methods**

5

6 The bovid collection from Lothagam was examined in the National Museums of  
7 Kenya (KNM) during several visits from 2005 to 2016. The present paper focuses on the  
8 Lower and Upper Members of the Nawata Formation, which are the richest (Table 1). I was  
9 able to see the bulk of the material, including all specimens figured by Harris (2003), but  
10 there is some material that I could not find, including some specimens whose dimensions  
11 were provided by him, and a few cranial pieces mentioned in his descriptions of  
12 *K. presigmoidalis*. However, from the catalogue, other missing fossils are unlikely to include  
13 important specimens. Comparisons with material from other sites in Kenya were conducted in  
14 the KNM; other relevant comparative material was examined in several institutions, mainly  
15 the Muséum National d'Histoire Naturelle, Paris (MNHN), National Museum of Ethiopia,  
16 Addis Ababa (NME), and Natural History Museum, London (NHMUK).

17 In the descriptions, tooth-rows are supposed to be horizontal. Divergence of the horn-  
18 cores is that of their main axes at the base, in front view. Their inclination is the angle  
19 between their posterior border and the top of the braincase, in lateral view. Measurements are  
20 in mm. Open nomenclature follows Bengtson (1988). 3D reconstructions of Supplemental  
21 material C and D were prepared with Agisoft Photoscan™.

22

#### 23 **Systematic Palaeontology**

24

25 Family **Bovidae** Gray, 1821

26

Subfamily **Bovinae** Gray, 1821

27

Tribe **Boselaphini** Knottnerus-Meyer, 1907

28

Genus *Tragoportax* Pilgrim, 1937 ?

29

*Tragoportax* ? sp.

30

(Fig. 1C)

31

32 **Remarks.** Harris (2003) identified three species of Boselaphini at Lothagam, a larger form  
33 and two smaller ones. All of them have horn-cores whose divergence is weak at the base and

1 decreases upwards, with a strong anterior keel and a less acute posterolateral one. There is in  
2 fact no compelling evidence for more than one species, as members of the *Tragoportax* group  
3 are known to be strongly dimorphic, females being even sometimes hornless (Spassov &  
4 Geraads 2004); for instance, KNM-LT-24214 (Harris 2003, fig. 11.7) taken as representing a  
5 small species, has small horn-cores relative to the braincase, and is almost certainly female.  
6 The same is true of KNM-LT-195 and KNM-LT-196 (*Tragoportax* sp. B of Harris 2003),  
7 whose relatively small horn cores are inserted wide apart on broad frontals. Differences  
8 within Lothagam boselaphins are smaller than at Sahabi, Libya (compare Thomas 1979, pl.1,  
9 fig.5, with Gentry 2008, fig. 1). A possible exception is the frontlet KNM-LT-23149 that has  
10 long, relatively slender horn cores; it was assigned to *T. aff. cyrenaicus* by Harris (2003) and  
11 Bibi (2011) but its horn cores, like those of the other Lothagam specimens, are definitely less  
12 divergent than in this species. Pending the discovery of more specimens (especially cranial)  
13 that would better document the variation at Lothagam and elsewhere, I tentatively assign the  
14 whole Lothagam material to a single species.

15       It much differs from '*Mesembriportax' acrae* Gentry, 1974 (transferred to  
16 *Miotragocerus* by Gentry 2010) from Langebaanweg, South-Africa, which has very divergent  
17 horn cores that are usually short, stout at the base but become cylindrical higher up, thus  
18 showing a change in cross-section that is better indicated than at Lothagam. The Lothagam  
19 form also differs from *Miotragocerus cyrenaicus* Lehmann and Thomas, 1987, from Sahabi  
20 and the Baynunah Formation of Abu Dhabi (Gentry 1999), in its much less divergent horn-  
21 cores. In the cross section, moderately indicated anterior demarcation, divergence, and course  
22 of the horn cores, most Lothagam horn cores (except perhaps KNM-LT-23149) are instead  
23 similar to those of *Tragoportax abyssinicus* Haile-Selassie, Vrba and Bibi, 2009, from the  
24 Kuseralee Member of the Sagantole Formation at Amba, Middle Awash, Ethiopia, and the  
25 type specimen of the Ethiopian species (Haile-Selassie, Vrba and Bibi, 2009, fig. 9.1)  
26 resembles KNM-LT-24214. The slight differences noted by the latter authors can probably be  
27 accommodated within intra-specific variation, as members of this group display significant  
28 shape variations, as noted as early as in the 19<sup>th</sup> century (Spassov & Geraads 2004, and refs  
29 therein). However, KNM-LT-23149 differs more from *T. abyssinicus*, and identification of  
30 the whole Lothagam sample with this species would be risky. I also prefer to leave open the  
31 genus identification, because some of the characters of the best specimen, KNM-LT-24214  
32 (depressed, rough fronto-parietal area, general shape of the horn-cores) fit *Tragoportax*,  
33 whereas some others (high occipital, median keel on the basioccipital) agree better with  
34 *Miotragocerus*.

1 Several dental remains were assigned to this tribe by Harris (2003), but their  
2 identification is not straightforward (see Supplemental material B). Some of them definitely  
3 do not belong here (such as the maxilla KNM-LT-13012 that has a far too small P4 for this  
4 tribe) but other specimens are of more uncertain attribution. On the relatively complete  
5 mandibles KNM-LT-203 and KNM-LT-204 (both from the right side; Fig. 1L–N) the pattern  
6 of the occlusal surface is suitable for a boselaphin, but the molars are rather hypsodont, and  
7 the premolars are much shorter than in *T. abyssinicus* from Amba (Haile-Selassie *et al.* 2009,  
8 fig. 9.4), *M. cyrenaicus* from Sahabi (Lehmann & Thomas 1987, fig. 1A), *M. acrae* from  
9 Langebaanweg (Gentry 1974, fig. 10, table 1), or late Miocene European forms (e.g., Spassov  
10 & Geraads 2004; Kostopoulos 2009a). Rather than assuming a shortening of the premolar  
11 row, which is unknown in related forms, I prefer to exclude these specimens from the  
12 Boselaphini.

13 Of the horn cores included by Harris (2003) in the Boselaphini, the only re-identified  
14 piece is KNM-LT-23980 that is probably reduncin.

15 A partial mandible with p4–m1 KNM-LT-26068, accessioned as from the Kaiyumung  
16 Member, was listed among the Reduncini by Harris (2003), but is definitely boselaphin in its  
17 large p4 relative to m1 and absence of goat fold (Fig. 1C). Given the absence of boselaphins  
18 in African contemporaneous sites, especially Kanapoi, I regard this stratigraphic origin as  
19 unlikely. Thus, the last definite occurrence of this tribe at Lothagam is in the Apak Member  
20 (horn-cores KNM-LT-23662 and KNM-LT-24021, as noted by Harris [2003]).

21  
22 Tribe **Tragelaphini** Blyth, 1863

23 Genus *Tragelaphus* Blainville, 1816

24 *Tragelaphus* cf. *kyaloi* Harris, 1991

25  
26 **Remarks.** Not much can be added to the description of this rare species by Harris (2003). The  
27 size and degree of anteroposterior compression of the few Lothagam horn-cores (only one of  
28 them from the Nawata Formation) are similar to those of *T. kyaloi* from Kanapoi whence it is  
29 best known, and intermediate between those of *T. moroitu* and *T. saraitu* (Haile-Selassie *et al.*  
30 2009; Geraads *et al.* 2009a) but their cross-section is less distinctly triangular than in these  
31 Ethiopian forms. They are also more anteroposteriorly compressed than those of the *T. cf.*  
32 *spekei* from Lukeino, Kenya (Thomas 1980), or *Tragelaphus* sp. from Langebaanweg (Gentry  
33 1980), which are likely to be early representatives of the *moroitu-saraitu-rastafari-nakuae*

1 lineage, and *T. kyalo* can be kept as a separate species, a distinction confirmed by its peculiar  
2 cranial shape (Geraads & Bobe, in press).

3  
4 Tribe **Bovini** Gray, 1821

5 Bovini gen. et sp. indet.  
6

7 **Remarks.** Harris (2003) listed several dental bovin remains from the Nawata Formation, but I  
8 could find none of them in the KNM. Bibi (2009) surmised that these teeth are too derived for  
9 confidently accepting their stratigraphic origin; on the basis of the photographs provided by  
10 him, I definitely agree.

11  
12 Sub-family **Antilopinae** Gray, 1821

13 Tribe **Reduncini** Knottnerus-Meyer, 1907

14 Genus ***Kobus*** A. Smith, 1840 ?

15 ***Kobus ? presigmoidalis*** Harris, 2003

16 (Fig. 1E–H)  
17

18 **Description and comparisons.** The best specimens of this species are the holotype partial  
19 cranium KNM-LT-189, and a similar frontlet KNM-LT-212, both from the Upper Nawata  
20 Member, but KNM-LT-486 establishes the occurrence of the species as early as the Lower  
21 Nawata Member. Unfortunately, a number of specimens listed by Harris (2003) could not be  
22 found in the KNM: these are KNM-LT-497 and KNM-LT-26575 from the Lower Nawata,  
23 and KNM-LT-233, KNM-LT-483, KNM-LT-496, KNM-LT-23661, KNM-LT-23713, KNM-  
24 LT-25951, and KNM-LT-25984 from the Upper Nawata. Some other specimens listed by him  
25 have large frontal sinuses and are probably not reduncin, such as KNM-LT-13009, KNM-LT-  
26 224, and KNM-LT-23671. Although not all reduncin specimens are identifiable to species,  
27 *K. ? presigmoidalis* seems to be an uncommon species at Lothagam. It is more clearly  
28 reduncin than '*K. laticornis*', discussed farther down, in the lack of frontal pneumatization,  
29 general course of the horn-cores, and extremely strong anterior tuberosities of the  
30 basioccipital.

31 Its main characters are: high and narrow occipital, narrow mastoid exposure (like  
32 *K. sigmoidalis* from the Turkana basin), supra-orbital foramina rather small for a reduncin,  
33 small postcornual fossa, extremely prominent anterior tuberosities of the basioccipital, horn-  
34 cores not very long, inserted uprightly and moderately curved backwards, with a hint of

1 sigmoid curvature, basal divergence moderate, and cross-section transversely compressed  
2 with a long axis moderately angled in respect to the sagittal plane.

3 Harris (2003) described the occipital as broad, but it is in fact distinctly less broad than  
4 that of *K. subdolosus* from Langebaanweg (Gentry 1980), in correlation with the more lateral  
5 orientation of the mastoid exposure, and these are the main differences with this South  
6 African form, which has also thicker, shorter and less compressed horn-cores, and larger  
7 supra-orbital foramina. The horn-cores of the Sahabi reduncin (Lehmann & Thomas 1987;  
8 Gentry 2008) are similar to those of the South African form, but more divergent.

9 Several dentitions from both members of the Nawata Formation are probably  
10 reduncin; the lower molars KNM-LT-23624, KNM-LT-23655, and KNM-LT-26052 have  
11 goat folds, but the lateral lobes are less rounded than in typical reduncins, and the lingual wall  
12 is more heavily folded (Fig. 1E–H). They resemble the teeth from Lukeino assigned to *Kobus*  
13 by Thomas (1980), and it is reasonable to associate them with cranial elements of  
14 *K. presigmoidalis*. The premolars KNM-LT-26007 also resemble those of the *?Hydaspicobus*  
15 cf. *auritus* of Pilgrim (1939), from the Siwalik Dhok Pathan Formation.

16 **Remarks.** Vrba (in Vrba & Haile-Selassie 2006, and in Haile-Selassie *et al.* 2009) thought  
17 that *K. presigmoidalis* was identical with the kob from the Kenyan sites of Mpesida and  
18 Lukeino, which Thomas (1980) described as *Kobus* aff. *porrecticornis* and regarded as  
19 identical with other Siwalik forms. Haile-Selassie *et al.* (2009) also described the species from  
20 the earliest Pliocene of the Middle Awash. In addition, an antelope from Baard's Quarry at  
21 Langebaanweg was described by Gentry (1980) as *K. ?porrecticornis*, and another one from  
22 Manonga, Tanzania, as *K. aff. porrecticornis* by Gentry (1997). All these reports suggest a  
23 wide distribution of this species or a closely related one (e.g., Bibi 2011). This is  
24 questionable, because it may be that these forms are mostly united by the lack of distinctive  
25 features, and because the horn core cross section significantly differs between them (virtually  
26 circular in '*Indoreduca*' *theobaldi* [Pilgrim 1939, pl. 3, fig. 10], more convex laterally than  
27 medially in the type of '*Dorcadoxa*' *porrecticornis* [Pilgrim 1939, pl. 1, fig. 9], laterally  
28 flattened at Lothagam) and I prefer to keep calling the Lothagam material *K. ?presigmoidalis*.

29 The early Pliocene of the Middle Awash Valley yielded other species assigned to the  
30 Reduncini, namely *Zephyreduncinus oundagaisus* Vrba and Haile-Selassie, 2006, *Kobus*  
31 *basilcookei* Vrba, 2006, *Kobus* aff. *oricornus* (see Haile-Selassie *et al.* 2009), and *Redunca*  
32 *ambae* Haile-Selassie, Vrba and Bibi, 2009. Distinguishing between all but the first of these  
33 taxa is not straightforward; their horn-cores look reduncin in their general course, but unlike  
34 in typical reduncins the brain-case is long, the anterior tuberosities of the basioccipital are not



1 extremely large, the occipital does not seem to be very broad, and the supra-orbital foraminae  
2 are of moderate size (these last two features as in *K. presigmoidalis*). Haile-Selassie *et al.*  
3 (2009) assigned to *R. ambae* dentitions said to be similar to those of *K. subdolos* from  
4 Langebaanweg, which Gentry (1980) showed to be morphologically closer to those of  
5 tragelaphins, but they also described more typical reduncin dentitions.

6 In summary, there are clear indications that most of these purportedly early reduncins  
7 from Sahabi, Lukeino, and the Middle Awash do not belong to the crown Reduncini. The  
8 Langebaanweg *K. subdolos* is also of uncertain position, because of its primitive teeth but  
9 reduncin-like broad braincase and large supra-orbital foramina. They all stand in sharp  
10 contrast with the typically reduncin cranial parts and dentitions from contemporaneous sites in  
11 Chad (Vignaud *et al.* 2002; Geraads *et al.* 2009b), suggesting that these early Pliocene East  
12 and South African forms are probably representatives of an early radiation of reduncins, and  
13 are not members of the clade including the Chadian reduncins + the Reduncini of modern  
14 type. By contrast, in spite of its earlier age, *Kobus ? presigmoidalis* seems to branch higher  
15 than *K. subdolos* and might be part of the crown group.

16  
17 Tribe indet.

18 Bovidae gen. et sp. indet. A

19  
20 **Remarks.** Harris (2003) assigned a few horn-cores to *Menelikia leakeyi* Harris, 1991, a  
21 species defined in the Moiti Member of the Koobi Fora Formation, but also known from more  
22 recent strata of the Turkana Basin. Harris' identification was mostly based upon the  
23 homonymous torsion of the horn-cores; the best preserved specimens (KNM-LT-178: Harris  
24 2003, fig.11.11; KNM-LT-487) do show it clearly, but other specimens are poorly preserved,  
25 and KNM-LT-26026 has an heteronymous torsion and must be of another species. The  
26 homonymous horn-cores are too incomplete for definite identification, because homonymous  
27 torsion is not exclusive to *Menelikia*, and because this genus is known only in much younger  
28 sediments, and it is safer to remove it from the Lothagam list, although these specimens could  
29 be related to it.

30  
31 *'Kobus' laticornis* Harris, 2003

32  
33 **Remarks.** This species is based upon KNM-LT-180, a partial cranium of large size, with  
34 widely divergent, virtually straight horn-cores. A few other specimens were assigned to the

1 same species by Harris (2003). Those that can be most confidently identified because they  
2 display the same features as the holotype are KNM-LT-199, a horn-core with associated  
3 occipital, and KNM-LT-200, a horn-core.

4 Vrba (2006) questioned the reduncin nature of this species, because on the holotype 1)  
5 the anterior tuberosities of the basioccipital are weaker than in reduncins, 2) there is no  
6 postcornual fossa, 3) the horn-cores have heteronymous torsion, no transverse ridges, but have  
7 keels. She noted instead resemblances with the Sahabi boselaphin. Boselaphin affinities can  
8 readily be discounted because the keels are far weaker than in this group, but Vrba's points are  
9 worth considering, and I may add that the frontals are hollowed by moderate-sized sinuses.  
10 All these features are unlike all or most reduncins; some species from Chad also lack  
11 transverse ridges and have incipient keels, but they are definitely reduncin in the course of  
12 their horn-cores with anterior recurvature distally, thick, solid frontals, and large supra-orbital  
13 foramina (Geraads *et al.* 2001, 2009b). None of the characters of *K. laticornis* is indeed  
14 exclusive of the Reduncini, and I follow Vrba (2006) in rejecting this identification, but  
15 alternative tribal assignment is not easy. It is obviously not a member of the Boselaphini,  
16 Tragelaphini or Antilopini, while the very likely absence of sinus in the pedicle rule out  
17 Alcelaphini or Hippotragini. The incipient frontal pneumatization, great horn-core divergence,  
18 and vestigial (?) keels suggest the Bovini, but the small size, and supra-orbital position of the  
19 horn-cores go against this. In any case, assignment to a modern tribe is tricky, if not  
20 impossible. A new generic name is certainly needed for '*Kobus*' *laticornis*, but knowledge of  
21 its anatomy is too incomplete for this name to be really useful.

22  
23 Bovidae gen. et sp. indet. B

24 (Fig. 1D)  
25

26 **Description and comparisons.** I assign to this species about 20 specimens from the Nawata  
27 Formation (Supplemental material B); they were all included in *Aepyceros premelampus* by  
28 Harris (2003). The best specimen is KNM-LT-26570 from the Lower Nawata (Fig. 1D); it  
29 consists of the right side of a braincase with horn-core, probably somewhat distorted by  
30 dorsoventral crushing. The occipital is remarkably low and broad, and the braincase itself is  
31 broad, with a flat dorsal side. The horn-cores are inserted very far apart and very uprightly  
32 (the angle between their posterior border and the top of the braincase is about 100°) on solid  
33 frontals. They diverge by about 90° (an angle perhaps augmented by distortion), curve  
34 moderately backwards but lack distinct torsion, transverse ridges, and keels. They have an

1 incipient triangular cross-section, the degree of outline curvature being greater anteriorly,  
2 posterolaterally, and medially, with similar transverse and anteroposterior diameters.

3 The broad braincase and course of the horn-cores are totally unlike *Aepyceros*; the lack  
4 of frontal sinus and shape of the horn-core are unlike alcelaphins, and no reduncin has  
5 similar-shaped horn-cores. The relatively small size and lack of frontal sinuses argue against  
6 the Hippotragini, but comparison with late Miocene Chadian forms (Geraads *et al.* 2008) is  
7 relevant here; *Tchadotragus* has horn-cores with a similar shape and cross-section, and  
8 *Saheloryx* resembles in its broad skull, curvature of the horn-cores, and solid pedicle, but the  
9 horn-cores have an oval cross-section. Again, this bovid is too poorly known for its affinities  
10 to be firmly established, but it certainly does not easily fit into any of the modern tribes.

11  
12 Tribe **Alcelaphini** Brooke in Wallace, 1876

13 *Damalacra* Gentry, 1980 ?

14 *Damalacra* sp. ?

15 (Fig. 1I–J)

16  
17 **Description and comparisons.** Several alcelaphin teeth, including all those assigned to the  
18 Hippotragini by Harris (2003), are accessioned as coming from the Nawata Formation; some  
19 of them (KNM-LT-507, KNM-LT-25432, KNM-LT-25960) have a very derived morphology  
20 and I suspect that they originate in fact from much younger sediments. The morphology of the  
21 remaining teeth is that of primitive alcelaphins; they resemble those of *Damalacra* from  
22 Langebaanweg (Gentry 1980, fig.40), except that the lobes are more evenly rounded buccally  
23 (Fig. 1I–J). Of the two horn-cores from the Nawata Formation that Harris (2003) assigned to  
24 the Hippotragini, KNM-LT-23709 can be included in the Alcelaphini, and KNM-LT-25968 is  
25 probably reduncin. Thus, there is no Hippotragini in the Nawata Formation; the tribe is also  
26 quite rare at Kanapoi (Geraads & Bobe, in press).

27 Nine basal horn-core pieces, some of them with partial frontals, are tentatively  
28 assigned to the Alcelaphini (Supplemental material B), although it may be than more than one  
29 species is represented. One of them (KNM-LT-456) was assigned by Harris (2003) to  
30 *Damalacra*, one to *Praedamalis* (KNM-LT-23709), and three (KNM-LT-13010, KNM-LT-  
31 23131, and KNM-LT-26037) to *Hippotragus*. The various identifications of the other  
32 specimens can definitely be rejected. By contrast, most of the specimens assigned to  
33 *Damalacra* by Harris (2003) belong to *Aepyceros*, with the exception of KNM-LT-231, which

1 is reduncin, and of a few unidentified (but non-alcelaphin) specimens (Supplemental material  
2 B).

3         These horn-cores are slightly larger and less compressed than the only specimen of  
4 *D. harrisi* Geraads, Bobe and Manthi, 2013 from Kanapoi, and more primitive in their shorter  
5 pedicle. They resemble those of *Damalacra acalla* from Langebaanweg (Gentry 1980) but are  
6 smaller than males of this species (Gentry 1980, fig. 39) and more transversely compressed;  
7 their divergence does not increase and their diameters remain more constant upwards, so that  
8 they do not have the odd shape of *D. acalla* and many other alcelaphins. These morphological  
9 differences bring them closer to the Hippotragini, an identification that would be equally  
10 acceptable in regard of the large frontal sinuses extending into the pedicle, but is unlikely  
11 because of the strongly arched frontals between the horn-cores (distinctly more so than in the  
12 roughly contemporaneous horn-core from Sahabi assigned by Lehmann & Thomas [1987] to  
13 *Hippotragus*). In addition, no tooth in the Lothagam collection is definitely identifiable as  
14 hippotragin, in sharp contrast to the late Miocene of Chad, where primitive hippotragins are  
15 abundant (Geraads *et al.* 2008).

16         If correctly identified, this alcelaphin is more primitive than the Kanapoi and  
17 Langebaanweg *Damalacra*; it is more like the single basal horn-core from Sahabi assigned to  
18 this genus by Lehmann & Thomas (1987). Other similar horn-cores, from the Kuseralee  
19 Member in the Middle Awash, have been described by Haile-Selassie *et al.* (2009) as  
20 *Hippotragus* sp. The difficulties in telling apart the Alcelaphini and Hippotragini around the  
21 Mio-Pliocene transition support a relatively late divergence of these tribes, but the Lothagam  
22 material is too incomplete to contribute significantly to this issue.

23  
24                     Tribe **Aepycerotini** Gray, 1872

25                     Genus *Aepyceros* Sundevall, 1847

26                     *Aepyceros* sp.

27                     (Fig. 1A–B)

28  
29 **Remarks.** Harris (2003) assigned the majority of Lothagam bovids to his new species  
30 *Aepyceros premelampus*; most of them indeed belong to *Aepyceros*, but the holotype and  
31 paratype are notable exceptions (see below), so that the Lothagam impala, which is relatively  
32 common in the Nawata Formation, remains without a species name. Several of the *Aepyceros*  
33 specimens were assigned by Harris (2003) to other taxa, especially *Damalacra*, as noted  
34 above (Supplemental material B). The genus is also present in the Apak and Kaiyumung

1 members. Since the best specimen displays no remarkable feature, I prefer not to suggest  
2 species identification.

3 **Comparisons.** KNM-LT-23673 (Fig. 1A–B) consists of a frontlet and poorly preserved upper  
4 part of the braincase. As in the modern *A. melampus*, the supra-occipital extends far anteriorly  
5 on the cranial roof, but is less rectangular. The frontals are distinctly up-arched between the  
6 horn-cores, and are much inflated, with small supra-orbital foramina. The braincase KNM-  
7 LT-188 additionally shows that on the basioccipital the posterior tuberosities are less broad  
8 than in *A. melampus* but, as in this species, they are unconnected to the anterior ones by  
9 longitudinal ridges. A number of horn-cores differ from modern ones in their simpler course,  
10 especially lack of strong increase in divergence shortly above the base; they are not much  
11 compressed transversely, and have a rounded cross-section with only an incipient increase of  
12 outline curvature postero-laterally, so that the main axis of the cross-section remains almost  
13 antero-posterior. In these features, and in size, they resemble early Pliocene fossil impalas  
14 from Kanapoi (Geraads *et al.* 2013; Geraads & Bobe, in press), the Kuseralee Member in the  
15 Middle Awash (Haile-Selassie *et al.* 2009), Kossom Bougoudi in Chad (Geraads *et al.*  
16 2009b), and perhaps Mpesida ('Tribu indét.' in Thomas 1980, fig.1.12), but differ from  
17 *A. afarensis* from Woranso Mille (Geraads *et al.* 2009a) and *A. dietrichi* from Laetoli (Gentry  
18 2011), which are also distinctly larger (Fig. 2). The course of the horn-cores resemble that of  
19 '*Prostrepsiceros*' *libycus* from Sahabi (Lehmann & Thomas 1987, fig.7), later tentatively  
20 referred to their new genus *Dytikodorcas* by Bouvrain & Bonis (2007), but the cross-section  
21 of the Libyan horn-cores is more compressed, they are grooved anteriorly, and the frontals are  
22 not inflated. Several isolated teeth and partial tooth-rows confirm the presence of *Aepyceros*,  
23 but none allows to estimate the premolar/molar index.

24  
25 Tribe indet.

26 *Afrotragus* nov. gen.

27 **Type-species.** *Aepyceros premelampus* Harris, 2003

28 **Diagnosis.** That of the single species.

29 **Derivation of name.** *Afro-*, from Africa; *-tragus*, Greek for goat, often used in bovid names.

30  
31 *Afrotragus premelampus* (Harris, 2003)

32 (Fig. 1L–P; Fig.3; Supplemental material C)

33

1 **Types.** Harris (2003) designated as holotype of this species the braincase with horn-cores  
2 KNM-LT-184, from the Upper Nawata (Harris 2003, fig.11.19; Supplemental material C),  
3 and as paratype the cranium KNM-LT-23153 (Fig.3; Harris 2003, fig.11.20), from the Lower  
4 Nawata. It is likely that these two specimens are indeed of the same species, but many of the  
5 other specimens listed under this name by Harris (2003) belong to several different species,  
6 which explains the exceedingly large range of horn-core measurements (Harris 2003, tab.  
7 11.30). In addition, I assign to *Afrotragus premelampus* several specimens that were listed by  
8 him under different names (Supplemental material B).

9 **Diagnosis.** Antelopes of medium size. Face slightly inclined on the neurocranium; preorbital  
10 fossa present; premaxilla not very broad, but with a distinctly square outline in ventral view;  
11 frontals lacking sinuses, supraorbital foramina of medium size; braincase and occipital broad  
12 and low; mastoid exposure not very broad; basioccipital with relatively large anterior  
13 tuberosities. Horn-cores long and slender, inserted rather upright, without transverse ribs, with  
14 a well-marked heteronymous torsion, main axis of the cross-section much angled in respect to  
15 the sagittal plane. Upper molars with weak styles, poorly indicated paracone rib, U-shaped  
16 central valleys, central enamel island, and seemingly late fusion of the lobes in the central part  
17 of the tooth.

18 **Description.** The most complete specimen is the imperfectly cleaned cranium KNM-LT-  
19 23153 (Fig. 3), which displays a number of differences with *Aepyceros*. It is long and narrow,  
20 but the braincase is broad, longer and less inclined in respect to the facial axis than in this  
21 genus, and less rounded dorsally. The nasal bones are missing, but were certainly rather  
22 narrow, in contrast to *Aepyceros*. They probably had a shorter contact with the premaxillae  
23 than in the impala, and the right side of the skull, well-preserved in this area, shows the  
24 absence, between the premaxilla and the maxilla, of the large gap that is a characteristic  
25 feature of *Aepyceros* (modern *A. melampus*, and Hadar *A. datoadeni*, the only fossil form in  
26 which this area is known). As observed by Gentry (1985), this gap is otherwise present only  
27 in *Neotragus* and *Nesotragus*, two small antelopes that are regarded as the sister-group of  
28 *Aepyceros* by Hassanin *et al.* (2012) and Yang *et al.* (2013): it follows that this gap is not just  
29 a synapomorphy of Pliocene to modern *Aepyceros*, but of this whole group, and its absence in  
30 *Afrotragus* strongly speaks against its inclusion in it.

31 The most noticeable feature of the premaxillae in KNM-LT-23153 is the square  
32 outline of their rostral end, quite distinct from the rounded shape in *A. melampus* and  
33 *A. datoadeni*; this almost certainly indicates a grazer (compare Fig. 3A with Solounias &  
34 Moelleken 1993, fig. 1), unlike them. Both sides of the face are hollowed by a large ante-

1 orbital depression, absent in *Aepyceros*. The medial part of the frontals are depressed between  
2 the orbits and were certainly devoid of sinuses, in contrast to *Aepyceros*, and the supra-orbital  
3 foramina are larger than in this genus. The area of the postcornual fossa is unclear. The  
4 mastoid exposure is narrow, and has a much smaller extent on the occipital surface than in the  
5 impala. The anterior tuberosities of the basioccipital are strong and somewhat splayed out  
6 laterally, and the bone is much broader at this level than in *Aepyceros*. The horn-cores (Harris  
7 2003, fig. 11.20) are long, with a distinct sigmoid curvature; the main axis of the cross-section  
8 is strongly oblique, so that the moderate compression appears antero-posterior.

9 The premolars are missing, and the molars poorly preserved. They much differ from  
10 those of *Aepyceros* in their greater relative breadth, much weaker styles, more convex  
11 paracone pillar buccally, a tendency to pinching of the lingual lobes, and presence of a  
12 transversely elongated central enamel island or valley between the lobes, which seem to fuse  
13 only late in wear at this level.

14 The holotype partial skull KNM-LT-184 (Supplemental material C) is generally  
15 similar to KNM-LT-23153; it shows additionally that the postcornual fossa, not observable in  
16 the complete skull, is well indicated. This specimen differs in the better expressed central  
17 groove on the basioccipital, the broader mastoid, and perhaps larger supra-orbital foramina.  
18 Similarities outweigh these differences, and I regard them as co-specific, which is also a more  
19 parsimonious option.

20 Several horn-cores with parts of the frontals, all of them from the Nawata Formation,  
21 can tentatively be assigned to the same species on the basis of the lamination, very oblique main  
22 axis of the cross-section, and depressed frontals lacking pneumatization (Fig. 1O–P). Some  
23 dental remains (Fig. 1L–N) could also belong here, but the teeth of the holotype are too  
24 poorly preserved to allow reliable identification of other specimens.

25 **Comparisons.** *Afrotragus premelampus* is unlike most other African bovids, but it does  
26 resemble the '*Prostrepsiceros*' *libycus* from Sahabi (Lehmann & Thomas 1987; NHMUK  
27 M32981 and M32982 are casts of two horn-cores). They share long, slender, spiralled horn-  
28 cores, and a frontal poorly bent anteroposteriorly and lacking sinuses; some Lothagam horn-  
29 cores, especially KNM-LT-219, display an incipient anterior groove, as at Sahabi. The main  
30 axis of the cross-section of '*P.*' *libycus* horn-cores is oblique in respect to the sagittal plane,  
31 but this is mainly due to a strong posterolateral longitudinal ridge, absent at Lothagam; they  
32 are also more inclined backwards, and M32981 shows no postcornual fossa, in contrast to  
33 KNM-LT-184. The upper teeth share similar characters. Thus, the Sahabi species is  
34 conceivably related to *Afrotragus premelampus* (rather than to *Dytikodorcas* to which it was

1 assigned by Bouvrain & Bonis 2007, but which is a much smaller form); however, the fact  
2 that it is very poorly known, and some differences, preclude identification at species level.

3 Another possible relative is the '*Aepyceros* aff. *premelampus*' from Lemudong'o  
4 (Hlusko *et al.* 2007), but it is too incompletely preserved for identification.

5 *Afrotragus* must also be compared to the late Miocene Eurasian forms of the  
6 *Prostrepsiceros* group (Gentry 1971; Bouvrain 1982; Bouvrain & Thomas 1992; Kostopoulos  
7 2004, 2006), which is widespread but remains imperfectly known (especially the facial part).  
8 They resemble *Afrotragus* in their broad occipital, basioccipital usually with a central groove,  
9 presence of an ante-orbital depression, horn-cores with heteronymous torsion and much  
10 angled main axis of the cross-section, and in their upper molar shape, but they differ in their  
11 smaller size, absence of clearly marked longitudinal ridges on either side of the basioccipital  
12 (but they are conspicuous on KNM-LT-184 only), narrower mastoid exposure, and especially  
13 shorter and stouter horn-cores with tighter spiralling and usual presence of keels (much  
14 reduced in *P. rotundicornis*). The earliest *Prostrepsiceros* is *P. vallesiensis* Bouvrain, 1982,  
15 from the early late Miocene of Greece; it is primitive in its narrow occipital, but derived in its  
16 short nasal bones, relatively strong cranial flexure, and early fusion of the molar lobes. It  
17 might belong to a group of antelopes known only by horn-cores that resemble those of  
18 *Afrotragus* in being loosely spiralled (in contrast to typical *Prostrepsiceros*) and whose main  
19 axis of the cross section tends to be strongly angled in respect to the sagittal plane. They  
20 centre on '*Prostrepsiceros*' *vinayaki* (Pilgrim, 1939) and are known from the Siwaliks  
21 (Pilgrim 1939), Afghanistan (Kostopoulos 2009b), the Arabian peninsula (Gentry 1999),  
22 Maragha (Kostopoulos & Bernor 2011), Turkey (Gentry 2003), and the Ethiopian Middle  
23 Awash (Bibi 2011). Their horn-cores differ from those of *Afrotragus* in being smaller, more  
24 compressed transversally, and with a tendency to develop anterior and posterior keels but,  
25 despite these differences, they might have given rise to this genus, as well as to  
26 *Prostrepsiceros* itself, but no Eurasian species of *Prostrepsiceros* displays the long, slender  
27 horn cores of *Afrotragus* and, if they share a common ancestor, the divergence must date to  
28 the earlier part of the late Miocene.

29

30 Tribe indet.

31

32 Genus *Turkanatragus* nov. gen.

33

34 **Type species.** *Turkanatragus marymuunguae* nov. sp.

35 **Diagnosis.** That of the single species.



1 **Derivation of name.** *Turkana*-, from the Turkana people; *-tragus*, Greek for goat, often used  
2 in bovid names.

3 *Turkanatragus marymuunguae* nov. sp.

4 (Fig. 4; Supplemental material D)

5  
6 **Holotype.** KNM-LT-28752, incomplete braincase with almost complete horn-cores, from the  
7 Lower Nawata Member. In spite of a longitudinal crack, it is almost undistorted.

8 **Diagnosis.** Frontal little hollowed if at all; long, wide braincase, but mastoid facing mostly  
9 laterally; occipital narrow, with both sides facing posterolaterally on either side of a raised  
10 central part, top of the occipital produced caudally into a strong process; basioccipital with  
11 thick longitudinal ridges; horn-cores slender, with gentle sigmoid curvature and no transverse  
12 compression. Differs from *Afrotragus* in its much longer braincase, distinctly narrower  
13 occipital with strong central process and mastoid exposure facing more laterally, and more  
14 slender horn-cores.

15 **Derivation of name.** Dedicated to Mary Muungu, former chief collections manager at the  
16 Palaeontology Section of the KNM, for her invaluable help there.

17 **Comparisons.** The holotype was included in *Aepyceros premelampus* by Harris (2003). It  
18 does resemble *Aepyceros* in the poor cranial flexure, deep postcornual fossa, high, narrow  
19 occipital (much narrower than in *Afrotragus*), and horn-cores with slight sigmoid,  
20 heteronymous curvature and no transverse compression. However, it differs from the modern  
21 *A. melampus* and fossil *A. datoadeni* from Hadar (Geraads *et al.* 2012) and *A. shungurae* from  
22 Omo (Gentry 1985) in the lack of frontal sinuses, much longer braincase with a poorly convex  
23 dorsal outline, and presence of thick ridges connecting the anterior and posterior tuberosities  
24 of the basioccipital. In addition, the most remarkable feature of KNM-LT-28752 is the shape  
25 of the occipital. The mastoid exposure faces almost completely laterally, and is wider  
26 ventrally; the occipital is high and rather narrow, and much decreases in width upwards; both  
27 halves of the occipital face posterolaterally on either side of a caudally salient medial part that  
28 is ridge-like in its central part, and ends dorsally into a large triangular process, protruding  
29 caudally.

30 I do not formally include any other specimen in this species; some horn cores may  
31 belong here, but since there are at least three species of spiral-horned antelopes at Lothagam,  
32 identification of every specimen is impossible.

33 KNM-LT-28752 resembles *Afrotragus premelampus* in its fronto-parietal area, and  
34 general course of its horn-cores (Fig. 4), but differs in their stronger torsion, and especially in

1 its occipital, which is much broader and facing wholly caudally in the latter species. The  
2 proportions and shape of the occipital may display significant variations in modern forms but  
3 none closely resembles KNM-LT-28752. Thus, unless it is a pathological specimen, which is  
4 an unsupported assumption, the differences in occipital shape and proportions with  
5 *A. premelampus* leave no doubt as to their taxonomic distinctness. The only modern occipital  
6 reminiscent of the highly characteristic shape of that of KNM-LT-28752 is that of the  
7 gerenuk, *Litocranius walleri*, but in this species the whole dorsal part of the occipital is  
8 protruding and, remarkably, the parieto-occipital suture is straight and transverse, in contrast  
9 to KNM-LT-28752 that retains the central extension of the supra-occipital into the parietal,  
10 which is the usual condition in bovids. Thus, the resemblance between KNM-LT-28752 and  
11 the gerenuk is very superficial; it is perhaps linked with a similar head posture (the gerenuk is  
12 often bipedal when browsing).

13 A possible relative of *Turkanatragus marymuunguae* is the species from Kanapoi that  
14 Geraads *et al.* (2013) and Geraads & Bobe (in press) called aff. *Dytikodorcas* sp. (KNM-KP-  
15 29277). They share a complicated parieto-frontal suture, a long braincase, an occipital that is  
16 quite narrow dorsally with at least some caudal expansion medially (broken off in KNM-KP-  
17 29277), and horn-cores with some heteronomous curvature; the main difference is that KNM-  
18 KP-29277 has a transversely compressed horn-core. Both specimens are too incomplete for  
19 definite conclusions about their relationships but, along with *Aepyceros*, *Afrotragus* and the  
20 Sahabi '*Prostrepsiceros*', they attest to the diversity of spiral-horned taxa in the late Miocene  
21 of Africa.

22  
23 Tribe **Antilopini** Gray, 1821

24 Genus *Gazella* Blainville, 1816 ?

25 *Gazella* sp. ?  
26

27 **Remarks.** KNM-LT-13008, assigned to *Gazella* by Harris (2003), has a large frontal sinus  
28 and is probably alcelaphin. By contrast, the basal horn-core KNM-LT-23736 assigned by him  
29 to *Damalacra* lacks a frontal sinus and better fits *Gazella*, of which it would document a  
30 rather large species. KNM-LT-463 has a small frontal sinus anterior to the supra-orbital  
31 foramen and also better fits *Gazella* s.l. KNM-LT-22990 is a mandible with dp2–m2, possibly  
32 also of *Gazella*. KNM-LT-503 is a lower m1 (L = 10.9) that was the only Nawata specimen  
33 assigned to *Raphiceros* by Harris (2003) but is larger than the fossils assigned below to this  
34 genus, and its size corresponds to that of *Gazella* s.l.

1 The mandible KNM-LT-23599 (Fig. 1K) is puzzling; it is *Aepyceros*-like in  
2 morphology, but the premolars are too short for this genus. They are even shorter than in  
3 modern *Ourebia*; in addition, the central valleys of the molars are shorter than in the oribi,  
4 and the hypoconid of p4 is less clearly demarcated from the protoconid. It was assigned by  
5 Harris (2003) to *Gazella*, but might as well belong to one of the spiral-horned Lothagam  
6 antelopes.

7  
8 Genus *Raphicerus* H. Smith, 1827 ?

9 *Raphicerus* sp. ?

10  
11 A few dental remains assigned by Harris (2003) to *Madoqua* are too large for this  
12 genus, but could belong to *Raphicerus* or a related form; those from the Nawata Formation  
13 are: KNM-LT-177, KNM-LT-22981, KNM-LT-23612, and KNM-LT-28733.

14

## 15 **The Late Miocene diversification of African Bovidae**

16

17 The Nawata Formation of Lothagam and the roughly contemporaneous sites of Toros  
18 Menalla in Chad have yielded the only large bovid assemblages from the late Miocene of  
19 Africa, contemporaneous with European Turolian faunas. They are thus critical, along with  
20 the much less diverse assemblages of Sahabi, Libya (Lehmann & Thomas 1987; Gentry  
21 2008), Lemudong'o (Hlusko *et al.* 2007) and Lukeino (Thomas 1980), Kenya, to reconstruct  
22 the early history of some of the present-day African tribes, the Tragelaphini of the subfamily  
23 Bovinae and, in the subfamily Antilopinae, the sister-tribes Hippotragini and Alcelaphini, the  
24 more distantly related Reduncini, and the enigmatic Aepycerotini, which recent genetic  
25 analyses (Hassanin *et al.* 2012; Yang *et al.* 2013) place at a basal position within this sub-  
26 family. It should be noted that these genetic analyses, their major discrepancies aside, have  
27 shown that the classical tribes have very unequal status in a phylogenetic taxonomy, most of  
28 them being paraphyletic; for instance, the (Aepycerotini + Neotragini) clade branches as the  
29 sister-group of all other Antilopinae (Hassanin *et al.* 2012; Yang *et al.* 2013; but see Decker *et*  
30 *al.* 2009), whereas the Alcelaphini-Hippotragini divergence occurs very high in the tree.

31 In recent studies, all late Miocene to modern African bovids have been assigned, even  
32 if tentatively, to these modern tribes. However, even previous to the present revision of the  
33 Lothagam material, some fossils suggested the presence, in the Late Miocene of Africa, of

1 taxa that could not be easily assigned to the crown groups of these various tribes. Indeed, as  
2 observed by Bibi (2013:10), '... in almost all cases, the stem branches leading to these  
3 originations [of the crown groups] are long, stretching back to the middle Miocene, which  
4 makes it possible that their late Miocene "radiation" is actually an artefact of differential (non-  
5 random) extinction of older lineages.' For instance, Geraads *et al.* (2008) assigned *Saheloryx*  
6 *solidus* from Toros-Menalla in Chad to the Hippotragini because its teeth could not be told  
7 apart from those of *Tchadotragus*, but it lacks some of the derived features of the modern  
8 forms, and is certainly not a member of the crown Hippotragini. The case of the Reduncini is  
9 extreme; Bibi (2013) estimates their divergence at ca. 14 Ma, before the splits within the  
10 Caprini-Hippotragini-Alcelaphini clade, but the crown Reduncini are not much older than 5  
11 Ma. Thus, it is likely that some, or many, of the early reduncins were not members of the  
12 crown-group, making them hard to identify on the basis of the characters of the modern  
13 forms. *Kobus ? presigmoidalis*, many of the late Miocene to early Pliocene '*Kobus*', and the  
14 various forms centred on *K. porrecticornis* are probably such early offshoots.

15 Fossils cannot falsify a phylogeny based upon genetics of modern taxa, but there is no  
16 reason to forcefully include fossil taxa into a taxonomy based upon this phylogeny, unless  
17 they display features of the crown groups. As shown above, several of the Lothagam bovids  
18 do not fit into the modern tribal arrangement. *Tragelaphus kyaloi* much differs from modern  
19 tragelaphins in the shape of its braincase (Geraads & Bobe, in press) but can reasonably be  
20 regarded as a stem tragelaphin, as it shares some of the horn-core and dental characters of this  
21 tribe. By contrast, '*Kobus*' *laticornis* fails to display any clear reduncin character, but is too  
22 poorly represented for assignment to another (new ?) tribe. The Bovidae gen. et sp. indet. A  
23 and B, described above, are also of uncertain position because they are poorly known, and at  
24 least the latter one does not easily fit into a modern tribe. The newly recognized spiral-horned  
25 Lothagam antelopes, *Afrotragus* and *Turkanatragus*, are better represented. Each of them  
26 display sets of characters that are quite unlike those of any of the crown-groups, and  
27 assignment to any existing tribe would be unsupported; a phylogenetic analysis might reveal  
28 the need for a new tribe to which the incompletely known *Turkanatragus* could also belong,  
29 as suggested by the shape of its horn-cores. Together with the '*Prostrepsiceros*' *libycus* from  
30 Sahabi, they document the occurrence, in the late Miocene of Africa, of several spiral-horned  
31 antelopes that might belong to a single group. In spite of a similar course of the horns, they  
32 are unrelated to *Aepyceros*, and putting them in the Antilopini, together with *Prostrepsiceros*,  
33 merely reflects the lack of characters that define the present-day African tribes, in agreement  
34 with the basal position of the 'Antilopini' relative to them.

1 As discussed in Supplemental material A, the Lothagam bovid fauna and its spiral-  
2 horned antelopes have no clear ancestors in the first part of the African Late Miocene, but it  
3 may be that the dearth of sites of Vallesian-equivalent age in this continent hampers their  
4 recognition. By contrast, the North Tethysian realm has a number of spiral-horned antelopes  
5 among which it is tempting to search for the ancestors of the Lothagam forms. I shall leave  
6 the issue open but, if true, this biogeographic history would be shared by several other large  
7 mammals that may have dispersed into Africa at roughly the same period, e.g., *Dinocrocuta*,  
8 *Giraffa*, *Ancylotherium*, *Ceratotherium*, perhaps *Kolpochoerus-Dasychoerus*; some people  
9 even list hominins. Remarkably, these spiral-horned antelopes all vanish shortly after Nawata  
10 Formation times, as they are absent from the Nachukui Formation and from Kanapoi.

## 12 **Conclusion**

14 Today, the Bovidae are by far the most diverse group of large African ungulates, but it  
15 seems that this great modern diversity, by comparison with other groups, led researchers to  
16 regard it as representative of the whole history of the family. The Lothagam fossil record  
17 shows that it may have been still greater in the past, not because of a greater number of  
18 individual species, but because of the existence of genera not belonging to the crown groups,  
19 which could even attest to the presence of tribes that are now wholly extinct and remain  
20 hidden in classifications based upon modern taxa. The Eurasian radiation at roughly the same  
21 time-period also led to the appearance of numerous genera that are usually tentatively  
22 regarded as close to one of the modern tribes, but might as well belong to extinct groups  
23 warranting tribal status.

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33  
34 **Figure Captions**

1 **Figure 1. A-B**, *Aepyceros* sp., frontlet KNM-LT-23673 (**A**, close-up of the frontals; **B**,  
2 anterodorsal view); **C**, *Tragoptax* ? sp., left tooth-row p4–m2 KNM-LT-26068; **D**, Bovidae  
3 gen. et sp. indet. **B**, right lateral view of horn-core with braincase KNM-LT-26570; **E–H**,  
4 Reduncini ? (*Kobus* ? *presigmoidalis* ?); **E**, right m1–m3 KNM-LT-23624, occlusal view; **F–**  
5 **G**, m3 KNM-LT-26052 (**F**, occlusal view; **G**, buccal view); **H**, left m2–m3 KNM-LT-23655,  
6 occlusal view; **I–J**, *Damalacra* sp. ?, mandible fragment with m1 and partial m2 KNM-LT-  
7 235 (**I**, lingual view; **J**, occlusal view); **K**, Bovidae gen. et sp. indet. (*Gazella* ?), left mandible  
8 with p2–m3 KNM-LT-23599, occlusal view; **L–N**, *Afrotragus premelampus* ?; **L–M**, right  
9 mandible KNM-LT-204 (**L**, occlusal view; **M**, lingual view); **N**, right mandible KNM-LT-  
10 203, occlusal view; **O–P**, *Afrotragus premelampus*, left horn-core with frontal KNM-LT-185  
11 (**O**, lateral view; **P**, front view). Scale bar equals 20 cm for Figs. B and O–P, 10 cm for Figs.  
12 A and D, 5 cm for all others.

13  
14 **Figure 2.** Plot of basal diameters of *Aepyceros* horn-cores: *Aepyceros* sp. from Omo Mursi  
15 Formation (Gentry 1985, Drapeau *et al.* 2014); *Aepyceros datoadeni* from Hadar (Geraads *et*  
16 *al.* 2012); *Aepyceros afarensis* from Woranso-Mille (Geraads *et al.* 2009a); *Aepyceros* cf.  
17 *afarensis* from Kanapoi (Geraads & Bobe, in press); *Aepyceros dietrichi* from Laetoli (Gentry  
18 2011, and original measurements); *Aepyceros* sp. from the Nawata Formation of Lothagam.

19  
20 **Figure 3.** *Afrotragus premelampus* cranium KNM-LT-23153. **A**, dorsal view; **B**, occipital  
21 view; **C**, ventral view; **D**, occlusal view of M2–M3; **E**, right lateral view. Scale bar equals 5  
22 cm for Fig. D, 10 cm for all others.

23  
24 **Figure 4.** *Turkanatragus marymuunguae*, holotype KNM-LT-28752. **A**, left lateral view; **B**,  
25 front view. Scale bar equals 20 cm.

## 26 27 **Supplemental material**

28  
29 **Supplemental material A.** Additional notes on the Bovidae from the Apak and Kaiyumung  
30 Members, and on the origin of the Lothagam bovid fauna.

31  
32 **Supplemental material B.** Catalogue of the Lothagam Bovidae, with previous and revised  
33 identifications, and main measurements.

34

1 **Supplemental material C.** 3D reconstruction of KNM-LT-184, holotype of *Afrotragus*  
2 *premelampus* (Harris, 2003).

3

4 **Supplemental material D.** 3D reconstruction of KNM-LT-28752, holotype of *Turkanatragus*  
5 *marymuunguae* gen. et sp. nov.