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Bovidae (Mammalia) from the lower Pliocene of Chad

DENIS GERAADS, ^{*,1} CECILE BLONDEL, ² HASSANE TAISSO MACKAYE, ³ ANDOSSA
LIKIUS, ⁴ PATRICK VIGNAUD, ⁵ and MICHEL BRUNET ⁶

¹ CNRS UPR 2147, 44 rue de l'Amiral Mouchez, 75014 Paris, France, denis.geraads@evolhum.cnrs.fr;

² IPHEP, CNRS UMR 6046, Université de Poitiers, 40 Avenue du Recteur Pineau, 86022 Poitiers
cedex, France, cecile.blondel@univ-poitiers.fr;

³ Département de Paléontologie, Université de N'Djamena, BP 1117, N'Djamena, Chad,
mackaye_taiisso@yahoo.com;

⁴ Département de Paléontologie, Université de N'Djamena, BP 1117, N'Djamena, Chad,
andossa.likius@yahoo.fr;

⁵ IPHEP, CNRS UMR 6046, Université de Poitiers, 40 Avenue du Recteur Pineau, 86022 Poitiers
cedex, France, patrick.vignaud@univ-poitiers.fr;

⁶ Collège de France, Chaire de Paléontologie humaine, 11 Place Marcelin Berthelot, 75232 PARIS
cedex 05, michel.brunet@college-de-france.fr

* Corresponding author

RH: GERAADS ET AL.—BOVIDAE FROM THE LOWER PLIOCENE OF CHAD

ABSTRACT—The sites of Kossom Bougoudi (KB) and Kollé (KL) are intermediate in age between the *Sahelanthropus* sites of Toros Menalla and the *Australopithecus* sites of Koro Toro, and their bovid faunas are also intermediate in composition and stage of evolution. Four new taxa are erected. The hippotragine *Tchadotragus fanonei* nov. sp. is more derived than the type-species of the genus, from Toros Menalla. *Kobus ammolophi* nov. sp. is also clearly related to the most common reduncine of the latter sites, rather than with other African forms. However, *Jamous kolleensis* nov. gen. nov. sp., a new bovine with extremely divergent, horizontal horn-cores, is unrelated to other Chadian Bovini. The KB and KL assemblages document the gradual replacement of hippotragines by alcelaphines in Northern Chad, but it is not necessarily linked with environmental change, as all Chadian assemblages virtually lack indicators of bush or woodland like Tragelaphini and *Aepyceros*. In spite of a significant endemic component, the KB and KL Bovidae compare best with some of those from Sahabi in Libya, confirming North-South connections.

INTRODUCTION

The main sets of fossiliferous localities where the "Mission Paléolithologique Franco-Tchadienne" has been conducting paleontological field research in the Djurab region of Northern Chad since 1994 are 1) the middle Pliocene of Koro-Toro (KT), with the first australopithecines west of the Rift (Brunet et al., 1995, 1996), whose age was estimated by biochronology at 3–3.5 Ma; 2) the lower Pliocene of Kollé (KL) with an estimated age of 4–4.5Ma (Brunet et al., 1998); 3) the lowermost Pliocene of Kossom Bougoudi (KB), with an estimated age of ca.5.5Ma (Brunet and M.P.F.T., 2000); and 4) the upper Miocene of Toros-Menalla (TM), which yielded the earliest known hominid, at ca. 7Ma (Vignaud et al., 2002; Brunet et al., 2002, 2005). These ages have been confirmed by radiometric dating (Lebatard et al., 2008).

As is usual in African faunas of these periods, the Bovidae make up a large proportion of the fauna. Those from Koro-Toro have been described previously (Geraads et al., 2001); some of those from Toros-Menalla have been published (Geraads et al., 2008), while the remaining specimens currently are under study. We describe here those from Kossom Bougoudi and Kollé. This material is not as well preserved as that from KT or TM. Most specimens consist of isolated teeth, or incomplete horn-cores and limb bones, and almost all of them suffered wind abrasion, obscuring some anatomical details, and introducing some uncertainties in the measurements.

The main localities from the KB area (N 16°20', E 18°40') are KB3, KB4 and KB7, which are all close to each other and were even lumped together during some field campaigns. These localities yield a homogeneous faunal assemblage and are referred to collectively as "KB" here. Other KB localities are much poorer. The bovids from KB15, KB16, KB18, KB22, and KB26 suggest that these localities could be of the same broad age as the main ones, and this is probably true also of other KB localities, except KB24 which is much younger. The Kollé sites (N 16°20', E 19°00') are also located very close to each other, and nothing suggests that they are diachronic.

All specimens belong to the "Département des Collections" of the Centre National d'Appui à la Recherche (CNAR), N'Djamena, Chad. Authors of family-group names are given according to Grubb (2001), and when describing cranial material the skull is oriented so that the tooth row is horizontal.

Abbreviations—APD: antero-posterior diameter; TrD: transverse diameter; HC: horn-core.

SYSTEMATIC PALEONTOLOGY

Bovidae from Kossom Bougoudi

Family BOVIDAE Gray, 1821

Sub-family BOVINAE Gray, 1821

Tribe BOVINI Gray, 1821

Bovini gen. et sp. indet.

This tribe is represented at KB by some post cranial elements, two small horn-core fragments, KB3-98-090 and KB3-97-003, a lower molar KB7-97-009, an m3 KB3-98-106, and a fragment of mandible KB3-98-042; the length of both m3s at mid-height is 43.5 mm. Since all teeth are mandibular, they cannot be directly compared with those from Kollé (see below), but they are roughly at the same evolutionary stage, being decidedly more bovine-like than those of *S. demissum* from Langebaanweg. There is no goat-fold but a strong parastylid, the labial pillars are pinched, the lingual pillars well rounded, but the ectostylid is not larger than in the latter site; the least worn m3 has a distal flange and a small fossette in the third lobe. They are slightly larger than the bovine teeth from Toros-Menalla, and the parastylid is stronger. Unfortunately, lack of significant cranial or horn-core remains precludes generic assignment of the KB bovine.

Sub-family HIPPOTRAGINAE Sundevall in Retzius and Lovén, 1845

Tribe HIPPOTRAGINI Sundevall in Retzius and Lovén, 1845

Genus *TCHADOTRAGUS* Geraads et al., 2008

Type-species—*Tchadotragus sudrei* Geraads et al., 2008, from Toros-Menalla.

Diagnosis—A primitive hippotragine of medium size, with a braincase slightly or only moderately inclined on the splanchnocranium and broad over the mastoids, both halves of occipital surface facing partly laterally, a basioccipital with strong anterior tuberosities, large orbits with very prominent rims, a short face with a small jugal and a short and deep lacrymal bone, a large diffuse anteorbital fossa, a relatively large ethmoidal fissure, premaxillae not contacting nasals, long slender curved horn-cores with some sigmoid curvature in antero-dorsal view, usually without transverse ridges, uprightly inserted and close to the midline, a large sinus in the pedicle, rather small supraorbital foramina, molar pattern simpler than in modern hippotragines, and premolars neither shortened nor enlarged (type-species description slightly modified after Geraads et al., 2008).

TCHADOTRAGUS FANONEI nov. sp.

aff. *Protoryx* sp. in Brunet and M.P.F.T., 2000

Holotype—KB3-97-146, left part of a brain-case with incomplete horn-core (Fig. 1B).

Paratype—KB3-97-200, frontlet with complete horn-cores, both halves of the mandible (the right one with complete tooth-row), tibia and talus (Fig. 1A, C, D; 2A; 3A).

Referred Specimens—About 60 specimens are definitely identified from KB3, KB4, KB7, and one from KB22, but most medium-large size bovids from these and other sites in the KB area are probably also of this species, which is the most common bovid there.

Derivatio Nominis—In memory of our colleague Fanoné Gongdibé.

Diagnosis—A species of *Tchadotragus* differing from the type-species by horn-cores with a longer pedicle, stronger cranio-facial angle (as shown by the anterior border of the horn-core pedicle more in line with the horn-core itself), longer and narrower neurocranium, and better expressed goat folds on lower molars.

Description and Comparisons—The holotype is the only specimen preserving part of the braincase, which is slightly longer (length from front of pedicle to top of occipital = 161 mm vs. 138-147 mm, mean 142 mm, N = 3, in *T. sudrei*), higher (occipital height, from top of foramen magnum = 50 mm vs. 40-48 mm, mean 43 mm, N = 6, in *T. sudrei*) and narrower (width over mastoids = ca. 96 mm vs. 94-120 mm, mean 107 mm, N = 9, in *T. sudrei*) than at Toros-Menalla. This difference in braincase proportions is reflected in the closer approach of the poorly defined temporal lines posteriorly, in the narrower supra-occipital bone, both sides of the occipital facing still more laterally, and more lengthened basicranium and basioccipital. It may be that the anterior tuberosities of the basioccipital reached the level of the missing foramen ovale, in contrast to the type-species, and this character has accordingly been removed from the generic diagnosis. We regard all these differences as significant, as the single *T. fanonei* specimen stands apart from all *T. sudrei* specimens.

As in *T. sudrei*, the horn-cores of the types are very uprightly inserted (their posterior border makes an angle of about 95° with the parietal profile in lateral view), slightly divergent, with an incipient anticlockwise torsion on the right horn-core, and a strong backward curvature. The latter is less clearly localized around mid-length than in *T. sudrei*, but too few specimens are known for this apparent difference to be included in the diagnosis; in some distal fragments (e.g., KB3-97-238 and KB3-97-070), the curvature is more localized near the tips, showing that these horn-cores were not very long. Other specimens consist mostly of basal parts. Together with the types, they all show that the pedicle is longer than at TM, so that its lateral side is less deeply concave in front view. This difference is increased by the slightly less prominent orbital rims, although none is completely preserved at KB. Other consequences of the pedicle being longer are that the supra-orbital foramen is farther away from the horn-core, and that the front edge of the pedicle is almost straight and in line with that of the horn-core itself in lateral view, instead of being concave in *T. sudrei*. However, this is also because the face is more inclined in respect to the brain-case, and the angle between the facial profile and the horn-core would have been larger. It may also be that the maximum diameter of the cross-section is located less

posteriorly than at TM (Fig. 2A-C), but the difference in this regard between the left and right horn-cores of KB3-96-056 makes us cautious about the validity of this difference.

Horn-core measurements are virtually identical with those from TM (mean APD x TrD: 48.1 x 35.4 mm for 12 specimens from KB, vs. 48.1 x 35.7 mm for 55 specimens from TM).

The teeth do not differ much from those of *T. sudrei* from Toros-Menalla. Neither the morphology, nor the hypsodonty, measurements, nor premolar/molar proportions of the few complete specimens differ significantly (Table 1).

The p4 has a poorly distinct paraconid, widely separated from the bulbous metaconid. On the molars, the ectostylid is moderate but, on the average, the goat fold is definitely stronger than at TM, where it is incipient, at most. Here, it varies from completely absent to rather strong, but never reaches the top of the crown.

The post-cranial skeleton is best illustrated by associated elements KB7-97-050, the paratype tibia KB3-97-200, and several other short bones and fragments. The distal articulation of the humerus corresponds to our second type at Toros-Menalla (Geraads et al., 2008). It resembles modern hippotragines, but is less cylindrical. Measurements (Table 2) are also very similar to those from TM. On the radius, the palmar outline of the proximal surface is not sharply broken, the lateral tuberosity is of moderate size, and the distal extensor grooves are slightly concave; all these features are found in modern hippotragines. On the metacarpal, the lateral sides of the distal condyles are moderately divergent, as in modern hippotragines, but in contrast to them, the unciform facet is not much lower than the capitato-trapezoid facet, and the epiphysis is not depressed just above the condyles. The femur is represented by the shaft only. Accounting for the slightly larger available measurements of KB3-97-200 compared to KB7-98-050, the tibia is about one tenth longer than the radius, a difference comparable with modern hippotragines (Gentry & Gentry, 1978, fig.19), but smaller than in alcelaphines, and larger than in reduncines or tragelaphines. The central distal process of the tibia is narrower than in tragelaphines and alcelaphines, and the anterior fibular facet is offset medially, as at

TM and in modern hippotragines (Fig. 1A). Although the post-cranial skeleton from KB can be referred definitely to *Tchadotragus*, it does not solve the problem of postcranial identification at TM (Geraads et al., 2008). Dimensions of the talus, the most common bone, cover the whole range of those of the larger antelopes at TM, falsifying the idea that *Saheloryx* averages larger than *Tchadotragus*. Thus, it could be that the former is illustrated by the first type of humeri that we recognized (Geraads et al., 2008), and by some tibiae without offset anterior fibular facet; this would confirm our hypothesis that *Saheloryx* is less closely related to modern hippotragines than is *Tchadotragus*.

There is no doubt that *T. fanonei* is closely related to *T. sudrei*, and it is tempting to believe that it is its descendant. The longer horn-core pedicle, greater cranial flexure, and stronger goat-folds are more derived, and the younger geological age of the former does not contradict this succession. It would follow that other cranial differences, the proportions of the braincase and the orientation of the occipital, are also derived in *T. fanonei*, but they draw it farther away from modern hippotragines, confirming that *Tchadotragus* is a distinct lineage.

Dentitions similar to those of *Tchadotragus* are present at Kanapoi (KNM-KP29274, KP29276, and KP29279; the latter two specimens were referred to the Reduncini by Harris et al., 2003, but they might as well be hippotragine). Of the horn-cores from Lothagam referred to *Hippotragus* sp. by Harris (2003), some (like KNM-LT23598) are too obliquely inserted for this genus, but LT23131, as well as LT23709, both from the Upper Nawata, referred to *Praedamalis* by Harris, could belong to the modern genus or to *Tchadotragus*, but are too incomplete for detailed comparisons.

Sub-family indet.

Tribe REDUNCINI Knottnerus-Meyer, 1907

Genus *KOBUS* A. Smith, 1840

KOBUS AMMOLOPHI n.sp.

Kobus sp.nov. in Brunet and M.P.F.T., 2000

Holotype—KB3-97-154, a braincase with both horn-cores, and four associated upper molars (Fig. 1E-H; 2F).

Referred Material—About 40 specimens definitely can be assigned to this species, and some postcranials must belong here too. Besides the type, the best specimen is KB3-97-171, a less well preserved braincase with left horn-core. KB7-97-088 is a right tooth-series p4-m3 (Fig. 3C), KB7-97-095 a left series m2-m3, and KB7-97-098 right and left P2-M3 (Fig. 3B), all presumably of the same individual.

Derivatio Nominis—Because sand dunes (Greek *αμμόλοφος*) are widespread in the Djurab desert.

Diagnosis—A species of *Kobus* of medium size. Horn-cores small, upright, with a moderate divergence which increases upwards, with little compression and backward curvature, and no transverse ridges. Braincase with a flat dorsal profile, mastoid exposure with a distinct mastoid process. Teeth of advanced reduncine morphology,

Description—On KB3-97-154, the cranial flexure was similar to that of *K. kob*. The supra-orbital foramina open directly into the orbit; they are incompletely preserved but it seems that the frontal depression around them was rather shallow. The fronto-parietal suture is almost straight, with only a very shallow median indentation. The post-cornual fossa is small and shallow. The horn-cores are very short compared to the size of the braincase, although complete fusion of the basisphenoid-basioccipital suture shows that the specimen was fully adult. They are inserted uprightly in side view (the angle between the base of their posterior edge and the top of the braincase is about 75°), slightly curved backwards for most of their length but are straight or even have a weak forward curvature near the tip. The divergence is moderate (about 55°) and increases upwards. The cross-section is oval (Fig. 2F,G), with no tendency towards a postero-lateral keel, and is moderately compressed near the base but less so distally. Its main axis makes an angle of about 45° to the sagittal plane, and the maximum transverse diameter is closer to the anterior side. There are no transverse ridges.

The braincase has an almost flat dorsal profile and widens posteriorly. The temporal lines are indistinct because of weathering, but seem to approach closely posteriorly, on either side of a narrow supra-occipital. The occipital is broad, with a triangular rather than semi-circular outline, and its sagittal part is slightly raised above the lateral sides, which face somewhat laterally. The mastoid exposure faces postero-laterally; it is triangular and broadens regularly from its dorsal tip around the small mastoid foramen to its ventral base. A vertical blunt ridge marks the limit between a posterior concave part, which belongs more to the occipital plane, and an anterior one which ends ventrally by forming a distinct rather large mastoid process, the tip of which is broken. The cranial base is not preserved, except for part of the basioccipital, showing posterior tuberosities not wider than the very incompletely preserved anterior ones.

On KB3-97-171, the horn-core is slightly larger and longer and was slightly more divergent from its counterpart (about 60°) but the divergence increases very little upwards. The auditory bulla (not preserved on KB3-97-154) is large and inflated, but the rest of the braincase is similar to that of the previous specimen. Measurements are given in Table 3.

Other horn-cores are mostly incomplete and weathered. They confirm the above-mentioned features; however, some may show a tendency towards flattening of the lateral side, a tip slightly curving forwards, or a deeper post-cornual fossa.

The teeth have a modern reduncine pattern. On the upper ones, the lobes are well outbowed between the styles, the entostyle is transversely lengthened, and the protocone is pinched lingually. Corresponding features can be seen on lower teeth, and the goat fold is long. On KB7-97-088, the paraconid and parastylid of p4 are fused into a narrow blade up to the top of the crown, but they were probably distinct on KB4-97-001, where they are broken; on the three available p4s, this anterior complex remains widely separated from the metaconid, and the talonid is antero-posteriorly compressed with a hypoconid strongly salient labially. The lengths of the upper premolar and molar

series of KB7-97-098 are 33.5 and 53.5 mm, respectively. Those of the lower molar series of KB7-97-088 and KB4-97-008 are 56.5 and 53 mm, respectively.

Comparisons—There are two species of *Kobus* at Koro-Toro. *Kobus korotorensis* Geraads et al., 2001 is mostly known by its horn-cores; their basal divergence is comparable to that of the KB *Kobus*, but it strongly decreases upwards. The cross-section is also different, being more triangular, with a flattened postero-medial surface. The second species, *K. tchadensis* Geraads et al., 2001, has very long and very divergent horn-cores with a circular cross-section, the face is much less bent on the cranium, and the ventral part of the mastoid is much narrower, the mastoid process being much smaller. Thus, the most common species of *Kobus* at KB has no close relationship with the KT ones.

Some reduncine specimens from TM, instead, are clearly related to the KB species. They share a similar length, orientation, course, and cross-section of the horn-cores, similar braincase size and morphology, including a wide occipital, straight dorsal profile, large mastoid exposure with a well-developed mastoid process, and a frontal much bent along the midline. Differences are that the KB horn-cores are on the average slightly larger and less compressed, slightly more divergent, and the main axis of the cross section is more inclined in respect to the midline, but the main difference is in the shape of the mastoid exposure, which is shorter dorsally and more triangular, whereas its squamosal and occipital sutures are more nearly parallel at TM.

From sites outside Chad, only a few reduncines of medium or large size have horn-cores short enough to be compared to the KB species. *Kobus subdolus* Gentry, 1980, from Langebaanweg, has horn-cores with a similar degree of compression and a similar course in lateral view; its braincase also widens posteriorly, has a flat upper profile, and no indentation of the parieto-frontal suture. It differs first by its much more primitive teeth, but also in that the horn-cores are usually slightly larger, with a flattened lateral surface, are inserted more obliquely and with the main axis of the cross-section seemingly less angled in respect to the sagittal plane, and with a weaker basal divergence which

decreases upwards; its occipital faces wholly posteriorly and includes most of the mastoid exposure, which is small.

Another species from Langebaanweg (*Kobus* sp.2 of Gentry, 1980) has more divergent and more curved horn-cores, the top of the braincase is convex, and the posterior ridges on the basioccipital are more transversally elongated.

The horn-cores of the *Kobus* aff. *subdolus* from the earliest Pliocene of Tinde at Manonga (Gentry, 1997) are on average slightly less compressed, less curved and more divergent than those from KB, but similar in their increasing divergence upwards. Its teeth are more primitive than those from KB because of the weaker labial ribs of the paracone and metacone, the lack of pinching of the protocone, weak or absent basal pillars, weaker goat folds and short disto-lingual arm of the hypoconid on p4.

Redunca darti Wells & Cooke, 1956, from Makapansgat is a species of small size, with massive horn-cores with a similar divergence and antero-lateral to postero-medial compression, but they are extremely short. The skull has not been described in detail, but the dorsal cranial profile looks more rounded, and the occipital condyles protrude less, posteriorly, meaning that the occipital is more in a single plane.

Lehmann & Thomas (1987) described as *Redunca* aff. *darti* two frontlets and a horn-core from an unknown level of Sahabi, Libya. They differ mainly from the KB fossils by their larger size and presence of transverse ridges on one specimen but nothing is known of the skull.

Kobus presigmoidalis Harris, 2003, from Lothagam, is about the same size as *Kobus ammonophi* but the horn cores have a distinct sigmoid curvature so that the divergence diminishes upwards, the supra-orbital foramina are more triangular and narrower, the braincase has a convex dorsal profile, the occipital is narrower, and the mastoid exposure is wholly lateral, with an anterior expansion behind the auditory foramen; these differences show that they are distinct species.

Kobus ammonophi differs from *K. porrecticornis* from the upper part of the Dhok Pathan Formation of the Siwaliks, and from related forms from Lukeino (Thomas, 1979) and the Beard's

Quarry at Langebaanweg (Gentry, 1980) by its larger size and more upright horn cores, the divergence of which increases upwards rather than remaining constant or decreasing.

Kobus khroumirensis (Arambourg, 1979) is based upon a poorly preserved incomplete braincase from Lake Ichkeul, an early Pliocene site in Tunisia. It is slightly larger, the occipital is relatively still lower, the dorsal braincase profile is more convex, but the mastoid exposure is similar, with a depressed posterior part in the occipital plane, and an incipient mastoid process anteriorly. A detached horn-core has a similar divergence that increases upwards, a similar cross-section whose major axis is strongly angled on the sagittal plane, but has a slight forward curvature.

The teeth of *Kobus ammolophi* are much more derived than those of *Kobus subdolos* Gentry, 1980, from Langebaanweg. However, as noted by Gentry, the latter are remarkably primitive for their geological age, and more typical reduncine teeth are known as early as the late Miocene in the Middle Awash (Haile-Selassie, 2001), at Lukeino and Mpesida (Thomas, 1980), and in the early Pliocene of the Nkondo Formation of Uganda (Geraads & Thomas, 1994). The fact that dental morphology evolved at different rates in the various reduncine lineages is confirmed by *Kobus sigmoidalis* from Olduvai, where the labial pillars of upper molars are only weakly rounded (Gentry and Gentry, 1978). Therefore, it would be premature to draw any biochronological conclusion from the morphology of the KB teeth.

KOBUS cf. *KOROTORENSIS* Geraads et al., 2001

Description—KB3-98-038 and KB4-97-031 are two heavily weathered horn-cores whose cross-section outline is too different from that of *Kobus ammolophi* for them to be included in the same species, and they are more like *K. korotorensis* from Koro-Toro (Geraads et al., 2001). Their antero-posterior as well as transverse diameters are in the 30-32 mm range, but cannot be precisely measured. At least KB4-97-031 was more inclined than in the latter species, but too little is preserved of their bases for their divergence to be estimated. Their cross-section has the shape of a rounded triangle, but

the lateral side is narrower than at Koro-Toro, so that one of the adjoining surfaces is posterior rather than postero-medial. We provide no definite identification for these specimens.

Sub-family ANTILOPINAE Gray, 1821

Tribe AEPYCEROTINI Gray, 1872

Genus *AEPYCEROS* Sundevall, 1847

AEPYCEROS sp.

Description—There are only two definite *Aepyceros* specimens at KB: KB3-97-361, a crushed and deformed frontlet, but with the base of the left horn-core well-preserved (APD = 37.8 mm; TrD. = 36.2 mm), and KB3-97-081, the weathered base of a right horn-core; KB7-97-130 and KB3-97-247 are doubtful horn-core fragments. On KB3-97-361, the frontal is poorly preserved, but it was not thickened as in the modern impala, and sinuses were much reduced or absent; nothing can be said about the supra-orbital foramina or post-cornual fossa. The horn-cores are large relative to the size of the frontal; at the base their angle of divergence is about 70°, but it increases upwards for about 10 cm before decreasing; they also have a regular backward curvature in side view, and therefore a clear normal torsion. The cross-section at the base is almost circular, with only a hint of a postero-lateral keel underlined by a shallow groove; there is only a slight indication of transverse ridges. KB3-97-081 differs from *Kobus* by its smaller size and weaker compression, weak but distinct spiralling, and presence of sinus in the frontal bone.

Comparisons—The reduced or absent pneumatization rules out the inclusion of KB3-97-361 in *A. melampus*, while the clear spiral of the horn-cores differs from several unnamed middle Pliocene forms, such as those from Hadar or from the oldest Omo sediments. *Aepyceros shunguruae* from the Turkana basin may have more clearly spiralled horn-cores, but they are smaller. The KB *Aepyceros* horn-cores best match those of *A. premelampus* Harris, 2003, from Lothagam, except that the latter are almost always more compressed; Harris (2003) noticed that their size decreases through the Lothagam

sequence, and KB3-97-361 is larger than all those from the Apak Member, and close to the largest specimens of the Nawata Fm. However, we prefer not to attribute these specimens to species, as the evolution of *Aepyceros* is still poorly understood, with several lineages co-existing in the Pliocene of Africa.

Tribe ANTILOPINI Gray, 1821

Genus *GAZELLA* Blainville, 1816

GAZELLA sp. A

Material—KB3-97-009 is a mandible with the labial walls of m2-m3 and the alveoli of other teeth. No Antilopini horn-cores are known from KB.

Description and Comparisons—The third lobe of m3 is large, but shorter than the other two; the premolar series includes a two-rooted p2, and is rather long (estimated length = 22.5 mm ± 0.5 mm, vs. ca 44 mm for the molars). A specimen of similar premolar length, but with longer molars, was referred by Geraads et al. (2001) to an *Antidorcas* with primitive, long premolars. We believe that those of the present specimens are too long for this genus.

GAZELLA sp. B ?

Material—KB3-98-012 is a mandible fragment with m2-m3 (estimated length m1-m3 = 35 mm), KB26-97-001 is a mandible with p4-m3 (length m1-m3 = 38).

Description and Comparisons—These specimens indicate smaller animals than KB3-97-009, and we tentatively refer them to another species, which could be close to a species from TM.

Bovidae from Kollé

Sub-family BOVINAE Gray, 1821

Tribe BOVINI Gray, 1821

Genus *JAMOUS* nov. gen.

Type-species—*Jamous kolleensis* nov. sp.

Diagnosis—That of the single species

Derivatio Nominis—Arabic جاموس, buffalo.

JAMOUS KOLLEENSIS nov. sp.

Simatherium sp. in Brunet et al., 1998

Holotype—KL3-96-013, skull lacking the left part of the face, front of the muzzle and premolars; three horn-core segments found nearby have a quite satisfactory fit onto the skull and are taken as being part of the holotype (Figs. 2E, 4).

Type-locality—Locality KL3, Kollé, Djurab Erg, Chad.

Diagnosis—A bovine with horn-cores of moderate length and almost without curvature, inserted horizontally above the post-orbital bar, almost completely divergent, not much compressed dorso-ventrally, with a rounded triangular cross-section, the antero-dorsal and antero-ventral edges being almost keel-like, and a slightly concave postero-ventral face. Face short and deep, no frontal bosses or rugosities, parietal depressed and separated by a transverse thick ridge from the supra-occipital which is not fully deflected into the occipital plane.

Derivatio Nominis—From Kollé, the area of the type-locality.

Description—The holotype skull is that of an adult with well-worn M3. The sutures are not traceable, and most of the bone surface is weathered, but the skull is not distorted. The face was deep, as shown by what remains of the right maxilla, M3 being far below the orbit. The dorsal edge of the maxilla is blunt, suggesting that it had no contact with the missing nasal, and that at least a remnant of ethmoidal fissure might have been present. There is no sign of a pre-orbital fossa. The lateral palatal notches reach the level of the middle of the second lobe of M3, while the choanae are more caudal than M3. The vomer is not visible in the nasal fossae, and was thus widely separated from the palate. The

lateral border of the masseter insertion forms a tubercle under the orbit, but the zygomatic arch is otherwise lightly built. The orbital border is only slightly raised above the plane of the maxilla, and the orbital rim is not tubular as in some bovines, such as *Bison*. The supra-orbital foramina are small and moderately wide apart. Between them, the frontals are slightly depressed on either side of the sagittal suture, but between the horn-cores the frontal is transversely flat. There is no sign of frontal boss or rugosities. The horn-cores were inserted above the post-orbital bar and partly overhang the orbits, in a position not more caudal than in many antelopes. The detached right horn-core has some missing parts around the base, but the left one fits closely onto the skull, especially along the temporal fossa, ensuring that all four specimens belong to the same individual. The horn-cores emerge transversally from the skull, almost horizontally, and diverge by an angle of about 170° (both in anterior and dorsal views). Although the front part of their base is above the orbits, they extend well behind it, so as to cover most of the temporal fossa. They are not much dorso-ventrally compressed, and the cross-section is that of a rounded triangle, with an anterior dorsal keel, an antero-ventral one (the primitive postero-lateral keel), and a rounded posterior border. The dorsal face of the left horn-core is eroded, but on the right one it was more convex than the other two, the postero-ventral face being flattened or even slightly concave near the base, reminiscent of some Pliocene East-African bovines. The base of the distal fragment shows that towards the tip, the section becomes more compressed and more oval, and that the horn-cores, although broad at the base, were not very long compared to the size of the skull. The two specimens together indicate that the horn-core was virtually straight, with only a hint of downward curvature basally, and a slightly stronger upward and backward curvature distally. The frontal sinus extends into the first few centimeters, but the right horn-core shows no more sinus at 8 cm above the base, showing that pneumatization was limited to the base.

Between the horn-cores, the frontal is significantly arched antero-posteriorly (Fig. 4A), but this convexity abruptly ends with a small tubercle at the level of the posterior horn-core border (presumably the limit between the frontal and parietal bones), where the profile becomes concave for 35 mm. Thus,

the parietal was relatively long for a bovine. Behind this, a thick, raised, well-delimited ridge (ca. 28 x 68 mm) extends almost from one temporal fossa to another, where they come closest to each other, but still remain far apart. Further back, the supra-occipital area forms a well-delimited trapezoidal area, at an angle to both the parietal and occipital planes. Although it is not easy to measure precisely, the distance between the horn-core and this supra-occipital area is short, but this is due to the large size of the horn-core base, not to their backward shift. The occipital proper is broad, with a straight dorsal edge separating it from the supra-occipital. The mastoid exposure looks narrow, and its ventral part faces ventro-laterally. The left paroccipital process is directed ventro-caudally and is transversely compressed, but perhaps eroded. The basioccipital is triangular, as is usual in bovines, and long compared to its width over the posterior tuberosities; the poorly expressed (but eroded) anterior tuberosities reach the level of the small oval foramen. The bulla is oval and well inflated.

The premolars and the buccal walls of the molars are missing. The central valleys of the latter are simple, without extremely rounded pillars of the labial lobes as in derived bovines, and only small enamel spurs; the lingual lobes are angular, especially the protocone; there is a central enamel island, and a strong entostyle, Y-shaped on M3. The molars are large compared to the size of the skull.

Measurements of the skull and horn-cores are given in Table 4.

The only other bovine remains from Kollé are a few weathered tali.

Comparisons—The Bovini are relatively uncommon elements of the late Miocene and Pliocene African faunas. *Brabovus nanincisus* Gentry, 1987, from Laetoli, is a small species with *Cephalophus*-like horns totally unlike the Kollé bovine. *Pelorovis*, from the late Pliocene and Pleistocene of East and perhaps North Africa, has forward curving and/or extremely long horn-cores with an oval cross-section, and is also quite unlike the Kollé bovine. Other taxa form a complex group within which relationships are hard to decipher. Following the taxonomy of Gentry (2006), they include *Ugandax demissum* (Gentry, 1980), from the early Pliocene of Langebaanweg, perhaps also present in Uganda (Geraads & Thomas, 1994); *Ugandax coryndonae* Gentry, 2006, from the middle Pliocene of Hadar; *Ugandax*

gautieri Cooke & Coryndon, 1970, from Kazinga, Uganda, whose age is not precisely known but might be close to 5 Ma. (Pickford et al., 1993: 104); *Simatherium kohllarseni* Dietrich, 1941, from the middle Pliocene of Laetoli (Dietrich, 1942, 1950; Gentry, 1987) and perhaps also Koobi Fora (Harris, 1991); and *Simatherium shungurensense* Geraads, 1995, from the late Pliocene of Omo.

They have horn-cores that are usually massive but not very long (compared to skull size), are inserted above the back of the orbits or slightly behind them, are moderately to strongly inclined in side view, but never horizontally (dorso-ventral crushing probably increased their inclination in the holotype skull of *S. shungurensense*), and are more divergent than in most antelopes, but never extremely so, and the divergence lessens distally. They are not much compressed medio-laterally (i.e., dorso-ventrally if very divergent), with a cross-section which is not neatly triangular, because the three faces are usually convex, but they may have a more or less marked anterior keel, and the position of the primitive postero-lateral keel may sometimes be discerned. According to the results of Gentry's cladogram (2006), a shift in the position of the postero-lateral keel towards a more anterior position would characterize *Syncerus* which includes, besides the living African buffaloes (*S. caffer*), *Syncerus acoelotus* Gentry & Gentry, 1978, from Olduvai, a *Syncerus* sp. from Omo Shungura Mb. C (Gentry, 1985), and, to remain monophyletic, both species of *Simatherium*. Although one might argue about the robustness of such parsimony analyses (see Geraads, 1992 and Geraads, 1995 for alternative results), it is clear that none of the species referred to *Simatherium* or *Ugandax* has horn-cores as divergent as the Kollé form. Since the Kollé faunal assemblages are of early Pliocene age, comparisons can be made primarily with the Uganda Nkondo faunas and the late Miocene Middle Awash faunas (Haile-Selassie, 2001). A skull fragment from Nkondo, referred to *Simatherium* aff. *demissum* by Geraads & Thomas (1994) has an almost flat dorsal profile, and horn-cores which were less divergent. In the Middle Awash, horn-cores fragments from Asa Koma and Kabanawa, dated to ca. 5.5 Ma, were also more uprightly inserted (Haile-Selassie, 2001, Fig.5.37) than at Kollé. The same is true at least of the most complete of the Lothagam specimens, KNM-LT 23724. An unpublished relatively complete skull from

Lissasfa, Morocco, well-dated to ca. 5.5 to 6 Ma. (Raynal et al., 1999), also displays horn-cores which are only moderately divergent and inclined. Last, the poorly known bovine from Toros-Menalla has a long braincase and moderately divergent horn-cores, and is also very different from the Kollé one.

The teeth of the Kollé bovine are larger than those from Lukeino (Thomas, 1980, fig. 1.3) and the entostyle is stronger; they differ by the same characters from those of Toros-Menalla. They are also more modern-looking than the very primitive teeth of *S. demissum* of Langebaanweg, but not than those of the Lothagam bovine, which are quite advanced, in spite of their early age.

The modern *Syncerus* is represented today by a wide morphocline ranging from the large South-African Cape buffalo to the small forest buffalo of Central Africa. The former has large horns emerging from frontal bosses that can be huge in the males, and are directed transversally at the base but with a strong downward curvature. The latter has smaller horns without frontal bosses and without downward curvature, but they are less divergent, being directed backwards as well as laterally. Fossil *Syncerus acoelotus* from Olduvai (Gentry and Gentry, 1978) and Omo (Gentry, 1985) are as large as the Cape buffalo, but their horn-cores lack the downward curvature, although they are more divergent than those of the forest buffaloes, but they are curved backwards, unlike those of *Jamous*. Their cross-section is variable (Gentry, 2006, fig. 7) but may be similar to that of *Jamous*. Nothing in the descriptions of Gentry and Gentry (1978) and Gentry (1985) suggests that the parieto-occipital area resembled that of *Jamous*. We have not seen the holotype of *S. acoelotus*, but its dorsal view (Gentry and Gentry, 1978, pl. 2) shows that, as in modern *Syncerus*, the horns were close to the occipital, and that the frontal is convex; the best specimen from Omo (National Museum of Ethiopia, Addis Ababa, L-607-1), has the parietal and the very low occipital at right angle to each other, and separated by a sharp nuchal crest; both specimens are therefore very different from *Jamous*. The middle to late Pleistocene "*Pelorovis antiquus*" has still larger horns that are even directed forwards at the base before curving backwards. All these buffaloes differ from *Jamous* by a number of features: 1) their horn-cores are inserted more posteriorly, their anterior border being always more posterior than the orbit; 2) although there is some

intraspecific variation (Gentry, 2006, fig. 7); the horn-core cross-section is more triangular, notably with a posterior keel probably secondarily sharpened; in *Jamous* the posterior border is rounded; 3) the horn-cores have at least a moderate curvature backwards; the weakest curvature is found in *Pelorovis kaisensis* Geraads & Thomas, 1994, but the very long horn-cores of this poorly known species have a completely different cross section; 4) in connection with 1), the fronto-parietal area is much shortened behind the horn-cores, and the supra-occipital is no longer part of the cranial roof, having been pushed back into the occipital plane. Thus, all African buffaloes are clearly more derived than *Jamous* in their cranial morphology.

It is instead in some Eurasian bovines that we can find a parieto-occipital morphology reminiscent of *Jamous*. In *Proamphibos* from the Tatrot zone of the Upper Siwaliks (Pilgrim, 1939, fig. 30, pl. 5, fig. 3-4), a modest ridge runs between the closely approaching temporal fossae in front of the suture between the parietal and the supra-occipital, but these bones are in the same plane. In *Parabos cordieri* from the Pliocene of France, the supra-occipital is slightly deflected towards the occipital plane, but there is no transverse ridge. *Leptobos* is known from both Europe and the Siwaliks; the supra-occipital is oriented as in *Jamous*, but is much smaller, being both shorter antero-posteriorly between the transverse ridge and the nuchal crest, and narrower because the temporal lines approach closely above the occipital plane (in "*Epileptobos*" from Java, fusion of these structures produces an occipital "chignon"). The subcircular cross-section of the horn-cores in *Leptobos* and several cranial characters rule out any close relationship between *Leptobos* and *Jamous*, but they are at a similar stage of reorganization of the neurocranium, marked by the beginning of parietal shortening and deflection of the supra-occipital into a more vertical plane, together with thickening of the cranial roof at the limit between these bones.

Three incomplete skulls from Sahabi were described as *Leptobos syrticus* by Petrocchi (1956) and, from the description and figures, photos kindly provided by M. R. Palombo and direct examination of one of Petrocchi's specimens, the parieto-occipital area is indeed similar to that of *Leptobos*.

Compared with Kollé, the horn-cores are longer, slightly less divergent, curved backwards and upwards instead of being almost straight, with a more definite antero-dorsal keel, the supra-orbital foramina are less wide apart, the temporal fossae are closer to each other, but the most conspicuous differences are the smaller supra-occipital without a strong transverse ridge, and the fronto-parietal sagittal profile less arched antero-posteriorly. Still, the Sahabi bovine might be the form closest to the Kollé one. All known material of *Leptobos syrticus* was collected by the Italian parties in 1934-1939, and nothing is known of its stratigraphic origin, but the absence of this species among the material collected by the American-Libyan team (Lehmann and Thomas, 1987) suggests that it might originate from different strata than those worked out by the latter group.

Sub-family HIPPOTRAGINAE Sundevall in Retzius and Lovén, 1845

Tribe HIPPOTRAGINI Sundevall in Retzius and Lovén, 1845

Genus *TCHADOTRAGUS* Geraads et al., 2008

TCHADOTRAGUS cf. *FANONEI*

Description—KL2-98-135 is a frontlet with virtually complete horn-cores, but so crushed that very few characters are visible. The crushed left pedicle suggests that it was hollowed; the horn-cores are upright, long (about 300 mm along anterior curve), without keels or ridges, transversely compressed, with a backward curvature which regularly increases upwards, and there is no more than a shallow post-cornual fossa. This frontlet is certainly hippotragine. The curvature is distinct from what is typical in *Tchadotragus*, where there is normally a rather straight terminal portion, but is similar to that of some terminal portions from KB, mentioned above. Specific identification is likely, but more specimens are needed before we can say whether the variability is the same as at KB, or if only one of the KB morphs is present at KL.

Tribe ALCELAPHINI Brooke in Wallace, 1876

Alcelaphini gen. et sp. indet.

Material—KL11-98-012, strongly weathered braincase with base of right horn-core.

Description and Comparisons—The parieto-occipital angle is obtuse, and there is a small indication of a parietal boss. The horn-core is inserted almost vertically, its posterior edge making an angle of about 120° with the top of the long braincase, it has a slight forward curvature, a large sinus in the pedicel, and its cross-section is roughly circular (basal diameters ca.40 x 40), with a hint of a postero-lateral keel. This latter character is unlike alcelaphines, but the others do not fit any other tribe. The very upright horn-cores and small parietal boss suggest affinities with *Damalacra* from the Miocene or early Pliocene of Langebaanweg (Gentry, 1980), Sahabi (Lehmann and Thomas, 1987), Manonga (Gentry, 1997), Kanapoi (Harris et al., 2003) and Lothagam (Harris, 2003). It is by no means certain, however, that all these early forms really belong to the same genus.

Sub-family indet.

Tribe REDUNCINI Knottnerus-Meyer, 1907

Genus *KOBUS* A. Smith, 1840

KOBUS cf. *AMMOLOPHI*

cf. *Kobus* sp. in Brunet et al., 1998

Material—Twelve horn-cores, mostly incomplete and weathered, plus a few teeth and postcranials.

Description—KL3-98-003 (basal diameters: 36.5 x 28.3 mm) and KL3-98-004 (35 x 28.5 mm, L = 227 mm) are the best horn-cores, probably not of the same individual. They are similar to those from KB and probably of the same species; the flattening of the lateral side and tendency towards a postero-lateral keel are better marked, but this is not true of all specimens from KL. KL20-98-008 (38.5 x 35 mm) and KL11-98-025 (40 x 34.8 mm) are two basal fragments of large size, almost lacking basal compression, but otherwise similar; we tentatively include them in the same species.

KOBUS cf. *KOROTORENSIS* Geraads et al., 2001 ?

Description—KL2-98-101 is a poorly preserved basal fragment, similar to the few specimens from KB described above under this name, but it is not fully certain that it is not merely a weathered specimen of the previous species. We refer to the same species an m3, KL2-98-035 (mid-height length = 22.3 mm), with an ectostylid weaker than at KB, and a few isolated teeth, also from KL2. Some post-cranials cannot be identified to species, as both are not very different in size; a complete but crushed metacarpal KL2-98-123 has the following dimensions:

Length = 227 mm; min. width of shaft = 20 mm; distal width = 28.7 mm

Subfamily ANTILOPINAE Gray, 1821

Tribe ANTILOPINI Gray, 1821

Genus *GAZELLA* Blainville, 1816

GAZELLA sp.

Description—A calcaneus, KL2-98-136, is of the right size for Antilopini, and must be of a large *Gazella* (max. length = 60.5 mm).

CONCLUSIONS

The distribution of Bovidae in the Djurab sites is shown in Table 5 (the list for Toros-Menalla is currently being revised).

The two bovid assemblages with the greatest similarities are KB and KL. They probably share *Tchadotragus fanonei* and the same two species of *Kobus*. Remains of the other bovids are too incomplete in one or the other site to be certain about their differences. The bovids do not even provide clear evidence that KL is younger than KB. *Tchadotragus* and *Kobus ammolphii* are the main positive

similarities with the TM sites (although the latter might include more than one *Kobus* species), and these similarities may extend to the Antilopini, currently under study. However, a noticeable difference is the disappearance of *Saheloryx*, a common form at TM. *Jamous* from KL is quite distinct from the TM Bovini, and the rare Boselaphini of TM went extinct before KB.

Fara et al. (2005) have shown that the ecological structure of the faunal assemblages underwent no major changes from KB to KT, and figure 2 of Zazzo et al. (2000) does not indicate any major change in the C3/C4 proportion in the diet of each bovid tribe (even though, on the whole, there are more grazers in the KT faunal assemblage). What does change, however, is the proportion of the various tribes (as estimated by the number of horn-cores); figure 5 shows that in this respect KB is more different from KL than it is from TM, as though *Tchadotragus* had replaced the now extinct *Saheloryx*, before all hippotragines become rare. The KT assemblage differs markedly from the TM-KB-KL ones in that 1) it includes almost no hippotragines, 2) it has a large species of *Kobus* which is rather common, 3) it has abundant alcelaphines, quite rare in earlier sites, and 4) it has a number of antilopines (most of the "Others" in figure 6) that were less common at TM and quite rare at KB-KL.

In comparison with East Africa, the most noticeable absence in all these sites is that of the Tragelaphini, of which not a single fossil has been found, and the scarcity of *Aepyceros*, a very successful genus further East. It should be noted that a similar situation is found in the only rich (but significantly younger) Pliocene site of North Africa, Ahl al Oughlam (Geraads and Amani, 1998), which has no *Aepyceros* and very rare tragelaphines. We may suspect that this is linked with lighter tree cover in central and north-west Africa. Studies in progress on Chadian paleoecology might tell us more about these differences.

However, similarities with North Africa extend beyond the resemblances in tribal composition that reflect ecological conditions, because it is with the Libyan site of Sahabi, rather than with East African ones, that some of the TM, KB and KL bovids compare best, suggesting that some lineages may be endemic to this part of Africa. Indeed, Chadian bovid assemblages have a significant endemic

component that suggests that longitudinal exchanges were restricted, at least in the latest Miocene and early Pliocene.

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Captions to figures

FIGURE 1. **A-D**: *Tchadotragus fanonei*; **A**, distal view of left tibia KB3-97-200; the arrow points to the medially shifted anterior fibular facet; **B**, KB3-98-146, holotype, lateral view; **C-D**, KB3-97-200, lateral and anterior views of frontlet; **E-H**: *Kobus ammolophi*, KB3-97-154, holotype, in **E**, dorsal, **F**, anterior, **G**, lateral, and **H**, occipital views. Scale bar equals 20 cm for **C-D**, 10 cm for **A**, 15 cm for all others. [planned for page width]

FIGURE 2. Cross-sections of horn-cores at base, all shown as if from the right side; anterior side to the top of the page, lateral side to the right, except for **E**. **A-C**: *Tchadotragus fanonei*; **A**, KB3-97-200; **B**, KB3-96-056; **C**, KB4-97-151. **D**, *Aepyceros* sp., KB3-97-361. **E**, *Jamous kolleensis*, KL3-96-013; **F-G**: *Kobus ammolophi*; **F**, KB3-97-154; **G**, KB4-97-087. Scale bar = 5 cm. [planned for column width]

FIGURE 3. **A**, *Tchadotragus fanonei*, lower tooth-row KB3-97-200. **B-C**: *Kobus ammolophi*; **B**, upper tooth-row P2-M3 KB7-97-098; **C**, lower tooth-row p4-m3 KB7-97-088. Scale bar equals 4 cm for **A**, 3 cm for **B-C**. [planned for column width]

FIGURE 4. *Jamous kolleensis*, holotype KL3-96-013, in **A**, lateral, **B**, posterior, **C**, dorsal, **D**, ventral, and **E**, oblique postero-dorsal views. Detached horns-cores missing on **A** and **D**. Scale bar equals 20 cm. [planned for page width]

FIGURE 5. Proportion of horn-cores of the various tribes in the Djurab assemblages. "Others" includes Bovini, Antilopini, and *Aepyceros*. [planned for column width]