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NEW HIPPOTRAGINI (BOVIDAE, MAMMALIA) FROM THE LATE MIOCENE OF
TOROS-MENALLA (CHAD)

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RH: GERAADS ET AL.—HIPPOTRAGINI FROM THE LATE MIOCENE OF CHAD

ABSTRACT—Until now, the pre-Pleistocene record of the bovid tribe Hippotragini was rather poor. We describe here two new taxa from the late Miocene of Toros-Menalla in northern Chad, which yielded the earliest known hominid, *Sahelanthropus tchadensis*. *Tchadotragus sudrei* n.gen. n.sp. is known by complete skulls and numerous horn-cores. It has typical hippotragine features such as long slender, curved horn-cores, weak cranial flexure, large frontal sinus, and hippotragine-like dentition, and is here taken as a basal member of the tribe, branching before the divergence between *Oryx-Praedamalis* and *Hippotragus* s.l. *Saheloryx solidus* n.gen. n.sp. is less well-known; it differs mainly by the lack of sinus in the frontal and horn-cores, shorter horn-cores, and rounded brain-case, but it shares with *Tchadotragus* a large number of features that prompt us to classify it also at the base of the hippotragine tree, perhaps as the sister-taxon of *Tchadotragus*.

No other African taxon looks like *Saheloryx*, and the only one similar to *Tchadotragus* is from Sahabi, Libya. The abundance of hippotragines sharply distinguishes Toros-Menalla from the East African late Miocene bovid faunas.

INTRODUCTION

Since 1994, the "Mission Paléoanthropologique Franco-Tchadienne" has conducted paleontological field research in the Djurab region of Northern Chad, leading to the discovery of over 500 fossil vertebrate localities, most of them ranging in age from the late Miocene to the lower Pliocene, that help filling a wide geographic gap in the African fossil record. The major fossiliferous areas are Koro-Toro, with middle Pliocene strata (age estimated by biochronology at 3–3.5 Ma), which yielded the first australopithecines West of the Rift (Brunet et al., 1995, 1996), Kollé (Brunet et al., 1998), lower Pliocene (age estimated by biochronology at 4–4.5Ma), Kossom Bougoudi (Brunet and M.P.F.T., 2000), with Mio- Pliocene boundary faunas (age estimated by biochronology at ca.5.5Ma), and Toros-Menalla, which yielded the earliest known hominid (Brunet et al., 2002), of late Miocene age, ca.7 Ma (Vignaud et al., 2002; Brunet et al., 2005).

In all these deposits, the Bovidae constitute a large proportion of the faunal remains, as in other African sites of this time-period. Those from Koro-Toro have been described previously (Geraads et al., 2001). Here we describe two new taxa, ascribed to the tribe Hippotragini, from several localities of the anthracotheriid unit of Toros-Menalla (TM) (Vignaud et al., 2002), including TM266, type-locality of *Sahelanthropus tchadensis*. Other bovids, which include bovines, rare boselaphines, *Aepyceros*, gazelles, and numerous reduncines, will be described later. Extensive sand-dunes prevent direct stratigraphic correlation between localities, but their homogeneous faunal contents suggest that all localities are roughly contemporaneous; further research is in progress to refine their precise stratigraphic correlation. All specimens belong to the "Département des Collections" of the Centre National d'Appui à la Recherche (CNAR), N'Djamena, Chad.

SYSTEMATIC PALAEOLOGY

Family BOVIDAE Gray, 1821

Sub-family HIPPOTRAGINAE Sundevall in Retzius and Lovén, 1845 (see Grubb, 2001)

Tribe HIPPOTRAGINI Sundevall in Retzius and Lovén, 1845

Genus *TCHADOTRAGUS* nov. gen.

Type-species—*Tchadotragus sudrei* nov.sp.

Diagnosis—That of the type and only species.

Derivatio nominis—from Tchad-, French name for Chad, and -tragus (Greek τράγος, goat), a name frequently used for bovids.

Tchadotragus sudrei nov. sp.

Holotype—TM12-97-23, virtually complete skull, but lacking the premaxillae, right nasal, zygomatic arches, and most of the auditory region (Fig. 1–2).

Diagnosis—A primitive hippotragine of medium size, with a braincase slightly inclined on the splanchnocranium and broad over the mastoids, both halves of occipital surface facing partly laterally, a basioccipital with strong anterior tuberosities not reaching the level of the foramen ovale, large orbits with very prominent rims, a short face with a small jugal and a short and deep lacrymal bone, a large diffuse ante-orbital 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.

Derivatio nominis—In honour of our colleague and friend Dr Jean Sudre (EPHE, Montpellier), who found the holotype.

Material—There are about 85 horn-cores and skull pieces of *T. sudrei*. Among the ca. 450 mandibular and maxillary pieces that are assignable either to the same species or to the other taxon described below, only the mandibles TM266-01-177 and TM301-02-01 are definitely of *T. sudrei*, as they are associated with horn-cores. The identification of other specimens is discussed further down.

Description of the holotype—The cranium is almost complete except for the right nasal and both premaxillae. During fossilization, the maxilla was shifted upwards, and slightly rotated, crushing the jugal and lachrymal areas. All these bones were therefore cleaned and separated, and the facial part of the cranium reconstructed. Some imperfections remain, but the present condition and especially the relationship of the neurocranium and splanchnocranium are certainly very close to the real ones.

The skull is of medium size (Tab. 1), comparable to those of *Gazella granti* or *Kobus kob*. Its most noticeable feature is the length and slenderness of the horn-cores which are curved backwards, more strongly so in the middle part, but with a distal part that is even very slightly curved upwards. They are inserted above the orbits, not very far apart, and situated upright (the angle between their posterior border and the skull roof is greater than 90°). The divergence is weak at the base but increases upwards to decrease again near the tip; thus they have a weak but distinct graceful torsion. There is no hint of a keel or of transverse ridges. The cross section of each horn-core is moderately compressed (Tab. 1–2; Fig. 1F), with some flattening of the lateral surface, and the maximum transverse diameter is situated posteriorly; thus, the shape of the cross-section is that of a rounded triangle. Its main antero-posterior axis is oblique in respect to the sagittal plane.

The face is moderately bent on the cranial axis, the fronto-nasal profile being inclined at an angle of 130° on the parietal one. In lateral view, the base of the occipital condyles is approximately at the same level as the tooth-row. A short length of the suture of the premaxilla with the maxilla is preserved; it shows that a wide gap separated the former bone from the nasals, of which only the narrow posterior part of the left one is preserved. There is an extensive ante-orbital fossa, but none of its limits is clear. The infra-orbital foramen is located high above P3. The lacrymal bone is large and deep (Fig. 2). There is a rather small and narrow ethmoidal vacuity, but it is larger than in modern hippotragines and free from bone internally. The contribution of the maxilla to its anterior border must have been very limited, as the large lacrymal bone certainly came very close to the nasal at this point. The jugal has no great extension on the face. The orbits are large, and their rims are extremely salient, giving them an almost tubular shape. Between them, no depression surrounds the supraorbital foramina, and the frontals are rather flat; they are not elevated between the horn-cores. Both the inter-frontal and fronto-parietal sutures form slightly elevated rims, and are almost fused, although the animal was not very old. The elongate post-cornual fossa is faint and shallow. The braincase is long, with a flat top surface; its width increases posteriorly, and the skull is broad at the post-tympanic level (Tab. 1). The temporal crests are well-marked and approach rather closely posteriorly, so that the supraoccipital is not broader than long. The parietal is long, as it reaches the nuchal crest, and might even have had a very short contact with the mastoid; its central part is slightly raised in a V-shaped structure, also present in some other bovids, which Morales et al. (2003) thought to be a remnant of the ancestral sagittal crest. The area of insertion of the M. temporalis is long and trapezoidal. The top of the occipital has the shape of an inverted V; below it, the two halves of this bone belong to two different planes facing laterally as well as posteriorly, but their meeting line in the sagittal plane does not form a crest. The paroccipital processes are flattened, slightly

curved medially, and directed posteriorly. The mastoid exposure is broad, but remains wholly behind the nuchal crest, mostly in the occipital plane, because the auditory region is antero-posteriorly short. The basioccipital has a long sagittal groove; the posterior tuberosities are quite strong; the anterior ones are long, but remain more posterior than the foramen ovale. The postglenoid foramen is large. The bulla is missing, and the petrous bone is much eroded. In the palate, the palatines are of moderate length (they extend as far as the anterior lobe of M2), and the foramina open at their suture with the maxilla. The anterior border of the choanae is at the same level (posterior lobe of M2) as the lateral indentations.

The teeth are large relative to skull size, and are moderately worn. On the lateral walls, the styles are moderately prominent; the ribs are pronounced and rounded. The molars are broad relative to their length; they have a central enamel island and an entostyle arising from the cingulum, connected to the rest of the occlusal surface on M1. The central valleys lack accessory spurs. The protocone is slightly pinched, at least on M2.

Referred specimens—*Tchadotragus sudrei* is the most common bovid at Toros-Menalla, but it would be superfluous to describe in detail the other specimens, none of which is as well preserved as the holotype. However, skull TM58-98-02, although slightly crushed transversely, is more complete, as it preserves part of the premaxillae, well-separated from the nasals, and the auditory bulla, large but narrow, probably not as an effect of crushing. The chief interest of the other specimens is to confirm the features of the holotype. Some variation occurs in the horn-cores, which can be slightly more divergent (e.g., TM38-98-01), straighter (e.g., TM100-00-01), or have faint transverse ridges (TM251-01-01). The amount of flattening also varies; the outline of the cross-section may be either more rounded, or the posterior face may be less rounded than the medial and lateral faces (in contrast to the type), or they can all be flattened, giving the cross-section a more triangular outline, but the degree of transverse compression is rather constant

(index between 0.66 and 0.90, mean 0.75), and slightly greater than in most modern *Hippotragus*. Broken horn-cores show that the pedicle is hollowed by an extensive sinus, usually undivided, extending about one cm into the base of the horn-core itself, and that antero-medial to it and the supraorbital canal, another sinus hollows the frontal bone. By their fully hollowed base and pedicle, horn-cores of *Tchadotragus* can easily be told from those of the next species, provided that the base is preserved.

Neither the distribution of the antero-posterior dimension nor that of the transverse one are significantly different from normal distributions (Shapiro-Wilk tests: resp. $W = 0.980$, $p = 0.49$ and $W = 0.987$, $p = 0.83$, $N = 55$), but the antero-posterior dimension displays a shortfall of values around the mean, suggesting that a weak sexual dimorphism might have been present, as in modern hippotragines (Klein, 1974). The lack of hornless skull supports this hypothesis, but only weakly, as hornless bovid skulls are extremely rare in the whole bovid collection from TM.

Teeth—There are a number of tooth-rows of the appropriate size to belong to *Tchadotragus sudrei*, but their detailed morphology is often obscured by breakage or weathering. Furthermore, despite careful attempts, it has proven impossible to tell their teeth apart from those of the next species, which can be expected to be slightly larger. The only associated set of upper and lower teeth is TM266-01-131 (from the *Sahelanthropus* site), that we assign to *Tchadotragus sudrei* because the morphology of the upper teeth closely matches that of the holotype. The lower premolars (Fig. 4F) are rather short, the paraconid is weak, the metaconid is slanting distally on p3 but transverse on p4, the talonid of which is short and separated by a deep labial groove from the trigonid. The lower molars have a moderate ectostylid, no goat fold, the labial lobes are slightly pinched, and the third lobe of m3 is labially offset. Less worn specimens (e.g., Fig. 4G) show that the teeth are hypsodont (m3 is as high as it is long), with rounded or even blunt cusps, but with high relief, and that the metaconid of p4 is mesially shifted. The paraconid may be

stronger and distinct from the parastylid in the middle and upper part of the crowns of p3 and p4, and there may be an incipient goat fold, at least on m1, but there is no clear association of these features that would allow to separate the two taxa. Table 3 shows that the larger specimens (TM153-01-10 and TM297-01-04) had relatively shorter premolars, and one might hypothesize that this reflects a taxonomic distinction, but from their molar lengths (71 and 75 mm), the two specimens that are definitely of *Tchadotragus* (see **Material**) would then be assigned to different species. More specimens with their complete set of cheek-teeth are needed before both taxa can be told apart from their teeth.

Comparisons—There is no doubt that *Tchadotragus* belongs to the Hippotragini, as it shares a number of similarities with living members of this tribe: (1) a skull moderately bent on the facial axis; (2) horn-cores long, without keels, little or no flattening of the lateral or medial surfaces, usually without transverse ridges; (3) an ethmoidal fissure smaller than in most Reduncini, Tragelaphini or Antilopini; (4) high infra-orbital foramina; (5) hollowed frontals; (6) a small shallow post-cornual fossa; (7) a parietal reaching the nuchal crest, and perhaps contacting the mastoid; (8) a low and wide occipital; (9) a mastoid facing mostly posteriorly, even in its lower part; and (10) a basioccipital with strong anterior and posterior tuberosities, with a groove between them.

The tribe Hippotragini has a poor fossil record, besides the Pleistocene *H. gigas*, best known from East Africa (Gentry and Gentry, 1978; Harris, 1991), but also reported from Algeria (Geraads, 1981) and South Africa (Gentry and Gentry, 1978; Klein and Cruz-Urbe, 1991).

Hippotragus gigas is more primitive than living *Hippotragus* by its tooth morphology, but the premolars are very short, there are large goat folds, and it further differs from *Tchadotragus* by its larger size, less upright horn-cores, and base of horn-core higher above the upper orbital rim; the

facial characters are unknown. *Hippotragus cookei* Vrba, 1987, is a poorly known form, reported only from Makapansgat.

A horn-core from the late Miocene or earliest Pliocene of Sahabi, Libya, was referred to ?*Hippotragus* sp. by Lehmann and Thomas (1987). It is long and slender, but slightly less uprightly inserted than those from Chad. The backward curvature is also perhaps stronger than the average at Toros-Menalla, but it would certainly have been referred to *T. sudrei* if found there. Although more material from Sahabi would be welcome, we believe that this horn-core definitely documents *Tchadotragus* from Libya, confirming this biogeographic connection (Lihoreau et al., 2006).

No hippotragine is known from Lukeino and Mpesida (Thomas, 1980). From Lothagam, Harris (2003) reported a *Hippotragus* sp. which differs from all other species of this genus, and from *Tchadotragus*, by the low insertion of its horn-cores, but the material is poor, and the identification is debatable. In any case, hippotragines are quite rare at Lothagam, in sharp contrast to Toros-Menalla.

From Kanapoi, Harris et al. (2003) described as Hippotragini gen. indet. a horn-core fragment (KNM-KP-30361) that could as well be reduncine; however, at least one mandibular fragment is certainly hippotragine, but this tribe is certainly rare, as at Lothagam.

The genus *Praedamalis* includes two species: *P. deturi* Dietrich, 1950, from Laetoli and Hadar, and *P. howelli* Vrba and Gatesy, 1994, from Maka in the Middle Awash. All these occurrences are in the 3–3.7 Ma time-range, but the genus has also been reported from Lothagam (Harris, 2003). *Praedamalis* has nearly straight horn-cores, which are less inclined than in *Oryx*, but more so than in *Hippotragus*, and well-marked goat folds: thus, it is sharply distinct from *Tchadotragus*.

From the Upper Siwaliks, Pilgrim (1939) erected the genus *Sivatragus* for his new species *S. bohlini*, added *S. brevicornis* as a second species, and included both of them in the Hippotragini. Gentry and Gentry (1978:352) suspected that the latter species "is not hippotragine at all". The type-frontlet has a very sharp fronto-parietal flexure, and the basal part of the horn-cores is swollen; both features remind of the Alcelaphini, and we believe that *S. brevicornis* fits better this tribe. *Sivatragus bohlini* resembles *Tchadotragus* by its braincase which is broad at the mastoid level and with strong temporal ridges, and by the prominent orbital rims. However, the braincase is shorter, its top surface is not flat, the occipital faces caudally (Pilgrim, 1939, pl. 2, fig. 3), the horn-cores are less upright, and their maximum width is less posterior. The face and most of the horn-cores being unknown, the comparisons cannot go much beyond this, but *S. bohlini* could be close to the ancestry of *Hippotragus*. Vrba and Gatesy (1994) even concluded from a parsimony analysis that it is more specifically related to the early Pleistocene *H. gigas*.

In the late Miocene of Europe, Asia, and North Africa, an array of antelopes centered on the genera *Protoryx* Major, 1891 and *Pachytragus* Schlosser, 1904 have some resemblance to *Tchadotragus*. Many authors (Solounias, 1981; Köhler, 1987; Bosscha Erdrink, 1988; Bouvrain, 1994, 1997) considered *Pachytragus* as synonymous with *Protoryx*, and often linked them with the Hippotragini. Gentry, instead, repeatedly (1971, 2000, 2003; Gentry et al., 1999) insisted on their generic distinction, and on the caprine affinities of *Pachytragus*. Indeed, *Tchadotragus*, which is contemporaneous with the last representatives of *Pachytragus*, is a much better candidate for hippotragine ancestry. The following set of features shared by *Pachytragus* and modern hippotragines are also present in *Tchadotragus*; they are therefore clearly primitive for the whole group, and of no help to support exclusive *Pachytragus*-Hippotragini relationships: (1) some inclination of the face on the cranium; (2) a long braincase; (3) a small, shallow post-cornual fossa; (4) wide posterior and strong anterior tuberosities on the basioccipital, with a

longitudinal groove; and (5) pedicle and horn-core base hollowed by a large, dome-shaped, sinus. On the other hand, *Tchadotragus* has derived hippotragine features, absent in *Pachytragus*: (1) a braincase widening posteriorly; (2) long slender horn-cores; (3) rounded lingual walls on lower molars and labial walls on upper molars; (4) large entostyles and ectostylids; and (5) a bulbous metaconid on p4. By contrast, *Pachytragus* has several caprine features that are absent in *Tchadotragus*. They were discussed at length by Gentry (1971, 2000, 2003; Gentry et al., 1999); the tooth characters of *Pachytragus*, especially, are almost as different as possible from those of the hippotragines (very short premolars, weak or absent accessory columns, narrow styles and weak pillars on upper molars, flat labial walls of upper teeth and lingual walls of lower teeth). To these can be added (1) the tendency towards anterior keel development on the horn-core, never met in the Hippotragini, and (2) the strong bending of the face on the cranium, with a frontal between the horns which is much higher than the orbital rims; this occurs only in *H. niger* among the Hippotragini, and even in this species the base of the occipital condyle is not lower than the tooth-row.

The only feature shared by *Pachytragus* and *Hippotragus*, but not by *Tchadotragus*, is the central position of the maximum transverse diameter of the horn-core, although some *Hippotragus* also have a maximum diameter situated posteriorly. However, the triangular cross-section of most *Tchadotragus* horn-cores might be a secondary consequence of their being very long and curved, implying reinforcement of the posterior part. Thus, we do not believe that *Tchadotragus* is closely related to *Pachytragus*, nor that its ancestry should be searched in the Eastern Mediterranean.

In Africa, early forms are not well known, as the late Miocene African record is poor. Those referred to *Caprotragoides* Thenius, 1979, by Thomas (1981, 1984) were included by Azanza and Morales (1994) in their new genus *Gentrytragus*. *Gentrytragus gentryi* (Thomas,

1981), from Ngorora, Kenya, has a skull which is not unlike that of *Tchadotragus*, with horn-cores uprightly inserted, transversely compressed and curved backwards, a weak post-cornual fossa, a braincase broadening posteriorly and only slightly angled on the face, and rather hypsodont teeth and short premolars. However, some of these features are probably primitive, and *G. gentryi* differs from *Tchadotragus* in that its cranial basis is shorter, the orbit smaller and more anterior, the horn-cores are also more anterior, their pedicle is not hollowed, the upper teeth have flatter lingual walls and no entostyle, the p4 may be fully molarized and the lower molars are alcelaphine-like by their rounded outline, reduced ectostylid, and lack of goat-fold. These tooth characters bring it closer to caprines or alcelaphines than to hippotragines. From the earlier site of Fort Ternan, Kenya, *Gentrytragus thomasi* Azanza and Morales, 1994 (described as ? *Pseudotragus potwaricus* by Gentry, 1970) has a more primitive p4, but its aegodont teeth are also unlike those of *Tchadotragus* and the Hippotragini.

Genus *SAHELORYX* nov.gen.

Type-species—*Saheloryx solidus* nov.sp.

Diagnosis—That of the type and only species.

Derivatio nominis—from Sahel-, the semi-arid belt south of the Sahara, and -oryx, a living hippotragine.

Saheloryx solidus nov. sp.

Holotype—TM108-00-08, cranium with bases of horn-cores (Fig. 4A-E).

Diagnosis—An hippotragine of rather large size, with a low, broad braincase, rounded in antero-posterior and transverse directions, a low occipital surface facing mainly posteriorly, a basioccipital with anterior tuberosities reaching the level of the foramen ovale, horn-cores uprightly inserted and wide apart, slightly divergent and slightly curved backwards, without

transverse ridges, no sinus in frontal and horn-core pedicle, and supraorbital foramina in wide depressions, teeth similar to those of *Tchadotragus*.

Derivatio nominis—from Latin solidus, solid, not hollowed, because the horn-core bases are not pneumatized.

Material—About 75 horn-cores and skull pieces (measurements: Tab. 4), plus many mandibular and maxillary pieces.

Description—All crania are broken at the orbits, and the face is unknown, except for specimen TM38-98-02 showing a hint of shallow preorbital fossa. The horn-cores are inserted wide apart on a low pedicle, and are rather upright (in lateral view, the angle between their posterior border and the braincase is always close to 90°). They are moderately long, slightly divergent at the base and straight in anterior view, regularly and moderately curved in lateral view, without any twisting or spiraling, without keels or transverse ridges, but often with an antero-medial longitudinal groove. The cross-section is an almost regular oval, with slight lateral flattening (Fig. 4B); in contrast to *Tchadotragus*, it never tends to be triangular. Its long axis is not very oblique in respect to the sagittal plane, and the maximum transverse diameter is variable in position, but never very posterior.

The angle between the top of the braincase and the fronto-nasal line can be estimated at about 130°. The mid-frontal suture is raised as a low broad ridge. In profile, it is weakly convex antero-posteriorly between the horn-cores, but concave in its most anterior part. At this level, the frontal bone is deeply sunken on either side, antero-medially to the supraorbital foramina. The latter are large and open in triangular depressions. These last features are linked with the complete lack of sinuses, both in the frontal and pedicle. The orbital rims are moderately prominent. There is no post-cornual fossa, and no depression postero-medially to the horn-cores.

The mid-frontal suture is fairly thick, and never fuses. The parieto-frontal suture is complex and indented medially.

The braincase is low and wide, especially in the supra-auditory region, which is splayed out laterally. Its upper profile is rounded, and continues in a regular curve that of the frontal bone. The temporal crests are strong anteriorly, along the parieto-frontal suture, but vanish posteriorly; the area of insertion of the M. temporalis is short and rounded. The occipital is strongly inclined, low, and very wide. Both halves are almost in the same plane, although the sagittal part is raised. The mastoid exposure is large, and its lower part faces mostly laterally, because the auditory region is antero-posteriorly stretched. The auditory foramen is small, especially on the holotype. The paroccipital processes may be very strong, as on cranium TM229-01-13, and are directed posteriorly. The postglenoid foramen is large. The basioccipital has moderate to large anterior tuberosities that reach the level of the foramen ovale; the posterior ones are wide but they are not prominent ventrally, and there is no clear sagittal groove.

No hornless cranium is known and we take this as an indication of the females being horned, but sexual dimorphism must have been weak, as the plots of the basal diameters of the horn-cores (Fig. 3) are not significantly different from normal distributions (Shapiro-Wilk tests: antero-posterior $W = 0.981$, $p = 0.71$; transverse $W = 0.989$, $p = 0.95$, $N = 42$).

Comparisons—the main differences between these two bovid taxa of Toros-Menalla are summarized in Table 5.

These differences much exceed those between male and female of any other species of the Bovidae. In this family, the most obvious expression of sexual dimorphism, when present, lies in the horn-cores. In females, they are often absent or small; whenever they have a different morphology than those of the males (e.g., Antilopini), they are much smaller, whereas the difference here is in shape, not in size (Fig. 3). The frontal sinus may slightly differ between

males and females of some species (Schaffer and Reed, 1972; Farke, 2007) but it is never extensive in one gender and absent in the other. Sexual dimorphism may also affect horn supporting structures and some cranial measurements (Hooijer, 1958; Cooke, 1996; Puzachenko and Rautian, 2001; Massei et al., 1993) but the set of differences listed above has no equivalent in any fossil or modern species. Therefore, the hypothesis that *Saheloryx solidus* and *Tchadotragus sudrei* are two sexes of one and the same species can be definitely ruled out. These differences are even far greater than those between two species of the same genus, especially those involving the proportions of the braincase, pneumatization of the frontal and related features. The crania of both taxa reflect two different building designs that cannot be accommodated within a single genus. Such a coexistence of two or more closely related bovid taxa of similar size and similar abundance is not a rare occurrence both in the modern and fossil records. Among the former, we may mention the topi and kongoni in the Serengeti, two species of *Tragelaphus* in the Kruger Park, both species of *Hippotragus* in the Okavango delta, or two species of *Redunca* in the Umfolozi Park, etc.; among the latter, two Alcelaphini at Ternifine (Geraads, 1981), four Reduncini in area 103 of the KBS Member of the Koobi Fora Formation (Harris, 1991), or four Alcelaphini at Olduvai BK II (Gentry and Gentry, 1978).

Among African tribes of large bovids, only the Reduncini and Tragelaphini normally have solid frontals and horn-core pedicels; *Saheloryx* is otherwise so different from the Tragelaphini that no detailed comparison is necessary, but a relationship with the Reduncini is less unlikely. It shares with members of this tribe: (1) a low and broad braincase, as in the large members of the genus *Kobus*; (2) the lack of sinus in the frontal and pedicle; and (3) the opening of the supraorbital foramen in depressions of the frontal. It differs by: (1) the probable presence of horns in females, whereas they are always absent in female reduncines; (2) the very upright insertion of the horn-cores, their weak divergence, and the lack of post cornual fossa; the lack of transverse

ridges is also unlike most reduncines; (3) the moderate size of the anterior tuberosities of the basioccipital; and (4) the lack of derived reduncine features on the teeth, such as prominent pillars, pinching of the lobes, strong goat folds and entostyles/ectostylids, which are all quite clear, by contrast, in the Toros-Menalla reduncines. Thus, *Saheloryx* cannot be included in the Reduncini.

No bovid from Lothagam or Kanapoi resembles *Saheloryx*, but a comparison can be sought more to the North. *Damalavus boroccoi* Arambourg, 1959 is based upon a poorly preserved frontlet from the early late Miocene of Algeria; some of the few available features (short, much inclined horn-cores; narrow frontal) are quite unlike the Toros-Menalla hippotragines.

The Eurasian *Palaeoryx* Gaudry, 1861 (Gentry, 1970), mainly known from Turolian sites, is contemporaneous with, or slightly older than, Toros-Menalla. The main resemblances between *Saheloryx* and *Palaeoryx* are: (1) the general shape of the horn-cores; (2) the low and wide cranium, rounded dorsally; and (3) the slanting occipital, with both halves nearly in the same plane. However, the horn-cores of *Saheloryx* are relatively smaller, more upright, and more compressed. Another difference is the lack of frontal hollowing in the Chadian form, hence large sunken supraorbital pits. Upper teeth do not differ much, but those of *Palaeoryx* have definitely less rounded labial pillars. Its lower teeth are not known with certainty, but most of the largest dentitions from Pikermi and Samos in Greece probably belong to this genus (some others might be of *Samokeros*, as suggested by Solounias, 1981). Their teeth are broad relative to their length, they have more flattened lingual walls, there is no hint of a goat fold, the ectostylid is weak or absent, the p4 does not look antero-posteriorly compressed and the metaconid has an anteriorly directed flange that may even close the median valley. All these differences show that *Saheloryx* is not closely related to *Palaeoryx*.

Pseudotragus capricornis Schlosser, 1904, from Samos, is a poorly known species, and the only known braincase (Schlosser, 1904, pl. 10, fig. 8) was apparently destroyed (Solounias, 1981:206). Both the female and very large male horn-cores are significantly more compressed than those of *Saheloryx*, and the supraorbital foramina open into narrow grooves. The teeth are similar to those of *Palaeoryx*, and the p4 further differs from those of *Saheloryx* by its shallow labial groove. Thus, just as for *Tchadotragus*, no bovid of the well-known Aegean late Miocene looks close to *Saheloryx*.

Hippotragine Postcranials

Many postcranial bones have been recovered from TM, some of them complete, but the similar size and probable close relations between the two common large species renders definite identifications impossible.

Humerus—Two types can be distinguished among the larger forms. In one, the distal articulation is conical, with the diameter of the lateral condyle much smaller than that of the medial part of the trochlea, which is somewhat rounded. This type resembles modern reduncines (and cervids), but it clearly belongs here either to *Tchadotragus* or to *Saheloryx*. In a second type, the distal articulation is more cylindrical, with the diameter of the lateral condyle not much smaller than that of the medial part of the trochlea. This type looks more what is found in modern alcelaphines and hippotragines, but the distal border of the lateral epicondyle is less oblique, the cylindrical shape is less clear than in hippotragines, and the lateral ridge caudal to the insertion of the extensor of the lateral digit is less caudal than in alcelaphines (see Peters et al., 1997, pl.6-7).

Radius—The lengths of three specimens can be estimated with reasonable precision. These are TM153-01-03 (length ca. 320), TM153-01-09 (length ca. 325) and TM55-98-04 (length = 290). These values are not much smaller than those of two complete tibias and, unless all radii

are from a different species than all tibiae, they imply that at least one of the larger TM forms had high forequarters.

Tibia—At the distal end, the median beak of the largest specimens is narrow, as in modern reduncines and hippotragines, and the cranial fibular facet is medially offset, a feature today known only in hippotragines (Peters et al., 1997, pl.16, character 73), but also present at Koro Toro in some other tribe (Geraads et al., 2001).

Calcaneus—The sustentaculum tali is weaker than in all modern African bovids, except alcelaphines, with its plantar border more cranial than that of the main part of the bone.

Metatarsus—The distal pulleys are not splayed out laterally, in contrast to modern alcelaphines and hippotragines. Non-tragelaphine African bovids are not otherwise very different for this bone.

On the whole, the relative lengths of the preserved bones (radius slightly longer than metatarsus, and not much shorter than tibia) best match those of *Oryx* among modern forms, but the similar size of the two taxa, and their similar frequency, as deduced from the horn-cores, imply that both were represented among the postcranial remains. This is confirmed by the co-occurrence of two different types of humeri, which also suggests that *Tchadotragus* and *Saheloryx* had somewhat different locomotory adaptations, but it is unlikely that the two genera had very different limb proportions.

RELATIONSHIPS

Based on the dataset of Vrba and Gatesy (1994), we assessed the relationships of *Tchadotragus* and *Saheloryx* with other Hippotragini by parsimony analysis (using an exhaustive search with Hennig86, command "ie"). We converted their qualitative estimates of the character

states (e.g., "low", "high") into quantified ones, so as to keep, as far as possible, the same character states.

We made only a few changes to their data matrix, which includes an outgroup with hypothetical ancestral states (Tab. 6). We removed the Lothagam hippotragines (except *Praedamalis*) from the analysis, because their status is unclear. Specimen KNM-LT-188, used by Vrba and Gatesy (1994), is now referred to *Aepyceros* (Harris, 2003); among the most hippotragine-like fossils, KNM-LT-13010 has a deep post-cornual fossa, whereas KNM-LT-23131 has none, and they must belong to different taxa. We also removed *Wellsiana* and *Brabovus*, as Vrba and Gatesy (1994) concluded that they are not hippotragine, and *Sivatragus brevicornis*, for the reasons given above. We removed their characters 4 (proportion of upper molars, because its estimate depends too much upon wear stage), and 6 (width of the premaxilla, because it is known in only very few terminals, and because the state in the outgroup is disputable), but we added seven more characters (numbers 24 to 30 in Tab. 6). Finally, we hypothesized that the angle of the face to braincase in the outgroup is low instead of high, which better conforms to the primitive condition in bovids.

The strict consensus tree (length = 59; ci = 66; ri = 81) of the 18 shortest trees (length = 58; ci = 67; ri = 82) shows *Praedamalis* + *Oryx* as the sister-group of *Hippotragus* + *Sivatragus*, a conclusion already reached by Vrba and Gatesy (1994), and *Saheloryx* + *Tchadotragus* as the sister-group of all others (Fig. 5, left). In a slightly longer tree that we favour (Fig. 5, right; length = 60; ci = 66; ri = 81), *Saheloryx* would be the sister-group of all other taxa, with *Tchadotragus* branching next, but probably not much later. The detailed lists of apomorphies supporting each clade are given in the caption to Fig. 5; the main ones, common to both trees, are as follows (character numbers in brackets). Node 1: metaconid of p4 bulbous (4); braincase more angled on the face (9); broader occipital (24); longer (21), larger (22), less compressed (15), and probably

more upright (19) horn-cores. Node **3**: goat-folds well developed on lower molars (26); longer face (30), with longer lachrymal bone (28), and a shallow or absent pre-orbital fossa (29), and perhaps an occipital facing caudally (27; parallel change in *Saheloryx*). Node **4**: supra-orbital foramina wider apart (7); straighter (16) and more caudal (17) horn-cores. Node **5**: horn-cores more divergent (23), with a less angled main axis of the cross-section (18), and perhaps an ethmoidal fissure blocked by bone (5). Node **7**: braincase less inclined on the face (9); very long horn-cores (21). Node **8**: horn-cores with strong backward curvature (16). Node **9**: braincase less inclined on the face (9), strong temporal lines (10, parallel change in *Tchadotragus* + *Saheloryx*). Node **10**: Y-shaped basal pillars (2); pinched medial lobes of upper molars (3); longer braincase (11).

Node **2** of the consensus tree is supported by strong temporal lines (10) and paroccipital processes slanting backwards (25), while Node **1'** of our preferred tree (Fig. 5, right) is supported by acquisition of the frontal sinus (8, which is thus non-homoplastic in this topology).

Both topologies are in good agreement with chronology. They also allow explaining the postcranial differences between the Chadian taxa and all modern hippotragines; if the latter form a monophyletic group not including the Miocene forms, their post-cranial characters may have been acquired recently, as was suggested at Koro-Toro for reduncines and alcelaphines (Geraads et al., 2001).

The cladograms presented here imply that the tribe Hippotragini is at least 7 Ma old, and we believe that it is not much older. By contrast, by calibrating their super-tree of the ruminants, Hernández Fernández and Vrba (2005) have estimated the age of divergence between *H. niger* and *H. equinus*-*H. leucophaeus* at 8.8 Ma, and that of the *Addax*-*Oryx* and *Hippotragus* groups at about 11 Ma. This would put the divergence of *Saheloryx* and *Tchadotragus* back into the Middle Miocene; however, no definite Hippotragini is known at that time, nor in the first part of the

Upper Miocene (Namurungule, Ngeringerowa, Nakali and Ngorora in Kenya; Bled Douarah and Jebel Krechem in Tunisia; Bou Hanifia and Oued Mya in Algeria). It would also imply a long ghost lineage leading to modern *Hippotragus*, as no definite *Hippotragus* is known in the Mio-Pliocene (Langebaanweg in South Africa; Manonga in Tanzania; Lukeino, Mpesida and Lothagam in Kenya; the Middle Awash in Ethiopia; Nkondo in Uganda; Toros-Menalla and Kossom Bougoudi in Chad). We believe that this long list of localities without Hippotragini or *Hippotragus* comprises a reasonable case for "absence of evidence". Correspondingly, we suggest that the dates proposed by Hernández Fernández and Vrba (2005) are over-estimated, perhaps by a factor of two.

At a higher taxonomic level, there is now a consensus that the Hippotragini are closely related to the Alcelaphini, the Caprinae branching next (Gentry, 1992; Vrba and Schaller, 2000; Kuznetsova et al., 2002; Ropiquet and Hassanin, 2004; Price et al., 2005; Hernández Fernández and Vrba, 2005). Therefore, there is little doubt that both tribes originated in Africa, and *Tchadotragus* shows what a primitive hippotragine looked like, at a time when *Pachytragus* had already diverged towards the Caprini, from the ancestral Caprinae-Alcelaphini-Hippotragini stock.

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Captions to figures

Figure 1. *Tchadotragus sudrei*, holotype skull, TM12-97-23. **A**: lateral view; **B**: dorsal view of the braincase; **C**: occipital view; **D**: occlusal view of the right tooth-row; **E**: ventral view of cranial base (stereo); **F**: cross-section of right horn-core (anterior side towards the top, lateral to the right); **G**: lateral view; **H**: anterior view. Scale bar = 20 cm for Figs G-H, 5 cm for Fig. D, 10 cm for all others. [planned for page width]

Figure 2. Sketch-drawing of the holotype skull of *Tchadotragus sudrei*, to show extent of the lacrymal bone (nasal reconstructed from the left side). Numbers refer to some of the characters listed in Table 6. [planned for column width]

Figure 3. Basal diameters of the horn-cores of the Toros-Menalla hippotragines, of *Praedamalis* from Lothagam (Harris, 2003), and of modern *Hippotragus* (mean values, from Klein, 1974). [planned for column width]

Figure 4. **A-E**: *Saheloryx solidus*, holotype, TM108-00-08. **A**: anterior view; **B**: cross section of right horn-core (anterior side towards the top, lateral to the right); **C**: occipital view; **D**: lateral view; **E**: dorsal view of braincase; **F**: *Tchadotragus sudrei* ?, TM266-01-131, occlusal view of lower left tooth-row; **G**: Hippotragini indet. (*Saheloryx solidus* ?), TM82-99-02, occlusal and lingual views of lower left tooth-row. Scale bar = 10 cm for Figs A-E, 5 cm for Fig. F-G. [planned for page width]

Figure 5. Cladograms of the Hippotragini. Left : the strict consensus tree (length = 59; ci = 66; ri = 81) of the 18 shortest trees (length = 58; ci = 67; ri = 82); right: the tree preferred here (length = 60; ci = 66; ri = 81). Unambiguous character changes supporting nodes **1–10** on both trees are (character numbers are those of Tab. 6): Node **1** = 4(1), 9(1), 15(1), 21(1), 22(1), 24(1); Node **3** = 26(1), 28(1), 29(1), 30(1); Node **4** = 7(1), 16(0), 17(1); Node **5** = 18(0), 23(1); Node **7** = 9(0), 21(2); Node **8** = 16(2); Node **9** = 9(0), 10(1); Node **10** = 2(1), 3(1), 11(2). With the early change option, they are further supported by: Node **1** = 27(1); Node **3** = 1(0); Node **4** = 12(1), 19(1); Node **5** = 5(1). With the late change option, they are supported instead by: Node **3** = 27(1); Node **4** = 1(0); Node **9** = 1(0); Node **10** = 5(1). Other unambiguous changes for the consensus tree are: Node **1** = 11(1); Node **2** = 10(1), 25(1); Node **5** = 6(1); Node **9** = 14(0), and for the preferred tree: Node **1** = 12(0), 19(2); Node **1'** = 8(1); Node **6** = 8(2). [planned for column width]