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NEW FOSSILS OF ALCELAPHINI AND CAPRINAE (BOVIDAE: MAMMALIA) FROM AWASH, ETHIOPIA, AND PHYLOGENETIC ANALYSIS OF ALCELAPHINI

by

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ABSTRACT

Alcelaphine antelopes comprise one of the most species-rich groups among the mammalian assemblages from the Middle Awash, Ethiopia, and in Africa as a whole. I describe a new genus and species *Awashia suwai* from Matabaietu 3, and other new alcelaphine species, *Damaliscus ademassui* from Gamedah 1 and *Beatragus whitei* from Matabaietu 3-5, all dated ca. 2.5 m.y. (millions of years). Other new alcelaphine fossils from Middle Awash include an Early Pliocene species allied to *Damalops*, Late Pliocene records of *Parmularius* cf. *pandatus* and *Beatragus antiquus*, and Middle Pleistocene records of *Megalotragus kattwinkeli*, *P. angusticornis*, *Damaliscus niro*, *Connochaetes taurinus olduvaiensis*, *Numidocapra crassicornis*, and *Alcelaphus buselaphus*. My comparisons of these fossils with all other known fossil and Recent Alcelaphini includes a cladistic analysis. The results suggest that during or before the Miocene-Pliocene transition two alcelaphine subtribes diverged for which I suggest the names Alcelaphina and Damaliscina. Alcelaphina consists of two ancient subclades: (1) the sister-group of *Damalacra neanica* and *Beatragus* known since 5.0-4.5 m.y. ago, and (2) a large clade first recorded 4.4 m.y. ago (genera *Damalops*, *Numidocapra*, *Alcelaphus*, *Rabaticeras*, *Megalotragus*, *Oreonagor*, and *Connochaetes*) that had a high diversification rate since 3 m.y. ago. The earliest record of Damaliscina is the form that Gentry (1980) named *Damalacra acalla*, which emerges as the hypothetical direct ancestor of the Early-Middle Pliocene split into *Parmularius* and the *Damaliscus* group. The placement of the new genus *Awashia* remains problematic. A new ovibovine genus and species, *Nitidarcus asfawi*, and a new caprine genus and species, *Bouria anngettyae*, both from Bouri 1, are also described. I discuss some evolutionary and biogeographic implications of the new fossils from Middle Awash.

KEYWORDS: Alcelaphini, Caprinae, Awash, Ethiopia

INTRODUCTION

Excavations of Plio-Pleistocene sedimentary deposits in eastern Ethiopia's Middle Awash Valley have recently yielded large new assemblages of fossil vertebrates including Hominidae (White *et al.* 1993; Clark *et al.* 1994; White *et al.* 1994). This description of antelopes in Alcelaphini and Caprinae known to date from Middle Awash will need additions and amendments in future as new fossils are discovered in the ongoing Awash project. A cladistic analysis of Alcelaphini will be presented that includes the entire record of this tribe and places the new Awash fossils in genealogical and chronological context. This analysis includes many more taxa than did my previous cladogram of Alcelaphini (Vrba 1979), and new characters and new evaluations of previously used characters, and is therefore a major revision of that analysis. A similar previous paper described the fossil Hippotragini of the Awash in the context of a cladistic analysis of all known taxa in that tribe (Vrba and Gatesy 1994). Table 1 gives fossil sites and stratigraphic subdivisions referred to in this paper and Figure 1 the chronology of the Awash strata. The living and fossil species of Alcelaphini are introduced in Table 2.

MATERIALS AND METHODS

This study is based on observations and measurements on all living and known extinct alcelaphines with emphasis on the new Awash fossils. Some of these data were obtained for previous analyses (Vrba 1971, 1976, 1977a, 1977b, 1979, 1984, Laubscher *et al.* 1972). Figure 2 gives cross-sections of the basal horncores, and Figures 3-17 photographs of the Awash fossils. Their measurements (Tables 3-12) are compared to those of other alcelaphines in Figures 18-20. Comparison of the 40 skull characters in Table 13 across alcelaphine taxa resulted in the codes in Table 14 that were used in the cladistic analyses.

To estimate the cladistic codes (Table 14), ontogenetic growth patterns and graphs of measurements were compared across taxa. My aim was to arrive at code separations that are independent of body size. Characters 1-3, 9, 14, 15, 19-24, 28-30, and 38 (Table 13) were analysed quantitatively. The others were coded qualitatively because the presence or absence of the states could readily be evaluated (e.g., horncore torsion, 12, 13 in Table 13), or because it was difficult to quantify the character differences (e.g., the extent of the preorbital fossa, 32 in Table 13). In order to explore the extent of

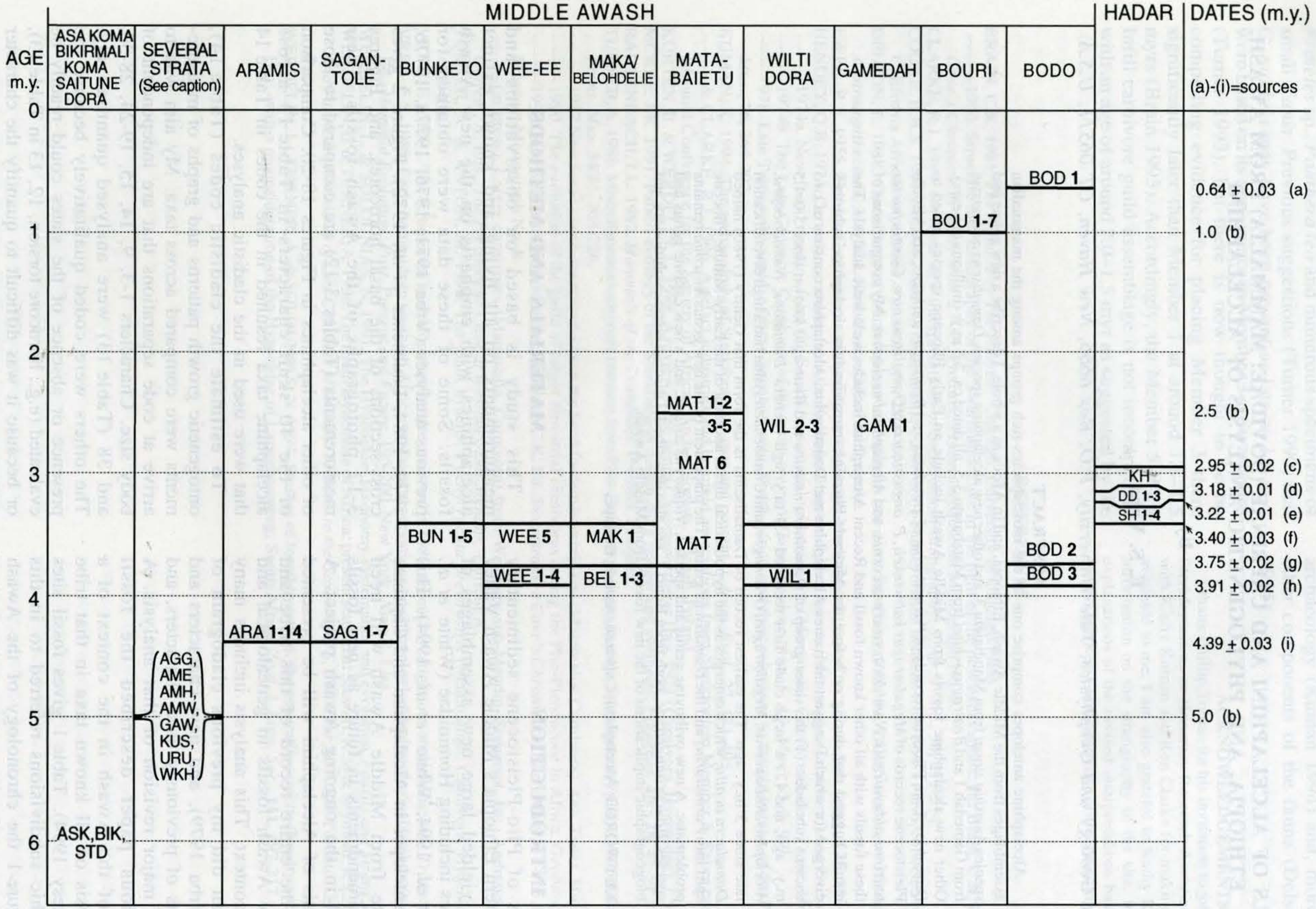

Figure 1. Chronology of stratigraphic sections and fossiliferous units in the Middle Awash, and also Hadar, from which bovid fossils come. See Table 1 for names and acronyms. This scheme is subject to revision as field and laboratory analyses progress. Tuff names and sources for dates are as follows: (a) pooled estimate of weighted mean age for the tuff represented by MA90-20 at Hargufia and MA90-23 at Bodo which are homologous based on stratigraphic and geochemical criteria (Clark *et al.*, 1994); (b) preliminary, approximate, unpublished determinations (White, pers. comm.); (c) tuff BKT-2L, (d) tuff KHT, (e) tuff TT4 ((c)-(e) are after Walter, pers. comm., as in Kimbel, 1995); (f) based on the following tuffs that are chemically homologous (review in White *et al.*, 1993): MA90-28 at Wee-ee, MA90-39 at Bunketo South, MA90-14 at Wilti Dora, SHT at Hadar, a tuff from the Gulf of Aden core 231, and Tulu Bor beta tuff in the Turkana Basin; (g) tuff VT-3 (=Wargolo tuff, White *et al.*, 1993); (h) tuff VT-1 (White *et al.*, 1993); (i) GATC tuff complex (WoldeGabriel, *et al.*, 1994).

allometric effects on the characters, for each of the 16 quantitative characters a least squares regression line was calculated for the individual values regressed against a proxy for body size. The proxy used was basal horncore size as defined in Figure 20. In the cases of the angle measurements (9, 14, 15, 19, Table 13), no significant correlation with body size was found and the code separations were estimated directly by inspection of the variation. Figure 18 illustrates this approach for characters 15 and 19. Horncore compression (1 in Table 13) was taken to have state 0 below and state 1 above the line along which the ratio of the basal diameters is 80% (Figure 19). (For this as for some other characters there seems to be variability with increasing body size in certain taxa. Such ontogenetic variation will be discussed in the relevant taxonomic sections.) For other quantitative characters, the regression lines with confidence intervals were used as an approximate guide to code separations, as illustrated in Figure 20 for basal horncore separation. In this case, taxa with mean values below, between, and above the 99% confidence intervals were respectively assigned codes of 0, 1, and 2. About 10% of codes are uncertain (coded ? in Table 14) mostly due to missing data on incomplete fossils. In a few cases the variation within a taxon for a character is large. For instance, because the values for horncore compression in living *Alcelaphus buselaphus* vary extensively (Figure 19), and because the original state in this taxon is unknown, a ?-code was assigned (Table 14). In each of a few additional cases a ?-code was assigned because the mean of a small sample, or the only available value, was found to be intermediate. An example is the the angle between the maximum horncore diameter and and the midfrontal suture (15 in Tables 13 and 14) in the single known specimen of *Awashia suwai* (AsMAT3 in Figure 18). Multistate characters were ordered on the basis of ontogenetic progression and similarity between adjacent states (see Lipscomb 1992). The meaning of ?-codes in two-state characters is uncertainty between states 0 and 1, but in multistate characters it is open to additional interpretation. In the final cladistic result (Figure 21) all cases of ?-codes in multistate characters were interpreted appropriately.

The codes in Table 14 were analysed using outgroup rooting. Cladistic results from mitochondrial DNA (Gatesy 1993; Gatesy *et al.*, 1992; Gatesy *et al.* in press) and nuclear DNA sequences (Gatesy pers. comm.) gave independent information on alcelaphine outgroups. While these results varied to some extent depending on the combinations of DNA sequences and computational methods used, they consistently supported monophyly of Alcelaphini and identified five additional monophyletic taxa as being among the outgroups or as subclades of outgroups: Caprinae (Caprini, Ovibovini, Rupicaprini), Hippotragini, Reduncini, *Aepyceros*, and Antilopinae (Antilopini, Neotragini). In all the DNA cladograms, Caprinae (1) or Hippotragini (2) are either the first two outgroups or the sister-clade Caprinae-Hippotragini (3) is the first outgroup. The next-nearest outgroup is always a clade Reduncini-Antilopinae-*Aepyceros* (4) or a clade Reduncini-Antilopinae (5), or *Aepyceros* (6). I arrived at the outgroup codes in Table 14 by estimation of the plesiomorphic states for skull characters for each of clades (1) – (6) using previous analyses of bovid skull morphology (Vrba *et al.* 1994, for Reduncini; Vrba and Gatesy 1994, for Hippotragini; Vrba and Schaller, in prep., for Caprinae and Antilopinae; see also Gentry 1992). For six characters in Table 14, decisions on character polarity at the alcelaphine outgroup node remain uncertain, and the codes I used reflect my current best estimates (characters 2, 6, 19, 21, 23, 30). For the remaining characters the outgroup states in Table 14 are more securely based as they appear to be the plesiomorphic states in each of clades (1) – (6).

The cladistic analyses used options (outgroup rooting, mhennig*, bb*, and NELSEN for consensus trees) of the HENNIG86 program (Farris 1988). Mhennig* constructs several trees, each by a single pass through the data, and then applies branch-swapping to each of these initial trees. The bb* option applies more extended branch-swapping to the initial trees and generates all the shortest trees it can find. Mhennig* and bb* are not certain to find all trees of minimal length. The full data set is too large to use the ie option of HENNIG86 which does find all trees of minimal length. This option was applied after treating as single taxa the most strongly-supported terminal clades in the consensus tree (e.g., *Beatragus*, Figure 21). The results confirmed that the consensus tree for each of my cladistic analyses does represent the consensus of all trees of minimal length.

The systematics of *Megalotragus* and *Awashia* were subjected to additional cladistic explorations. In the case of *Megalotragus*, the codes in Table 14 were analysed in two cladograms that differed only with respect to taxonomic subdivision of this genus. In one analysis, *M. kattwinkeli* as previously recognized (e.g., Gentry and Gentry 1978), *Megalotragus* from Bouri in the Awash, and *M. isaaci* from the Koobi Fora Formation (Harris 1991) were treated as three separate taxa (Mk, MkBOU, Mki in Table 14). The second analysis treated these three forms as one variable species (Mk* in Table 14). The results, which differ only with respect to branching within *Megalotragus*, will be discussed. In the case of *Awashia*, many character states that turned out to be important to the basal branching sequence in Alcelaphini are difficult to interpret in the single known skull, either because it is intermediate or because its eroded condition leaves open what the correct states are. I will report on the outcomes of using different interpretations of such characters in *Awashia*.

TABLE 1.

Fossil sites and stratigraphic subunits referred to, with codes in capital letters that are used in tables and figures. Stratigraphic subunits are arranged roughly from latest at the top to earliest at the bottom. Table 2 cites sources for bovid records. For stratigraphy and chronology see Figure 1 for the Middle Awash, and Vrba's (1995b) review for other sites. Loc. = Locality; F. = Formation; M. = Member; sm. = submember.

Site	**Country**	**Time period**	**Acronym**
Ain Boucherit	Algeria	Late Pliocene	AINB
Ain Hanech	Algeria	Early Pleistocene	AINH
Ain Jourdel	Algeria	Early Pleistocene	AINJ
Anabo Koma	Djibouti	Early Pleistocene	AK
Awash, Middle (Figure 1)	Ethiopia	Plio-Pleistocene	
Bodo Loc. 1		Middle Pleistocene	BOD1
Bouri Loc. 1, 2, 6		Middle Pleistocene	BOU1, 2, 6
Matabaietu Loc. 1-5		Late Pliocene	MAT1-5
Gamedah Loc. 1		Late Pliocene	GAM1
Wilti Dora Loc. 2-3		Middle-Late Pliocene	WIL2-3
Matabaietu Loc. 6, 7		Late Pliocene	MAT6, 7
Bunketo Loc. 1-5		Middle Pliocene	BUN1-5
Maka Loc. 1		Middle Pliocene	MAK1
Wee-ee Loc. 1-5		Middle Pliocene	WEE1-5
Belohdelie Loc. 1-3		Middle Pliocene	BEL1-3
Wilti Dora Loc. 1		Middle-Late Pliocene	WIL1
Aramis Loc. 1, 4, 6, 8		Early Pliocene	ARA1, 4, 6, 8
Sagantole Loc. 1-7		Early Pliocene	SAG1-7
Agera Gawetu Loc. 1		Early Pliocene	AGG
Amba East Loc. 1		Early Pliocene	AME1
Amba West Loc. 1		Early Pliocene	AMW1
Amboul Hareli Loc. 1		Early Pliocene	AMH1
Gawto Loc. 1		Early Pliocene	GAW1
Kuseralee Loc 1, 2		Early Pliocene	KUS1, 2
Urugus Loc. 1		Early Pliocene	URU1
Worku Hassan Loc. 1		Early Pliocene	WKH1
Asa Koma Loc. 1		Late Miocene	ASK
Bikirmali Koma Loc. 1		Late Miocene	BIK1
Saitune Dora Loc. 1		Late Miocene	STD1
Cornelia	South Africa	Middle Pleistocene	COR
Elandsfontein	South Africa	Middle Pleistocene	E
Florisbad	South Africa	Late Pleistocene	FLOR
Hadar Formation	Ethiopia	Middle-Late Pliocene	
Kada Hadar M.			KH
Denen Dora M., sm. 1-3			DD
Sidi Hakoma M., sm. 1-4			SH
Isimila	Tanzania	Middle Pleistocene	ISI
Kakesio	Tanzania	Early Pliocene	KK
Kanapoi	Kenya	Early Pliocene	KP
Kromdraai A	Transvaal, S. Africa	Middle Pleistocene	KA
Koobi Fora Formation	Kenya	Plio-Pleistocene	
Chari Member			CHA
Okote Member			OKT
KBS Member			KBS
Upper Burgi Member			UBU
Tulu Bor Member			TUL
Lokochot Member			LOK
Langebaanweg, Varswater F.	Cape, South Africa		LAN
Laetoli Beds	Tanzania	Early Middle Pliocene	LIT
Makapansgat Limeworks M. 1-5	South Africa	Late Pliocene	M1-5
Nachukui Formation	Kenya	Plio-Pleistocene	
Upper Lomekwi Member			ULM
Olduvai Gorge Beds I-IV	Tanzania	Pleistocene	
Peninj	Tanzania	Pleistocene	PE
Rabat	Morocco	Pleistocene	R
Rusinga Island	Kenya	Late Pleistocene	RU
Shungura Formation, M. B-J	Ethiopia	Plio-Pleistocene	S-B - S-J
Siwaliks formations, Pinjor	India and Pakistan	Plio-Pleistocene	P
Swartkrans Formation, M. 1-3	South Africa	Lower Pleistocene	SK1-3
Sterkfontein Formation, M. 4	South Africa	Late Pliocene	ST4
Tadzikistan, Kuruksai	Tadzikistan	Late Pliocene	TAD
Ternifine	Algeria	Middle Pleistocene	T
Upper Ndolanya Beds	Tanzania	Late Pliocene	UN
Wadi Natrun	Egypt	Earliest Pliocene	WADN

Vrba *et al.* (1994) used significance tests to estimate code separations in quantitative characters. Most of the present samples are too small to apply such methods. The difficulties inherent in cladistic coding are especially felt in an analysis such as this one with its small samples for closely related taxa. There remain problems of homology among taxa, of which characters to exclude so as to eliminate overlap between characters, and of where the code separations should be located in the spectrum of variation. Each statement about a character in Table 14 is an hypothesis to be tested, and to be rejected by additional data. These hypotheses test each other in the cladistic analysis.

SYSTEMATIC RESULTS

The cladistic analysis that treated Mk, Mki and MkBOU in Table 14 as three separate taxa resulted in the consensus tree in Figure 21. I will argue below that all three belong to a single species, an inclusive *M. kattwinkeli*. The analysis that treated them as a single species (Mk* in Table 14) resulted in a consensus tree of identical branching topology to that in Figure 21, except for the *Megalotragus* clade in which *M. atopocranion*, *M. priscus* and the inclusive *M. kattwinkeli* formed a trichotomy. The phylogenetic tree in Figure 22 is based on this second result, with taxa plotted against time using the dates in Table 2. Each taxon without autapomorphies in the consensus tree (Figure 21) is the hypothetical potential ancestor of its sister-group. Such taxa are shown in the appropriate ancestral positions in Figure 22.

Some taxa have been cited as alcelaphine in the past, but are not included in my cladogram. *Aepyceros* (impalas) has been regarded as alcelaphine (Gentry 1978) or as the sister-taxon of Alcelaphini (Vrba 1979), but cladistic results from DNA sequences cited earlier strongly suggest that Alcelaphini are more closely related to caprines and hippotragines than to *Aepyceros*. Thomas (1984) proposed that Alcelaphini consists of two basal sister-lineages: *Maremmia haupti*, a small, dentally advanced antelope from the Turolian of Baccinello, Italy, and the sister-group (*Aepyceros* + [Alcelaphini *sensu* Figure 21]). I doubt that this is correct. Alcelaphini in my sense, their closest relatives based on DNA studies (living Caprini and Hippotragini), and *Aepyceros*, all share some kind of hollowing at the horncore bases, while *Maremmia* lacks this feature. I prefer the second alternative offered by Thomas (1984): that *Maremmia* may be the sister-taxon of the Middle Miocene, Afro-Eurasian *Caprotragoides*. Klein and Cruz-Uribe (1991) described a form from Elandsfontein as ?*Parmularius* sp. nov. It shares with *Parmularius* a lateral horncore boundary that is posteriorly much lower than anteriorly; very low horncore separation and divergence, and long pedicels. It shares with *P. pandatus* strong backbending of the horncore, and with *P. braini* strongly compressed horncores, but it is unlike *Parmularius* in the shape of the horncore-pedicel boundary, clockwise torsion in the right horncore and in lacking posterolateral basal horncore swellings. There are resemblances in horncore torsion and course (e.g., in the horncores remaining very close along their entire length and being strongly backbent with rapid diminution), and in the shape of the horncore-pedicel boundary to caprines like *Sinotragus wimanni* (Bohlin 1935). However this latter Late Miocene form is geographically and temporally far removed from Elandsfontein. I see the Elandsfontein form as either a very aberrant alcelaphine allied to or basal within *Parmularius*, or as a caprine.

The following are alcelaphines, and included in Table 2 as such, but were omitted from the cladistic computations because they are based on scant material. *Damaliscus "hipkini"* (the name that the late L. H. Wells once intended to give this species, although he never described it, pers. comm.; *Damaliscus* sp. nov. of Klein and Cruz-Uribe 1991) is a small form known from the Middle Pleistocene of Elandsfontein (based on frontlets EFT 3781 and EFT 5143) and Cornelia. (I stress that specific names in quotation marks, like "*hipkini*", are not formally described. I use these informal descriptive names in quotation marks, rather than a less intelligible numbering system, to make more comprehensible to the reader my extensive references to several undescribed species.) *D. "hipkini"* has strongly compressed horncores with flattened lateral surfaces, lacking basal swellings and arising from moderately long pedicels. These features suggest that it belongs in *Damaliscus*. *Damaliscus* or *Parmularius "makapani"* is based on a small frontlet M8246 from Makapansgat Member 3. Features that resemble *Parmularius* are horncores with some basal swelling and lacking lateral flattening, long pedicels and a definite parietal boss. The species may be a new small *Parmularius* species or a juvenile of a larger *Parmularius* species, rather than connected to the ancestry of *Damaliscus* as I previously suggested (Vrba 1995b). The next taxa, although omitted from the cladogram, will be discussed in relation to similar Awash fossils. *Beatragus "elandsfonteini"* (*Beatragus* sp. of Gentry 1978; *Damaliscus* aff. *lunatus* of Klein and Cruz-Uribe 1991) is known from Elandsfontein and may be conspecific with a horncore from Swartkrans Member 2 (Vrba 1976). I argue below (following Gentry 1978), that this form is closely allied to, and perhaps descended from *B. antiquus*. *Damaliscus gentryi* (Vrba 1977a), based on a single horncore from Early Pleistocene Makapansgat Member 5 may be close to *D. niro*. (*Damalops*) sp. indet. in Table 2 is based on *Parestigorgon gadjingeri* from Upper Ndolanya, Tanzania, which was described by Dietrich (1950) based on a horncore and some dentitions. These fossils are related to *Damalops palaeindicus* (Gentry

TABLE 2.

Living and extinct alcelaphine taxa and their first and last appearance data (FAD, LAD, first and last entries). Other sites are cited in some cases. See Table 1 for letter codes for fossil sites, Figure 1 for Awash dates, and Vrba's review (1995b) for other dates and literature sources. Only subspecies that appear in this paper are given. Genus names in brackets refer to past assignations that are not upheld by the cladistic results in Figure 21 as monophyletic and/or worthy of generic distinction. Such cases include taxa assigned to a genus during original description or later revision, as well as undescribed new species that were loosely associated with a genus in the literature. As the following undescribed species, will be extensively referred to, it will be done by descriptive names in quotation marks rather than use a less intelligible numbering system (at least one good specimen and its source site are added in each case in brackets): (*Damalops*) "*sidihakomai*" (AL 208-7, Hadar SH), (D.) "*denendorai*" (AL 161-5, Hadar DD), (*Rabaticeras*) "*lemutai*" (S.208, Olduvai Bed II), *Damaliscus* "*hadari*" (AL 146-1, Hadar SH, *Damaliscus* "*hipkini*" (EFT 3781 and EFT 5143, Elandsfontein), *Beatragus* "*elandsfonteini*" (EFT 16561, Elandsfontein), and *Damaliscus/?Parmularius* "*makapani*" (M8246, Makapansgat Member 3).

Genus	Species Subspecies	Site of FAD Site of LAD	FAD m.y. LAD m.y.	Extinct = † Common name	Taxon acronym
Damalacra	*neanica*	LAN	5.0	†	ne
		WADN	4.5		
(*Damalacra*)	*acalla*	LAN	5.0	†	ac
		LAN	5.0		
Damalops	*palaeindicus*	TAD	2.6	†	Dop
		PIN	2.6 - 2.0		
(*Damalops*)	"*sidihakomai*"	ARA	4.4 - 4.2	†	Dos
		KK	4.4		
		KP	4.1		
		LIT	3.76 - 3.46		
		MAK	3.75 - 3.40		
		WEE5	3.75 - 3.40		
		LOK	3.50 - 3.36		
		TUL	3.36 - 2.68		
		SH	3.40 - 3.22		
	"*denendorai*"	DD	3.22 - 3.18	†	Dod
		S-B	2.9		
		KH	2.9		
(*Damalops*)	sp. indet.	UN	2.9 - 2.6		Do?UN
(*Parestigorgon*)					
Beatragus	*hunteri*	CHA	1.39 - 0.67	Hunter's Hartebeest	Bh
	antiquus	WIL2	2.5	†	Ba
		GAM	2.5		
		OII Kit K	>1.48±.05		
	whitei sp. nov.	MAT3-5	2.6	†	Bw
		MAT3-5	2.6		
	"*elandsfon-*	?SK1	1.8	†	Be
	teini"	E	0.6		
Awashia	*suwai* sp. nov.	MAT3	2.6	†	As
gen. nov.		MAT3	2.6		
Damaliscus	*dorcas*	SK2	1.1	Blesbok etc	Dd
	lunatus	SK3	0.7	Tsessebes etc	Dl
	l. jimela			Topi	Dlj
	l. korrigum			Korrigum	Dlk
	l. lunatus			Tsessebe	Dll
	niro	OII SHK	1.66 - 1.48	†	Dn
		BOU	1.0		
		BOD1	0.6		
		FLOR	.2 - .1		
	agelaius	OII FLK	1.75 - 1.66	†	Da
		OIII JK2	1.33 - 0.96		
	gentryi	M5	1.8 - 1.6	†	Dg
		M5	1.8 - 1.6		
	ademassui	GAM	2.5	†	Dad
	sp. nov.	GAM	2.5		
	"*hadari*"	SH	3.40	†	Dha
		SH	3.40		
	"*hipkini*"	COR	0.8 - 0.6	†	Dh

TABLE 2. continued

Genus	Species Subspecies	Site of FAD Site of LAD	FAD m.y. LAD m.y.	Extinct = † Common name	Taxon acronym
		E	0.6		
Parmularius	*pandatus*	LIT	3.76 - 3.46	†	Ppan
		?WIL2	?2.5		
	braini	M3	2.8 - 2.6	†	Pb
		M3	2.8 - 2.6		
	eppsi	S-C	2.6	†	Pe
		OKT	1.6 - 1.39		
	altidens	AINB	2.7 - 2.5	†	Pal
		OI HWK	1.8 - 1.75		
	angusticornis	OI FLKN	1.80 - 1.75	†	Pan
		BOU	1.0		
		ISI	0.8 - 0.6		
	rugosus	OII HWK	1.75 - 1.66	†	Pru
		OIV HWK	0.78 - 0.7		
	parvus	KA	1 - 0.7	†	Ppar
		OIV	0.78 - 0.7		
	ambiguus	T	0.7	†	Pam
		T	0.7		
Parmularius or *Damaliscus*	*cuiculi*	AINB	2.7 - 2.5	†	D/Pc
		AINB	2.7 - 2.5		
	"*makapani*"	M3	2.8 - 2.6	†	D/Pm
		M3	2.8 - 2.6		
Alcelaphus	*buselaphus*	BOD1	0.6	Hartebeest	Ab
	b. buselaphus			†	Abb
	b. caama			Cape Hartebeest	Abca
	b. cokii			Coke's Hartebeest	Abco
	b. jacksoni			Jackson's Hartebeest	Abj
	b. lelwel			Lelwel Hartebeest	Abl
	b. major			Western Hartebeest	Abm
	b. swaynei			Swayne's Hartebeest	Abs
	b. tora			Tora Hartebeest	Abt
Alcelaphus (*Sigmoceros*)	*lichtensteini*	SEM LT	0.5 - 0.3	Lichtenstein's Hartebeest	Ali
Rabaticeras	*arambourgi*	OIII JK2	1.33 - 0.96	†	Ra
		OIV PDK	0.8		
		R	0.6		
		E	0.6		
(*Rabaticeras*)	*porrocornutus*	SK1	1.8	†	(R)p
		SK1	1.8		
(*Rabaticeras*)	"*lemutai*"	OII Tuff IIA	1.66	†	(R)le
		OII Tuff IIA	1.66		
Numidocapra	*crassicornis*	AINH	1.7	†	Nc
		AK	1.6		
		?OII SHK	1.5		
		BOU	1.0		
Megalotragus	*kattwinkeli*	MAT1	2.5	†	Mk
		SH-D1	2.5		
		ST4	2.6 - 2.4		
		BOU	1.0		
		OII-IV	1.5 - 0.6		
	k. isaaci	UBU	2.0 - 1.88	†	Mki
		OKT	1.6 - 1.39		
	priscus	COR	0.8 - 0.6	†	Mp
		NBC	.012 - .009		
Megalotragus	*atopocranion*	RU	Late	†	Ma
(*Rusingoryx*)			Pleistocene		
Connochaetes	*taurinus*	OII MNK	1.66 - 1.48	Blue Wildebeest	Ct
	t. olduvaiensis	OII MNK	1.66 - 1.48		
		PE	1.1		
		BOU	1.0		
	gnou	COR	0.8 - 0.6	Black Wildebeest	Cgn
	africanus	OII	1.75 - 1.33	†	Ca
		OII	1.75 - 1.33		
	gentryi	ULM	2.5	†	Cg
		OII	1.66 - 1.48		
Oreonagor	*tournoueri*	AINB	2.7 - 2.5	†	Ot
		AINJ	1.8		
?*Oreonagor*/?*Megalotragus* sp.		BOU	1.0	†	?Osp.BOU
		BOU	1.0		

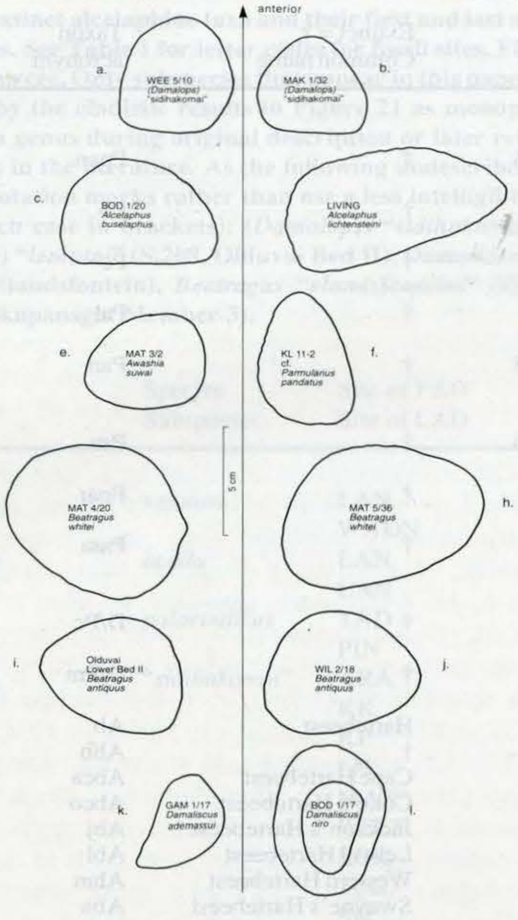

Figure 2. Cross-sections of basal alcelaphine horncores from Middle Awash, Olduvai Lower Bed II (i. = OLD/'71 HWK E Rootlet Clay S. 217), and living Lichtenstein's Hartebeest (d.). The smaller cross-section for *D. niro* horncore BOD 1/17 is from 120 mm above the base. The cross-sections to left and right of the central line are of actual left and right horncores respectively, except that of left horncore *D. niro* BOD 1/17 (l.) which was transposed to the right. Actual horncore separation is represented by distance from the central line.

and Gentry 1978) and may belong to (*Damalops*) "*denedorai*" (see below).

Numidocapra crassicornis (Arambourg 1949), a large antelope from Ain Hanech, Algeria, and Anabo Koma, Djibouti, Ethiopia (Bonis *et al.* 1988), and now also from Bouri in the Awash, was considered by Geraads (1981) as alcelaphine, but by Gentry (1978, 1990a) as caprine. I will discuss why I see *crassicornis* as specifically distinct from, but closely related to and perhaps directly ancestral to *R. arambourgi*.

When I refer in the systematic descriptions to clockwise or anticlockwise torsion of horncores, I mean in the right horncore from the base up. The following terms will also be used: the 'craniofacial angle' is the angle between the forehead and the dorsal braincase (character 19 in Table 13), and the 'parietal-occipital angle' is that between the straight line from bregma to occiput, and the straight line from occiput to the top of the foramen magnum.

Tribe Alcelaphini (Rochebrune 1883)

1883 Alcelaphidae Rochebrune
1898 Bubalinae Trouessart
1945 Alcelaphini Simpson

Alcelaphini are medium to large antelopes in which females as well as males have horns. They have a sinus in the frontal, in the area of the pedicel and horncore base, that is extensively developed such that the surrounding bones are thin relative to sinus volume and there are hardly any bony intrusions into the sinus. An associated feature is the high level of the frontals between the horn bases relative to the orbital rims. Shallow elongated post–cornual fossa. Supraorbital foramina flush with the frontal surface, in very small pits. Preobital fossae and glands pleisiomorphically well-developed. The large premaxillae rise with roughly even width to have a long contact with the long nasal bones. Ethmoidal fissures are absent in adults. Tooth rows are set anteriorly. The zygomatic arch deepens anteriorly beneath the orbits. Basioccipital with a central longitudinal groove between well-developed longitudinal ridges behind the anterior tuberosities. Occipital surface facing partly laterally as well as backwards. Mastoids large. Temporal ridges wide apart on the posterodorsal braincase. Teeth hypsodont, without goatfolds on lower molars (protostylids), without basal pillars (the ectostylids on lower and entostyles on upper molars) except in some earliest forms and juveniles, with small hypoconids on P_4 and with rounded molar lobes. Repeated trends within the tribe include shortening of the braincase, decrease of the craniofacial angle, lengthening of the face, reduction of preorbital fossae, reduction of premolar rows, and fusion of paraconid and metaconid on P_4. In living species: pedal glands present on forefeet only; no inguinal glands; one pair of mammae; tail either long, crested and bordered on top with a fringe of black hair (*Alcelaphus* and *Damaliscus*) or white hair (*Beatragus*), or very long horse-like tail with long hair (*Connochaetes*); whithers higher than rump. (See also Gentry and Gentry 1978; Gentry 1980; Vrba 1979).

Subtribe Alcelaphina, nom. nov.

Alcelaphina are medium to large alcelaphines. The basal horncore margin is lower laterally than medially. The horncore in lateral view is concave soon above the base such that the horncore recurves in an anterior direction. The angle of the basal horncore to the midfrontal suture is pleisiomorphically large. There is no distinct parietal boss on the dorsal braincase. The braincase roof is straight to concave. A feature that evolves early within the subtribe is clockwise horncore torsion.

Gen. indet. aff: *Damalops* Pilgrim, 1939, (here referred to as "*Damalops*")

Several cranial pieces and dentitions from Aramis, Maka and Wee-ee (Figures 3, 4, Tables 3, 11, 12) belong to a single evolving lineage and species that is best known from the Hadar Sidi Hakoma Member (I will use the short form Hadar SH). It is also known from Kakesio in the Laetoli area, Kanapoi, the Laetoli Beds, and the Lokochot and Tulu Bor Members in the Koobi Fora Formation. The fossils from Hadar and Laetoli were discussed in Gentry (1980, 1981) as ?*Damalops*. Harris (1991) discussed those from Koobi Fora under different names, including as *Parmularius* cf. *P. angusticornis*. This species has not yet been formally described, and I refer to it informally as (*D.*) "*sidihakomai*". A similar species, that in my analysis emerges as the direct – although substantially changed – descendant of "*sidihakomai*", is represented best in the Hadar Denen Dora and Kada Hadar Members (Hadar DD and KH). This form is also undescribed, and I refer to it as (*D.*) "*denendorai*". It is also present probably in Shungura B11 (= Shungura Member B subunit 11) ca. 2.9 m.y. and in the Upper Ndolanya assemblage by horncores previously assigned to *Parestigorgon gadjingeri* (Dietrich 1950; Gentry 1987). Gentry (1980, 1981) regarded Hadar "*sidihakomai*" and "*denendorai*" as successive parts of a single species, ?*Damalops* sp., and as a close relative of *D. palaeindicus* from the Pinjor Formation of the Siwaliks (Pilgrim 1939) and Tadzhikistan (Dmitrieva 1977). Pilgrim's (1939: 67) original diagnosis for *Damalops* and for the type (and only known) species *D. palaeindicus* included the following: "horn-cores mounted on a ridge, but not far away from the orbits, close together, at first almost parallel and at right angles to the braincase, then curving very gradually outward and backward", an almost straight profile of the dorsal braincase, anteriorward expansion of the nasals and muzzle, long narrow nasals and face, very deep and extensive preorbital fossa, and presence of P_2 where this can be seen. Gentry (1981: 14) noted the following features of *D. palaeindicus* in comparison with the Hadar forms: similarities include "high and narrow skull; horn cores inserted closely together and not very uprightly above the backs of the orbits, nearly parallel proximally but increasingly divergent distally; ... braincase rather long by comparison with presumed later alcelaphines; braincase roof inclined with little sign of a parietal boss; preorbital fossa large; nasals pronouncedly narrow as a ridge between the preorbital fossae; and a deep face. [Differences include that] *D. palaeindicus* shows backward curvature of its horn cores, horn cores not tapering rapidly above the base, sides of braincase parallel and not widening posteriorly, and probably also longer horn cores, shorter braincase,

TABLE 3.

Measurements of horncores and frontlets related to *Damalops*: (*Damalops*) "*sidihakomai*" horncores and partial frontlets: ARA-8/3 frontlet with left horncore, MAK-1/32a and b left and right horncores, WEE-5/10 left horncore, compared with AL349-3 left horncore from Hadar cf. SH, Laetoli cranium 1959.233 probably from the Laetoli Beds; and (*Damalops*) "*denendorai*" right horncore from Hadar cf. DD. Length in mm; two values for horncore length are preserved/estimated complete lengths; e = estimated, ee = very rough estimate; max. = maximum.

	(*Damalops*) "*sidihakomai*"					(*D.*) "*denendorai*
	ARA-8/3	MAK-1/32	WEE-5/10	AL349-3 (cf. SH)	Laetoli 1959.233	AL169-26 (cf. DD)
Horncore max. diameter (HMAX)	38.4	48.2	55e	51e	51.5	60.5
Horncore min. diameter (HMIN)	37.63	43.5	48e	47.4	43.5	50ee
Horncore ratio (HMIN/HMAX)	0.90	0.87	0.93	0.90	0.90	83ee
Horncore length	110/140	230/290	190/270		-	130/210
Horncore basal separation	22.4	30ee			27.0	
Angle of basal horn divergence	30°					
Angle of HMAX to midfrontal suture	70°	60-70°		90°ee		
Width across horn pedicels		123ee			110.1	
Craniofacial angle	120°ee		105°e			
Max. separation supra-orbital foramina (SOF)			82e		67.7	
Distance orbit to horncore			38e			

and a toothrow positioned more anteriorly. P_2 is absent on the only two Hadar specimens (both in middle wear) on which its state is determinable, and this contrasts with its presence on a single *D. palaeindicus*."

D. palaeindicus lacks the specializations in horn shape, associated with the evolution of horn torsion, that characterize its relatives from recent common ancestry, *Alcelaphus*, *Megalotragus*, *Oreonagor* and *Connochaetes*. It also lacks most of the innovations in skull and facial shape of these taxa. As a result *D. palaeindicus* retains the strongest overall resemblances to the ancestral lineage from "*sidihakomai*" to "*denendorai*" as noted by Gentry (1980, 1981). In terms of my results, this resemblance rests on plesiomorphic retention of ancestral characters. That is, a genus *Damalops* including the species *palaeindicus*, "*sidihakomai*", and "*denendorai*" is paraphyletic, and lacks autapomorphies and definition in the sense of De Queiroz and Gauthier (1994). If *Damalops* is left to include only *palaeindicus*, then a separate new genus including "*sidihakomai*" and "*denendorai*" would also represent a paraphyletic grade. Nevertheless, I suggest that we need a single genus name for such an unbranching lineage of successive distinct morphologies in spite of its ancestral status and, if my hypothesis of ancestry (Figure 22) is upheld, then a new generic name is needed for this long-lasting, basal lineage from "*sidihakomai*" and "*denendorai*". Until these forms are described, we need to refer to them using some provisional nomenclature that maintains links with previous usage to facilitate communication. To this end I suggest the temporary names (*Damalops*) "*sidihakomai*" and (*D.*) "*denendorai*".

Damalops sidihakomai sp. nov. from Aramis 1, 4, 8 and 9, and also Maka 1, and Wee-ee (Figures 3, 4, Tables 3, 11, 12):

The Aramis localities at which this taxon is found are dated 4.4 m.y. and Maka 1 and Wee-ee 5 ca. 3.4 m.y. (Figure 1). The earlier form from Aramis was about the size of a large blesbok. The later ones from Maka and Wee-ee are of the larger size of a living topi, with the Wee-ee material being the largest. ARA-8/3 is a broken frontlet with most of the left and part of the right horncore (Figure 3). (Catalogue numbers for Middle Awash vertebrate fossils contain the letters VP, ARA-VP-8/3 in this case, but I use the shorter form. Also, I abbreviate the names of Middle Awash localities, e.g., Aramis 8 for Aramis Locality 8.) The horncore is little compressed (Figure 19), with a distinctly flattened posterior surface and approach to a posterolateral keel, inserted moderately closely to its neighbour (Figure 20) on pedicels that are not short but ill-defined with sloping sides, and quite uprightly with a gentle anterior concavity. The pedicel-horncore transition is distinct, and laterally lower than

Figure 3. (*Damalops*) "*sidihakomai*" sp. nov. from Aramis: a. and b. ARA-8/3 frontlet with left horncore in left lateral and anterior views; c. ARA-8/9 left maxilla with P^3-M^2; d. ARA-4/1 left mandibular teeth M_1 fragment and M_2.

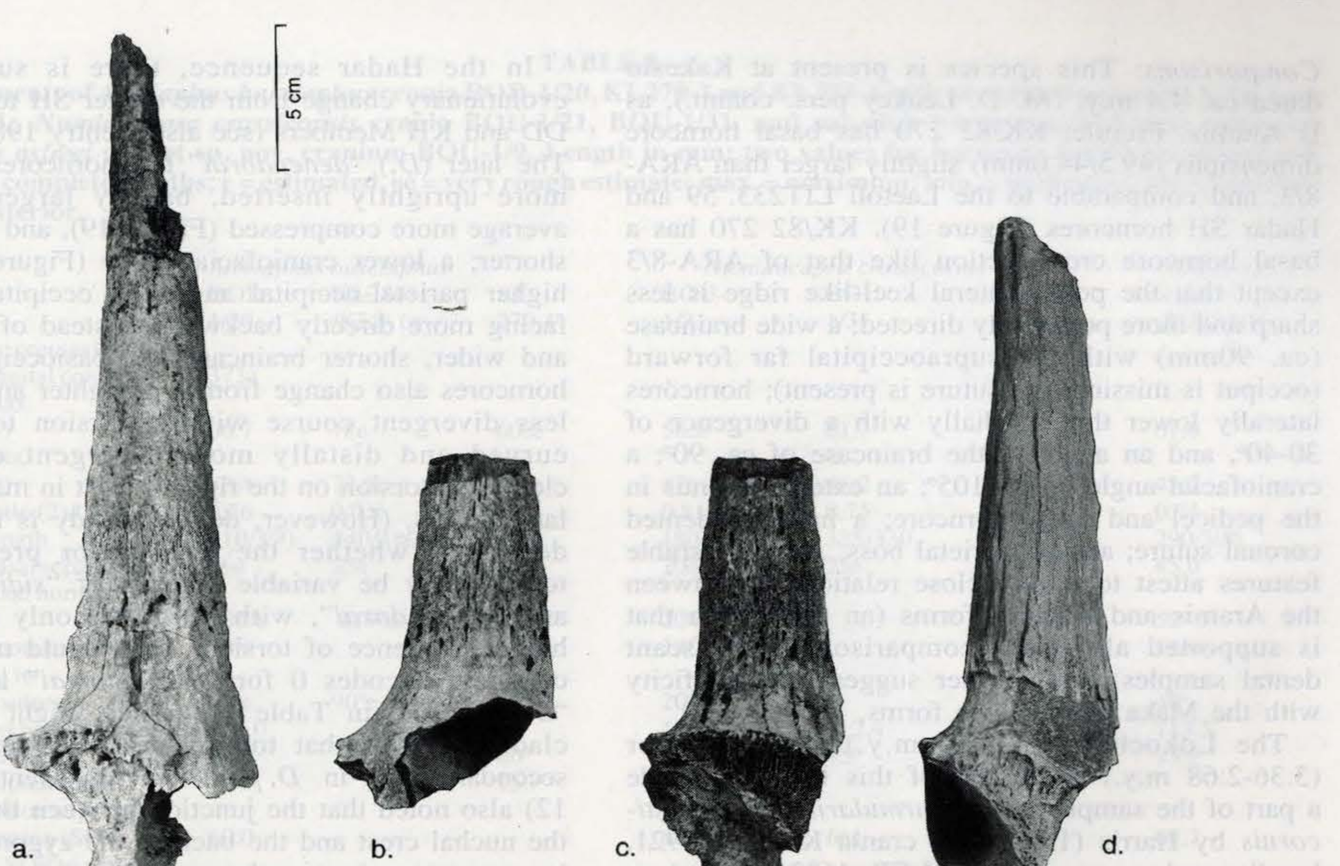

Figure 4. (*Damalops*) "*sidihakomai*" horncores (anterior always to the right; b. in right lateral view, others in medial view): a. left WEE-5/10; b. and c. right and left MAK-1/32; d. left AL 349-3 from Hadar Sidi Hakoma Member.

medially. The horncores diverge moderately, with divergence increasing slightly distally but not by a sudden or marked change in course. The maximum diameter (which is barely the maximum one and only due to the posterolateral keel) is situated at a posterior angle of ca. 70° to the midfrontal suture. There is no horncore torsion. Closely-spaced transverse ridges can be seen on the anterior surface. The extensive smooth-walled sinus in the pedicel extends well into the horncore base. The coronal suture is hardly indented. The preserved pieces suggest that the craniofacial angle was large for Alcelaphini. Left horncore WEE-5/10 closely resembles ARA-8/3 in nearly all these features, but it is larger and longer with less of a protruding posterolateral keel although it also has an approach to a sharp edge lateral to a flattened posterior basal surface (Figure 2a); its anterior surface is less markedly concave; the angle of horncore to braincase may be higher; the basal sinus is a bit more extensive (ca. 10mm into the horncore base) with thinner surrounding bone. Right and left horncores MAK-1/32 (Figure 4b, c) compare closely with the previous specimens. In the large extent of the basal sinus and the thinness of the surrounding bone MAK-1/32 resembles WEE-5/10 more; in basal horncore cross-section (Figure 2b) it is closer to ARA-8/3 by its lesser anteroposterior depth than in WEE-5/10 and in the more pronounced posterolateral approach to a keel.

Figure 3 shows the best of a few dentitions from Aramis, and Figure 17a and b two mandibles from Maka. The single right P_4 from Aramis (Table 11) is from a dentition in advanced wear. Yet its paraconid and metaconid had fused only recently, forming a simpler central enamel cavity (interior to the fusion) than in later alcelaphines. (When I mention 'simpler' central enamel cavities, in distinction to 'more complex' ones, I mean less centrally constricted, or 'dumbbell-shaped'.) It is rather square in shape with the rear part less reduced than in later alcelaphines, with a thin transversely directed valley between endostylid and entoconid. The left maxilla with P^3-M^2, ARA-8/9, and the lower molars ARA-4/1 (Figure 3) are less advanced than those of later alcelaphines in having less 'pinching' of the lateral lobes of lower molars and medial lobes of upper molars (that is, anterior and posterior constrictions of the rounded parts of the lobes), and simpler central enamel cavities. Similar observations apply to the cf. (*Damalops*) dentitions from Maka and Wee-ee which I cannot meaningfully distinguish from the small Aramis sample. Of four available P_4 from Maka and Wee-ee, only one has fusion of paraconid with metaconid, while the other three are only close to fusion.

Comparisons: This species is present at Kakesio dated ca. 4.4 m.y. (M. D. Leakey pers. comm.), as is Aramis. Frontlet KK/82 270 has basal horncore dimensions (49.5/44.0mm) slightly larger than ARA-8/3, and comparable to the Laetoli LIT233.'59 and Hadar SH horncores (Figure 19). KK/82 270 has a basal horncore cross-section like that of ARA-8/3 except that the posterolateral keel-like ridge is less sharp and more posteriorly directed; a wide braincase (ca. 90mm) with the supraoccipital far forward (occiput is missing, the suture is present); horncores laterally lower than medially with a divergence of 30-40°, and an angle to the braincase of ca. 90°; a craniofacial angle of ca. 105°; an extensive sinus in the pedicel and basal horncore; a hardly indented coronal suture; and no parietal boss. All comparable features attest to a very close relationship between the Aramis and Kakesio forms (an impression that is supported also by a comparison of the scant dental samples), and further suggest conspecificity with the Maka and Wee-ee forms.

The Lokochot (3.5-3.36 m.y.) and Tulu Bor (3.36-2.68 m.y.) specimens of this lineage include a part of the sample called *Parmularius* cf. *angusticornis* by Harris (1991: e.g., crania KNM-ER 921, locality unknown, and KNM-ER 4680 labelled as from Tulu Bor on pp. 208-209, but listed as from Lokochot on p. 299). Previous to my seeing this material, A. W. Gentry (pers. comm.) pointed out that it is related to *Damalops*. (The characters that suggest (*Damalops*) rather than *P. angusticornis* are partly reflected by the code differences between these taxa, *Dos* and *Pan*, in Table 14.) In some respects these crania are intermediate between the SH and later DD/KH fossils from Hadar. Their high horncore-to-braincase and parietal-occipital angles resemble some DD specimens. The Koobi Fora horncores resemble ARA-8/3, MAK-1/32 and WEE-5/10 in compression, and in size KNM-ER 4680 is close to MAK-1/32, and KNM-ER 921 to WEE-5/10. Many other features of these specimens compare closely with those of other fossils of (*D.*) "*sidihakomai*", including the lack of horncore torsion, the basal horncore cross-section, and cranial features. This lineage is also present at Kanapoi dated 4.1 m.y. (Leakey *et. al.* 1995). For example, frontlet KP-71 is similar to ARA-8/3 and other (*D.*) "*sidihakomai*" in degree of horncore divergence, a basal horncore that is flattened posteriorly and with a lower lateral than medial margin, basal horncore separation, huge basal sinuses, a slight anterior concavity of the horncore in lateral view, absence of torsion, and horncore length. It differs from Aramis in a higher angle of horncores to braincase, in which respect it also resembles Hadar DD more closely than Hadar SH. Its relatively high brain width is a resemblance to Kakesio that cannot be assessed on the Awash fossils.

In the Hadar sequence, there is substantial evolutionary change from the earlier SH to the later DD and KH Members (see also Gentry 1980, 1981). The later (*D.*) "*denendorai*" has horncores that are more uprightly inserted, basally larger and on average more compressed (Figure 19), and relatively shorter; a lower craniofacial angle (Figure 18) and higher parietal-occipital angle; an occipital surface facing more directly backwards instead of laterally; and wider, shorter braincase and basioccipital. The horncores also change from a straighter and distally less divergent course without torsion to a more curved and distally more divergent one with clockwise torsion on the right at least in many of the later fossils. (However, detailed study is needed to determine whether the absence or presence of torsion may be variable in each of "*sidihakomai*" and "*denendorai*", with the latter only having a higher incidence of torsion. This would necessitate changes of codes 0 for "*sidihakomai*" and 1 for "*denendorai*" in Table 14, which might have the cladistic result that torsion does not need to be secondarily lost in *D. palaeindicus*.) Gentry (1981: 12) also noted that the junction between the base of the nuchal crest and the back of the zygomatic arch is more anterior in the earlier forms, and that horncore divergence in the early SH skull AL 208-7 "does not increase continuously but changes fairly sharply at a point about one third of the distance above the base. Other horn cores from SH are curved, however, and it can only be noted that no relatively straight horn cores occur above SH." Many Hadar SH horncores are almost entirely straight except for a gentle anterior concavity, while the DD horncores are less straight. The fairly sharp change "at a point about one third of the distance above the base" that Gentry noted in AL 208-7 is absent in the Aramis and Wee-ee horncores, while the Maka horncores are broken too near the base to be certain. However, there are SH (or cf. SH) horncores that resemble the Aramis and Wee-ee ones very closely in being almost straight except for a gently concave shape anteriorly, such as AL 349-3 (Figure 4). In general, the Aramis and Wee-ee horncores resemble most the relatively straight SH versions, and not the DD horncores that show torsion or/and more curvature and tend to be more compressed basally as well as much larger. The horncores from Upper Ndolanya (*Parestigorgon gadjingeri* of Dietrich 1950) and Shungura B11 differ from the Awash fossils in having greater compression and a hint of clockwise torsion like (*D.*) "*denendorai*" to which they may belong. The horncores of *D. palaeindicus* are much longer, more compressed and backbent than all those from the Awash, with smaller bases than those from Maka and Wee-ee (Figure 19). Cranium LIT 233.'59 either from the Laetoli Beds or a later stratum was discussed by Gentry (1980) who suggested that it may be conspecific with the

TABLE 4.

Measurements of *Alcelaphus buselaphus* crania BOD-1/20, KL270-1 and KL284-1 with associated palate KL8-1a, both cf. Bodo 1; *Numidocapra crassicornis* crania BOU-1/21, BOU-1/31, and subadult horncores BOU-6/1; ovibovine *Nitidarcus asfawi* gen. et sp. nov. cranium BOU-1/9. Length in mm; two values for horncore length are preserved/estimated complete lengths; e = estimated, ee = very rough estimate; max. = maximum; min. = minimum; ant. = anterior; post. = posterior.

	Alcelaphus buselaphus			*Numidocapra crassicornis*			*Nitidarcus asfawi*
	BOD 1/20	KL284-1 /KL8-1a	KL 270-1	BOU-1/21	BOU-1/31	BOU-6/1	BOU-1/9
Skull length: premaxilla to post. occipital condyle	373e						
Horncore max. diameter (1)	66.7	78e	60ee	58.2	61.7	40.9	61.6
Horncore min. diameter (2)	50.4	72.5e	50ee	47e	46.2	34.7	45.7
Horncore ratio (2)/(1)	0.76	0.93e		0.81	0.75	0.85	0.74
Horncore length	310/390	440/480		180/?	325/330	275/275	290/300
Horncore basal separation	26e	25e		20e	25e		45.0
Angle of basal horncore divergence	100°e	110°e		20°e			50°
Angle horncore to braincase	90°e			140°			145°
Angle of (1) to midfrontal suture	90°e	90°e		20°e			40°
Width across horn pedicels	104.0			106e	112.4		113.5
Craniofacial angle	78°		80°		85°		95°e
Parietal-occipital angle			150°				
Max. separation supra-orbital foramina (SOF)	60.0			60ee	66e		69.7
Distance of SOF to anterior horncore midpoint	80e						50.0
Distance across superior orbital margins	150e			152ee	148ee		163.0
Distance orbit to horncore	60e						44.5
Braincase width at parietal-squamosal suture	82.8			96.0	107.0		98.0
Braincase length: coronal suture to occiput	33.5		52e	68.7	75.8		63.2
Distance across mastoid exposures	108e	130ee					126ee
Occipital height: top foramen magnum to occiput	44.5			46.5			58.2
Min. separation temporal lines on dorsal braincase	34.0	37e	34e				61.0
Basioccipital width across anterior tuberosities	26.0						31.8
Basioccipital width across posterior tuberosities	34.2	38e		36e			47.6
Basioccipital length: ant. to post. tuberosities	30ee	31e					35e
Distance post. M^3 - occiput	190e						
Length of nasal bones	186e						
Width across nasal bones	29.8			23.5e			
Width across ant. premaxilla	53.0						
Maxillary breadth at M^3				78.9			
Length P^{2-4}	33.6						
Length P^{3-4}				29.0			
Length/breadth P^2	9.7/9.6						
Length/breadth P^3	11.4/10.6			14.4/12.2			
Length/breadth P^4	12.0/11.5			13.3/13.5			
Length M^{1-3}	55.8	62.5e		74.5			
Length/breadth M^1	16.5/14.5			22.2/15.5			
Length/breadth M^2	19e/15e	23e/19.5e		25.8/16.1			
Length/breadth M^3	20.7/15.7	22.3/14.4		26.1/14.6			
Length P^2-M^3	87.0						
Length P^3-M^3				102.65			

Hadar lineage and closely related to *D. palaeindicus*. LIT 233.'59 is clearly closer to Hadar (*D.*) "*sidihakomai*" than to (*D.*) "*denendorai*" in the following: the absence of horncore torsion, a narrower braincase relative to length, a longer thinner basioccipital with anterior tuberosities facing more nearly anteroposteriorly and not splayed out posteriorly as in the Hadar DD form, absence of localized frontal raising between horncore bases in the form of a ridge, and a substantially lower parietal-occipital angle. LIT 233.'59 does show some advance towards (*D.*) "*denendorai*" in the more upright insertion of the horncores relative to the braincase than in Hadar SH fossils, and in a slightly shorter braincase. It is possible that there was advance within (*D.*) "*sidihakomai*" from more nearly straight horncores before 3.4 m.y. (as at Aramis, Kakesio and Kanapoi) to the beginning within the SH Member of increased variation to include more distal horncore divergence that starts fairly abruptly some distance above the base, and more rapid tapering towards the tip. LIT 233.'59 does have these tendencies and thus resembles some SH horncores while the Hadar DD form is even more advanced in these respects.

The Aramis teeth are much more advanced than the 5-4 m.y.-old Langebaanweg dentitions of *Damalacra* (Gentry 1980) in more rounded medial lobes of upper and lateral lobes of lower molars, thinner more complex central enamel cavities and more outbowed walls between stylids on lower molars. The gap in tooth advancement between Langebaanweg and Aramis is very large compared to that between Aramis and living alcelaphines given the short time between the two fossil localities. The lack of completed fusion of paraconid with metaconid in three of four P_4 from Maka and Wee-ee compares as follows with the Hadar sample: of two from Hadar SH one was fused in middle wear and one only by late wear, while the DD sample of six appears more advanced in that five were fused by middle wear. The Hadar teeth from DD are more advanced than those from SH in other respects as well, such as in greater reduction and earlier fusion of the posterior parts of P_4, more enlarged posterior lobes (entostylids) on M_3, and in generally more complex molar morphology. The Maka dentitions are closer to those from Hadar SH (e.g., compare mandibles MAK-1/76 with AL401-7 from SH and AL358-8 from DD). The incidence of P_2 can be assessed on two Hadar DD specimens in middle wear (Gentry 1981) and on two Awash specimens. P_2 was absent in both mandibles from Hadar DD. It was present in one mandible in middle wear, and absent in a subadult one, from Awash.

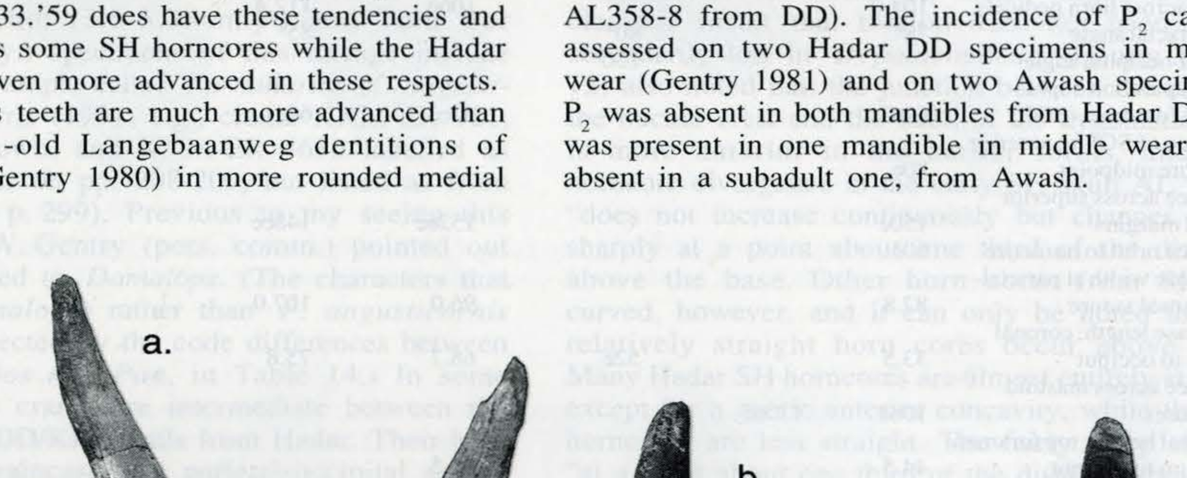

Figure 5 Partial crania from Bouri 1 in anterior view: a. *Numidocapra crassicornis* BOU-1/31, and b. holotype of *Nitidarcus asfawi* BOU-1/9.

Figure 6. Partial crania from Bouri 1 in right lateral view: a. *Numidocapra crassicornis* BOU-1/31, and b. holotype of *Nitidarcus asfawi* BOU-1/9.

Genus *Numidocapra* Arambourg 1949

Type species *Numidocapra crassicornis*
Arambourg 1949

Generic diagnosis: As for the single species.

Numidocapra crassicornis Arambourg 1949

Diagnosis: Medium to large alcelaphines with skulls nearer to high and narrow than to low and wide; frontals between horncore bases strongly raised; horncores have an oval cross-section and are more massive, longer, and often basally more strongly compressed and less basally and distally divergent, with weaker clockwise torsion from the base up on the right side, than in *Rabaticeras*. The horncores pass forwards and upwards from the base such that their basal to middle parts appear gently concave-forward in lateral view; basal horncores with low divergence and inserted closely, with small posterior angles of their maximum diameters to the midfrontal suture, and very uprightly with a large angle to the dorsal braincase; the frontal surface anterior to the horncores is not convex, but slightly concave with a shallow valley towards the midfrontal suture; supraorbital foramina widely separated; keels and basal swellings are absent on horncores and transverse ridges absent to weak; parietofrontal suture straight to gently indented anteriorly; dorsal orbital rims project less strongly than in *Rabaticeras*; postcornual fossa small to absent; braincase strongly angled relative to the face with sides parallel to slightly narrower towards the rear; no parietal boss; moderately large, somewhat shallow preorbital fossa that lacks definite rims; the nasal bones are narrow; occipital surface mainly facing backwards, narrowing a bit dorsally, with a slight vertical ridge. The teeth are large relative to skull size among alcelaphines. The occlusal morphology is quite advanced with large fairly complex central cavities and pinched buccal and lingual lobes. The premolar row is reduced. (Based on Arambourg 1949, 1979, with additions from the new Bouri fossils.)

Numidocapra crassicornis from Bouri 1 and 6
(Figures 5, 6, 17e; Tables 4, 11, 12):

There are three crania with horncores from Bouri Localities 1 and 6 dated ca. 1 m.y.: BOU-1/21 includes two pieces that join securely: a posterior cranium with both basal horncores, and an anterior piece with full maxillary dentition. BOU-1/31 is a dorsal cranium with complete right and most of the left horncore, and the subadult BOU-6/1 includes two complete horncores and fragments of the frontlet and braincase. These specimens, where the features are preserved, essentially support the diagnosis. There is variation: The unattached horncores of BOU-6/1, probably juvenile, show slight indications of diagonal ridges on the convex surfaces and stronger ones towards the concave surfaces. BOU-1/21 has the basioccipital encrusted in matrix, but one can see that it is somewhat rectangular (perhaps more so than on one *R. arambourgi* cranium from Elandsfontein) and has a longitudinal groove with flanking ridges as usual in Alcelaphini. Its occipital surface has slightly laterally-facing components and is dorsally less evenly rounded and a bit narrower than in some other alcelaphines. Its auditory bulla is somewhat thin and little inflated. The anterior piece of BOU-1/21 shows narrow posterior nasals; and a medium-sized preorbital fossa, rather shallow and lacking definite flanking rims, that is deepest over the M^2/M^3 junction. The dentition (Figure 17e) is the first known to be definitely associated with *Numidocapra*. A few other dentitions from Bouri have been assigned to this taxon (Tables 11, 12). The teeth are close in size to the smallest *Connochaetes taurinus* and the largest *Alcelaphus buselaphus* that I measured. They are large relative to skull size among alcelaphines. The occlusal morphology is quite advanced with large fairly complex central cavities and buccal and lingual lobes that are narrowed reminiscent of ovibovines. P^2 was absent in life.

Comparisons: *N. crassicornis* was described from Ain Hanech, Algeria, (Arambourg 1949), and is also known from Anabo Koma, Djibouti, Ethiopia (Bonis *et al.* 1988). Geraads (1981) considered it alcelaphine and Gentry (1978, 1990a) as a caprine. The larger Bouri specimens BOU-21 and BOU-31 bear a close resemblance in morphology to *N. crassicornis* from Ain Hanech (compare Figures 5 and 6 with Arambourg's, 1979, Plate 38: 4) and Anabo Koma. Similarities include compressed horncore bases of oval cross-section with a maximum diameter near-parallel to the midfrontal suture; very strong craniofacial angle and very high angle of basal horncore to braincase; comparable horncore length in relation to girth; and very low basal horncore separation and divergence. In fact, every feature cited in Arambourg (1979) and Bonis *et al.* (1988) seems to be present also at Bouri, but there appears to be a trend of decreasing size in this lineage from Ain Hanech (which by biochronology may be ca. 1.8-1.7 m.y. old) to Anabo Koma (ca. 1.6 m.y. old, Bonis *et al.*, 1988) to Bouri at ca. 1 m.y. (Figure 19). The most closely related species, *Rabaticeras arambourgi*, is smaller than the Bouri form and occurs in roughly coeval to later strata, thus continuing the size trend if it is indeed descended from *Numidocapra*. The Bouri form is larger than *R. arambourgi* from Rabat and Olduvai Beds III-IV and overlaps only with the largest Elandsfontein fossils. Gentry and Gentry (1978) proposed that *Rabaticeras* gave rise to *Alcelaphus*, which would further continue the same lineage, but this was questioned by Bonis *et al.* (1988). I return to this debate in the next section in which I describe the earliest known *Alcelaphus* from Bodo, ca. 0.6 m.y. in age. In addition to smaller size, the main differences of *R. arambourgi* from the Bouri *Numidocapra* are horncores that are averagely less strongly compressed, more widely separated and more divergent, with stronger clockwise torsion from the base up on the right side; a hardly marked postcornual fossa; parietals shorter especially in relation to braincase width; probably closer supraorbital foramina; and more strongly projecting dorsal orbital rims.

Gentry and Gentry (1978: 417) considered four specimens from Olduvai Bed II, SHK II 1953.280, SHK II surface 1957.92, SHK II 1953.234, and BK II East 1953.067/5460, as similar to *R. arambourgi* yet aberrant in comparison with it: "One [alternative], which we favour, is to regard them as a variant within the *R. arambourgi* lineage, and another is to regard them as possibly linked with ... *Numidocapra crassicornis* Arambourg (1949: 290) from Ain Hanech ... If the Olduvai horn cores are related to *Numidocapra*, it would be good to know whether they should be classified as Caprinae similar to *Procamptoceras brevicornis* ... or as Alcelaphini." I suggest assignation of these Olduvai specimens to *N. crassicornis*. BOU-1/31 and BOU-1/21 have strong resemblances to them: a size as large as the largest Olduvai specimen and high compression in BOU-1/31; weak torsion and forward curvature, although the Olduvai horncores may be even less curved. The Olduvai Bed II levels SHK and BK are dated ca. 1.7-1.4 m.y., comparable in age to Ain Hanech and Anabo Koma. On Gentry and Gentry's (1978) suggestion that *Numidocapra* may be caprine, the dentition of BOU-1/21 (Figure 17) does not support membership of Caprini. The central cavities are too complicated, probably too wide open, and the dentition is large relative to other skull measures whereas Caprini have relatively small teeth. The teeth resemble those of ovibovines in upper molars that are long relative to width and have pointed medial lobes; but the premolar row is too short, and the central cavities are not narrow enough for Ovibovini, quite apart from the numerous differences in horncore and skull morphology. The caprine *Procamptoceras brevicornis* from Seneze (Schaub 1923) differs decisively from the Bouri form: apart from being very much smaller (with basal horncore size that compares with the smallest Alcelaphini in Figure 19), it has no horncore torsion and much less distal divergence, hollows more than half-way up the horncore of which there is no sign at Bouri; and a much lower angle of the basal horncore to the braincase.

(*R.*) *porrocornutus* from Swartkrans resembles the Bouri fossils in strong basal horncore compression (shared with BOU-1/31) and widely separated supraorbital foramina. It differs in higher separation between horncore bases and between these and the supraorbital foramina, more divergent

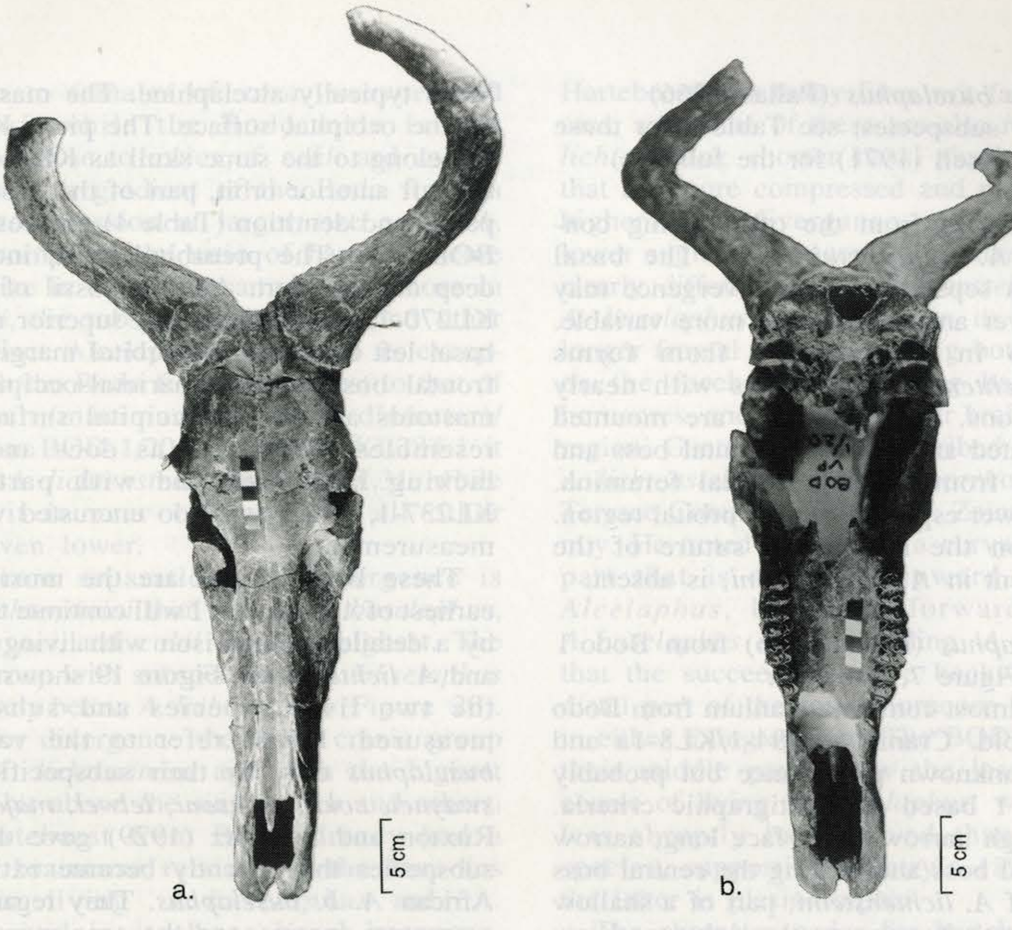

Figure 7. *Alcelaphus buselaphus* cranium BOD-1/20 from Bodo 1: anterior (a.) and palatal (b.) views.

horncores with strong and closely spaced transverse ridges, more prominent orbits, and in a higher craniofacial angle and a lower angle of the horncore to the cranium.

If *Numidocapra* and *Rabaticeras* are ancestor and descendant in their own monophyletic group separate from *Alcelaphus*, then the correct name for this group is *Numidocapra* Arambourg 1949. I suggest that nomenclatural changes at the generic level will be better made with additional information. It is possible that additional support emerges for a single ancestral-descendant lineage from *Numidocapra* to *Rabaticeras* to *Alcelaphus*. In that case the name of the group would be *Alcelaphus* with the other two generic names as synonyms. Also, a generic revision would be better based on a cladogram that includes *N. crassicornis* and with a branching sequence better resolved than the polytomy at node 18 in Figure 21.

It is interesting that the largest form in this proposed lineage was widespread at some time in the interval 1.8-1.4 m.y., implying continuity between the North African and Somalian-eastern Ethiopian biotas and their extension southwards to include at least the Olduvai area. In contrast, by the time of Bouri at 1 m.y. and some time within the interval of Olduvai Beds III-IV (ca. 1.3-0.7 m.y.), the Olduvai representative was a smaller and changed descendant while contemporaneous *Numidocapra* still persisted in eastern Ethiopia. This may indicate the effects of global cooling during the earlier time, and of later warming that affected Olduvai while cooler conditions persisted at higher latitudes and altitudes in the Awash area.

Genus *Alcelaphus* De Blainville, 1816

1775	*Bubalis* Frisch
1820	*Bubalis* Goldfuss
1827	*Damalis* H. Smith
1827	*Acronotus* H. Smith
1912	*Sigmoceros* Heller
1979	*Sigmoceros* Vrba

Type species *Alcelaphus buselaphus* (Pallas 1766)

Generic diagnosis: Medium to large sized alcelaphines with elongated crania that are moderately to very high and of low to medium width; horncores inserted far behind the orbits on a moderately to very long boss that results from backward protrusion of the frontal bone and possibly also from pedicel fusion; horncores with posterior flattening and with a large angle to the midfrontal suture; moderately long horncores that vary in compression and have strong clockwise torsion from the base up on the right; horncore tips recurving to point downwards in mature individuals; distance from posterior horncores to occiput short to extremely short; small craniofacial angle and large parietal-occipital angle; preorbital fossae of moderate size.

Alcelaphus buselaphus (Pallas 1766)

(Includes many subspecies; see Table 2 for those to which I refer; Ansell (1971) for the full list.)

Diagnosis: Differences from the other living congeneric species *A. lichtensteini* are: The basal horncores are less separated. Their divergence may be as high to lower and is therefore more variable. They vary also in compression from forms resembling *A. lichtensteini* to forms with nearly round cross-sections. The horncores are mounted on a more elongated and narrower frontal boss and are more distant from the supraorbital foramina. The skull is narrower especially in the orbital region. A raised boss on the midfrontal suture of the forehead, as present in *A. lichtensteini*, is absent.

Alcelaphus buselaphus (Pallas 1766) from Bodo 1
(Figure 7, Table 4):

BOD-1/20 is an almost complete cranium from Bodo 1, ca. 0.6 m.y. old. Crania KL284-1/KL8-1a and KL270-1 are of unknown provenance but probably also from Bodo 1 based on stratigraphic criteria. BOD-1/20 is a high narrow skull; face long, narrow with a long frontal boss and lacking the central boss on the forehead of *A. lichtensteini*; part of a shallow postcornual fossa can be seen on the right; toothrow substantially anterior to the orbit; a long diastema; an extensive nasal-maxillary contact; anterior zygomatic arch with a strong deep ridge; elongated thin nasals with a central indentation of the frontonasal suture; horncores with bases flattened posteriorly (Figure 2c), marked clockwise torsion on the right, strong transverse ridges, strong basal divergence with distal parts reapproaching and with a downward component; horncores surprisingly long relative to basal size; oval and moderately sized foramen ovale; the spaces for the missing auditory bullae look fairly large; the basioccipital has a longitudinal groove with flanking ridges; occipital surfaces face partly laterally on either side of a moderately marked median vertical ridge; mastoids are large; a strongly developed preorbital fossa with superior and ventral rims; palate strongly domed upwards in the centre, with median palatal indentation far forward of lateral ones and narrowed to a point; the upper teeth not noticeably less advanced than in living *Alcelaphus* with comparably long premolar rows with P^2 present.

KL284-1 is a frontlet, with an adjoining ventral cranial piece, of a large hartebeest. It was encrusted with matrix at the time of study. It has fairly long, nearly complete horncores with little basal but stronger distal compression, strong clockwise torsion and basal divergence, curved back down in lateral view and slightly outwards in anterior view towards the tips, transverse ridges that are very faint near the base but marked over the curved anterior surfaces, and large smooth-walled basal hollows that extend some 20-30 mm into the horncore. The basioccipital looks typically alcelaphine. The mastoid is entirely on the occipital surface. The piece KL8-1a appears to belong to the same skull as KL284-1. It includes the left anterior orbit, part of the nose, and a partial palate and dentition (Table 4) that resemble those of BOD-1/20. The preorbital fossa includes a fairly deep anterior part. Another fossil of this species is KL270-1, a well-preserved superior cranium with a basal left horncore and orbital margin, a substantial frontal boss, a huge parietal-occipital angle, and mastoids all on the occipital surface. It strongly resembles BOD-1/20, as does another cranium lacking horncores and with partial dentition, KL237-1, which was too encrusted with matrix for measurement.

These Bodo fossils are the most complete and earliest of *Alcelaphus*. I will continue their description by a detailed comparison with living *A. buselaphus* and *A. lichtensteini*. Figure 19 shows the samples of the two living species and subspecies that I measured. I will refer to the varieties of *A. buselaphus* only by their subspecific names *tora*, *swaynei*, *cokii*, *jacksoni*, *lelwel*, *major*, and *caama*. Ruxton and Schwarz (1929) gave data on another subspecies that recently became extinct, the North African *A. b. buselaphus*. They regarded *caama* as a separate species, and the *tora-swaynei-cokii* group as more plesiomorphic than other *A. buselaphus* in their weaker, less twisted horns on a shorter, narrower frontal boss, but as more advanced in high horncore divergence. KL284-1 is much larger than BOD-1/20 and KL270-1, although the first two both have adult dentitions. This suggests that KL284-1 is male and the other two female, and I will refer to the fossils as such. The basal skull length of the female BOD-1/20 is closest to female means of *tora*, *swaynei*, *cokii*, *lelwel*, *caama*, *A. lichtensteini*, shorter than female means for *jacksoni* and *major*, and longer than values for one female and one male of the extinct *buselaphus*. Space constraints in Figure 19 did not allow me to show all individual points for hartebeests and information on sex. In a plot of all the data, BOD-1/20 and KL270-1 fall into a cluster of mostly female living hartebeests, and lie very close to *swaynei*, *tora* and *A. lichtensteini* females. KL284-1 is comparable in size to the largest horncores in *A. buselaphus*, namely of *caama*, *jacksoni*, and *major* males. (My comparative sample included no males of *tora* and *swaynei* which are today geographically closest to the Awash, the Tora Hartebeest in the Blue Nile area and Swayne's Hartebeest in eastern Ethiopia and Somalia.) Horncores in *caama*, *jacksoni*, and perhaps *major* are very little compressed and show a growth gradient towards lower compression with increasing size (Figure 19). Horncores in *swaynei*, *cokii*, and especially *tora* and *A. lichtensteini*, are more compressed. The sample of five *A. lichtensteini* suggests a growth gradient towards greater compression with increasing size. The Bodo females are very close to females of *tora*, *swaynei* and *A. lichtensteini*, while the Bodo male is less compressed and close to males of *cokii* and *major*. That is, the growth gradient of the Bodo form is towards less compression at larger size as in *A. buselaphus*. I compared the ratio of basal horncore size to tooth size in the Bodo sample with those in *A. lichtensteini*, the subspecies *jacksoni*, and other living and extinct Alcelaphini. The ratio is exceptionally large in the Bodo form and closest to that of *A lichtensteini*: (maximum horncore diameter)/(length M^{1-3}) for BOD-1/20 is 1.20, for KL284-1 it is 1.25, for an *A. lichtensteini* skull it is 1.31, while for *jacksoni* it is near 1.0, and for all other alcelaphines even lower.

Basal horncore separation and divergence is higher in *A. lichtensteini* than in any *A. buselaphus*, with *tora*, *swaynei*, and *cokii* the next highest. The Bodo fossils group with subspecies of *A. buselaphus* and fall decisively below *A. lichtensteini* (Figure 20). Surprisingly, for divergence the Bodo crania group closely with *A. lichtensteini* and with the highest *cokii*, being a bit above the single *tora* and others. This early hartebeest from Bodo already had a strongly bent braincase relative to the face (as extreme as in living *A. buselaphus* and *A. lichtensteini*), and in its large basal horncore-midfrontal angle it resembles *A. buselaphus* closely and may be less advanced than *A. lichtensteini* which has an even larger one (Figures 2, 18). In hartebeests, the angle between horncores and cranium increases with increasing horn size so that females tend to have less upright horncores than males. This angle in the female BOD-1/20 is closest to those of *tora*, *cokii*, and small *A. lichtensteini*, and substantially lower than those of other subspecies of *A. buselaphus*. In its moderately widely separation of the supraorbital foramina, BOD-1/20 lies above the *caama* mean, and close to other *A. buselaphus* and to the lowest *A. lichtensteini*. In the lengthening of the frontal boss, as measured by the distance from supraorbital foramina to basal horncores, the Bodo female is higher than *swaynei* and *cokii*, as advanced as *tora* and other *A. buselaphus* and above even the largest values in *A. lichtensteini*. In the width of its frontal boss, or fused pedicels, the Bodo female is close to *tora* and to the *jacksoni* and *caama* means, above females of *cokii*, *swaynei*, *jacksoni* and *caama*, and substantially below female *A. lichtensteini*, while the Bodo male has a boss as wide as the largest *A. lichtensteini*. Breadth across the mastoids and occipital height in the Bodo fossils are lower than in *A. lichtensteini* and more comparable to those in *A. buselaphus*.

In sum, in all respects the Bodo form resembles one or more of the *tora-swaynei-cokii* group, the most plesiomorphic group in *A. buselaphus*. In some of these features it is clearly less advanced than the specialized *jacksoni-major-caama* group. It has particularly close resemblances to the Tora Hartebeest that today lives not far from the Awash area, and some of these are also resemblances to *A. lichtensteini*: shorter basal skull length, horncores that are more compressed and possibly also longer, higher basal divergence and separation, and the lower angle of horncore to cranium. The Bodo form clearly differs from *A. lichtensteini*, and resembles *A. buselaphus* as a whole in its more slender and longer frontal boss, in lacking both a central raising on the forehead and strong basal expansion of horncores, and in its narrower braincase and mastoid region. Gentry (1990b) described the earliest secure *A. lichtensteini* specimen, a horncore from the Lower Terrace Complex of Semliki, Zaire, dated ca. 0.5-0.3 m.y. He noted that it has a curvature in the middle part that is not only upward as is typical of *Alcelaphus*, but more forward than in living *A. buselaphus* and resembling *A. lichtensteini*, and that the succeeding curve backwards in the more distal part of the fossil horncore is less abrupt than in either living species. The BOD-1/20 horncores in their middle parts show the less forward-curving course of living *A. buselaphus*, while their tips are less abruptly back-curved than in either living species, supporting Gentry's (1990b) notion that the latter is plesiomorphic.

The character codes for hartebeests in Table 14 were based on living *A. buselaphus* and *A. lichtensteini*, independently of the conclusion that the Bodo form belongs to *A. buselaphus*. It is a reasonable inference that *A. buselaphus* at its origin did not yet have the high level of polymorphism that it has today and, second, that *A. buselaphus* from Bodo should most closely resemble the common ancestor shared with *A. lichtensteini* and, third, that the features which Tora and Lichtenstein's Hartebeests share with that from Bodo, are plesiomorphic retentions. This hypothesis is supported for most of the characters by the present cladistic result and by comparison with the outgroups of the *A. buselaphus-A. lichtensteini* sister-group. These outgroups are the potential direct ancestor *Rabaticeras arambourgi*, (*R.*) "*lemutai*", (*R.*) *porrocornutus*, and *Damalops palaeindicus* (Figure 22). The observed strong horncore compression in all these outgroups, even in some populations of *R. arambourgi* although this taxon is variable (Figure 19), supports the notion that higher compression is plesiomorphic for the living *A. buselaphus* and *A. lichtensteini*. The hypothesis that horncores of intermediate length relative to basal size are plesiomorphic for the entire group from node 14 in Figure 21, with *D. palaeindicus* evolving increased and the *jacksoni* group decreased length, is consistent with the evidence. Horncore length is not known for (*R.*) "*lemutai*" and (*R.*) *porrocornutus*, but for some *R. arambourgi* it is intermediate, comparable to Bodo, shorter than in *D. palaeindicus* and longer than in advanced *A. buselaphus*. Basal horncore divergence is intermediate in *D. palaeindicus*, (*R.*) "*lemutai*", (*R.*) *porrocornutus* and varies in *R. arambourgi* with some Elandsfontein horncores being higher but still lower than *A. lichtensteini* and the Bodo *A. buselaphus*. Therefore the present hypotheses, that the high divergence of the last two forms is plesiomorphic and that *R. arambourgi* is ancestral to them, require that higher divergence was attained by at least one late population of *R. arambourgi* as indicated by the ambiguous change at node 27 in Figure 21 (character 9: 1->2). If true, then this population is likely to have been derived from a form such as the Elandsfontein *R. arambourgi*. Basal horncore separation is intermediate in *D. palaeindicus*, (*R.*) *porrocornutus* and *R. arambourgi* (Figure 20). This is consistent with the hypothesis that horncore separation was pleisiomorphically intermediate and then narrowed towards the advanced *jacksoni* group and widened towards *A. lichtensteini*. (In that case (*R.*) "*lemutai*" would have had to evolve independently a separation as high as in *A. lichtensteini*.) The angle of the basal horncore to the cranium was scored conservatively such that the score 1 was given only to taxa with the highest values (Table 14). *D. palaeindicus*, (*R.*) "*lemutai*" and (*R.*) *porrocornutus* are lower than *R. arambourgi* and the average *A. buselaphus*, which supports the notion that the primitive state before origin of *R. arambourgi* was indeed a lower angle. *A. lichtensteini* has a ?-code as it varies from moderately high in the smallest adults to very high in the largest, and this allowed the cladistic outcome of a high angle as a synapomorphy of *R. arambourgi* and living hartebeests. A less conservative coding would have to acknowledge that *R. arambourgi* has a higher angle than even the highest *A. buselaphus*, namely the *jacksoni* group (and an even higher angle than the other supposed descendants: the Bodo, Tora and Lichtenstein's Hartebeests). Thus the hypothesis that a lower angle was plesiomorphic for living hartebeests does not fit the data without admitting homoplasy.

Recently there has been increasing interest in our field in heterochrony – particularly in the kind of paedomorphosis known as neoteny and in its inverse, the form of peramorphosis called acceleration – in relation to phylogeny and climate. (Reviews and examples can be found in Vrba *et al.* 1994; Vrba 1994, in press). Heterochrony includes all evolutionary changes in the timing of appearance of characters during ontogeny, and in the rates of shape and size development. In neoteny the descendant adult, in spite of being of the same size or larger, retains phenotypic characters that appeared in ancestral juvenile stages. In acceleration the descendant adult, in spite of retaining the ancestral size or being smaller, has characters that appear more advanced than the ancestral adult – or 'hyper-adult'. On average colder climates are often associated with larger bodies (Bergmann's Rule) that retain neotenic components; while warmer environments correlate with smaller bodies and with features that evolved by acceleration. Thus, evolution in warmer climate by acceleration is expected to result in relative increases in features such as horn curvature, torsion and girth, angulation of the basal horncore to the midline, length of frontals and frontal bosses, and premolar length (all of which were relatively larger in the ancestral adults than juveniles), and decreases in other characters such as separation of horncores and supraorbital foramina (which generally become relatively reduced with growth to maturity). These are precisely most of the changes that did evolve towards *Alcelaphus* (given descent from *Rabaticeras*). Thus acceleration in response to occupation of increasingly warmer habitats provides a viable hypothesis for evolution of a lineage from *Numidocapra* to *Rabaticeras* to *Alcelaphus*. Size reduction also occurred within *Numidocapra* and between it and *Rabaticeras* and early *Alcelaphus*. However, one cannot explain by acceleration the evolution of less steep horncore insertions (with lower and higher angles of horncores to braincase and face respectively), that we observe in *Alcelaphus* if it evolved from *Rabaticeras*. As noted above, in hartebeests and many other bovids steepness of horncore insertions tends to increase with maturation and growth to larger sizes. For this character in *Alcelaphus* one would need to invoke the simpler kind of heterochrony called hypomorphosis (the smaller descendant adult has the subadult shape of the ancestor at that size), evolving in mosaic fashion alongside the overall imprint of acceleration. Bonis *et al.* (1988) noted the problem that the carriage of the head in *Numidocapra* and *Rabaticeras* would have differed from that in living *Alcelaphus* because the horns of the first two are more extremely angled to the braincase with lower basal angles to the face. I agree with that. Based on it, they suggested that *R. arambourgi* is not a suitable ancestor of living *Alcelaphus*. Nevertheless, I suggest that Gentry and Gentry's (1978) notion that *Alcelaphus* evolved from *Rabaticeras* remains viable. There are in fact models that predict mosaic evolution in the same lineage, of different kinds of heterochrony for different characters depending on their ancestral growth profiles, as required in this case (e.g., Vrba 1994, in press).

Genus *Megalotragus* Van Hoepen, 1932
1925 *Rhynotragus* Reck: 451
1932 *Pelorocerus* van Hoepen: 65
1953 *Lunatoceras* Hoffman: 48
1965 *Xenocephalus* Leakey: 62
1984 *Rusingoryx* Pickford and Thomas: 445

Type species *Megalotragus priscus* (Broom 1909)

Generic diagnosis: Gentry and Gentry (1978:356) gave the diagnosis: "Very large extinct alcelaphines, including the largest known, with narrow skulls and

TABLE 5.

Measurements of *Megalotragus kattwinkeli* crania BOU-2/21, BOU-1/99, frontlet BOU-2/20, and horncores BOU-1/6 and MAT-1/13; and cranium of *?Oreonagor*/*?Megalotragus* sp. BOU-1/97. Length in mm; two values for horncore length are preserved and estimated complete lengths; e = estimate, ee = very rough estimate; max. = maximum; min. = minimum.

	Megalotragus kattwinkeli					*?O./?M.* sp.
	BOU-2/21	BOU-1/99	BOU-2/20	BOU-1/6	MAT-1/13	BOU-1/97
Horncore maximum diameter (1)	68.2	76.6	90e	98.3	70.0	68.8
Horncore minimum diameter (2)	53.0	67.4	77e	80.0	59.3	55.8
Horncore length	300/420					390/460
Horncore basal separation	33.0	40ee				65e
Angle of horncore divergence	40°					55°e
Angle horncore to braincase	60°e	80°ee				80°e
Angle of (1) to midfrontal suture	70°e	135°e				50°e
Width across horn pedicels	115.5	170ee				135.0
Craniofacial angle	110°e	110°e				110°
Parietal-occipital angle	140-160°					130°
Maximum separation supra-orbital foramina (SOF)	110ee					
Distance SOF to horncore	118e					
Distance orbit to horncore	83e					
Braincase width at parietal-squamosal suture		106.5				104.0
Braincase length: coronal suture to occiput	15e					35e
Min. separation temporal lines		86.7				75.2
Basioccipital width across anterior tuberosities						37.5e
Basioccipital width across posterior tuberosities						41e
Basioccipital length: anterior to posterior tuberosities						45ee
Length M^{1-2}	58.5					
Length/breadth M^1	27.5/19.7					
Length/breadth M^2	31e/?					

horncores inserted obliquely in side view, behind the level of the orbits and close together, with a torsion that is clockwise from the base upwards on the right side; molar teeth tending to have a simple occlusal pattern; very short premolar rows; long legs." The present analysis adds the following. The preorbital fossae are minimally developed to absent. The distance between the coronal suture and the occiput on the dorsal braincase is markedly reduced, while the occipital surface is relatively high and wide across the mastoids. The tendency to at least incipient development of horn pedicel fusion into a joint boss is present within each species. Although the nasal area of the face is unknown in *M. priscus*, an upward-doming of the posterior nasals and adjacent bones to form a crest probably characterizes the entire genus, as also concluded by Gentry *et al.* (1995).

Megalotragus kattwinkeli (Schwarz 1932)

1925 *Rhynotragus semiticus* Reck: 451, unnumbered figure
1932 *Alcelaphus kattwinkeli* Schwarz: 4, no figure
1937 *Gorgon taurinus semiticus* Schwarz: 60, 85, in part
1965 *Alcelaphus howardi* Leakey: 60, Plate 79
1965 *Xenocephalus robustus* Leakey: 62, Plates 81 and 82
1965 Incertae sedis Leakey: 69 (d) in part
1976 *Megalotragus ?kattwinkeli* Gentry: 285
1976 *Megalotragus* cf. *M. kattwinkeli* Harris: 298
1978 *Megalotragus kattwinkeli* Gentry and Gentry: 356, Plate 12:2, Plate 13
1985 *Megalotragus* sp. nov. Harris: 156
1991 *Megalotragus isaaci* Harris: 187, Figures 5.46 to 5.48

Diagnosis: An alcelaphine that varies in size from large-medium to very large. Horncores short to moderately long, with transverse ridges that are better developed above the base, insertions that vary from far behind the orbits to very far such that their bases overhang the occipital surface, with associated variation in the distance from horncore bases to occiput; horncore bases strongly angled to the midfrontal suture, with compression that is mostly low at the base and increases towards the mid-horncore. Divergence above the horncore bases varies from low to moderate, with tips that have a greater tendency to reapproach and to curve inwards distally in the smaller individuals whereas in the larger individuals they curve less inwards and rather more upwards. In smaller individuals most of the basal part of the horncore is anteriorly concave. Towards larger skull sizes there is an increasing tendency to strong backward curvature of the horncore above a more upright basal stem. The horncores have anterior basal swellings that are especially marked in larger horncores with well-developed basal backward curvature. There is a

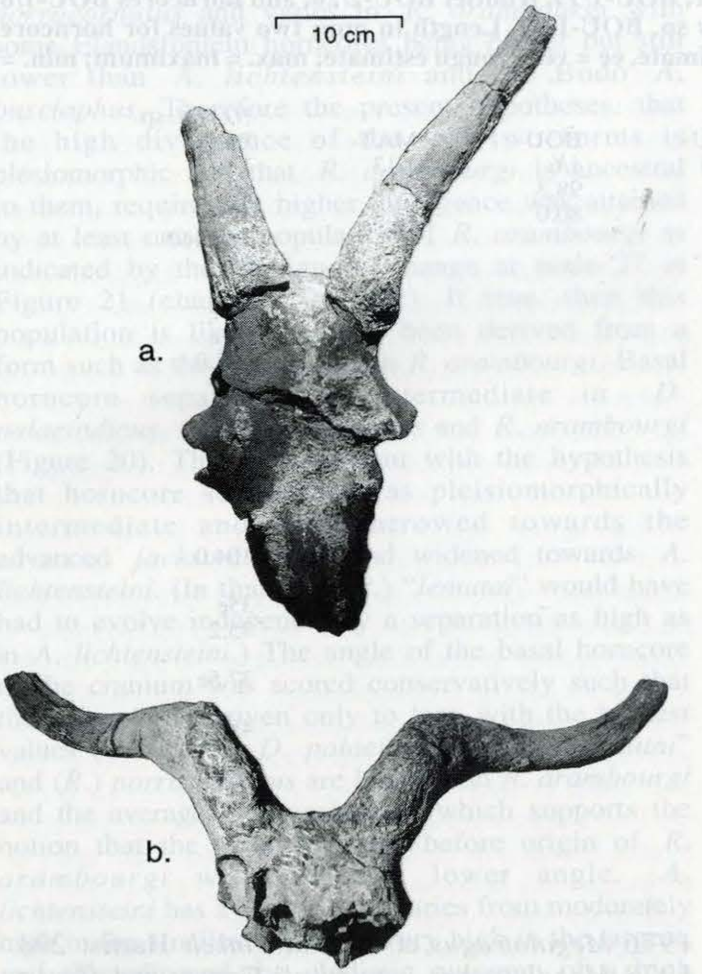

Figure 8. Partial crania from Bouri 1 in anterior view: a. BOU-2/21 of *Megalotragus kattwinkeli* and b. BOU-1/97 of *?Oreonagor/?Megalotragus* sp.

variable tendency, increasing in larger specimens, for the frontals between the horncores to be raised such that the pedicels appear fused into an incipient joint boss. The orbits project prominently relative to the narrow distance across the horn pedicels. A prominent nasal crest, formed by upward-doming of the posterior nasals and adjacent bones, is present. The cranium has an occipital surface that faces mainly backwards and only a little laterally and has a median vertical ridge, a wide basioccipital with large anterior tuberosities, and small, little inflated auditory bullae.

Comments on synonymy and diagnoses: The nature and sequence of discoveries in this group has resulted in a complicated systematic history (Gentry *et al*. 1995). The holotypes of *Rhynotragus semiticus* and *Megalotragus kattwinkeli* were collected during a 1913 expedition to Olduvai Gorge. Because it was thought that they had been destroyed during the second world war, Gentry and Gentry (1978) designated as neotype of *M. kattwinkeli* the skull BM (NH) M21447. They were unsure of the affinities of *R. semiticus* just as Reck (1925, 1935) had been. Pickford and Thomas (1984) described material from Late Quaternary strata on Rusinga Island in Kenya as a new genus and species of Alcelaphini, *Rusingoryx atopocranion*. They did not mention any possible affinity of this form with *Megalotragus*, just as by that date no one had yet suspected any affinity between *Rhynotragus* and *Megalotragus*. It was not until 1991 that the close relationship between these three taxa was recognized. Harris (1991) described new fossils from Koobi Fora as a new species *M. isaaci*. He argued that *Rusingoryx* is a junior synonym of *Megalotragus*, and that *M. atopocranion* is a species separate from other members of the genus. My own analyses strongly support both of these conclusions (see also Gentry 1990a; and Gentry *et al*. 1995). Pickford and Thomas (1984) thought that some features of *atopocranion* are unique among bovids, notably the very large craniofacial angle. I agree with Harris (1991) that this angle only appears so large because the nasals and anterior frontals are strongly domed upwards in a nasal crest; and that this nasal crest in *atopocranion* is homologous with the inflated nasal region that he described in *M. isaaci* and that Reck (1935) noted in *R. semiticus* from Olduvai.

Recently Gentry *et al*. (1995) reported the discovery, during 1992 in the Universitäts-Institut fur Paläontologie und Historische Geologie in Munich, of many of the bovid fossils from the 1913 Reck expedition to Olduvai Gorge, including the holotypes of *R. semiticus* and *M. kattwinkeli*. They reported that a horncore listed by Schwarz (1937) as *Gorgon taurinus* fits exactly onto the *R. semiticus* holotype, and confirmed that *R. semiticus* is conspecific with *M. kattwinkeli*. With this astonishing discovery, the name *Rhynotragus* became the senior generic synonym for *Megalotragus*, and *R. semiticus* the senior specific synonym for *M. kattwinkeli*. A petition to the International Commission on Zoological Nomenclature from A. W. and A. Gentry to conserve the use of the names *Megalotragus* and *M. kattwinkeli*, which have been much used in recent years, is pending.

The new fossils of *Megalotragus* from Bouri confirm many essential conclusions of Harris (1991) and Gentry *et al*. (1995). Yet they do add yet a new perspective. Harris (1991) argued that the Koobi Fora form is a new species, *M. isaaci*, separate from *M. kattwinkeli* but conspecific with *R. semiticus*. In partial contrast, Gentry *et al*. (1995) regarded *R. semiticus* as a synonym of *M. kattwinkeli* as known from Olduvai Beds II to IV and elsewhere, and accepted *M. isaaci* as a separate species. I shall argue below that the combination of features preserved in the new Bouri fossils, in the context of all the other evidence, suggests that all three belong to a single variable species, namely that both *R. semiticus* and *M. isaaci* are synonyms of *M. kattwinkeli*. Thus my diagnosis refers both to

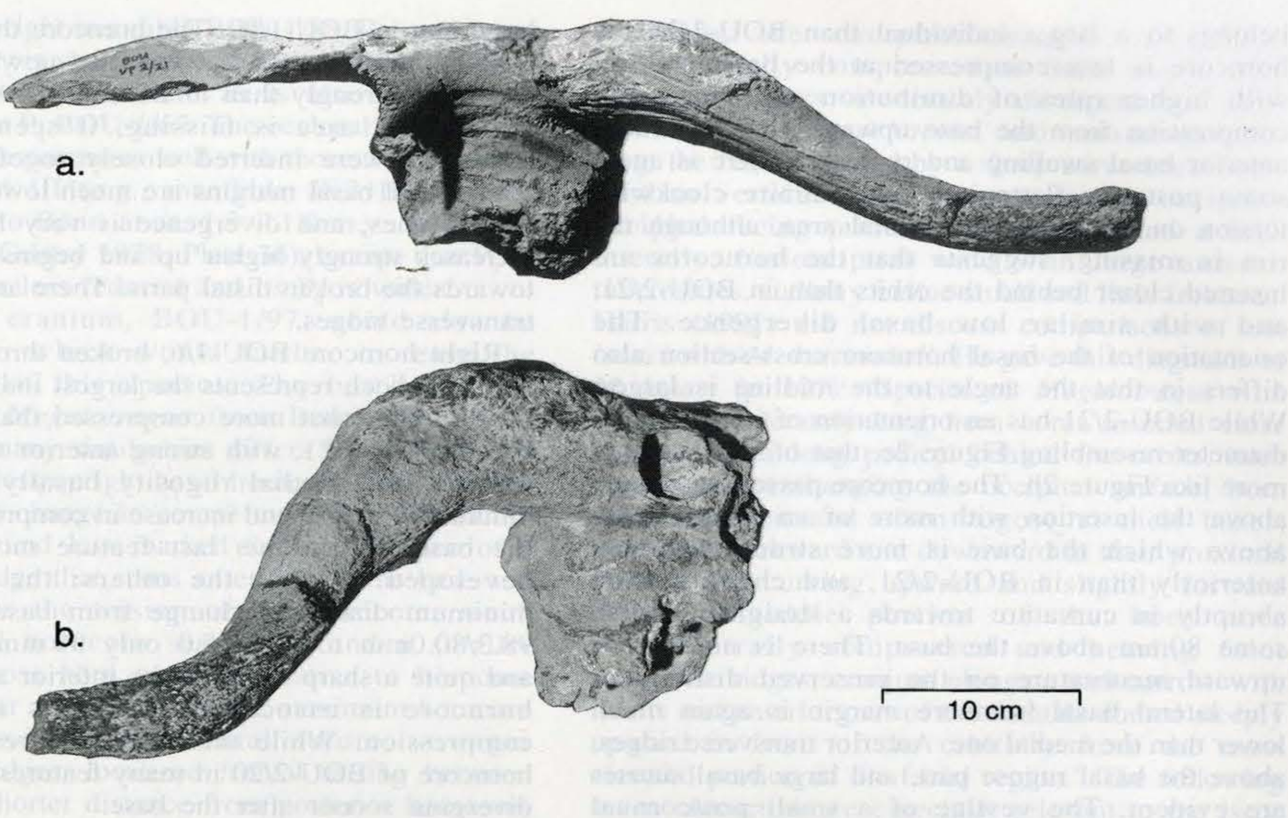

Figure 9. Partial crania from Bouri 1: a. BOU-2/21 of *Megalotragus kattwinkeli* in left lateral view, and BOU-1/97 of ?*Oreonagor*/?*Megalotragus* sp. in right lateral view.

characters cited in Gentry and Gentry's (1978:356) diagnosis of *M. kattwinkeli*, and to characters in Harris's (1991:187) diagnosis for *M. isaaci*, and differs from both in being the diagnosis of a more variable species.

Megalotragus kattwinkeli from Bouri 1-2 and
Matabaietu 1 (Figures 8, 9, Table 5):

Bouri 1 and 2, ca. 1 m. y. old, have yielded four cranial fossils of *Megalotragus*: crania BOU-2/21 and BOU-1/99, frontlet BOU-2/20, and horncore BOU-1/6. BOU-2/21 (Figures 8, 9) includes a large part of the face up to parts of both orbital rims and much of the nasal and maxilla bones, most of the left and the basal part of the right horncore, the dorsal braincase, and some associated teeth. The horncore bases are compressed, with some posteromedial flattening, and not particularly swollen anteriorly. The horncores are quite long, near 420 mm in life, and have definite clockwise torsion on the right side. They are inserted very far behind the orbits and close to the occiput with their major axes at a fairly strong angle to the midfrontal suture (the posterior angle being ca. 70°), and at a moderate angle to the braincase. They pass gradually backwards above the insertion such that the bases are moderately convex anteriorly, then straighten out in their mid-sections, and recurve gently upwards towards the tips. They are inserted closely together, with their lateral basal margins much lower than their medial ones, and with divergence that is basally low, increases higher up, and lessens slightly towards the tips. Fairly well-marked transverse ridges are evident anteriorly above the basal third of the horncore. The frontals between the horncores are raised, and from the back this raising can be seen to be localized underneath the horncores such that the pedicels appear fused into an incipient joint boss. The orbits project outwards quite prominently relative to the narrow diameter across the horn pedicels. There is a small supraorbital foramen on the right set almost flush with the slightly convex frontal, with a long groove anterior to it, and notably distant from the midline and the horncores. A long, shallow, thin postcornual fossa can be seen on the left. Near the anterior orbit, the posterior nasals and adjacent bones start to dome upwards strongly to form a prominent, rounded nasal crest that extends forward on the face. Enough of the lateral face is preserved to determine that there was either no preorbital fossa or only a very small one. The dorsal braincase behind the horncores is extremely abbreviated with a supraoccipital exposure that is anteroposteriorly so thin that it is confined to the nuchal crest. The facial updoming and extreme shortness of the exposed braincase make it difficult to judge the craniofacial angle, but my estimate makes it surprisingly high, ca. 110°, while the parietal-occipital angle was very high, perhaps as high as 160°. The occipital surface faces mainly backwards. It has a rounded dorsal margin that shows the beginnings of only gentle lateral concavities towards its missing basal parts. The very hypsodont teeth show that this was a young adult.

Cranium BOU-1/99 includes about 200 mm of the right basal horncore and the dorsal braincase. It belongs to a larger individual than BOU-2/21. Its horncore is less compressed at the base, shorter, with higher rates of diminution and increasing compression from the base upward, and with more anterior basal swelling and rugosity. There is again some posterior flattening, and definite clockwise torsion on the right. The orbital area, although the rim is missing, suggests that the horncores are inserted closer behind the orbits than in BOU-2/21, and with similar low basal divergence. The orientation of the basal horncore cross-section also differs in that the angle to the midline is larger: While BOU-2/21 has an orientation of its maximum diameter resembling Figure 2e, that of BOU-1/99 is more like Figure 2h. The horncore passes backwards above the insertion with more of an upright stem above which the base is more strongly convex anteriorly than in BOU-2/21, and changes more abruptly in curvature towards a straighter course some 80mm above the base. There is no sign of upward recurvature on the preserved distal part. The lateral basal horncore margin is again much lower than the medial one. Anterior transverse ridges, above the basal rugose part, and large basal sinuses are evident. The vestige of a small postcornual fossa can be seen on the right. There is a rugose ridge on the frontal anterior of the horncore passing from anterolateral to posteromedial. The face as far as preserved (up to the middle of the orbit and above the missing supraorbital foramina) is quite flat, showing no sign of the facial up-doming in BOU-2/21. This is nevetheless consistent with the notion that these specimens are conspecific, as the rounded nasal crest in BOU-2/21 is present only from the anterior orbit forward. The craniofacial angle is ca. 110°. The coronal suture is not centrally indented. The surface of the posterior braincase roof and occipital surface is damaged such that the position of the occiput is uncertain, but one can see that the supra-occipital exposure was again anteroposteriorly very thin, while the distance from the posterior horncores to the occiput was longer than in the previous specimen. There is no sign of a parietal boss. The occipital surface faces mainly backwards and is basally very wide. The poorly marked temporal lines on the braincase are very far separated at their closest approach.

Frontlet BOU-2/20, with much of the right horncore, is from an even larger individual than the previous one. The horncore base is hardly compressed and quite swollen anteriorly. The complete horncores were of comparable length as in BOU-2/21, but shorter relative to their much greater girth. They are inserted more steeply relative to the anterior part of the dorsal braincase than in the previous specimens. They pass abruptly backwards (some 60 mm above the base), unlike the gentler curvature in BOU-2/21 and with more of a basal upright stem as in BOU-1/99, although the backward curvature commences sooner above the base than in BOU-1/99. The horncore then has only a short straighter part, recurving upwards sooner and more strongly than in BOU-2/21. Although the mid-frontal area is missing, it seems that the horncores were inserted closely together. Again, their lateral basal margins are much lower than their medial ones, and divergence is very low basally, increases strongly higher up and begins to decrease towards the broken distal parts. There are prominent transverse ridges.

Right horncore BOU-1/6, broken through the top of the pedicel, represents the largest individual. It is basally somewhat more compressed than the others except BOU-2/21, with strong anterior swelling and anterior and medial rugosity basally, and rapid diminution in size and increase in compression above the base. It has this last feature more strongly developed than do the others: the maximum/minimum diameters change from basal values of 98.3/80.0mm to 68.0/35.0 only 90 mm higher up, and quite a sharp ridge on the inferior aspect of the horncore is associated with this increase in compression. While this specimen resembles the horncore of BOU-2/20 in many features it differs in diverging sooner after the base.

The four specimens seem to belong to the same species of *Megalotragus*. That this species probably showed considerably variation in adult body size is suggested by the fact that the teeth of the smallest specimen BOU-2/21 show it to have been already a young adult. It was possibly a female while the largest specimens come from males. I argue below that the considerable variation, even in this small sample, in characters other than size such as basal and distal horncore course and horn orientation relative to the cranium, is consistent with large size variation in a single, averagely large-bodied species.

The right horncore base from Late Pliocene Matabaietu 1, MAT-1/13, may also belong to *Megalotragus*. It shows a large, smooth-walled sinus extending at least 20 mm up into the horncore base. Like the other horncores, it has clockwise torsion, and rapid diminution and increasing compression shortly above the anteriorly swollen and uncompressed base. There is rugose keel-like ridge extending from the anterolateral base in a mediodistal direction.

Some lower dentitions have been referred to cf. *Megalotragus* (Table 11) and upper isolated molars to cf. *Megalotragus* or *Connochaetes* (Table 12). They are larger than the largest *C. taurinus* I measured, and compare well with *Megalotragus* from Chesowanja and Olduvai Beds II and III (Gentry and Gentry 1978). The two Bouri M_3 have lengths of 40.9 and 39.1mm. This compares with the means (sample sizes in brackets) of samples of M_3 from the Koobi Fora Formation as follows (see Harris 1991): 40.1 mm (9) for the Upper Burgi Member, 35.0 mm (9) for the KBS Member, and 43.5 mm (1) for the Okote Member. The best Bouri specimen is right mandible BOU-1/88. P_2 was absent in life. Its P_4 is shortened and wide with fully fused paraconid and metaconid as is also true of the isolated right P_4 BOU-1/67. The occlusal morphology of these teeth compares well with those from Olduvai Beds II and III (e.g., mandible JK2 III A.3261, dated close to Bouri at ca. 1.3 – 1.0 m.y., figured in Gentry and Gentry 1978: Plate 36), except that P_3 in BOU-1/88 is less reduced and its P_4 is wider.

Another cranium, BOU-1/97, could also be conspecific, which would further increase the variability of this species. The best-preserved cranium of *Megalotragus* from Bouri, BOU-2/21, in spite of many similarities differs from BOU-1/97 in having a less upright basal horncore stem, absence of an abrupt change in course towards the horncore mid-section and less marked torsion; absence of a thickened ridge that starts anteriorly at the base and then follows the torsion of the horncore; much lower basal horncore separation and a smaller distance across horn pedicels relative to horncore size; a greater angle between the maximum horncore diameter and the midfrontal suture; stronger transverse ridges; localized frontal raising between horncores; shorter distance from posterior horncores to nuchal crest; a much smaller supraoccipital exposure on the dorsal braincase; a more widely rounded dorsal margin of the occipital surface with lesser tendency to concavities on either side of it; occipital surface facing more nearly backwards; and a higher parietal-occipital angle. In order to explore the affinities of this enigmatic cranium, I cladistically coded and analysed BOU-1/97 separately from the *Megalotragus* specimens that I described above. BOU-1/97 was coded as having horncores with stronger torsion, with bases more separated and with their major axes at lower angles to the midline, and a longer braincase (Table 14). I present the cladistic result, that groups BOU-1/97 with *Oreonagor*, for discussion (Figures 21, 22). While I discuss BOU-1/97 as a possible ?*Oreonagor* sp. in the next section, I regard it as quite likely that it actually is part of *M. kattwinkeli*. This would substantially increase the already marked variation of that assemblage and also of *M. kattwinkeli* as a whole.

Comparisons: The main comparisons are with *M. kattwinkeli* from Olduvai Beds II to IV (to which I will refer as OLD) and elsewhere (Gentry and Gentry 1978), and with fossils described as *M. isaaci* from the Upper Burgi, KBS and Okote Members of the Koobi Fora Formation (to which I will refer as KF), and to a lesser extent with *M. priscus* from southern Africa. The most recent available diagnosis of *M. kattwinkeli* (Gentry and Gentry 1978: 356) could not be framed relative to the KF assemblage which had not yet been discovered: "Horn cores short to moderately long, inserted behind the orbits but not so far back as to overhang the occipital surface, sometimes dorsoventrally compressed at their bases, with transverse ridges, moderately divergent but much less than in *Connochaetes*, and curved upwards from the base followed by a sharp curve backwards. Median vertical ridge present on the occipital, occipital facing primarily backwards and a little laterally, basioccipital wide with large anterior tuberosities, auditory bullae small and little inflated." Harris (1991) did not discuss comparisons of *M. isaaci* with *M. kattwinkeli*. He gave this diagnosis of *M. isaaci* (p. 187): "Species of *Megalotragus* with short to moderately long horn cores inserted close together on a long pedicel behind the orbits, horn core bases overhanging the occipital surface; horn cores swollen and often rugose at their bases, diverging backward and downward in their proximal portion but curving upward and slightly forward distally; middle portion of the horn core dorsoventrally compressed and bearing faint transverse ridges; cranium elongate and narrow with nasals and anterior part of the frontals domed steeply upward in front of the orbits to form the most elevated portion of the facial region." The following seven characters are especially relevant to the issue of whether these assemblages represent one or more species: 1. horncore and body size, 2. the nasal crest, 3. proximal and distal horncore course, 4. horncore separation and divergence, 5. horncore insertion relative to cranial landmarks such as occiput, 6. horncore length, and 7. pedicel fusion.

1. *Variation in horncore and body size*: Mean basal horncore size increases from the smallest Olduvai Bed IV sample, through that from Upper Burgi, through the considerably larger one from Olduvai Bed II, to the largest set from KBS, Bouri and the Omo Shungura Members D (ca. 2.5 m.y.) and K (1.5-1.4 m.y.) (Figure 19). There is a tendency for less compressed horncores in the larger individuals within each of the OLD, KF and Bouri samples, while each includes one or more strongly compressed specimens. The large size range within each of these samples probably largely reflects sexual dimorphism. I have mentioned that BOU-2/21 with its adult dentition is probably female and the other much larger Bouri specimens males. In the sample from Olduvai Beds III and IV, the neotype of *M. kattwinkeli*, M. 21447, is likely to be among the males as it is markedly larger than others such as JK2 III A.72 and GTC IV 068/6664. Gentry and Gentry (1978) suggested that the last two are females. These inferences are consistent with the somewhat small horncores relative to a large cranium in the best Bouri cranium BOU-2/21 as expected in adult females of a population of averagely larger body size, while the best Olduvai fossil M. 21447 has horncores that are larger relative to other cranial measures which would

be appropriate for an adult male from a population of smaller size.

The variation in horncore size and compression within each of the OLD, KF and Bouri samples is so large, and they overlap so extensively with each other, that these characters can be used neither to support specific separation between a form *kattwinkeli* from Olduvai and a form *isaaci* from Koobi Fora, nor to support the distinction of the Bouri form from either of the other two. Extensive variation in size in many large-bodied living bovids (such as *Alcelaphus buselaphus*, see Figure 19) is known to correlate allometrically with high variation in other characters, especially those of horncores in species with strong horncore torsion. In many cases intraspecific variation in size and morphology is enhanced by extended growth that continues throughout life in males, so that the allometric variation between adult males of differing ages is added to that between the sexes and between juveniles and adults (e.g., Geist 1971; Sinclair 1977; Spinage 1986). In fact, these modern examples suggest that the total variation in size and compression across all samples from OLD, KF and Bouri is consistent with membership of a single species. Only the later southern African *M. priscus* differs decisively from other *Megalotragus* by its consistent high compression at large body size.

2. *Nasal crest*: The strongest expression of the crest is seen in the KBS sample, notably in crania ER 2000 and ER 6032 (Harris 1991) and in the holotype of *Rusingoryx atopocranion* which is more remote from the present comparison. The crest in ER 2000 starts to rise closer to the horncores than it does in BOU-2/21. In ER 2000 the crest is already domed considerably by a level above the middle of the orbits, while in BOU-2/21 the crest commences near the anterior orbit and is less elevated. In the only OLD cranium in which this feature is seen, the holotype of *R. semiticus* VII-1111 (Gentry *et al.* 1995: Figure 3), the crest is of much lower elevation relative to the orbit than in the KBS crania and perhaps closer to the level of prominence in BOU-2/21, although the crest of VII-1111 starts higher up than in BOU-2/21. This might thus be cited as a feature that supports species separation of *isaaci* from *kattwinkeli*, and that aligns the Bouri form with *M. kattwinkeli*, but such a feature is a prime candidate for varying with sex and body size. Harris (1991) suggested a thermoregulatory function, and the structure might also have functioned in sexual signalling. The argument that the Bouri skull BOU-2/21 with its less marked crest may be female is relevant. In fact, some variation *within* populations in the prominence of the crest is already indicated. Some KBS specimens must have had a weaker crest than ER 2000 and ER 6032 from the same member. For instance, each of ER 2591 and ER 1756 has part of the frontals anterior to the horncores preserved on which no obvious large updoming of a crest is present such as can be seen in the equivalent position relative to the orbit in ER 2000 and ER 6032. Thus, what we know so far of the incidence of this feature seems consistent with conspecificity of the OLD, KF and Bouri forms.

3. *Proximal and distal horncore course*: Olduvai *M. kattwinkeli* horncores tend to curve upwards from the base (with concave-forward shape), with lower basal angles to the dorsal braincase, and their tips recurve inwards and in some cases downwards as well. The KBS *M. isaaci* differs in that the course from the base starts with a more upright basal stem (with a higher angle of that basal horncore stem to the braincase), then curves backwards more strongly (with convex-forward shape), and the tips curve upwards rather than inwards. The Bouri *Megalotragus* is closer to *M. isaaci* in having more of a basal upright to backward-curved horncore stem. Yet it is intermediate between OLD and KF in that its basal stem is less upright and the distal horncores of two Bouri specimens may show a bit more of a tendency to reapproach than in *M. isaaci*. The Bouri and KF morphologies resemble horncores from Shungura G3 (ca. 2.3 m.y.) and K (1.5-1.4 m.y.) that also have an approach to a basal upright to backward-curved stem (Gentry 1985). The Shungura K horncore F203-34 shows a mosaic of resemblances to the Olduvai form on the one hand and to the KF and Bouri forms on the other: it is like the former in strongly inward-curving horncore tips and fairly high divergence, and like the latter in its large, long horncores with at least a partial basal upright and back-curving stem.

I suggest that these variants can be explained to a large extent as successive stages within a common growth allometry: namely, OLD males reach adulthood at a size and morphology that basically resembles a subadult male from Bouri and an even younger stage from the KF population. During earlier growth stages in living hartebeests, the horncores tend to have the shape of a bracket in anterior view with high basal divergence and the orientation of the tips has inward and and downward components, resembling the morphology in many OLD fossils, e.g., frontlet M. 14950. After additional basal growth has rotated the horncores outwards, the tips point less inwards and downwards and more outwards and upwards, resembling the KF sample. In the advanced subspecies of *A. buselaphus*, a stage of higher basal divergence resembling the condition in OLD *Megalotragus* precedes the lower divergence in adult horncores that resembles the KF *Megalotragus*. In all living bovids that have horncore lyration in adults (as has the KF *Megalotragus*; that is, a basal more or less upright stem followed by backward curvature and still higher up by forward recurvature of the tips), there is a juvenile stage during which the horncore base is concave-forward in shape resembling the OLD *Megalotragus*. For instance, during the ontogeny of the topi, the earliest horncore is a spike with slight concave-forward curvature, while the long back-bending basal stem of that taxon grows upward from the base later during ontogeny carrying the forward-recurving tip aloft. Thus, one might expect that, if an ontogeny like that of the OLD *M. kattwinkeli*, which lacks this last growth phase that produces basal back-curvature, were to change towards extended growth, the resulting larger individuals, with longer horncores that include a basal back-curving stem, would resemble the KF and Bouri populations. Conversely, evolutionary truncation of the growth period would result in a paedomorphic descendant like the OLD form from an ancestor like the KF or Bouri forms. Such differences in growth period occur within many living bovid species among subspecies that live in different ecosystems. I will return to that later.

A measure of the degree to which an upright basal stem is present on a horncore is the angle between the basal horncores and the cranium. Within several living alcelaphine species there is a clear trend of increase in this angle with growth to increasing basal horncore size. A plot of minimum basal horncore diameters against estimates of this angle shows not only that the Bouri *Megalotragus* follows such a trend, but also that the few available points for OLD and KF appear to lie along the same curve: BOU-2/20 and ER 1756 with the largest horncores (see the two points in the upper righthand corner of Figure 19) have similar and largest angles, smaller specimens like BOU-2/21 and the neotype of *M. kattwinkeli* from Olduvai Beds III-IV have similar low angles, while BOU-1/99 lies on the line between them as it is intermediate for both variables. If the OLD, KF and Bouri samples overlap along the same growth gradient, then it is unsatisfactory to propose that they should be separated specifically based on this character.

4. *Horncore separation and divergence*: Two Olduvai Bed IV *M. kattwinkeli* specimens have basal horncore divergence of 60-90° and two of KBS *M. isaaci* of 30-55°. Two Bouri fossils resemble *M. isaaci* in basal divergence (ca. 40°) while BOU-2/20 is more divergent and within the Olduvai range. Figure 20 shows that, while the Olduvai sample has averagely higher separation than the other two, there is overlap between all three samples. I mentioned earlier that basal horncore divergence decreases during hartebeest ontogeny; and separation decreases as basal horncores grow larger in several living species (Figure 20). Therefore, while one can score as a valid difference the fact that the Olduvai Bed IV form grows to averagely smaller horn size (and by inference, based also on other skull measures, to smaller body size), this difference may entail the allometric changes in the other two variables. That is, horncore divergence and separation on their own provide an unsatisfactory basis for specific separation of these samples.

5. *Overhanging by horncore bases of the occipital surface*: This character, which features in the diagnoses of *M. kattwinkeli* (Gentry and Gentry 1978) and *M. isaaci* (Harris 1991), needs to be broken up into its components. Two important characteristics of the basal horncore that promote it are low divergence and strong back-bending after a sufficiently high upright stem. The horncores of the neotype of *M. kattwinkeli* would overhang the occipital surface if they were basally more back-bending and less divergent. In fact, even a low divergence would suffice.

   If it is correct that (as argued under 3. and 4.) neither divergence nor backbending is satisfactory for species separation among the OLD, KF and Bouri samples, then their consequence of overhanging, or failing to overhang the occipital surface, is not satisfactory either. The Bouri form is closer to *M. isaaci* in both divergence and the backbending of basal horncores than it is to the OLD sample. Therefore it does have horncores that overhang its occipital surface, although less markedly so than in *M. isaaci*.

6. *Horncore length*: The *M. isaaci* horncores are longer (two measurements I took are 400 and 490 mm) than those of *M. kattwinkeli* from Olduvai (a range of 250-385 mm for five, Gentry and Gentry,1978). The Bouri average is probably intermediate, with BOU-2/21 with an estimated 420 mm within the KF range and close to the two horncores from Shungura G3 (430 mm) and K (498 mm; Gentry, 1985), while BOU-1/99 is shorter and resembles the OLD fossils.

7. *Pedicel fusion*: This feature changes during ontogeny and varies within and especially among subspecies of living *A. buselaphus*. Harris (1991) cited pedicel fusion in his diagnosis of *M. isaaci*, but I found that some *M. isaaci* specimens have it much less marked than others, as in the Bouri sample in which BOU-2/21 has stronger expression of it than the other fossils.

One or two characters of the Bouri form could be advanced relative to the OLD and KF samples, such as the expansion of its forehead. It perhaps has larger separations of horncores from orbital rims and from supraorbital foramina, and a larger separation of the latter. The Bouri crania may have an averagely larger craniofacial angle than the KF crania, and be closer in this character to OLD *M. kattwinkeli* (Figure 18). Overall the Bouri form resembles the KBS and Omo variants most closely. Cranium BOU-1/99 even has the rugose ridges in front of the horncores, passing from a lateral position towards the posterior midline that Harris (1991) also found in KBS specimens. Nevertheless, there is a mosaic pattern of resemblances of the Bouri sample to the others from Olduvai, Koobi Fora and Omo, and among these other samples. This mosaic pattern of variation – particularly its *temporal* distribution – suggests that all these variants belong to a single long-lasting and polytypic species *M. kattwinkeli*. I conclude that both *Rhynotragus semiticus* and *Megalotragus isaaci* are synonyms of *Megalotragus kattwinkeli*. (I have referred in tables and figures to the KF subspecies as *M. k. isaaci*.)

It is interesting that the Bouri *Megalotragus* (dated ca. 1.0 m.y.) has less resemblance to the temporally closer *Megalotragus* from Olduvai Beds III-IV (ca. 1.3-0.7 m.y.) than it has to Late Pliocene and Early Pleistocene *Megalotragus* from KBS (ca. 1.9-1.6 m.y.), and Shungura G3 (ca. 2.3 m.y.) and K (1.5-1.4 m.y.). The Bouri form is also closer in several characters to the earlier Olduvai *Megalotragus* from Middle and Upper Bed II (1.7-1.4 m.y.) than to the Bed III-IV variant. There are several other bovid examples of single, long-lasting polytypic lineages such as *Tragelaphus strepsiceros* (known since ca. 2.5 m.y.), *Kobus kob* (since ca. 2.9 m.y.), *Alcelaphus buselaphus* (since 0.6 m.y. at Bodo), the single lineage of *Aepyceros shungurae* and *A. melampus* (since ca. 2.9 m.y.; Gentry, 1985), and *Syncerus* (since ca. 2.7 m.y.). In some of these lineages, later populations share more characters with earlier variants than they do with contemporaneous populations. For instance, horncores of living impalas, *A. melampus*, from Shaba in Zaire and Ndola in Zambia are more similar to fossil *Aepyceros* from Shungura B11 (ca. 2.9 m.y.) than they are to horncores of larger living conspecifics (Gentry, 1985); both the small, forest subspecies and the much larger woodland savanna forms of the living buffalo *Syncerus* may have had Late Pliocene counterparts existing together in Africa in different ecosystems, just as they do today; and the closer similarity of the living *A. b. tora* to the Bodo hartebeest than to most of its larger living conspecifics was discussed earlier.

The polytypic variation in some living species arises from differing maturation times in response to local ecology. For instance, *Syncerus caffer caffer* reaches its larger body size and associated allometric differentiation by growing longer (Sinclair 1977) probably in response to seasonally cooler environments at the generally higher latitudes and altitudes where it lives, while *S. c. nanus* is typical of many warmer-adapted forest forms in its shorter growth period to smaller size. In fact, these two are among many bovids that exemplify Bergmann's and probably also Allen's Rules (reviewed in Vrba 1994; see also Geist 1971 for caprine species). Such intraspecific differences in growth period may be based on genetic differentiation and/or on ecophenotypic responses to local differences in temperature, nutrition, and other factors (e.g., Geist 1971 for caprines; T. Robinson, pers. comm., for the springbok *Antidorcas marsupialis*).

The recognition of a single long-lasting polytypic species (a 'species' in the sense of reproductive cohesion is meant here) is based on evidence of genetic continuity, and on the pattern in which the variants recur over time and geography. The presence of some of both kinds of evidence for *Megalotragus* from Olduvai, Koobi Fora, Bouri and Omo militates against specific separation of these samples: For at least most of the variation, each character appears to be situated along a common growth allometry. There is also extensive overlap between the samples, and one of the latest samples, that from Bouri, is intermediate in several respects between the extremes from much earlier KBS and contemporaneous Olduvai Bed IV.

There are additional reasons for interpreting this mosaic pattern of variation as consistent with intraspecific variation in response to differing local environmental conditions. Recall that the Bouri *Megalotragus* at ca. 1.0 m.y. has less resemblance to the temporally closer and smaller *Megalotragus* from Olduvai Beds III-IV than it has to Late Pliocene and Early Pleistocene *Megalotragus* from the KBS Member and Shungura G3 and K. If large bodies are often a response to seasonally cooler climates, then the difference between the Bouri and Olduvai Beds III-IV fossils may reflect a cooler climate ca. 1 m.y. ago at Bouri due to higher altitude and maybe also higher latitude, than at Olduvai. And recall the related inference from the *Numidocapra-Rabaticeras* lineage: the larger *Numidocapra* extended into the Olduvai area, perhaps due to a cooler phase, during the Early Pleistocene of Bed II. The smaller *R. arambourgi* had replaced it there by Bed III-IV in spite of the fact that *Numidocapra* was present contemporaneously in the Awash, perhaps because Olduvai was warmer at some time during the Bed III-IV interval while the higher latitudes and altitudes in the Awash area still remained cool enough to allow *Numidocapra* to persist there. In a survey of the bovine fossil record (Vrba 1987) I concluded that the presence of the giant buffalo *Pelorovis* indicates seasonally cool and vegetationally open environments. It may be significant that *Pelorovis* disappears from Olduvai in Bed III or IV and that *Parmularius angusticornis* disappears before 1.0 m.y. by Bed III (Gentry and Gentry 1978), while both are still present at Bouri.

The cladogram based on separate taxa from OLD, KF, and Bouri has a poorly resolved branching pattern within a monophyletic *Megalotragus* (Figure 21). The second analysis treated *M.*

kattwinkeli as synonymous with *M. isaaci* and including the Bouri variant, with all character codes adjusted accordingly (Mk* in Table 14; codes that vary among the OLD, KF and Bouri forms were recoded as ?). The cladogram from this suggests that *M. kattwinkeli* (from KF, Olduvai, Bouri and elsewhere) has no autapomorphies and is therefore the potential ancestor of *M. priscus* and *M. atopocranion*. In fact, several features particularly of the Bouri form hint at evolution towards *M. priscus*, such as the huge elongation of the frontal anterior to the horncores, and reduction of the dorsal parietal. In spite of the fact that the samples are small and variable, it may also turn out to be significant that the average ratio of horncore compression decreases from earlier *M. k. isaaci* (0.88, n=6), to *M. kattwinkeli* from Olduvai (0.86, n=9) and Bouri (0.83, n=4), to the later *M. atopocranion* (0.81, n=1) and *M. priscus* (0.69, n=3). Perhaps it was a late, smaller and warmer-adapted population of the polytypic *M. kattwinkeli*, like that from Olduvai Bed III-IV, that gave rise to *M. atopocranion*, and a larger and cooler-adapted one like the one from Bouri that gave rise to the species *M. priscus* of higher latitudes.

Genus *Oreonagor* (Thomas 1884)

Type species *Oreonagor tournoueri* (Thomas 1884)

Generic diagnosis: Alcelaphines of medium to large size, smaller than *Connochaetes taurinus*. The anterior cranium is large; orbits project slightly; horncores very long with strong clockwise torsion on the right side and inserted far apart and quite far above the back parts of the orbits; posterior cranium moderately short; face not strongly angled relative to the cranium; parietal-occipital angle moderately to large; occipital surface fairly low and widening towards the mastoids; shortened premolar rows with P_2 absent; limb bones robust with posterior and anterior metapodials subequal. (Largely after Arambourg 1979: 101.)

?Oreonagor/*?Megalotragus* sp. from Bouri 1 (Figures 8, 9, Table 5):
BOU-1/97, from Bouri 1 dated ca. 1 m.y., includes most of the posterior cranium and both horncores. The horncores are uncompressed, ca. 440 mm long in the complete state, with marked clockwise torsion. The horncore surfaces are damaged and encrusted so that the hints of some posterior, lateral and medial flattening and of moderate anterior basal swelling may be misleading. The widest mediolateral horncore diameter is situated posteriorly. They are inserted widely apart with their major axes at an angle of ca. 50° to the midfrontal suture. What remains of the orbital margins suggests that they were not prominent and that the horncores are inserted far above them. On the right side can be seen an extensive frontal sinus in the pedicel and horncore base with a posterolateral bony strut intrusion. The horncores rise at an angle of ca. 80° to the braincase. The pedicels are short and the lateral basal horncore margins somewhat lower than the medial ones. Each horncore has a basal upright stem over some 100 mm with almost parallel sides in anterior view and diverging from its partner at an

TABLE 6.

Measurements of cranial fossils of *Connochaetes taurinus olduvaiensis* from Bouri 1: fragmentary frontlet with most of right horncore BOU-1/5, right horncore BOU-1/57, and much of left basal horncore BOU-1/47, in comparison with *C. t. olduvaiensis* from Olduvai Beds II to IV (from Gentry and Gentry, 1978). Length measurements in mm; two values for horncore length are preserved/estimated complete lengths; e = estimated, ee = very rough estimate; max. = maximum.

	Connochaetes taurinus olduvaiensis					
			Holotype			
	BOU-1/5	BOU-1/57	BOU-1/47	BM(NH) M21451	BM(NH) M21452	BK II 1955 P.P.F.1
Horncore maximum diameter (1)	90.7e	71e	60e	75.2	84.2	75.5
Horncore minimum diameter (2)	68e	54ee		53.9	61.9	55.5
Horncore ratio (2/1)	0.75e	0.76ee		0.72	0.74	0.74
Horncore length	395/460	345/345	290/400			385/385
Horncore basal separation	128ee					
Angle of basal horn divergence	120°e					
Max. separation supra-orbital foramina (SOF)	128ee					
Distance SOF to anterior horncore midpoint	66.5ee					

angle of ca. 50°, whereafter it enters its mid-region by a fairly abrupt change towards a posterolateral course. This middle part of each horncore also has a slight downward direction which gradually changes to an upward course towards tips that may have been quite strongly upcurved. As the horncores enter this middle region, some 100 mm above the bases, their divergence changes to a much higher angle which diminishes towards the tips. The horncores are rounder at the base, then assume an increased diminution rate and higher compression in the middle region, and thereafter resume a lower diminution rate and rounder cross-section. Weak transverse ridges can be discerned distally on the anterior surface, and these could have been stronger and more extensive in the undamaged state. In spite of the encrusting matrix one can discern a thickened ridge on each horncore that, on the right horncore, starts slightly laterally to the anterior basal midpoint and then follows the clockwise torsion by passing upwards towards the medial and then the posterior part of the horncore. Discrete frontal raising between the horncores is absent. The craniofacial angle is ca. 110°. The parietal-occipital angle is ca. 130°. The supraorbital foramina are missing. The forehead is flat rather than transversely convex. The coronal suture is close to the posterior horncore bases, may have been slightly indented, and is separated from the occiput by ca. 35mm. The braincase has a more or less flat roof with far-separated temporal lines, with a supraoccipital that extends quite far anteriorly, and is fairly wide in its middle part with lateral sides more or less parallel. The margin of the occipital surface is dorsally rounded over a somewhat narrow area, and then becomes concave laterally towards the mastoids. The occipital surfaces on either side of the central ridge have definite lateral-facing components. The mastoid exposures seem to be situated entirely on the occipital surface. The basicranium is damaged, but it can be seen that the basioccipital was quite long and rectangular with a deep, wide central longitudinal groove flanked by prominent longitudinal ridges. The space that was occupied by the missing auditory bulla looks narrow.

Comparisons: The species had originally been described from Ain Jourdel, Algeria, as *Antilope tournoueri* (Thomas 1884). Arambourg (1979) described material from the earlier Ain Boucherit in Algeria, in which *O. tournoueri* is one of the most abundant species, and gave new generic and specific diagnoses. He nominated the most complete Ain Boucherit cranium, 1954-8:266, as a neotype and some dentitions as neosyntypes. The resemblances of BOU-1/97 to *O. tournoueri* include overall size, long horncores with strong clockwise torsion, a long, basal upright stem of low divergence followed above ca. 100 mm by an abrupt change in course to a backward and much more divergent course, upward-curving tips, a thickened ridge that, on the right horncore, starts slightly laterally to the anterior basal midpoint and then follows the clockwise torsion; a coronal suture that passes closely behind the horncore bases; a similar distance between this suture and the nuchal crest; a similarly substantial exposure of the supraoccipital on the dorsal braincase; and similar craniofacial and parietal-occipital angles. The neotype of *O. tournoueri* differs from BOU-1/97 in longer horncores with less basal and greater distal divergence above the bases (more of a transverse and even forward, and less of a posterior component, to the course after the base); higher basal separation; distal horncores that recurve in an anterior direction with longer upward-directed tips; a greater tendency to a swollen antero-lateral horncore base that is laterally more markedly lower than medially; possibly higher basal horncore compression (Arambourg 1979, gave the basal diameters as 68 and 48 mm, but I suspect that his larger diameter was measured obliquely to encompass the antero-lateral swelling on the neotype horncores making the compression seem greater than it is); orbital margins that project outwards closer to the horncore base; and a more convex forehead.

I listed earlier the differences from the Bouri specimens described as *Megalotragus*. I currently see the differences from *O. tournoueri* as possibly even more compelling, especially the larger basal horncore separation of the latter. I nevertheless present the alternative of affinity with *Oreonagor* for discussion in the hope that additional finds will clarify the matter.

Genus *Connochaetes* Lichtenstein 1814
1816 *Cemas* Oken
1821 *Catablepas* Gray
1934 *Pultiphagonides* Hopwood
1850 *Gorgon* Gray

Type species *Connochaetes gnou* (Zimmermann 1780)

Generic diagnosis: Fairly large alcelaphines with low, wide skulls and long faces that are broader across the orbits than anteriorly; horncores inserted wide apart and behind the orbits, strongly divergent in earlier species and emerging transversely or forwards in later species. Torsion is clockwise from the base upwards in the right horncore. Coronal suture centrally indented; preorbital fossae absent or shallow without an upper rim; posterior suture of nasals indented centrally; greatest width of nasals lying anteriorly; anterior expansion of premaxillae; anterior tuberosities of basioccipital more localized than in *Alcelaphus* and *Damaliscus*; auditory bullae large and inflated; occipital surface faces backwards rather than laterally; premolar rows very short with

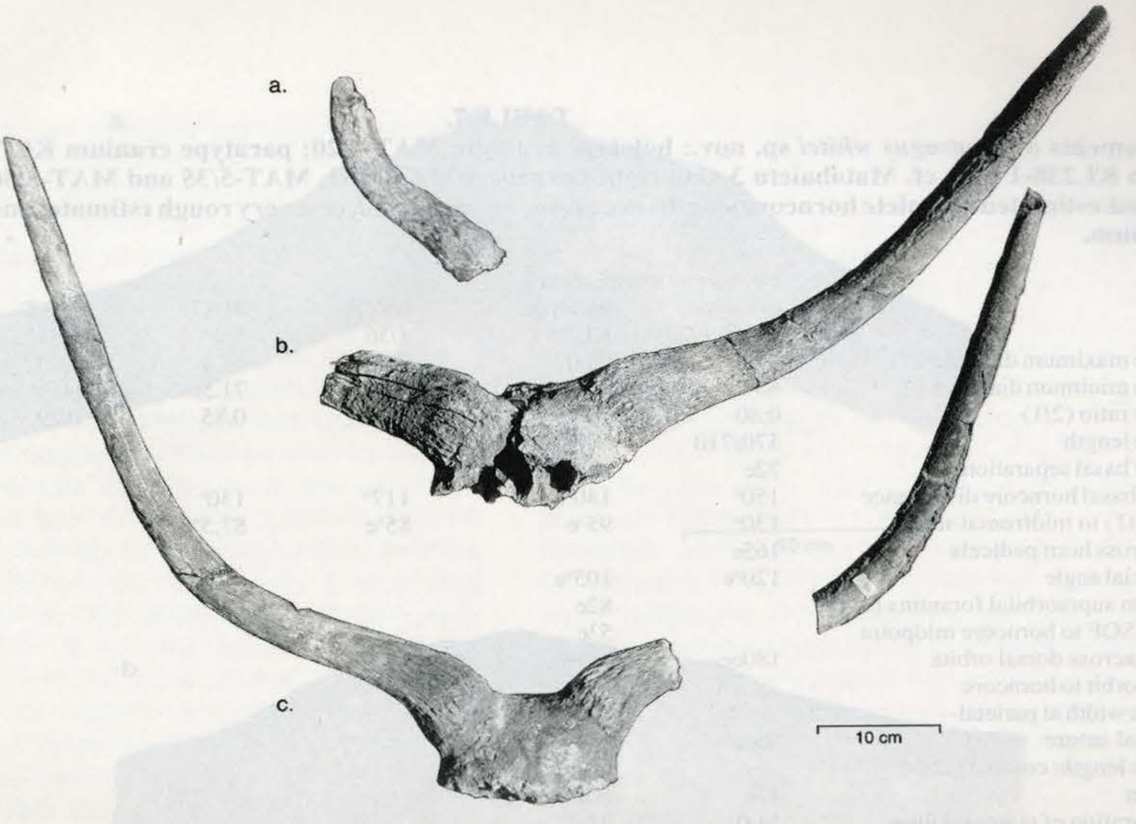

Figure 10. a. Right horncore of *Beatragus antiquus* WIL--2/18 from Wilti Dora 2; b. holotype cranium with most of left horncore of *Beatragus whitei* sp. nov. MAT-4/20 from Matabaietu 4; c. paratype cranium, with separate piece of left horncore, of *B. whitei* sp. nov. KL75-1 of unknown provenance but possibly from Matabaietu 3 (T. White, pers. comm.), all in anterior view.

P_2 tending to disappear. (Partly from Gentry and Gentry 1978).

Connochaetes taurinus (Burchell 1823)

Diagnosis: A larger wildebeest with a more convexly-domed forehead than *C. gnou*; horn cores inserted at the back of the skull above the occipital surface, emerging transversely, having tips turned upwards and inwards; a long face and nasals; zygomatic arch deep anteriorly below the orbits; large shallow preorbital fossa; jugal with two broad anterior lobes; wide premaxillae ascending to a long contact on the nasals; no median vertical ridge on the occipital. (Largely based on Gentry and Gentry 1978.)

Connochaetes taurinus olduvaiensis (Leakey 1965)

Diagnosis: An extinct subspecies differing from living *C. taurinus* in horn cores inserted less far back and passing less downwards as they emerge from the skull (Gentry and Gentry 1978).

Connochaetes taurinus olduvaiensis from Bouri 1(Table 6):

Specimens from Bouri 1 of this taxon are BOU-1/5, a frontal with right horncore, BOU-1/57 a complete right horncore, and BOU-1/47 much of a left horncore. BOU-1/5 includes much of the forehead and a piece of the anterior braincase. The forehead consists of fragments that were found aligned but not securely joined. Thus, observations on orientation are tentative. The fossil is large. In dorsal view the horncore base is strongly compressed and expands at the base, with rugose features on the frontal surface anterior and medial to it. The horncore passes posteriorly from the base and then laterally. In anterior view, the horncore is raised 30-40mm above the base, then undergoes marked diminution in maximum diameter as it passes transversely and a bit downwards, then recurves upwards, and eventually inwards towards the tip. Faint transverse ridges are discernible. Although the orbital rim was broken, the distance from basal horncore to orbit must have been distinctly shorter than in living *C. taurinus*. Basal horncore separation is very large (see CtBOU in Figure 19). The almost complete right horncore BOU-1/57 is similar except that it is smaller, shorter, and has tips that do not curve inwards but only upwards. Also, it has a rugose ridge on the anterior and dorsal base that runs from the lateral (inferior) base to a postetro-medial position a bit above the base, and continues as a keel-like ridge along the posterior surface above the base. (The presence or absence of this ridge in BOU-1/5 cannot be ascertained as the area is too damaged in that fossil.) Left horncore BOU-1/61, broken through its base and pedicel, is basically similar to the other two.

Comparisons: The specimens compare well with *C. t. olduvaiensis* from Olduvai Beds II-IV (Gentry and Gentry 1978). In horncore size and basal compression they are particularly close to fossils from Beds III and IV (Figure 19). While they do not

TABLE 7.

Measurements of *Beatragus whitei* sp. nov.: holotype cranium MAT-4/20; paratype cranium KL75-1 and subadult cranium KL238-1 both cf. Matabaietu 3, and right horncores MAT-5/31, MAT-5/35 and MAT-5/36. Length in mm; preserved/estimated complete horncore lengths are given; e = estimated, ee = very rough estimate; ant. = anterior; min. = minimum.

	Beatragus whitei sp. nov.					cf. *B. whitei*
	holotype MAT-4/20	paratype KL75-1	MAT-5/36	MAT-5/35	MAT-5/31	KL238-1
Horncore maximum diameter (1)	79.0	76.0	78.0	84.5	77.0	56e
Horncore minimum diameter (2)	63.2	65.5	68e	71.5e	60.5	54e
Horncore ratio (2/1)	0.80	0.87	0.87	0.85	0.79	0.96e
Horncore length	570/710	695/720				
Horncore basal separation	72e	66.0				89e
Angle of basal horncore divergence	150°	140°e	117°	130°		
Angle of (1) to midfrontal suture	130°	95°e	85°e	87.5°e		
Width across horn pedicels	165e					
Craniofacial angle	120°e	105°e				
Separation supraorbital foramina (SOF)		82e				84.0
Distance SOF to horncore midpoint		53e				71e
Distance across dorsal orbits	180ee	175ee				
Distance orbit to horncore		38e				
Braincase width at parietal-squamosal suture	96ee	98e				97.0
Braincase length: coronal suture to occiput	47e	50ee				53e
Min. separation of temporal lines	51.0	41.3				
Occipital height: top foramen magnum to occiput	69e	61.5e				59e
Length/width of auditory bulla						46.4/27.8
Basioccipital width across anterior tuberosities		31.5e				29.5
Basioccipital width across posterior tuberosities		47.5e				41.7
Basioccipital length: ant. to post. tuberosities		33e				36.3

resemble other fossil *Connochaetes* very much, there is one puzzling aspect: Gentry and Gentry (1978:364) saw a ridge in *C. africanus* from Olduvai Bed II that passes "across the base of the top surface of the horn core from its anterolateral extremity to its posterior edge", and wrote on p. 368 that in living and fossil *C. taurinus* the horncores are "without a ridge passing across the base of the horn core from its anterolateral extremity." Yet, at least one of the three Bouri specimens has such a feature. I have also noted a similar phenomenon in some specimens that Gentry and Gentry (1978) ascribed to *Connochaetes* sp., and that Harris (1991) described as *C. gentryi*. The ridge described above in *?Oreonagor*/*?Megalotragus* sp. from Bouri and *O. tournoueri*, and that I have also observed in *Megalotragus kattwinkeli* from Bouri and in some *M. k. isaaci* specimens, may be homologous. If that is correct, then the ridge may be plesiomorphic for the *Megalotragus*-(*Oreonagor*-*Connochaetes*) sistergroup, being subsequently lost independently in several lineages. Gentry and Gentry (1978) considered that *C. africanus* might have evolved into *C. gnou* through intermediate stages from South Africa *C. ?gnou laticornutus* from Cornelia, *C. gnou ?laticornutus* from Elandsfontein, and *C. gnou antiquus* from Florisbad. These three South African forms show progressive expansion of the horncore base in dorsal view and spreading of rugose bone over the adjacent frontal. They may represent successive stages in the evolution of the enlarged basal bosses and unusual course of horncores in living *C. gnou*. These South African fossils have very much more marked basal horncore expansion and raising, and frontal rugosity, than have the Bouri fossils.

Genus *Beatragus* Heller, 1912
1971 *Damaliscus* Ansell (in part)
1977 *Alcelaphus* Van Gelder (in part)
1979 *Damaliscus* Vrba (in part)

Type species *Beatragus hunteri* (P. L. Sclater 1889)

Generic diagnosis: The earliest known forms were of moderately large size and the later forms decreased towards medium size. Long horncores that are pleisiomorphically widely separated, with some reduction in separation towards the Recent species. The maximum horncore diameter is strongly angled to the midfrontal suture. The horncores are situated closely above the orbit and diverge very strongly from their bases. The horncores curve backwards and then recurve in an upward direction to end in markedly elongated tips that point upwards and

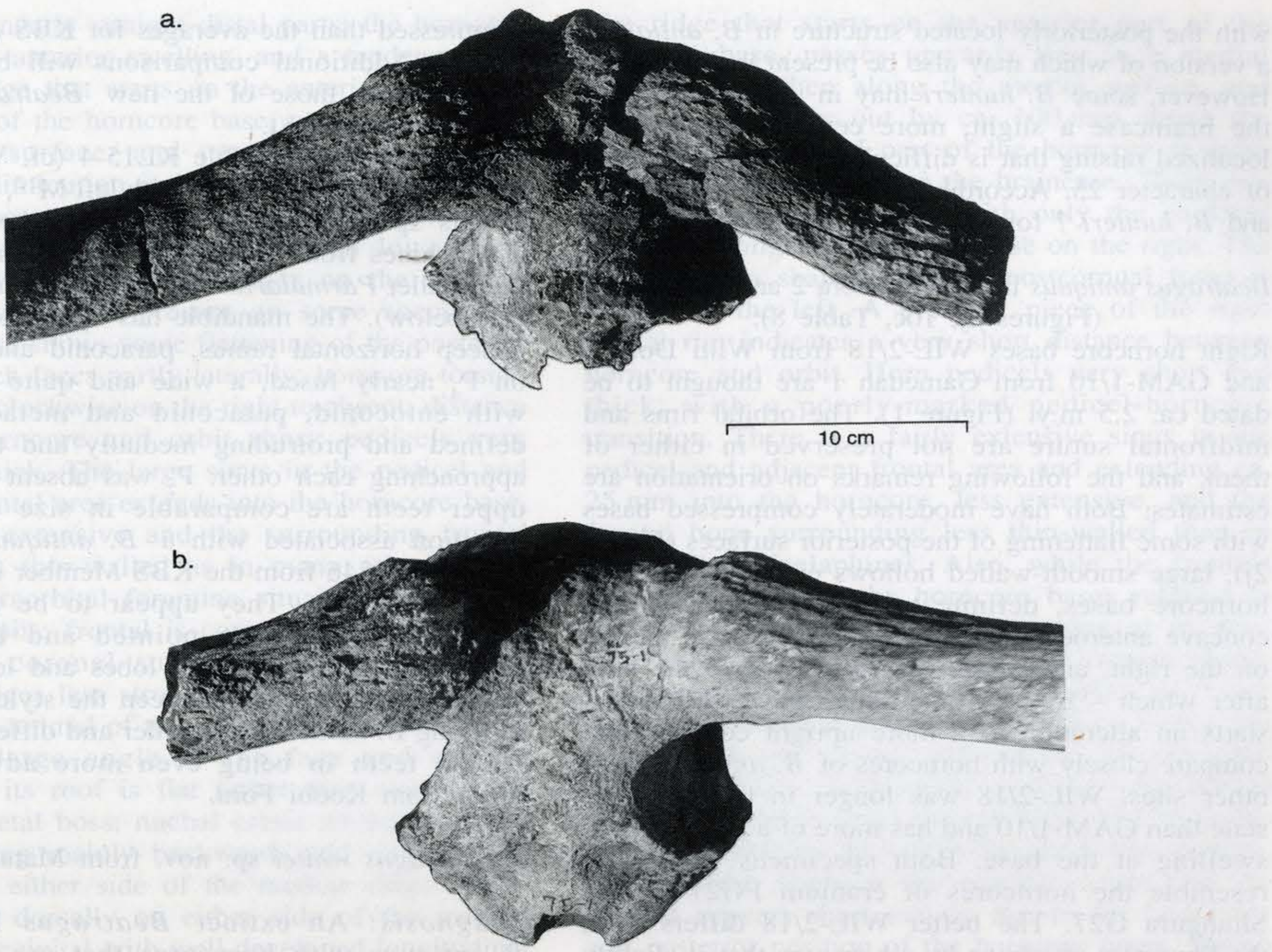

Figure 11. *Beatragus whitei* sp. nov.: a. holotype cranium of MAT-4/20 from Matabaietu 4; b. paratype cranium KL75-1 possibly from Matabaietu 3, both in superior view.

vary in divergence from outwards to nearly parallel to each other. Anticlockwise torsion of the right horncore is incipient in earlier and stronger in later forms. Transverse ridges well-marked except in the earliest and largest form. The frontal anterior to the horncores is convex although this is less marked in the Recent and smallest species. The supraorbital foramina are widely separated. Moderately high occipital height, as measured from the top of the foramen magnum to the top of the occiput. The following features are known only in the living *B. hunteri*: preorbital fossae of moderate size; P_2 usually absent. (See also Gentry and Gentry 1978.)

Beatragus antiquus Leakey 1965

1937 *Beatragus hunteri* Schwarz: 55, Plate 2: Figure 11

1965 *Beatragus antiquus* Leakey: 61, Plate 80

Diagnosis: A species of *Beatragus* larger than *B. hunteri* and smaller than *B. whitei*; horn cores with more upright insertions in side view than *B hunteri*, diverging from the very base as in *B. whitei* but more strongly than in *B. hunteri*, averagely less mediolaterally compressed in their lower parts than in *B. hunteri*, and with a less abrupt alteration in their course above the initial outward divergence than in *B. hunteri*; horncore torsion tends to be more pronounced than in *B. whitei* and resembling *B hunteri*; frontals wider and more convex in front of the horn core bases and less uparched between them than in *B.. hunteri* and comparable to the condition in *B whitei* (based on Gentry and Gentry 1978: 412 with additions).

Gentry and Gentry (1978; Gentry 1985) discussed the most complete cranium known, the possibly subadult FG27-1 from Shungura G27 dated ca. 2.0 m.y. They mentioned that it had more of a parietal boss than *B. hunteri*. I found this structure in FG27-1 to be a broad, raised, somewhat flat-topped part of the posterior cranium, that descends rather markedly along two lateral margins that converge posteriorly. This raised structure is placed very posteriorly on the parietal and partly on the supraoccipital. Another *B. antiquus* cranium has since been found, KNM-ER 4546 from the KBS Member of the Koobi Fora Formation which shows a similar flat-topped structure just anterior to the occiput with lateral margins that converge more closely posteriorly than in FG27-1. Character 25 in my analysis (Tables 13, 14) refers to a round parietal boss that rises slightly to markedly near the center of the dorsal braincase and gently descends to shallower parts of the bone right around it. I suggest that my character 25 is not homologous with the posteriorly located structure in *B. antiquus*, a version of which may also be present in *B. hunteri*. However, some *B. hunteri* may in addition have on the braincase a slight, more centrally placed and localized raising that is difficult to interpret in terms of character 25. Accordingly I coded *B. antiquus* 0 and *B. hunteri* ? for this character (Table 14).

Beatragus antiquus from Wilti Dora 2 and Gamedah 1 (Figures 2j, 10c, Table 8):

Right horncore bases WIL-2/18 from Wilti Dora 2 and GAM-1/10 from Gamedah 1 are thought to be dated ca. 2.5 m.y. (Figure 1). The orbital rims and midfrontal suture are not preserved in either of them, and the following remarks on orientation are estimates. Both have moderately compressed bases with some flattening of the posterior surfaces (Figure 2j), large smooth-walled hollows extending into the horncore bases, definite transverse ridges on the concave anterodorsal surfaces, anticlockwise torsion on the right, and strong divergence above the base after which – by ca. 100-130mm above the base – starts an alteration to a more upright course. Both compare closely with horncores of *B. antiquus* from other sites. WIL-2/18 was longer in the complete state than GAM-1/10 and has more of a slight medial swelling at the base. Both specimens essentially resemble the horncores of cranium FG27-1 from Shungura G27. The better WIL-2/18 differs from the Shungura specimen by a horncore that is slightly larger, remains divergent for longer after the base, and recurves medially less quickly and abruptly, has a lower diminution rate above the base and was therefore probably longer. The Awash horncores resemble those of *B. antiquus* FG27-1, KNM-ER 4546 from the KBS Member and one of the two horncores from Olduvai Bed I (Gentry and Gentry 1978) in basal compression. They are more compressed than the averages for KBS and Olduvai Bed II. Additional comparisons will be discussed together with those of the new *Beatragus* species that I describe next.

Subadult left mandible KL15-4 (cf. WIL-2) with full dentition, and KL22-2 with left M^{2-3}, are assigned to this species (Tables 11, 12) as the only other alcelaphines from Wilti Dora 2 and Gamedah 1 are the smaller *Parmularius* and new *Damaliscus* species (see below). The mandible has hypsodont teeth and a deep horizontal ramus, paraconid and metaconid on P_4 nearly fused, a wide and quite complex P_3 with entoconid, paraconid and metaconid well-defined and protruding medially and the last two approaching each other. P_2 was absent in life. The upper teeth are comparable in size to the only dentition associated with a *B. antiquus* horncore, KNM-ER 4546 from the KBS Member in the Koobi Fora Formation. They appear to be a little less advanced, with more pointed and less antero-posteriorly pinched medial lobes and less localized outbowing of the ribs between the styles. The teeth of living *B. hunteri* are smaller and differ from these Awash teeth in being even more advanced than those from Koobi Fora.

Beatragus whitei sp. nov. from Matabaietu 5-3

Diagnosis: An extinct *Beatragus* larger than *B. antiquus* with horncores that are the longest known among alcelaphines. Horncores basally not compressed, less so than in *B. hunteri* and comparable to *B. antiquus*, more compressed just above the base and rounder again distally; maximum basal diameter at a large angle to midfrontal suture; inserted far apart; highly divergent for a long part of the horncore after the base and then gradually recurving towards an upward and outward direction

TABLE 8.

Measurements of cranial fossils of *Beatragus antiquus*: right horncore WIL-2/18 and left horncore GAM-1/10; *Parmularius* cf. *pandatus*, complete right horncore KL11-2 cf. Wilti Dora 2; *Parmularius angusticornis* left horncore base BOU-1/11. Length in mm; two values for horncore length are preserved/estimated complete lengths; e = estimated, ee = very rough estimate.

	B. antiquus WIL-2/18	*B. antiquus* GAM-1/10	*P.* cf. *pandatus* KL11-2	*P. angusticornis* BOU-1/11
Horncore maximum diameter (1)	64e	59.0	55.5	65.6
Honcore minimim diameter (2)	52e	48e	42.6	54.7
Horncore ratio (2/1)	0.81	0.81	0.77	0.83
Horncore length			290/300	190/300
Horncore basal separation			12e	
Angle: basal horn divergence			25°e	
Angle of (1) to midfrontal suture			25°e	15°e
Width across horn pedicels			102ee	

of the long nearly straight distal parts; the horncore base has an anterior swelling, and a tendency to a keel-like ridge that starts on the anterior to anterolateral part of the horncore base, passes up towards the medial surface, and peters out some 10 cm higher up; diminution in horncore girth occurs soon after the base and is thereafter very slow. The basal horncore boundary is laterally much lower than medially. Weak transverse ridges on the anterior horncore surface are present on some specimens; horncore base shows some flattening of the posterior surface which faces partly laterally; horncore torsion is weak anticlockwise on the right to absent; distance between horncore and orbit short; pedicels very short and thick. The large sinus in the pedicel and adjacent frontal area extends into the horncore base, but is less extensive and the surrounding frontal bone not as thin-walled as in many other alcelaphines. Supraorbital foramina situated far apart in very small pits; frontal is convex near the anterior horncores; coronal suture indented anteriorly; temporal ridges less strongly marked than might be expected on animal of this size. The braincase has a relatively large angle to the face and widens posteriorly; its roof is flat rather than convex and lacks a parietal boss; nuchal crests strong; occipital surface facing mainly backwards and only a little laterally on either side of the median ridge. There are hollows dorsally on either side of the median ridge. Basioccipital with well-developed longitudinal ridges behind the anterior tuberosities and a deep central longitudinal groove between the ridges, fairly short and narrowing between the posterior and anterior tuberosities; posterior tuberosities wider than anterior ones. Mastoids with a strong dorsal rim, flaring out strongly to form a broad ventral occipital surface from a narrower dorsal one.

Holotype: The holotype MAT-4/20 includes much of the braincase and most of the left horncore (Figures 10b and 11a). The horncore cross-section is basally almost round (Figure 2), then becomes more compressed just above the base, and becomes rounder again distally. The maximum diameter is situated at a large angle to the midfrontal suture (Figure 18). The left side shows that the horncores were extremely long. After insertions that are far apart (Figure 20), they pass outwards at a highly divergent angle and a little backwards, and then recurve upwards as long nearly straight distal parts that pass outwards and upwards steadily and evenly. Some diminution in horncore girth occurs soon after the base and is thereafter very slow, the diameters at the base, and 50 mm, 100 mm, and 200 mm above the base being respectively 79.0/63.2 mm, 63.5/41.0 mm, 57.5/44.0 mm, and 47.9/46.3 mm. Faint transverse ridges can be seen on the anterior surface, especially above the base and into the concave part of the horncore. The horncore base has an anterior swelling, and there is a keel-like ridge that starts on the anterior part of the horncore base, passes upwards first in a medial direction and then along the medial surface, and lessens and peters out by ca. 100 mm above the base. The very basal part of the horncore is quite steeply inserted relative to the braincase. There is a virtual absence of torsion, with only the slightest hint that it might be anticlockwise on the right. The top part of a shallow, narrow postcornual fossa is visible on the left. A preserve piece of the right orbital rim indicates a very short distance between horncore and orbit. Horn pedicels very short and thick, with a poorly-marked pedicel-horncore transition. There is a fairly extensive sinus in the pedicel and adjacent frontal area and extending ca. 25 mm into the horncore, less extensive, and the frontal bone surrounding less thin-walled than in many other alcelaphines. Also, while the frontals are raised between the horncore bases relative to the orbits, this raising is not as strong as in most other Alcelaphini. The frontal has a convex shape. The coronal suture is moderately complex, ca. 5 mm wide, and indented anteriorly. Temporal ridges are definite but not strong, and are ca. 51 mm apart posteriorly. The craniofacial angle is large for an alcelaphine. There is no parietal boss. The braincase widens posteriorly. Its roof is flat rather than convex. The distance between the coronal suture and the occiput appears short mainly due to the large size and posterior position of the horncore bases. Strong nuchal crests; occipital surface facing mainly backwards and only a little laterally, with dorsal hollows on either side of the damaged median ridge. Mastoid with a strong dorsal rim, and situated at least mostly on the occipital surface; mastoid foramen not surrounded by a deep depression but more or less flush with the surrounding bone. In posterior view, the mastoids flare out strongly to form a very broad ventral occipital surface from a much narrower dorsal one.

Some cranial fragments also labelled MAT-4/20 that do not seem to belong to this cranium, and possibly not even to Alcelaphini.

Paratype: Cranium KL75-1 includes much of the right and a separate piece of left horncore (Figures 10, 11), the anterior frontal up to the supraorbital foramina, and much of the braincase including the basioccipital area. The most basal horncores and the long straight horncore tips diverge less than in the holotype. Supraorbital foramina situated flush with frontal surface in tiny pits and far apart; parietal boss absent; basioccipital with well-developed longitudinal ridges behind the anterior tuberosities and a deep central longitudinal groove between the ridges, short and narrowing between the posterior and anterior tuberosities; posterior tuberosities wider than anterior ones. Other features agree with those of the holotype.

Horizon: The holotype cranium, MAT-4/20, is from Matabaietu 4. The paratype cranium, KL75-1, is of unknown provenance but possibly from Matabaietu 3. Additional specimens come from Matabaietu 4 and 5. These localities are close to and just older than 2.5 m.y. (Figure 1).

Etymology: The new species is named after Tim White in recognition of his work in Middle Awash palaeontology.

Measurements: The measurements for all the *Beatragus whitei* cranial specimens are given in Table 7.

Referred specimens: MAT-5/36 is a right horncore base with parts of the frontal up to the midline suture and the anterior parietal. It is strongly divergent immediately above the base, and shows little compression at the base although compression increases shortly above that. The base is swollen medially, anteriorly and laterally, with a maximum diameter strongly angled to the midfrontal suture, and with some posterior flattening (Figure 2h). This horncore also has a thickened ridge running from the anterior surface in a clockwise and upward direction as in the holotype and paratype. In MAT-5/36 this ridge can be seen to end on the posterior surface some 80 mm above the base. The coronal suture is anteriorly indented at the midline. MAT-5/31 is another right horncore base with only a short piece of the horncore preserved. It also has the thickened ridge running from the anterior surface in a clockwise and upward direction, but the ridge is even more pronounced giving the anterodorsal surface a swollen and rugose appearance, and with the ridge becoming quite sharp dorsomedially. The sinus cavity in the horncore base is largely filled with spongy bone which differs from the general alcelaphine condition and may represent pathology. MAT-5/35 is a longer right basal horncore with associated parts of the frontal bones. It has the largest base of the *B. whitei* horncores, is as little compressed and with a similar basal cross-section and orientation to the midfrontal suture as the paratype and MAT-5/36, and the preserved part suggests a complete length similar to that in the paratype. The coronal suture is anteriorly strongly indented at the midline. The horncore is very rugose at the anterior base, more expanded at the base, then it thins and flattens immediately above the base and becomes broader and rounder again higher up. This specimen suggests very slight anticlockwise torsion from the base up. MAT-5/32 is the tip of a *B. whitei* horncore.

Cranium KL238-1, cf. MAT-3, could belong to *B. whitei*, or possibly to *Connochaetes gentryi*. It has the eroded bases of both horncores inserted very far apart. It may be subadult judging by the simple and open sutures and the spongy nature of the bone. It has a very broad, slightly and evenly convex forehead, a broad braincase that is short from occiput to the coronal suture, which is only slightly anteriorly-indented at the midline, curved temporal lines that remain very wide apart at their closest approach, no parietal boss, a supraoccipital that is very narrow anteroposteriorly but wide laterally and widely-spaced supraorbital foramina in tiny pits situated far anterior to the horncores. The basioccipital area shows well-developed longitudinal ridges behind prominently projecting anterior tuberosities and a definite central longitudinal groove between the ridges that is shallower than in the paratype, posterior tuberosities wider than anterior ones, and curved, long and not markedly inflated auditory bullae. Occipital surface facing mainly backwards. *C. gentryi* and *B. whitei* resemble each other in an expanded slightly convex forehead with far apart supraorbital foramina, uncompressed horncores (Figure 19) that are widely separated (Figure 20), horncore base with a high angle to the midfrontal suture, and a large craniofacial angle (Figure 18). Differences of *B. whitei* from *C. gentryi* include very much larger and longer horncores that lack clockwise torsion as in *C. gentryi* and with a different basal shape, lower distances from horncores to orbits and to supraorbital foramina, and a wider braincase and mastoid region. Unfortunately KL238-1 lacks horncores. The bases are close in dimensions to *C. gentryi*. It is also closer to the fine *C. gentryi* adult holotype cranium KNM-ER 287 from the Upper Burgi Member dated ca. 2.0 m.y. than to the *B. whitei* holotype and paratype in its very large distance from horncores to supraorbital foramina, and in the shallower longitudinal groove on the basioccipital. The fact that the specimen may be subadult complicates the evaluation of what these differences mean. KL238-1 is larger than the later *C. gentryi* skull in several of its measurements, such as widths of braincase and mastoids, and occipital height. In these respects it is closer to *B. whitei*. To propose that KL238-1 belongs to *C. gentryi* requires that the earlier, possibly juvenile cranium is larger than the later conspecific adult in some features but not in others. Additional material from Matabaietu may resolve this. Until then I tentatively assign KL238-1 to cf. *Beatragus whitei*.

Dentitions from Matabaietu 3 or 4 tentatively assigned to this species include an upper M^3, MAT-4/8 (Table 11), and several lower dentitions (Table 12). All three available P_4 are advanced in having fully fused paraconid and metaconid and fairly reduced posterior parts. All the molars are very hypsodont, and all the M_3 have large posterior lobes. The best mandible is shown in Figure 17d. It has a deep horizontal ramus, paraconid and metaconid on P_4 nearly fused, a wide and quite complex P_3 with entoconid, paraconid and metaconid well-defined and protruding medially and the last two approaching each other. P_2 was absent in life.

Comparisons: The closest comparison is with *B. antiquus*. There are numerous similarities, from the length and upward pointing tips of the horncores, through the basal horncore cross-section with some posterior flattening (Figure 2), to the convexly-domed forehead and short horn pedicels. The most informative adult fossil of *B. antiquus* is the frontlet S.217 from HWK East at Olduvai dated ca. 1.7 m.y., while other Olduvai fossils are horncores from Beds I and II (Gentry and Gentry 1978). A possibly subadult cranium KNM-ER 2570 with right horncore base from the Upper Burgi Member in the Koobi Fora Formation was the earliest fossil that was previously securely attributable to *Beatragus* (Harris 1991). Other later fossils from the Koobi Fora Formation are horncores from the KBS and Okote Members, between 1.9 and 1.6 m.y. old. One of these, KNM-ER 4546 from KBS, has an adult dentition associated with it. The most complete specimen of *B. antiquus* is the possibly subadult cranium FG27-1 of *B. antiquus* from Shungura G27 dated ca. 2.0 m.y. (Gentry 1985). Because the most complete crania are possibly from subadult animals, I shall first mention differences of *B. whitei* from the other presumably adult material: the horncore bases have an absolutely larger maximum diameter, an averagely larger minimum diameter, and averagely greater compression (Figures 2, 19). The horncores are substantially longer. The estimated lengths of 700 and 720 mm for *B. whitei* compare with presumably adult horncores of *B. antiquus* as follows: 535 mm (from Olduvai Bed I), 505 mm and 475 (Olduvai Bed II), and 440 mm (associated with adult dentition from KBS Member). Two *B. hunteri* lengths are 430 mm in a specimen from the Chari Member and 520 mm in a living skull. The distal and basal parts of the horncores are much more divergent (basal angles 150° and 140° in *B. whitei* compared with 115° in S.217 from Olduvai Bed II), and the angle of horncore to cranium angle is lower. The latter is related to the fact that in lateral view *B. whitei* horncores have only two major directional components (first backwards and upwards, then recurvature towards a more upward course) while those of *B. antiquus* tend to have three (first upwards, then backwards and upwards, and then recurvature towards an upwards direction in an S-shaped or lyrate course). *B. whitei* has far less pronounced transverse ridges on and torsion of the horncores and greater widths across orbits and horn pedicels. Most of these differences are even more pronounced in comparison with the subadult crania KNM-ER 2570 from the Upper Burgi Member and FG27-1 from Shungura G. Yet in some respects *B. whitei* resembles the subadults more closely. For instance, in horncore divergence and course, FG27-1 resembles the Awash fossils more closely than do the adult *B. antiquus*. This probably arises because bovid horncores grow mainly from the base (see Vrba *et al.* 1994) and the subadult has not yet undergone the late growth of the more upright basal stem of the horncore. That is, if *B. antiquus* evolved from *B. whitei* as my results suggest (Figure 22), then some of its features evolved by acceleration resulting in a 'hyper-adult' morphology. At the same time there was a decrease in size towards *B. antiquus*. Put another way, *B. whitei* is a neotenous (with proportions that are relatively juvenilized) giant relative to *B. antiquus*. Additional differences of *B. whitei* from the subadults KNM-ER 2570 and FG27-1 include larger occipital height and width across the mastoids, and a basioccipital with more of a central constriction between anterior and posterior tuberosities and with wider posterior tuberosities. *B. whitei* also has a shorter distance from the posterior horncore bases to the occiput which may be at least partly due to its more massive horncores. It is likely that many of the differences between *B. whitei* and *B. antiquus* are expressions at different body sizes of a common growth allometry such that relatively simple evolutionary change, for instance in the time of growth to maturation, occurred between these two taxa. Yet there are also indications for some characters that a dissociation of the ancestral growth allometry – a more fundamental kind of change – must have occurred. This can be seen in several proportional differences. For instance, the two taxa have similar braincase width, separations of temporal lines and of supraorbital foramina, and distance of supraorbital foramina from horncores. In strong contrast, *B. antiquus* is substantially lower in other dimensions such as horncore length, and widths across orbits and mastoids. It seems that *B. antiquus*, relative to its decreasing skull size, evolved a more expanded braincase and forehead.

The mandibles of cf. *B. whitei* agree with the single one referred to cf. *B. antiquus* in P_4 with nearly or fully fused paraconid and metaconid and fairly reduced posterior parts, hypsodont teeth in deep horizontal rami, and in similarly low premolar/molar ratios with P_2 absent in life. The referred M^2 in MAT-4/8 is longer but not wider, with less localized outbowing of the ribs between the styles than that in the only dentition associated with a *B. antiquus* horncore, KNM-ER 4546 from the KBS Member in the Koobi Fora Formation. The occlusal morphologies of the molars of the referred dentitions are very much larger and decidedly less advanced than in living *B. hunteri*.

Beatragus "*elandsfonteini*" from the Middle Pleistocene of Elandsfontein may be conspecific with a horncore from Swartkrans Member 2 (Vrba 1974). This species was considered as *Beatragus* sp. by Gentry (1978; Gentry and Gentry 1978), but as *Damaliscus* aff. *lunatus* by Klein and Cruz-Uribe (1991). My results support Gentry's view: The phylogenetic tree (Figure 22) suggests that the *Damaliscus* clade increased moderately in size in some *D. niro* populations and also towards *D. lunatus*; and that no *Damaliscus* lineage shows a large increase in the basal horncore-midfrontal angle (Figure 18). The Elandsfontein form was larger than the largest living *D. l. lunatus* I measured (Figure 19), with a large basal horncore-midfrontal angle. Affiliation with *D. lunatus* implies that it had the largest basal horncore size of any *Damaliscus* species, and requires first size increase and then secondary decrease in the *D. lunatus* lineage, and also unique increase of the basal horncore-midfrontal angle within *Damaliscus* followed by secondary decrease. In contrast, the phylogenetic tree (Figure 22) together with Figure 19 suggest that *Beatragus* overall decreased in size from the earliest *B. whitei*, through *B. antiquus* (although *B. antiquus* does show a great deal of variation) to *B. hunteri*. Between *B. antiquus* and living *B. hunteri* there was also a trend towards increased horncore compression. The Elandsfontein form is close in horncore size and compression to *B. antiquus*, being closest to the mean of Olduvai Bed II *B. antiquus* (Figure 19). The substantial anticlockwise horncore torsion and the large basal horncore-midfrontal angle of *Beatragus* (Figure 18) are present in the Elandsfontein form. Also, Olduvai *B. antiquus* shows a trend towards increasing approach of the distal horncores (see the latest-known horncore 1962.068/6654 from Kit K in Olduvai Bed II) which is even more strongly present in the Elandsfontein form. In sum, *B. "elandsfonteini"* is closely allied to *B. antiquus*, and perhaps the sister-lineage of *B. hunteri* after common descent from *B. antiquus*. Similarities between *B. whitei* and *B. "elandsfonteini"* include horncores with low compression and strong divergence immediately above the base, some flattening of the posterolateral surface, short thick horn pedicels, a short distance from horncore to orbit, and a more backward course immediately above the base than in *B. antiquus*, although *B. whitei* has this most marked. *B. whitei* differs from *B. "elandsfonteini"* more than it does from *B. antiquus* in its basal anterior rugosity that extends upwards on the horncores in a medial direction, in having very much longer horncores that lack any hint of inturning towards the tips which is strongly present in *B. "elandsfonteini"*, in horncores with the lateral basal margin much more lowered relative to the medial one, in a virtual absence of transverse ridges, and in the lack of a posterolateral keel.

Geraads (1979: 36-38, plate II, Figure 4) described a form from Melka-Kunture in Ethiopia as *Connochaetes taurinus* subsp. nov. It is abundant in the Garba IV strata dated ca. 1.3 m.y. and also known from later Sibirro. The best specimen, a complete left horncore Gar IV-72-2311, was 500 mm long in life, slender, with the basal part flattened dorso-ventrally and with anterodorsal swelling, uncompressed with basal diameters 58 and 54mm; transverse ridges and torsion absent; very strong divergence from just above the base and continuing for the lower half of the horncore, and is followed

Figure 12. a. *Damaliscus ademassui* sp. nov., holotype left horncore and partial cranium GAM-1/17 from Gamedah 1 in lateral view; and b. *Parmularius* cf. *pandatus*, right horncore KL11-2, cf. Wilti Dora 2 in medial view.

by a strong change in course to a straight upright distal part such that the basal and upright segments are situated almost at a right angle to each other. Geraads considered attribution to *Beatragus* and rejected it because in his view the horncores of *Beatragus* have stronger torsion and curvature near their bases and a relatively longer distal part. Having seen the new *B. whitei* material, I suggest that Gar IV-72-3211 could belong to a *Beatragus*, although probably specifically distinct from *B. whitei*. Geraads's figure suggests an insertion and basal course in anterior view very like that in the paratype of *B. whitei* (Figure 10c), with a short upward tendency immediately above the base followed by strong outward divergence. However, the basal segment seems more divergent and relatively longer than in *B. whitei*, the tips point more upwards and much less outwards, and the horncore is much shorter and basally less massive. Also, Geraads mentions that where slight torsion exists in similar specimens from Garba it is clockwise on the right which would fit his choice of *Connochaetes* better. Without seeing the Melka-Kunture specimens I cannot take the matter further except to suggest that detailed comparison of these two Ethiopian forms will be worthwhile.

I now believe that the fossil SK 3812 from Swartkrans Member 1 (cf. *Connochaetes* sp. in Vrba 1976) is a *Beatragus*, and probably *B. antiquus*. The horncores of this dorsal cranium are broken off showing large basal sinuses, and the remaining fragments suggest that the horncores were inserted wide apart and more closely behind the orbit than in *Connochaetes*. The forehead is convex as in *Beatragus*, and the supraorbital foramina were as wide apart as in *B. antiquus*. The upper part of a larger preorbital fossa than found in even earliest *Connochaetes* is present. If this is *B. antiquus*, then it would be the first evidence that *B. antiquus* had a preorbital fossa.

Some of the more startling aspects of my systematic hypothesis (Figures 21, 22) are the close relationship of *Beatragus* to *Damalacra neanica*, and the sister-group status of *Damalacra-Beatragus* with the *Damalops*-to-*Connochaetes* clade in Alcelaphina. Gentry (1980: pp. 70-72) noted that *D. neanica* resembles *Beatragus* in the large basal horncore-midfrontal angle (character 15 which is synapomorphous for Alcelaphina, Figure 21: node 2) and in some anticlockwise torsion in the right horncore (character 12). Yet he concluded that *D. neanica* "is too primitive to be satisfactorily related to *Beatragus*." The present alignment of *Beatragus* with hartebeests, wildebeests and allies offers some support for older views that are reflected in the name Hunter's Hartebeest for *B. hunteri*. The most significant characters supporting this relationship are a basal horncore margin that is markedly lower laterally than medially (character 6) and a strong angle of the basal horncore to the midfrontal suture (character 15, Figure 18), because these are the only two of five changes to Alcelaphina that occur uniquely at this node. Some additional characters that may support a sister-group relationship of *Beatragus* with *D. neanica*, are not represented among the cladistic codes (Table 14) because the information was available for too few taxa. *Beatragus* and *D. neanica* may share that the posterior tuberosities of the basioccipital are wider relative to the anterior ones than is usual in Alcelaphini. The ratio (width of anterior tuberosities)/(width of posterior tuberosities) in the relevant taxa is as follows: *D. neanica*: a mean ratio 0.76 (sample size n = 6) in contrast to (*Damalacra*) *acalla* from the same strata at Langebaanweg with a mean ratio of 0.82 (based on Gentry 1980); *B. whitei*: 0.71; *B. antiquus* from Upper Burgi: 0.74; one *B. hunteri*: 0.76. Many other alcelaphines appear to have ratios greater than 0.76. Another resemblance is the uninflated auditory bulla in *B. whitei*, *B. hunteri* (the bullae of the *B. antiquus* crania are not preserved, but the spaces for them look narrow), and in *D. neanica* while (*D.*) *acalla* has a larger bulla (Gentry 1980). Small, little-inflated bullae are also found in *Parmularius*, *Megalotragus* and some other alcelaphines. A feature that may be relevant is posterior flattening of the basal horncore (character 7, Table 13). I am uncertain whether *Beatragus* has this feature. One could argue that it is present (Figure 2g-j). This would require revision of the codes for *Beatragus* in Table 14. It would be another shared feature of *Beatragus* with the clade *Damalops*-to-*Connochaetes*, although *D. neanica* does not appear to have this state (Gentry 1980) and, in its present cladistic position, would require a reversal.

Subtribe Damaliscina, nom. nov.

Damaliscina includes alcelaphines of small to medium size. The basal horncore margin is posteriorly slightly to markedly lower than anteriorly. The horncore is anteriorly slightly to moderately convex, and lyrated in all but the most primitive forms (lyration here refers to anterior-ward recurvature towards the horncore tip after basal convexity). The posterior angle between the maximum horncore diameter and the midfrontal suture is low to moderate. A parietal boss on the dorsal braincase is slightly to well developed, although it is secondarily lost in more than one lineage. The braincase roof is slightly to strongly convex. The braincase is moderately to markedly wide and broad across the mastoids except in *Parmularius pandatus* in which this character shows secondary reversal. The braincase is pleisiomorphically long.

Genus *Parmularius* Hopwood, 1934

Type species *Parmularius altidens* Hopwood 1934

Generic diagnosis: Extinct small- to medium-sized alcelaphines. Horncores are moderately long to short, without torsion or keels, with transverse ridges in their distal parts, and generally with little basal compression. Basal swelling of the horncore is present posterolaterally, and sometimes also medially and posteriorly. The posterior angle between the maximum horncore diameter and the midfrontal suture is low. The horn pedicels are relatively long and parallel-sided, and the distance from the horncore base to the orbit in general is elongated. Preorbital fossae are small. Auditory bullae are fairly small. Premolar rows very short except in the earliest and one later form. There is a strongly developed parietal boss on the dorsal braincase. In all but the earliest forms, the braincase is short and wide with a large distance across the mastoid exposures, and a high occiput. (See also Gentry and Gentry 1978.)

Parmularius pandatus Gentry 1987

Diagnosis: "A species of *Parmularius* ca. the size of *P. altidens* or slightly smaller. Horn cores without a flattened lateral surface, inserted rather uprightly over the back of the orbits, not very divergent, curving rather sharply backwards just over halfway from base to tip, and with posterolateral swellings at the base. Braincase rather long for an alcelaphine and its roof not very inclined; frontals between the horncore bases at a higher level than the dorsal parts of the orbital rims, transverse coronal suture, low parietal boss on braincase roof, temporal lines rather close posteriorly, braincase sides parallel, supraorbital pits close together and with a concave and non-swollen area of the frontals between them, each side of the occipital surface facing partly laterally, narrow basioccipital" (Gentry 1987:390).

Parmularius cf. *pandatus*, cf. Wilti Dora 2 (Figure 2f, 12b, Table 8):
The right almost complete horncore KL11-2 is of unknown provenance but thought to come from Wilti Dora 2 dated ca. 2.5 m.y. (Figure 1). The horncore base is moderately compressed with its maximum diameter little angled to the midfrontal suture and the widest mediolateral diameter situated posteriorly (Figure 2f). There is a large sinus some 20 mm up into the horncore base. The basal horncore margin is markedly lower posteriorly than anteriorly, and the base has some posterolateral swelling. A preserved part of the orbital roof suggests that the horncore was situated above the posterior orbit. The lateral horncore shows some flattening and the medial surface less so. The horncore has a very upright part, that is very steep relative to the small preserved piece of the braincase and has little backbending, for ca. one third of the total length of 300 mm from the base. Then it bends back abruptly and strongly with some recurvature in an upward direction towards the tip. It has low basal divergence,

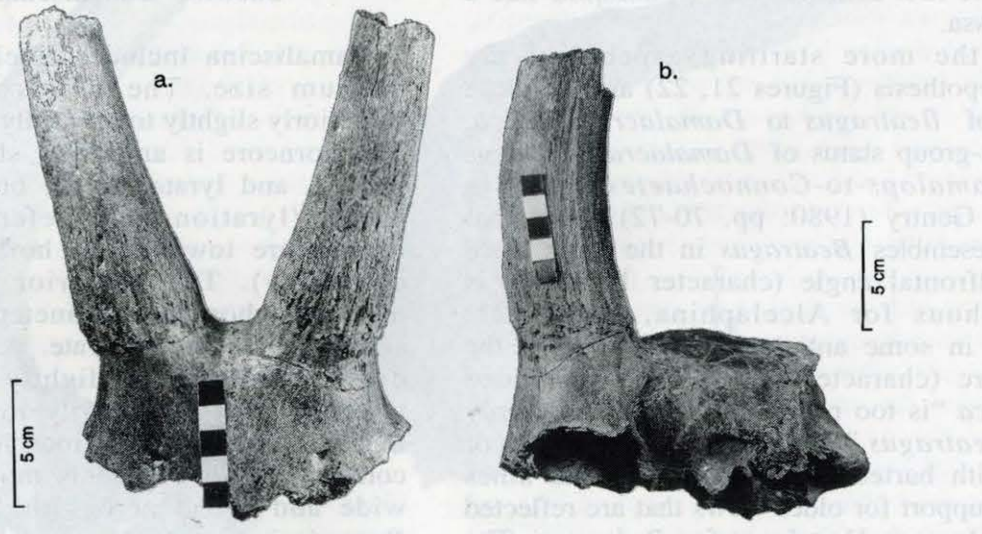

Figure 13. Cranium of *Damaliscus niro*, BOD-1/17, from Bodo 1 in a. anterior view, and b. left lateral view.

TABLE 9.

Measurements of crania: *Damaliscus ademassui* sp. nov., holotype GAM-1/17; *Damaliscus niro*, BOD-1/17; and *Awashia suwai* gen. et sp. nov., holotype MAT-3/2. Length in mm; two values for horncore length are preserved/ estimated complete lengths; e = estimate, ee = very rough estimate.

	D. ademassui	*D. niro*	*A. suwai*
	holotype		holotype
	GAM-1/17	BOD-1/17	MAT-3/2
Horncore maximum diameter diameter (1)	46.3	55.0	47.8
Horncore minimum diameter (2)	35.5e	46.5	42.7
Horncore ratio (2)/(1)	0.77e	0.85	0.89
Horncore length	260/260	137/?	280/300
Horncore basal separation	50ee	28.0	34.6
Angle of basal horncore divergence	45°ee	25°e	60°
Angle of horncore to braincase	90°ee	102°	90°
Angle of (1) to midfrontal suture	15°	10°e	60°e
Width across horn pedicels		109.0	117.3
Craniofacial angle	100°e	97°	113°e
Maximum separation supraorbital foramina (SOF)	63ee	65.0	57.5
Distance of SOF to anterior horncore midpoint	50e	48.5	57.5e
Distance of SOF to posterior auditory meatus	117.5	113.0	
Distance across superior orbital margins	120e	138ee	148.2
Distance orbit to horncore			41.0
Braincase width at parietal-squamosal suture	85ee	87.5	84.5
Braincase length: coronal suture to occiput	73e	70e	66e
Distance across mastoid exposures	115ee	113e	112ee
Occipital height: top foramen magnum to occiput		49e	57.5e
Basioccipital width across anterior tuberosities		28e	
Basioccipital width across posterior tuberosities		38.5	
Basioccipital length: anterior to posterior tuberosities		28.5	
Width across nasal bones			37e
Distance posterior M^3 to occiput			200e
Length M^{1-3}			60ee
Length M^{1-2}			43.8
Length/breadth M^2			21.1/20.0
Length/breadth M^3			23.7/15.0

then slightly increased divergence in its middle part, followed by inward-bending towards the tip. The upper part of a shallow postcornual fossa is preserved. Basal horncore separation was very low, and the horn pedicel is quite long. There is a slight hint of anticlockwise torsion. There are some strong longitudinal grooves on the middle posterior surface. There are transverse ridges circling the medial, anterior and lateral surfaces, very strong especially anteriorly, trending from higher lateral to lower medial positions, and separated 15-23mm from each other.

The closest resemblances are to *Parmularius pandatus* from the Laetoli Beds including the holotype cranium 1959.277 (see Gentry 1987; dated ca. 3.6 m.y.), *P. braini* from Makapansgat (Vrba 1977; ca. 2.9-2.7 m.y.), and to a lesser extent to *P. eppsi* from the Upper Burgi, KBS and Okote Members (Harris 1991; 2.0-1.4 m.y.) in the Koobi Fora Formation and Shungura C (ca. 2.6 m.y.). In comparison with these taxa, KL11-2 is intermediate in basal size and length of the horncore between the two large *P. braini* adult frontlets and the largest *P. pandatus* horncores. It is also intermediate in its ratio of basal horncore diameters, or compression, between the higher mean for *P. pandatus* (although its value of 0.77 fits into the range for *P. pandatus*, 0.75-0.87) and the lower mean for *P. braini*, while *P. eppsi* has a higher mean. The strong and abrupt backward curvature in the lower-to-middle part of the horncore of KL11-2, and a horncore tip that starts to recurve upwards soon after the backward bending, are less like *P. braini* and *P. eppsi* (in which backward curvature is less localized and more distal, and tip recurvature is also more distal) and much closer to *P. pandatus* although KL11-2 is more extreme in this respect than the Laetoli horncores. KL11-2, *P. pandatus* and *P. braini* share closer basal horncore separation than *P. eppsi*, and a low and gradual divergence from the base up with only the tips re-approaching (seen in *P. pandatus* frontlet LAET 245 Loc. 8, although not in the holotype 1959.277). The horncores of *P. eppsi* tend to re-approach slightly shortly after the base. The preserved part of the posterior orbital roof in KL11-2 suggests that the horncores were situated closer to the orbit and more nearly over its posterior part than in *P. braini* and *P. eppsi*, and again resembling *P. pandatus*. The posterolateral basal swelling in KL11-2 also resembles the Laetoli horncores more; in *P. braini* the posterior swelling is stronger and more medially situated. The lateral and medial basal swellings in *P. eppsi*, in addition to the posterior one, are absent in *P. pandatus* and in KL11-2. Gentry (1987) pointed out that horncores of *P. pandatus* have less pronounced anteroposterior thinning shortly above the horncore base than do those of *P. braini*. In this respect KL11-2, although it shows an approach to *P. braini*, is also more like *P. pandatus*.

While the Awash form has more resemblances to *P. pandatus*, it shows the following advances towards *P. braini*: an increase in horncore length and basal size; an increase in compression mostly by a larger maximum diameter with less tendency to posterior flattening of the basal horncore, increased prominence of transverse ridges, somewhat more pronounced anteroposterior thinning shortly above the horncore base, and more inward directed tips than in the *P. pandatus* holotype. I interpret it as a late population of *P. pandatus*, before the Late Pliocene evolution of the large suite of new features that characterize the *Parmularius* clade from *P. braini* upwards (node 13 in Figure 21), and perhaps close to the direct ancestry of *P. braini*. This would imply a date for KL11-2 that falls between 3.6 m.y. and 2.9-2.7 m.y., earlier than the 2.5 m.y. date implied by the tentative assignation to Wilti Dora 2.

A cranium KP30157 from Kanapoi (dated ca. 4.1 m.y.) is a *Parmularius* species that appears to belong to the lineage leading to *P. pandatus*, and may be a branch off the lineage that connects (*Damalacra*) *acalla* with *Parmularius* according to the present cladistic result (Figure 22). It is smaller than *P.* cf. *pandatus* from the Awash and also than *P. pandatus* from Laetoli. It resembles both the Laetoli and Awash forms in its degree of horncore compression, low basal separation and divergence of uprightly inserted horncores, and fairly long horn pedicels. It does not show the sudden backward curvature and strong transverse ridges of KL11-2.

Parmularius angusticornis (Schwarz 1937)
1937 *Damaliscus angusticornis* Schwarz: 55
1965 *Damaliscus angusticornis* Leakey: 51, Plates 63-66
1965 *Damaliscus antiquus* Leakey: 55, Plates 67-69
1965 *Parmularius* sp. indet. Leakey: 60, Plate 77
1965 cf. Alcelaphini Leakey: 66(b), Plate 91
1978 *Parmularius angusticornis* Gentry and Gentry: 382, Plates 23-24, Plate 25:

Diagnosis: Gentry and Gentry's (1978: 382) diagnosis is as follows. "A species of *Parmularius* about the size of *Alcelaphus buselaphus* or slightly larger; horn cores more massive with thicker bases and often more divergent in their distal parts than in *P. altidens*; most horn cores almost without backward curvature. Braincase more extremely shortened and more strongly angled on the facial axis than in *P. altidens*; parietal boss less marked than in *P. altidens*; suture of parietofrontals without a central indentation; large occipital surface retaining its median vertical ridge but facing backwards more clearly than in *P. altidens* or *rugosus*; auditory bullae small and little inflated; basisphenoid strongly bent upwards on plane of basioccipital."

Parmularius angusticornis from Bouri 1 (Table 8): Left horncore base BOU-1/11 comes from Bouri dated ca. 1 m.y. (Figure 1). The horncore is little compressed at the base with the greatest mediolateral diameter situated posteriorly, and may have been ca. 300 mm long in the complete state. The basal part rises at a steep angle to the small piece of the braincase that is preserved behind it and adopts a slightly more backward course upwards from some 50 mm above the base. The angle of horncore divergence was low to moderate, perhaps 30-40°. The basal horncore margin is lower posteriorly than anteriorly, and the base has a medial swelling. Its maximum basal diameter is hardly angled to the midfrontal suture which is very complicated anterior to the pedicel. The coronal suture is straight to only minimally centrally indented. The horncore has slight but definite transverse ridges on its anterior surface that are closely-spaced.

The previously known records of this species (Gentry and Gentry 1978) include Middle to Upper Bed II at Olduvai (dated ca. 1.7-1.5 m.y., Manega, 1993) and Kanjera of similar age, and also by a cranium from later Isimila probably dated close to Olduvai Upper Bed IV (ca. 0.7 m.y.). Thus, the Bouri and Isimila records are the latest. The Bouri form falls within the range for Olduvai and close to the Isimila fossil in basal size and compression (Figure 19), and closely resembles these previous records in its other preserved features.

Genus *Damaliscus* Sclater & Thomas, 1894
1846 *Damalis* Gray

Type species *Damaliscus dorcas* (Pallas, 1766)

Generic diagnosis: Small to medium sized antelopes. The skulls are high and narrow. The distance across the superior orbital margins is low except for departure from this basal condition in *D. lunatus lunatus*. The basal horncore sweeps smoothly upwards and backwards from the base without sudden alteration in course close above the base. The basal horncore is flattened laterally but not posteriorly, although this condition may have reversed in *D. agelaius*. The basal horncores are relatively strongly compressed with secondary loss of this feature in two taxa. The supraorbital foramina tend to be widely separated and not as far from the horncores as in most other alcelaphines. There is a slightly developed parietal boss. The braincase roof is slightly to markedly convex. The braincase is moderately long to long. The occipital height is low. Weak anticlockwise torsion in the right horncore is present in most species. The premolar rows tend to be relatively long for alcelaphines.

Damaliscus niro (Hopwood 1936)
1936 *Hippotragus niro* Hopwood : 640
1937 *Hippotragus leucophaeus* subspecies Schwarz: 87, Plate 2, Figure 14
1965 *Hippotragus* cf. *niger* Leakey: 50
1965 *Hippotragus* cf. *equinus* Leakey: 51 (in part)
1965 Other gazelles Leakey: 65(j) (in part)
1965 Alcelaphini indet. Leakey: 66(e), Plate 92
1965 *Damaliscus niro* Gentry: 335

Diagnosis: Gentry and Gentry (1978: 396) gave this diagnosis: "An alcelaphine about the size of *Damaliscus lunatus* or larger. Horn cores moderately long, strongly compressed mediolaterally especially distally (but less strongly compressed in some Olduvai specimens), frequently with flattened lateral and medial surfaces, the widest part of the cross-section situated anteriorly, inserted above the back of the orbits and obliquely in side view but more uprightly than in *D. lunatus*, divergent as much as in *D. lunatus korrigum* or more so, curved evenly backward (or in some Olduvai specimens with a fairly abrupt change of course about half way along the horn core length), many examples with strong and widely spaced transverse ridges on the front surface. Horn pedicels short compared with *Parmularius*; postcornual fossa shallow and rather long; braincase strongly angled on the facial axis; sometimes a slight indication of a parietal boss; orbital rims moderately projecting." The present analysis adds the following: Relative to basal horncore size, many *D. niro* horncores are very long, longer than those of other alcelaphines except *Beatragus*, *Damalops palaeindicus*, *Megalotragus*, and *Oreonagor*. The horn pedicels are shorter and the supraorbital foramina are closer than in other *Damaliscus*.

Damaliscus niro from Bodo 1 (Figure 13, Table 9):

Cranium BOD-1/17 and left horncore BOD-1/24 from Bodo 1 are dated ca. 0.6 m.y. (Figure 1). BOD-1/17 has the basal parts of both horncores, anterior frontals up to supraorbital foramina, and the almost complete posterior cranium. The horncores have bases that are large and oval in cross-section with little basal flattening medially, weaker lateral flattening at the base than higher up, and a largest mediolateral diameter that is situated anteriorly (Figure 2). The horncores have a low diminution rate over the preserved parts, are not as compressed as most *D. niro*, inserted steeply, close above the orbit on short pedicels, with low basal separation and divergence and at a low angle to the midfrontal suture, with some longitudinal grooves laterally and medially to posteromedially, without any torsion, and without basal swellings. On the anterior horncore surface there are strong transverse ridges widely spaced ca. 20-30mm apart; orbits not prominent. The cranium has widely spaced supraorbital foramina in small shallow pits on an almost flat to slightly convex forehead; part of a long shallow postcornual fossa visible on the left side; gently sloping parietal boss that is not localized on the braincase roof; parietofrontal suture only very slightly indented centrally; weak temporal ridges far apart on the posterior braincase roof; face strongly angled relative to braincase; braincase long and not widening posteriorly with a rather small supraoccipital exposure on the braincase roof; occipital surface with strong nuchal crests and not evenly and broadly rounded but with concave lateral borders, prominent spine on a prominent median ridge with deep dorsal flanking hollows on either side, occipital surface with strong laterally-facing components, mastoid with strong dorsal and ventral rims and situated entirely on the occipital surface; and a short basioccipital with a wide fairly deep longitudinal valley between flanking longitudinal ridges.

Left horncore BOD-1/24 shows the top of a smooth-walled basal sinus at its broken base. It is more compressed than the horncores of BOD-1/17. The maximum and minimum diameters of the base in the complete state are estimated roughly to be ca. 48.5 mm and 37.5 mm. Some 180 mm above this they are 32.0 mm and 17.7 mm. and the length may have been ca. 350 mm. Transverse ridges are only faintly perceptible and seem to be spaced far apart.

Comparisons: The Bodo cranium BOD-1/17 overall conforms closely with the diagnosis and previous descriptions of *D. niro* (see Gentry and Gentry 1978, for the most extensive treatment). It has smaller and less compressed horncores than the Olduvai Bed II mean and specimens from Peninj. It is closest in both respects to some of the smaller and least compressed specimens from Olduvai Bed III, although it has lower compression than the Olduvai Bed III mean (Figure 19). It compares as follows with South African *D. niro* from Kranskraal, Cornelia and Florisbad (see measurements in Gentry and Gentry 1978: 399; see also Brink 1987, 1988 for Florisbad). It is larger than all of them, being closest in size to the Cornelia form, and its compression is lower than in all Florisbad and Cornelia specimens but close to that of the Kranskraal cranium C.666, from which it differs in having less medial flattening of the basal horncores. The horncore BOD-1/24 is smaller with higher basal compression than BOD-1/17, and fits best in both respects with the larger Florisbad specimens. It is not possible to make extensive comparisons of other cranial features among African *D. niro* populations as BOD-1/17 is one of the most complete specimens known. The cast of a slightly smaller Kranskraal cranium, GHG303 at the Pretoria Geological Survey, has a braincase that is as long as that of BOD-1/17 although narrower with a narrower, longer basioccipital, a

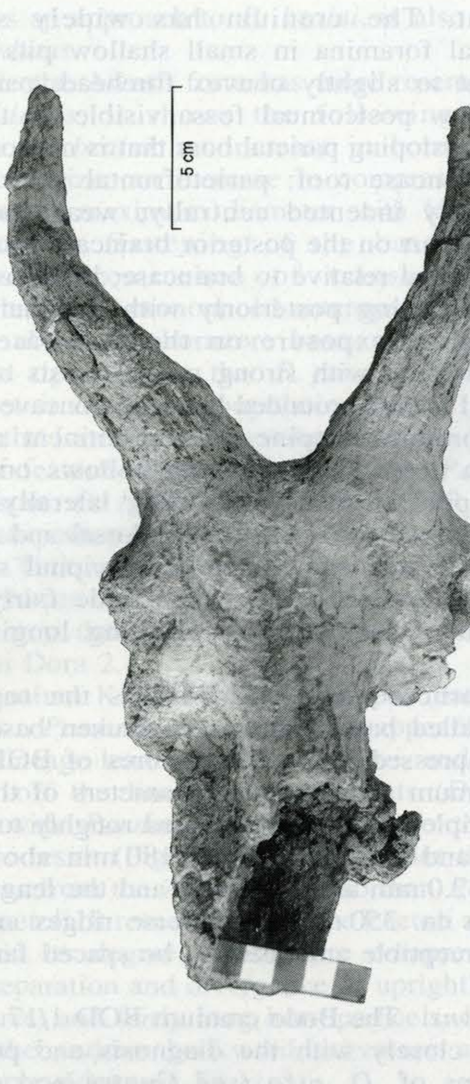

Figure 14. Holotype cranium of *Awashia suwai* gen. et sp. nov., MAT-3/2 from Matabaietu 3, in anterior view.

more prominent parietal raising, and is closely comparable in other respects. Comparisons of Bodo *D. niro* with the new species of *Damaliscus* from Gamedah will be discussed below. A taxon thought to be closely related to *D. niro* is *D. gentryi* known only as a single fragmentary frontlet from an Early Pleistocene stratum at Makapansgat (Vrba 1977). *D. gentryi* resembles BOD-1/17 in horncore size and degree of compression although it is slightly more advanced in both respects, in basal divergence, and in separation of the supraorbital foramina. It differs in a horncore-pedicel boundary that is more extremely lowered posteriorly than anteriorly, and in a more pronounced backbending of the lower half of the horncore that commences only a small distance above the anterior horncore-pedicel boundary. In this latter respect *D. gentryi* differs from all known *D. niro* specimens.

Damaliscus ademassui sp. nov.

Diagnosis: An extinct small species close in size to a large *D. dorcas*, with horncores that are moderately long although shorter than in secure *D. niro*, inserted right above the back of the orbit, and sweeping gently backwards and recurving in an anterior direction towards the tip. They show strong lateral flattening resembling some *D. niro* specimens, but no medial flattening as frequently found in *D. niro* such that the new species resembles *D. dorcas* and *D. lunatus* in this respect, and a stronger posterolateral keel than is present in *D. niro* and even in *D. dorcas*. Both the lateral flattening and the keel extend right up the horncore. The widest mediolateral basal horncore diameter is situated

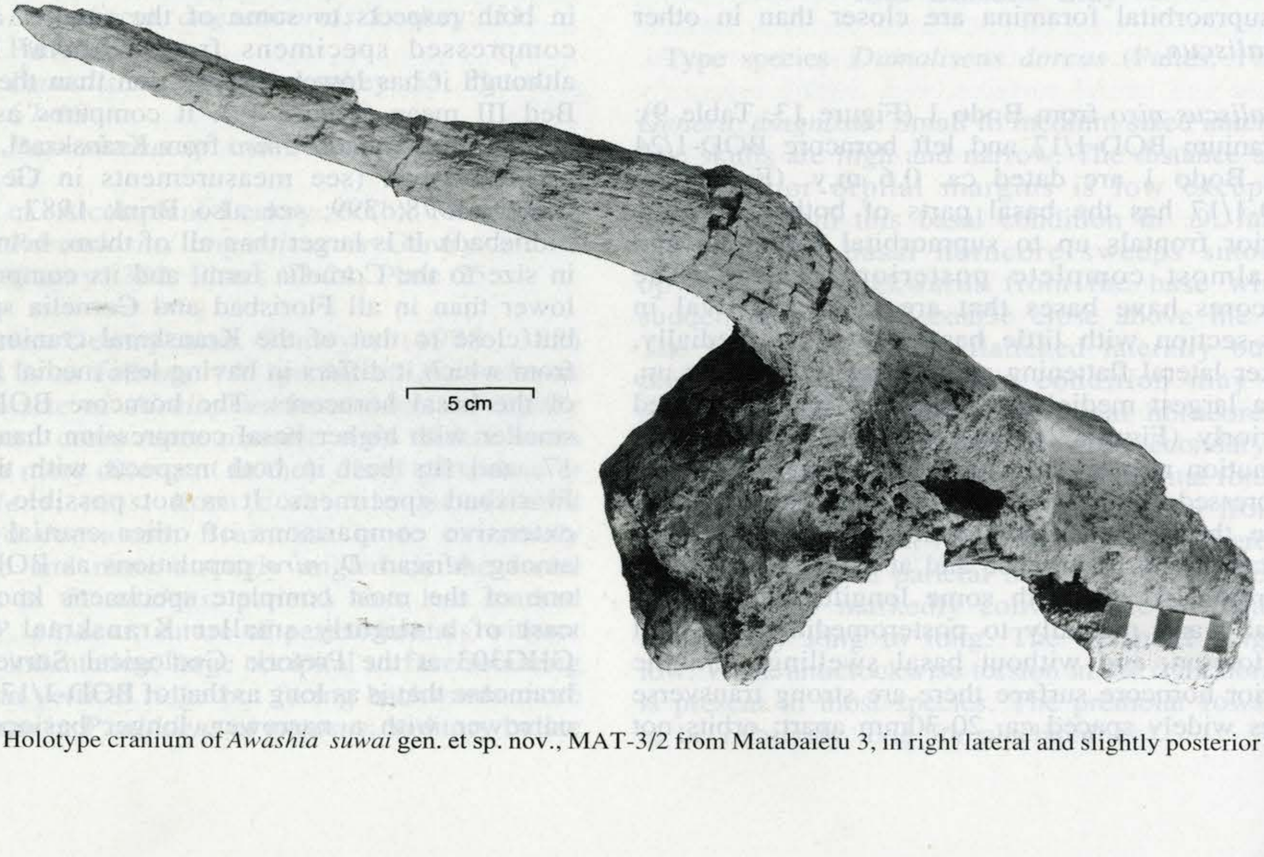

Figure 15. Holotype cranium of *Awashia suwai* gen. et sp. nov., MAT-3/2 from Matabaietu 3, in right lateral and slightly posterior view.

posteriorly as in *D. niro*. The horncores not as uprightly inserted as in *D. niro*, but resembling other *Damaliscus* species. The basal horncores are strongly compressed, unlike the rounder horncores of *D. agelaius* and resembling other *Damaliscus* species. Basal horncore divergence is higher than in many *D. niro* and in all the *D. dorcas* I have measured, but considerably lower than in *D. lunatus lunatus*, and the tips re-approach each other. The horncores have strong, widely-spaced transverse ridges, not as marked as but resembling the condition in *D. niro*. Basal horncore separation is moderate, higher than in *D dorcas* and *D. niro* but lower than in *D. lunatus lunatus*. The horncore pedicels are long and less well-defined and parallel-sided than in *Parmularius*, and longer than in *D. niro*. The orbit projects quite strongly. The angle of the forehead to the dorsal braincase is low as in *D. niro*, and lower than in other *Damaliscus* species. The braincase is as long as in *D. niro*, longer than in living *Damaliscus*, and shorter than in *D. agelaius*. There is weak anticlockwise torsion in the right horncore, resembling *D. dorcas* and *D. lunatus* but unlike *D. agelaius* and *D. niro*. The postcornual fossa is quite deep relative to length, unlike the shallow long fossa in *D. niro* and in many other alcelaphines. A large part of the mastoid faces laterally.

Holotype: GAM-1/17 includes the fragmentary part of a left side of a cranium with the almost complete left horncore (Figures 2k, 12a). The frontal is preserved only above the supraorbital foramen, but the position of that foramen can be inferred from the preserved piece of the supraorbital canal beneath. The dorsal part of the braincase is missing. The fronto-parietal and parieto-temporal sutures on the left side of the braincase are uncomplicated. The moderately long horncore curves back from the base up and then the tip recurves in an anterior direction. The tips re-approach one another. The transverse ridges are surprisingly strong for the size of the horncore, extending diagonally onto the antero-lateral and to a lesser extent onto the antero-medial surface. From what is preserved it appears that the braincase did not expand posteriorly. The orbit projects strongly below a long horncore pedicel. The anterior part of the temporal ridge is quite strong. A large part of the mastoid exposure is visible in lateral view.

Horizon: The holotype comes from the Gamedah 1, which is estimated to be ca. 2.5 m.y. old (Figure 1) although it remains possible that it will turn out to be closer to 2.0 m.y.

Etymology: The new species is named after Alemu Ademassu in recognition of his work in Middle Awash palaeontology.

Measurements: The measurements of the holotype are given in Table 9.

Referred specimens: Right and left horncore bases, KL307-2, 3 of unknown provenance, may belong to *D ademassui*. The specimens are damaged and incomplete. Similarities include size and strong compression. Basal horncore diameters on the left side in KL307-3 are 43.6 mm and 29.5 mm. One difference is the slight tendency to a posterolateral keel in this specimen in comparison with the strong keel in the *D. ademassui* holotype. I tentatively refer the small mandible KL25-1 (cf. WIL-2) to *D. ademassui* (Table 11). Its size is close to those of *D. agelaius*, *Parmularius altidens*, large *D. dorcas*, and small *D. lunatus*. It has a large, molarized P_3 and the alveolus of P_2 shows that it was present and perhaps larger than a simple peg during life. P_4 has the paraconid and metaconid fused. All this fits *Damaliscus* well, the species of which generally have relatively less reduced premolar rows than do *Parmularius* species. The valley between the entoconid and endostylid on P_4 is posteriorly directed in an open V-shape such that the posterior part of the tooth is less compact and reduced than in later *Damaliscus*. The molar occlusal morphology is comparable in complexity to that of *D. agelaius* from Olduvai Beds III-IV (see Gentry and Gentry 1978: Plate 30), and more complex than is usual in *Parmularius* dentitions.

Comparisons: GAM-1/17 of *D. ademassui* shows interesting differences from the *D. niro* skull BOD-1/17: In GAM-1/17 the anterior part of the temporal ridge on the dorsal braincase is much stronger than in the larger Bodo skull of *D. niro*. A much larger part of the mastoid faces laterally than in BOD-1/17. Also, the mastoid in the Bodo skull has as its dorsal rim the lateral nuchal crest, whereas in the Gamedah form the nuchal crest departs from the superior mastoid border in an anterior direction. Gentry and Gentry (1978) discussed two horncore varieties from Olduvai Bed II BK which they felt might be related to or conspecific with *D. niro*. They referred to them as type A and type B. Type A horncores differ from typical *D. niro* by less strong basal horncore compression, only lateral flattening of the basal horncore without the medial flattening (both are found in typical *D. niro*), the widest mediolateral basal horncore is situated posteriorly and not anteriorly as in *D. niro*, a more marked change in backward curvature about halfway along the horncore, a tendency to upturned tips, by having the transverse ridges on the horncore closer together, and by having a small posterolateral swelling at the base. Most of these features are reminiscent of members of *Parmularius*. Also the pronounced anteroposterior thinning shortly above the basal horncore swelling in some type A specimens like BK II Ext 140 resemble *P. braini*. However, the type A horncores have have shorter pedicels than in *Parmularius*. Type B horncores differ from typical *D. niro* by also having less strong basal horncore compression, again by the widest mediolateral basal horncore being situated posteriorly and not anteriorly as in *D. niro*, by having little or no lateral flattening of the basal horncore, by not having the same pronounced backward curvature as found in typical *D. niro* nor a sharp change in curvature halfway up the horncore, and by having a swelling of the whole medial surface at the horncore base. I have studied and measured both the type A and B horncores.

D. ademassui resembles type A horncores in uprightness and length of the horncores, and in having only a lateral and not medial horncore flattening. It differs from type A horncores in much more gentle backward curvature and more lyrate shape with more definitely upturned tips, greater basal divergence with tips re-approaching, slight anticlockwise torsion, much stronger lateral flattening culminating in a strong posterolateral keel, a definitely higher distance from the horncore to the supraorbital foramina relative to basal horncore size, transverse ridges on the horncore perhaps further apart in relation to horncore size, and by having the greatest mediolateral diameter situated more posteriorly. Type B horncores differ from *D. ademassui* in greater length and less compression, absence of a posterolateral keel and upturned tips, less marked transverse ridges, a small posterolateral swelling at the base, a greatest mediolateral diameter situated more posteriorly, and a swollen medial horncore base.

Arambourg (1979) described *Damaliscus cuiculi* based on horncore 154-15:72 and some referred dentitions from Ain Boucherit, Algeria (see also Geraads, 1987), which may be close in time to Gamedah 1. Horncore 154-15:72 has basal diameters of 45 mm and 35 mm and a total estimated length of 260 mm that are very close to those of GAM-1/17. I had previously thought that 154-15:72 might belong to *Parmularius* (Vrba 1977a) because it has its widest basal mediolateral diameter situated posteriorly and not anteriorly as in most *Damaliscus*, slightly posterior to posterolateral swelling of the horncore base, an absence of torsion as is usual in *Parmularius* but rarer in *Damaliscus*, and it situated all in one plane in anterior view suggesting little change in degree of divergence from the base up. *D. ademassui* differs from the Ain Boucherit form in a more rapid rate of diminution from the base up (giving GAM1-17 a much more gracile appearance than 154-15:72 in spite of their similar basal dimensions and lengths), a more gentle backward curvature and a more lyrate shape with definitely upturned tips (the Ain Boucherit fossil is much more strongly curved back in what above the base is nearly a single even arc), more divergence from the base with distal re-approach of the tips, definite torsion and a strong posterolateral keel, transverse ridges that are more widely spaced, and most of all in its very different and unusual basal cross-section (Figure 2k) with strong lateral flattening and a sharp keel. The last feature is utterly different from the nearly oval basal cross-section with a lesser degree of lateral flattening, with the largest mediolateral diameter posteriorly situated, in the Ain Boucherit horncore. In fact, the holotype of *D. cuiculi* has strong similarities with the type A horncores from Olduvai Bed II (Gentry and Gentry 1978).

Geraads (1979) discussed *Damaliscus*? sp. nov. from Garba IV at Melka-Kunture, Ethiopia, dated ca. 1.3 m.y. The best preserved horncore is Gar IV-75-143. Gam-1/17 resembles this and other similar specimens from Garba IV in size, at least some degree of anticlockwise torsion on the right, the presence of definite transverse ridges, basal divergence with re-approaching tips and lyration with tips pointing up. Gam-1/17 differs from the Garba IV horncores in greater compression and length, stronger and more widely spaced transverse ridges, a longer horn pedicel, a longer distance from horncore base to orbital rim, presence of a strong posterolateral keel, and a much less twisted shape.

Subtribe ?Alcelaphina or ?Damaliscina

Genus *Awashia* nov.

Type species *Awashia suwai* sp. nov.

Generic diagnosis: The type species is the only one in the genus, and a diagnosis is given under the species.

Awashia suwai sp. nov.

Diagnosis: An extinct, medium-sized alcelaphine species with uncompressed, and moderately long, upright and divergent horncores with a maximum diameter more strongly angled to the midfrontal suture than in *Damaliscus* and *Parmularius*. The horncores lack torsion, and their course abruptly alters to become less upright shortly above the bases. Transverse ridges are present. The horncore has a tendency to posterior and some medial flattening at the base and the maximum mediolateral width is situated posteriorly. It is inserted behind the posterior part of the orbit on moderately long pedicels. The supraorbital foramina are closer together and further away from the horncore bases than in *Damaliscus*. The postcornual fossa is deeper and more localized than in most alcelaphines. The orbit projects strongly from a broad face. The braincase is long, high, moderately wide, with a high occipital surface that faces markedly laterally on either side of a prominent median ridge. The nuchal crest is concave laterally. The preorbital fossae are very large with marked upper rims on either side of a broad flat nasal shelf. They have lower rims posteriorly.

Holotype: MAT-3/2 is much of a cranium (Figures 14, 15) with both horncores, right M^{2-3} and part of the left M^3 in medium wear, while parts anterior to that are missing. The basioccipital is obscured by matrix and may be missing. The horncores are uncompressed basally with a maximum mediolateral width situated posteriorly (Figure 2e), of medium length, without torsion, and inserted behind the posterior part of the orbit on moderately long pedicels. The angle of the maximum diameter to the midfrontal suture is difficult to estimate but may have been ca. 60°, and the craniofacial angle was quite large (Figure 18). The horncores approach a sigmoid curvature which arises from an anterior swelling over the basal 75 mm, with an abrupt alteration towards a less upright course at that point, and from a slight tendency for the horncore tips to recurve upwards. In spite of some damage to the surfaces, one can see that transverse ridges were present and spaced rather far apart. Flattening of the horncore base is approached posteriorly and less so medially (Figure 2). The posterolateral margin has no real keel although this is the most pointed part of the basal horncore. Divergence at the base is ca. 60° and decreases distally, and the angle of the most basal horncore to the cranium is ca. 90°. The horncore-pedicel boundary is indistinct, suggesting that this adult individual might have been a female. The supraorbital foramina are only moderately far apart, quite far anterior of the horncores, almost completely flush with a more or less flat frontal surface, and with small subsidiary foramina above them. The midfrontal suture is complex between the horncores, becoming simple and spare anterior to that. The coronal suture is strongly anteriorly indented at the midline. The postcornual fossa is deep and localized for an alcelaphine. The frontal between the horncores is raised relative to the orbit. The orbit projects strongly, jutting outwards immediately below the pedicel and then curving downwards towards the orbital margin, and the face anterior to the horn pedicels is broad. The temporal ridges are moderately strong anteriorly. It is not clear whether the slight indication of a parietal boss is genuine or an artefact of surface damage. The long, high, moderately wide braincase is dorsally only slightly convex and does not expand posteriorly. The high occipital surface faces markedly laterally on either side of a prominent median ridge. The fairly strong nuchal crest is not evenly rounded but concave laterally. The moderately large mastoids seem to be situated entirely on the occipital surface. The preorbital fossae are very large with marked upper rims where they descend almost vertically on either side of a broad flat nasal shelf. They have lower rims posteriorly. The occlusal morphology of the preserved molars is relatively simple without marked invaginations of the anterior and posterior parts of the central enamel islands, and with little outbowing and pinching of the buccal surfaces between the styles.

Horizon: The holotype comes from Matabaietu 3 which is slightly older than 2.5 m.y. (Figure 1).

Etymology: The new species is named after Gen Suwa in recognition of his work in Middle Awash paleontology.

Measurements: The measurements of the holotype are given in Table 9.

Referred specimens: There are two medium-sized dentitions that could belong to this species, as they agree in size and morphology with those of the holotype, and as the only other alcelaphine taxon recovered to date from Matabaietu Localities 3-5 is the definitely larger new species of *Beatragus whitei*. These dentitions are juvenile left maxilla with DP^4-M^3 MAT-4/37 (Table 12), and left mandible MAT-3/6, with P_4-M_3 (Figure 17c, Table 11). The mandible has a small triangular damaged depression, but no firm indication of an alveolus, in front of the fragmentary P_3. I tentatively conclude that P_2 was absent in life. The posterior lobe of M_3 is long and narrow and P_4 has fully fused paraconid and metaconid.

Comparisons: Even the basic affiliation of *Awashia* with one of the major alcelaphine groups remains in doubt because it is plesiomorphic in many respects. Also, some features that can be seen clearly tend to be intermediate, while others are difficult to assess on the eroded surfaces of the cranium. Due to surface erosion in the basal horncore and pedicel area, the estimated codes in Table 13 for characters 6, 7 and 17 are tenuous (Table 13): For character 6, the current estimate of state 2 (the basal horncore margin is lower posteriorly than anteriorly) should perhaps be replaced by state 0 (the margin is lower laterally than medially). For character 7, the alternative code 2 (posterior flattening of the basal horncore) seems possible rather than the current code 1 (no pronounced lateral or posterior flattening). Character 17 has state 1 in Table 13, namely horn pedicels are at least moderately long, but state 0 for short pedicels may be the correct one. Similarly, surface erosion of the anterior horncores leaves doubt on the interpretation in Table 13 that character 4 has state 1 (far apart transverse ridges are unmistakeable along the entire anterior horncore). For character 25, the incidence of a parietal boss, it remains unclear whether the current code 1 for a moderately developed boss should be replaced by code 0 for absence to slight development. It is also difficult to decide whether character 10 should have code 3 (as in Table 13: the horncores in lateral view are convex over much of their bases with tips recurving upwards) or an alternative code. Concerning character 15, the basal cross-sections of the left and right horncores of MAT-3/2 differ. The condition in the left horncore (Figure 2e) suggests an intermediate value for the posterior angle between the maximum horncore diameter and the midfrontal suture (Figure 18). Hence the code in Table 13 is ?, allowing membership of the Damaliscina clade (from node 3 in Figure 21). However, a code of 1 for a high angle may be the correct one, and this would imply membership of Alcelaphina (from node 2 in Figure 21). Repeated cladistic analyses that explored various combinations of the alternative character codes including ?-codes to denote uncertainty, invariably pulled *Awashia* right out of Damaliscina, and some of these results placed it into a basal position in Alcelaphina close to the *Damalops* group. The problem is that the characters that are doubtful in *Awashia* are also important to the basal branching pattern in Alcelaphini.

The principal comparisons for *Awashia* are with the *Damalops* group, *Damaliscus agelaius* and *D. lunatus*, and less so with *P. rugosus*. MAT-3/2 resembles *Damalops palaeindicus* in horncore and skull size, moderately high distances of supraorbital foramina from each other and from the horncores, absence of horncore torsion, deep preorbital fossae extending far forward with pronounced upper rims and sharply descending from the nasal shelf between them, and a moderately high to high basal horncore-midfrontal angle. *A. suwai* differs from *D. palaeindicus* in horncores that are not mounted on an elevated frontal ridge, less compressed, shorter and of higher diminution rate especially shortly above the base, more divergent at the base with lessening distal divergence, whereas in in *D. palaeindicus* divergence increases distally, with a marked alteration to a more backward course above the base that is absent in *D. palaeindicus*, and inserted less steeply relative to the dorsal braincase; a shorter deeper postcornual fossa; greater width across pedicels and orbits; much more prominently jutting upper orbits that are closer to the horncores; a larger craniofacial angle; a longer braincase with greater mastoid width; toothrow situated less anteriorly relative to the orbit probably indicating a shorter face; a wider nasal shelf between the preorbital fossae; and perhaps smaller upper molars relative to skull size. *A. suwai* is less advanced in most of these differences. It clearly does not even share the synapomorphies of the larger sister-group to which *D. palaeindicus* and *Alcelaphus* belong (node 18, Figure 21), and it is far from sharing the suite of diagnostic characters of *Damalops* (Pilgrim, 1939). *D. palaeindicus* is first recorded in Asia and close to the date of *A. suwai* at Matabaietu 3, and I wanted to test whether they could be sister-taxa descended from (*D.*) "*denendorai*". However, the evidence does not support this.

A. suwai resembles (*D.*) "*sidihakomai*" from Hadar SH in horncore size, separation, low compression, moderately steep insertion, a braincase that is long but only moderately wide; deep preorbital fossae extending far forward with pronounced upper rims and sharply descending from the nasal shelf between them; a fairly high craniofacial angle; occipital with surfaces facing strongly laterally and with strong hollows on either side of a median ridge; occipital surface narrowing dorsally; a braincase roof not curved or domed in profile, and possibly the tendency to a small parietal boss. In both taxa the moderately separated supraorbital foramina have additional foramina above them, which I have seen also in (*D.*) "*denendorai*" and other members of Alcelaphina. I do not know whether this last feature is primitive or advanced in Alcelaphini, but all the other similarities are shared plesiomorphies.

A. suwai differs from (*D.*) "*sidihakomai*" from Hadar SH in longer honcores that diminish less rapidly above the base and are basally more divergent. The SH horncores either have a straight course with divergence gradually increasing from the base or, after basally being nearly parallel, have an abrupt change in course to a more lateral direction about one-third of the length above the base (Gentry 1981). The abrupt change in horncore course in *A. suwai* occurs closer to the base and towards a more posterior direction (Figure 15). *A. suwai* has a broader face and orbital width, more prominently jutting orbits; a broader nasal shelf between the preorbital fossae; a higher occipital surface relative to the similarly long braincase that widens less posteriorly; shorter deeper postcornual fossae; and perhaps a lower parietal-occipital angle. *A. suwai* may be less advanced in the last two features, and perhaps more advanced in its other differences. I calculated the ratio (a = distance from junction of nuchal crest and zygomatic arch to the postorbital bar)/(b = posterior occipital condyle to the postorbital bar) because Gentry (1981) suggested that the nuchal-zygomatic junction evolved from a more anterior position in Hadar SH to a more posterior one with a higher ratio, in the Hadar DD descendant. The ratio a/b in *A. suwai*, 0.32, is lower than it is in two SH crania, 0.38 and 0.50. This further contradicts the notion that the form *suwai* is the last member of a lineage that passes from "*sidihakomai*" to "*denendorai*" to *suwai*, but the evidence might allow the hypothesis that *suwai* branched off after "*sidihakomai*" but before "*denendorai*".

The few resemblances of *A. suwai* to (*D.*) "*denendorai*" include an additional foramen above each supraorbital foramen. *A. suwai* differs in horncores that are not mounted on a raised frontal ridge, longer yet basally smaller and less compressed, more divergent at the very base, inserted less steeply without a forwardly curved course and without stronger distal divergence, lacking the clockwise torsion on the right of at least most Hadar DD specimens, and with a less extreme angle of the maximum horncore diameter to the midfrontal suture; a longer braincase despite the fact that the Hadar DD form is probably a larger animal; a longer distance between supraorbital foramina and horncores; a deeper postcornual fossa; a more prominently jutting orbit; a distinctly higher craniofacial angle and a much lower parietal-occipital angle; braincase not widening posteriorly; and an occipital surface that does not face backwards as much, and is dorsally much narrower and less broadly rounded.

D. lunatus is variable in horncore compression and course, and in orbital breadth. *A. suwai* resembles *D. l. lunatus* in basal size, low compression and steepness of horncores relative to the braincase, and in high pedicel width. *A. suwai* resembles *D. l. korrigum* and *D. l. jimela* in moderate separation of basal horncores. It fits within the ranges of *D. lunatus* as a whole in the high width and degree of projection of its orbits; angle of basal horncore divergence that is lower than in *D. l. lunatus* yet higher than in the *D. l. korrigum* and *D. l. jimela* that I measured; a deeper shorter postcornual fossa than in most alcelaphines; preorbital fossae with a posterior upper rim; moderately high wide braincase and mastoids; and an occipital surface that narrows dorsally with upward-facing concavities of the dorsal border on either side of the midline.

A. suwai differs from *D. lunatus* as a whole in horncores that change in course fairly abruptly towards a more posterior direction shortly above the base; in a lower craniofacial angle (while both have high angles, the mean for *D. lunatus* is 125° while the estimate for *A. suwai* is 113°); in a much flatter braincase roof which either lacks a parietal boss or has a smaller one; supraorbital foramina less separated from each other yet more distant from the horncores (the ratio between separation and distance to the horncores in *A. suwai* is 57.5/57.5 = 1, while the mean for 11 *D. l. lunatus* is 64/50.8 = 1.28 and the mean for three *D. l. korrigum* and *jimela* is 67/43.8 = 1.53); a decisively larger preorbital fossa that is much deeper anteriorly with strong inward-bending of the base of the fossa above the posterior toothrow (in *A. suwai* the fossa is still deep above M^{2-3} while in *D. lunatus* it is very shallow at that point); a larger braincase height from foramen magnum to occiput and a more angled and less rounded transition from the braincase roof to the occipital surface; an occipital surface that, while similar in narrowing dorsally, faces more laterally; and in a shorter premolar row if mandible MAT-3/6 (Figure 17c) has been correctly assigned to *A. suwai*.

The new Awash cranium belongs neither to *D. lunatus* nor to its direct ancestor as it is more advanced in features such as a lower craniofacial angle and greater distance of the supraorbital foramina from the horncores. The new species is clearly not a member of the *Damaliscus* clade because it is more advanced than all *Damaliscus* species in some characters, while it lacks all five of the character advances at node 12 in Figure 21. However, the performance within *Damaliscus* of none of these five hypothesized synapomorphies is flawless. Each shows either uncertainty (see ?-codes in Table 13) or reversal (such as the loss of the parietal boss in *D. agelaius*), while horncore compression shows both. Particularly *D. niro* and *D. agelaius* stand out by their reversals and insecure membership of *Damaliscus*. In fact, the presently hypothesized *Damaliscus* is precarious and future revision may well show that *D. niro* and *D. agelaius* are lower branches that are separated from the *dorcas-lunatus-ademassui* cluster.

A. suwai differs strongly from *D. niro* in its combination of characters. In comparing it with *D. agelaius*, it should be borne in mind that *D. agelaius* was overall probably somewhat smaller and that male and female crania of *D. agelaius* are known (see measurements and discussion in Gentry and Gentry, 1978). *A. suwai* resembles *D. agelaius* in moderately long horncores with low basal compression, without torsion or lateral flattening, basally moderately separated and divergent (one *D. agelaius* male has a basal divergence of ca. 55°, one female ca. 35°, and *A. suwai* ca. 60°), a similar horncore course to that in the *D. agelaius* female skull VFK III-IV 350 with divergence above the base followed by lessening divergence distally and tips trending upwards; dorsal orbital rims that are close to the horncores and prominently projecting, jutting outwards closely below the pedicel and then curving downwards towards the orbital margin; a deep forwardly-extending preorbital fossa with a marked upper rim from which the preorbital fossae descend steeply; a low parietal-occipital angle; perhaps similar widths of the braincase and mastoids relative to skull size (although the braincase width of 84.5 mm and mastoid width of ca. 115 mm in *A. suwai* exceed those of one male *D. agelaius* which are respectively 75.3 mm and 94.0 mm); perhaps a slight to absent parietal boss; and less convex frontals and lesser enamel complexity of upper molars than in living *Damaliscus*. The molar teeth may be small in relation to horn and skull size in both taxa: In two female *D. agelaius* the ratios (length of M^{1-3}/maximum horncore diameter) are 56.8/30.2 = 1.9 and 55.9/31.4 = 1.8 while in *A. suwai* it is estimated at ca. 60/48 = 1.25. *A. suwai* differs from *D. agelaius* in horncores that are basally larger with more posterior flattening and a larger angle to the midline, with a fairly abrupt change in course towards a more posterior direction shortly above the base; greater width of the forehead, horn pedicels and orbits; a lesser craniofacial angle (while both taxa have high angles, Figure 18, those in *D. agelaius* are higher); supraorbital foramina that are much closer especially in relation to facial breadth yet further from the horncores; a broader nasal shelf between the preorbital fossae; a braincase that is shorter in relation to overall size (although both taxa have long braincases), dorsally much flatter lacking the distinctly convex dome-shape in *D. agelaius*, and probably also wider in relation to basal horncore size and length of the upper molars; and a higher occipital surface. Almost all the similarities between these two taxa can be argued to be symplesiomorphic. The different proportions in *A. suwai* (e.g., the wider forehead area yet closer supraorbital foramina and shorter less domed braincase) show that it is specifically distinct from *D. agelaius*. The more advanced states in *A. suwai* (such as the lower craniofacial angle, and the higher separation of the supraorbital foramina from the horncores) disqualify it from direct ancestry of *D. agelaius*.

A. suwai has some resemblances to *Parmularius rugosus*: low horncore compression, moderately high craniofacial angle and angle of basal horncores to the cranium, and high orbital width. *P. rugosus* has a less marked parietal boss than other *Parmularius*, resembling *A. suwai* more closely. *A. suwai* differs in larger, longer horncores, greater breadth across the horn pedicels, basal horncore that are more separated and divergent and lack posterolateral swellings, more strongly projecting orbital rims (although they also project in *P. rugosus*) that are closer to the horncores, a deeper postcornual fossa, a decisively smaller parietal boss (if it exists at all as discussed above), much larger preorbital fossa, and a longer braincase especially in relation to brain width. The ratio (length from the back of the frontals to occiput)/(braincase width) in *A. suwai* is 66/84.5 = 0.78 while for the *P. rugosus* skull JK2 III TT 1 from Olduvai Bed III the ratio is ca. 0.4. In *A. suwai* the horncores re-approach distally while in *P. rugosus* they tend to diverge more, and the fairly abrupt change in horncore course towards a more posterior direction shortly above the base in *A. suwai* is absent in *P. rugosus*.

The dentitions referred to *A. suwai* compare in size with those of *P. pandatus* (Gentry 1987), and *D. agelaius* (Gentry and Gentry 1978). If the absence of P_2 on mandible MAT-3/6 has been correctly inferred, then the premolar/molar ratio is very low, as low as in *P. altidens* and lower than in any *D. agelaius* (see Gentry and Gentry 1978). Comparing only the ratios of P_{3-4}/M_{1-3}, MAT-3/6 has a ratio about as low as in *D. palaeindicus* and (*D.*) "*denendorai*" and lower than in *D. agelaius*. The enamel outlines of the molars look less advanced than those of *D. agelaius* in being less rounded and more angular.

In sum, the affinities of *A. suwai* remain unresolved to the extent that it may belong in Damaliscina (as in Figures 21, 22) or in a basal position in Alcelaphina, perhaps close to the *Damalops* group. The available indications are that *Awashia* is one of the more basal branches in Alcelaphini: The cladogram in Figure 22 implies first appearance of this branch between ca. 4.5 and 3.4 m.y. ago. If the branching event occurred after (*D.*) "*sidihakomai*" and before (*D.*) "*denendorai*", then it dates to 3.4-3.2 m.y. ago. This new taxon does not share the synapomorphies, and certainly not the diagnosis, of any previously named genus. Therefore, whatever its phylogenetic affinity turns out to be, it requires a new generic name.

Tribe Ovibovini (Gill 1872)

1872 Ovibovinae Gill
1872 Ovibovidae Gill
1945 Ovibovini Simpson

Taxa usually included in Ovibovini are large; have horncores inserted directly behind the orbits and often very steeply at an obtuse angle to the braincase, lacking transverse ridges, with torsion that may be anticlockwise but is more often clockwise on the right when present; extensive sinuses, often subdivided by bony struts, in the frontal and horn pedicels; shortened braincase; midfrontal suture not complicated; orbits strongly projecting; postcornual fossa absent; supraorbital foramina in small pits and wide apart; small auditory bullae; basioccipital often with a shape that is triangular rather than rectangular, with raised areas close together anteriorly, a tendency to hollows posterolaterally to these raised areas, without a wide deep longitudinal groove along its entire length, and posterior tuberosities further apart with a hollow between them which widens towards the rear; absence of basal pillars on molar teeth; upper molars long relative to width with fairly pronounced styles; premolar rows large; mandible not markedly deep below molars; paraconid of P_4 fused to metaconid (largely after Gentry 1970a, 1996).

A note on systematic status of Ovibovini:

Ovibos with *O. moschatus* the muskox, and *Budorcas* containing *B. taxicolor* the takin, are the only extant genera. Many extinct genera have variously been placed in Ovibovini. The systematics of these living and extinct taxa are more problematic than those of other bovids. It is not yet clear which among the genera would be excluded from a monophyletic Ovibovini, nor what the synapomorphies of such a clade might be. Gentry (1970a, 1996) discussed and reviewed this. So have Bouvrain and Bonis (1984), who proposed that basicranial specializations may define Ovibovini, including enlargement at the bases of the paroccipital processes, additional facets behind the posterior tuberosities of the basioccipital, and enlarged occipital condyles lying within the plane of the occipital surface. Gentry (1996) pointed out that in that case *Budorcas* as well as several extinct taxa like *Megalovis* and *Makapania* would cease to be ovibovine. He discussed two additional phylogenetic possibilities, only one of which results in monophyly of the living muskox and takin. Recent molecular analyses suggest that the muskox is allied with gorals (*Nemorhaedus*) and serows (*Capricornis*) (Groves 1995; Gatesy *et al.*, in press), while the takin belongs among sheep (Groves 1995). Major systematic revision of this group is needed.

Tribe ?Ovibovini

Genus *Nitidarcus* gen. nov.

Type species *Nitidarcus asfawi* sp. nov.

Generic diagnosis: The type species is the only one in the genus, and a diagnosis is given under the species.

Nitidarcus asfawi sp. nov.

Diagnosis: A medium sized ovibovine with moderately long horncores that pass forward at the base at a very high angle to the braincase and recurve backward strongly towards the tip; a large, smooth-walled sinus in frontals and pedicels extending up into the horncore base; horncores basally compressed, inserted moderately closely together and above the back and behind the orbit, moderately divergent, without transverse ridges, and with fairly strong clockwise torsion on the right; supraorbital foramina in small pits and wide apart on a broad, slightly convex forehead; dorsal orbital margins projecting strongly and closely beneath the horncore bases; midfrontal suture simple; temporal lines poorly marked and very far apart; braincase without a parietal boss, with sides nearly parallel, moderately to strongly bent relative to the face and fairly short; occipital surface facing mostly backwards, with a rounded dorsal outline, and with the mastoid situated entirely on it; basioccipital with an approach to a shape that is triangular rather than rectangular because the laterally splayed posterior tuberosities are distinctly wider apart than the anterior ones; anterior tuberosities posteriorly further apart than anteriorly with a shallow space rather than a deep longitudinal groove between them, a slight spine extending backwards behind the anterior tuberosities, followed by a valley that widens posteriorly towards a broad hollow between the posterior tuberosities; in the central part of the basioccipital there is some lateral constriction and marked longitudinal ridges are absent; auditory bulla moderately sized; paroccipital processes quite wide, with mediolaterally broadened proximal parts and distal parts pointing downwards rather than recurving in a medial direction.

Holotype: BOU-1/9 is a well preserved posterior cranium with the dorsal face and two complete horncores (Figures 5, 6; Table 4). The left horncore was broken through the pedicel when the fossil was found, showing an extensive, smooth-walled sinus up to 10-20mm into the horncore base; horncores basally strongly compressed, without swellings, with greatest mediolateral diameters situated posteriorly, inserted behind to above the back of the orbit at a posterior angle to the midfrontal suture of ca. 40° and moderately closely together, lacking transverse ridges, with fairly strong clockwise torsion on the right, with a welt that starts posterolaterally at the base and progresses upwards in a clockwise direction on the right always keeping a flatter surface ahead of it, passing forwards at the base at ca. 145° to the braincase and then recurving backwards strongly and in a smooth arc towards the tip; after initial divergence at ca. 50°, the horncores in anterior view pass straight up without re-approach of the tips; supraorbital foramina in small pits and wide apart; dorsal orbital margins projecting very strongly; postcornual fossa apparently absent; sutures very simple; the coronal suture is centrally indented forwards; temporal lines very far apart and poorly marked on the posterior braincase and not apparent at all anteriorly; braincase without a parietal boss, with sides nearly parallel, fairly short and bent moderately to strongly relative to the face; occipital surface quite high, facing mostly backwards, with a rounded dorsal outline, a central spine that is most marked dorsally, and with the mastoid situated entirely on it; the occiput protrudes upwards from the braincase; basioccipital with an approach to a shape that is triangular rather than rectangular because the prominent, laterally splayed posterior tuberosities are distinctly wider apart than the anterior ones; posterior tuberosities not transverse but with outer edges more posterior than inner ones and well in front of the occipital condyles; anterior tuberosities posteriorly further apart than anteriorly with a shallow space rather than a deep longitudinal groove between them; a slight spine extends backwards from the posterior parts of the anterior tuberosities, followed by a valley that widens posteriorly towards a broad hollow between the posterior tuberosities; in the central part of the basioccipital there is some lateral constriction and marked longitudinal ridges are absent; a moderately sized bulla is visible. In posterior view the paroccipital processes thicken dorsally where they abut against the upper parts of the occipital condyles.

Horizon: The holotype comes from Bouri 1 dated ca. 1 m.y. (Figure 1).

Etymology: The genus name is from the Latin *nitidus*, splendid, and *arcus*, an arc, arch or bow, and refers to the shape of the horncores. The species name is after Berhane Asfaw in recognition of his work in Middle Awash palaeontology.

Measurements: Measurements of the holotype are given in Table 4.

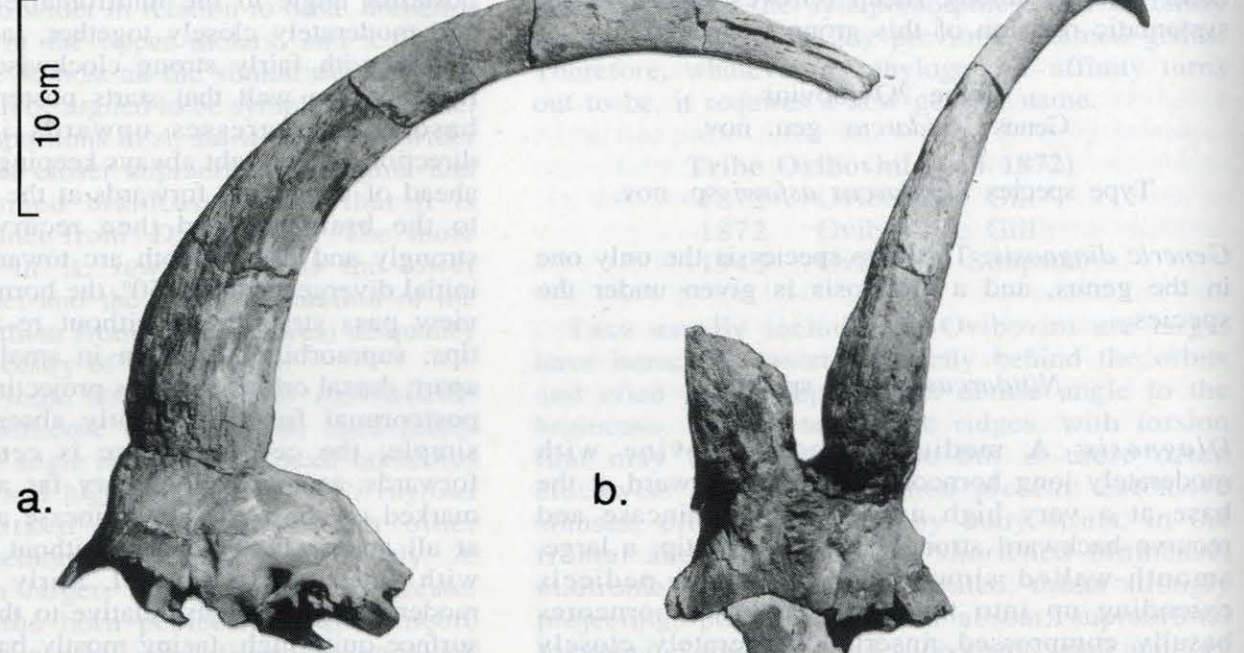

Figure 16. *Bouria anngettyae* cranium BOU-1/44, Bouri 1 in a. left lateral view, and b. anterior view.

Comparisons: The only possible comparison of BOU-1/9 with any other form from Bouri or from elsewhere in the Middle Awash is with the Bouri *Numidocapra*. This is why I present them together in Figures 5 and 6 and Table 4. Resemblances of BOU-1/9 to *N. crassicornis* include: size although BOU-1/9 is largest in many features; horncores lacking transverse ridges and of moderate length, with compression as strong as in BOU-1/31 (Figure 19), clockwise torsion on the right, and rising at a very high angle to the braincase; lack of postcornual fossae; occipital surface facing mainly backwards; and a straight to gently indented coronal suture. Differences of BOU-1/9 from *N. crassicornis* include (Figures 5, 6): horncores that are basally further apart and more divergent and distally less divergent, with some lateral flattening, a forehead that is more convex, more strongly projecting dorsal orbits, a somewhat lower and wider cranium, and a more inflated auditory bulla than that of BOU-2/21. Although the basioccipital of BOU-1/21 is too heavily encrusted for measurement, it shows narrower posterior tuberosities and a more rectangular shape, with a more marked longitudinal groove right along its length than present in BOU-1/9. The occipital surface of BOU-1/21 faces a bit more laterally with a less widely rounded dorsal margin than in BOU-1/9. The most dramatic difference is in the higher degree of torsion and in the course of the horncores (Figures 5, 6).

Resemblances of the Bouri form to one or more ovibovines are overall size; strong projection of the dorsal orbital rim close to the horncore base; simple midfrontal and other sutures; absence of transverse ridges on the horncores and of postcornual fossae; strong anteriorward direction of the basal horncores; short braincase; and a basioccipital that has posterior tuberosities far apart, with a hollow between them which widens towards the rear, and that lacks a longitudinal groove extending along its entire length. Differences from most ovibovines include the simple large sinus at the horncore base in BOU-1/9 which is smoothwalled and not subdivided by bony septa, and the auditory bulla which may be large for ovibovines. It is beyond the scope of this paper to appraise in depth the phylogenetic relationships of ovibovines (for which I refer the reader to Gentry 1970a, 1996; Bouvrain and Bonis, 1984). Instead, for each of several genera that others have regarded as ovibovine, I will cite some major differences from BOU-1/9 that debar this Bouri species from membership of that genus, and for some genera I mention similarities.

Gentry (1996) gave a new diagnosis of *Budorcas*. Features in this diagnosis that are present in BOU-1/9 include large size, moderately long horncores; the forward- and outward-facing surface of the horncore (anteroventral in the transversely-directed horncores of *Budorcas*, anterolateral in the less divergent ones of BOU-1/9) is more flattened than the surface on the opposite side; moderately close horncore insertions; skull wider at orbits than across the occipital, orbital rims strongly projecting (at least the preserved dorsal rim in BOU-1/9); frontals elevated between horn bases; midfrontal suture simple; basioccipital narrowing anteriorly giving it a basically triangular shape; and an occipital surface that faces mainly backwards. Features in which BOU-1/9 differs from the diagnosis of *Budorcas* include the moderate divergence of its horncore bases in contrast to the nearly transverse divergence in *Budorcas*, and its coronal suture with an anterior central indentation while the suture in *Budorcas* is straight. Additional differences are apparent in comparing BOU-1/9 with the only known species of *Budorcas*: the living takin *B. taxicolor*, the possibly Late Pliocene *B. teilhardi* (= *Budorcas* sp. of Teilhard de Chardin and Trassaert, 1938) from China, and *B. churcheri* from Middle or Upper Hadar (Gentry 1996), probably 3.2-2.9 m.y. in age. The takin differs from BOU-1/9 in having a protruding frontal ridge or boss under the horncores with a concavity between this rising ridge and the braincase behind it; basal horncore and frontal sinuses that are subdivided by bony partitions; relatively shorter horncores, averagely more compressed basally, with much higher basal divergence, and with a maximum diameter much more strongly angled to the midfrontal suture; a smaller orbit that is set lower in relation to the midfrontal surface; supraorbital foramina more widely apart yet less distant from the horncores; a shorter distance from coronal suture to occiput; a greater occipital height in relation to braincase width; less widely separated temporal lines on the posterodorsal braincase; larger parietal-occipital angle; basioccipital with more transversely directed posterior tuberosities that are closer to the occipital condyles; basioccipital lacking the anteriorly-converging shape of the anterior tuberosities in BOU-1/9, and with a less extensive posteriorly-widening valley between the longitudinal ridges. An important difference is the definite anticlockwise torsion on the right in the takin, while BOU-1/9 has strong clockwise torsion. I know of no case of congeneric bovid species that differ this strongly in torsion. While the takin and BOU-1/9 each have an approach to a ridge at least on the middle anterior horncore surface, in the takin this ridge starts posteromedially, and not posterolaterally as in BOU-1/9, and is sharper. Cranial remains of *B. teilhardi* include only horncores. They are close to BOU-1/9 in their higher compression and greater length than in the living takin, but differ from BOU-1/9 in anticlockwise torsion on the right and in a substantially different horncore course that carries the tips forward. The Late Pliocene *B. churcheri* from Hadar (Gentry 1996) differs from BOU-1/9 in having a large boss on which the horncores are mounted which rises at an angle of ca. 120° from the anterior face; in horncores diverging directly laterally at the base; in slight torsion that is clockwise on the better-preserved left side and would have been anticlockwise on the right as in the takin; orbits situated lower beneath the horncore bases; and a very large parietal-occipital angle (150-160° in contrast to 110-120° in BOU-1/9). The first three

TABLE 10.

Measurements of cranial fossils of the caprine *Bouria anngettyae* gen. et sp. nov., crania BOU-1/44, BOU-1/17 and frontlet BOU-2/18 from Bouri 1. Length in mm; two values for horncore length are preserved/estimated complete lengths; e = estimated, ee = very rough estimate.

	BOU-1/44	BOU-1/17	BOU-2/18
Horncore maximum diameter (1)	70.5	78.8	84ee
Horncore minimum diameter (2)	45.9	47.8	57ee
Horncore ratio (2)/(1)	0.65	0.61	58ee
Horncore length	460/500	315/380	420/500
Horncore basal separation	10.0	15ee	
Angle of basal horncore divergence	5°	3°	
Angle of horncore to braincase		98°	
Angle of (1) to midfrontal suture		5°e	
Width across horn pedicels	84.9	98ee	
Craniofacial angle	90°e	88°e	-
Maximum separation supraorbital foramina (SOF)	58ee		
Distance of SOF to anterior horncore midpoint	57.9		
Distance across superior orbital margins	130e		
Distance orbit to horncore	64.6		
Braincase width at parietal- squamosal suture	78.7	85.0	
Braincase length: coronal suture to occiput	44.8	42.2	
Distance across mastoid exposures		113e	
Occipital height: top foramen magnum to occiput	35.2	46e	
Minimum separation temporal lines on dorsal braincase	40.7	44e	
Basioccipital width across anterior tuberosities	29.5ee		
Basioccipital width across posterior tuberosities	32ee	34e	
Basioccipital length: anterior to posterior tuberosities		35ee	

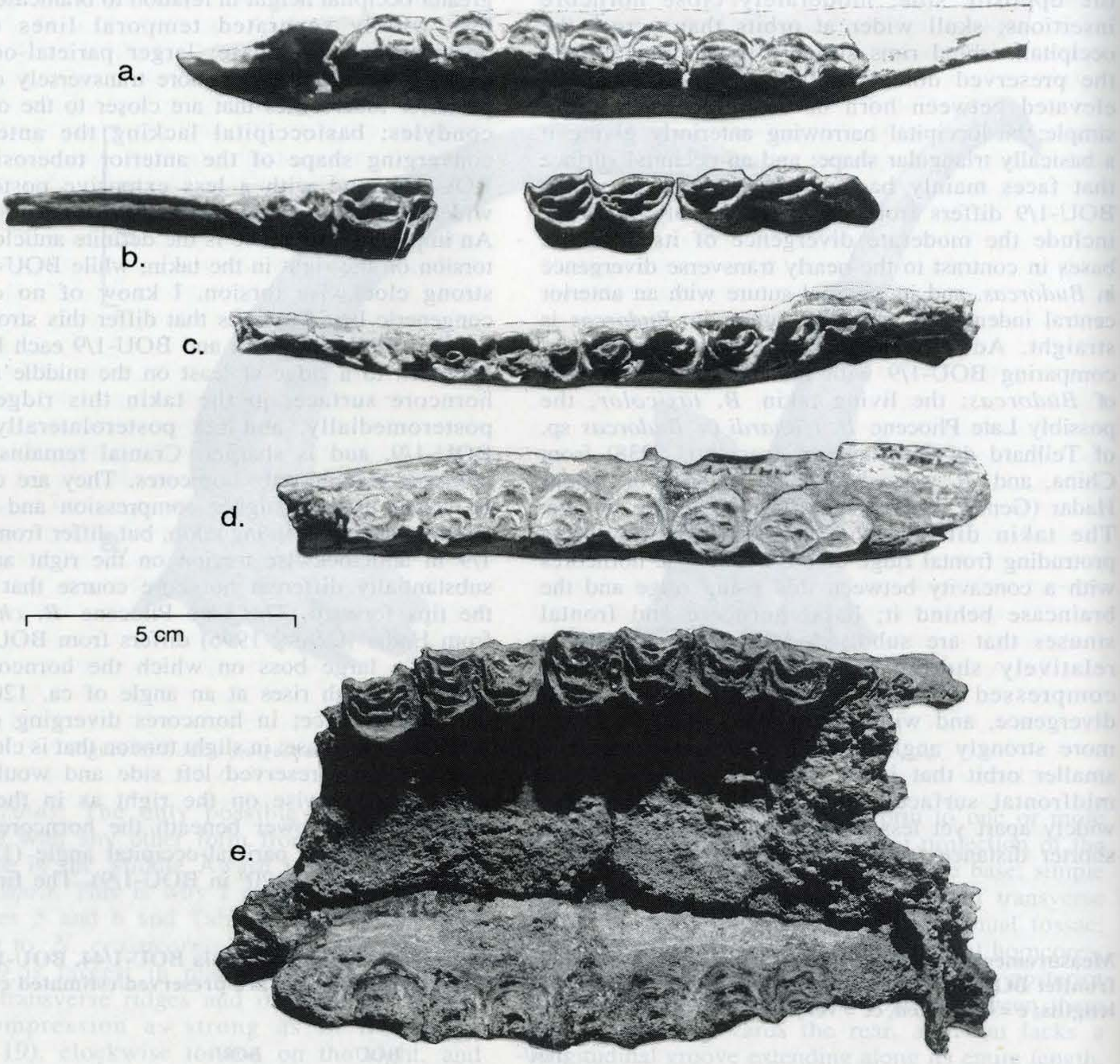

Figure 17. Middle Awash alcelaphine dentitions: a. right mandible MAK-1/76 with P_4-M_3, and b. left subadult mandible MAK-1/65 with P_3, P_4, M^{2-3}, both of cf. (*Damalops*) sp. nov. "*sidihakomai*"; c. left mandible MAT-3/6 with P_3-M_3 of cf. *Awashia suwai*; d. right mandible MAT-4/18 with P_4-M_3 of cf. *Beatragus whitei*; e. maxilla BOU-1/21 with left P^4-M^3 and right P^3-M^3 of *Numidocapra crassicornis* which belongs with a cranial specimen of the same number.

features are advanced similarities of *B. taxicolor* and *B. churcheri*. The fact that they were already present in the 3.2-2.9 m.y.-old *Budorcas* while the 1.0 m.y.-old BOU-1/9 lacks them suggests that the Bouri species is not allied to the *Budorcas* lineage at all. Gentry (1970a) thought that *Lyrocerus satan*, from the Early Pliocene of China (Teilhard de Chardin and Trassaert 1938), might be an early relative of the takin. *L. satan* differs from BOU-1/9 in horncores with more tightly-spiralled torsion that is strongly anticlockwise torsion on the right, with a strong sharp keel that passes far forward onto the face from the anteromedial horncore base, with deep longitudinal grooves, with a subdivided basal sinus, and mounted on a frontal boss reminiscent of the takin.

The muskox, *Ovibos moschatus*, is first recorded in Europe in the Steinheimian and in Asia from the Late Pleistocene. Close relatives are *Praeovibos* from Early to Middle Pleistocene Asian and North American strata, and *Bootherium* from the North American Middle and Upper Pleistocene. *Boopsis* from the Late Pliocene and Middle Pleistocene of China may be a more distant relative, and perhaps *Euceratherium* from Pleistocene North America as well (Gentry 1996). *O. moschatus* shares with BOU-

1/97 horncores with clockwise torsion on the right and a course that in lateral view has a strong anterior component above the base and recurves upwards and backwards towards the tip. Yet the horncores in other respects, in passing laterally and downwards from huge spread-out bases, and also the skull proportions, are so different that it is difficult to visualize anything closer than a distant common ancestry. Similarly, each of the extinct relatives of *M. moschatus* differs decisively from BOU-1/9 not only in horncore morphology but also in skull proportions.

The *Megalovis* group of ovibovines from sites of Villafranchian age (ca. 2.5-1.5 m.y.) in Europe and Asia includes *M. latifrons* and possibly conspecific or at least closely allied forms described under other names (*Deperetia ardea*, *Pliotragus ardeus*, and *Hesperoceridas merlae*), as well as *Soergelia elizabethae* considered by Gentry (1970a) as possible descended from *Megalovis*. Gentry (1996) suggested that the *Megalovis* group is close to *Makapania broomi* (Wells and Cooke 1956) from the Late Pliocene of the former Transvaal, South Africa, and that *Kabulicornis ahmadi* from the Early Pliocene of Afghanistan (Heintz and Thomas 1981) may be an earlier relative. *Makapania* has horncores of similar basal size and compression as BOU-1/9 (the basal horncore ratio in the *M. broomi* holotype, 48/62 mm, compares well with 45.7/61.6 in BOU-1/9) and perhaps also length. *Makapania* differs in horncores that emerge transversely and are inserted much wider apart, less curved with only a gentle ascent towards the tip, and mounted on a raised frontal area the sinus in which is not smooth-walled but contains bony struts; and in having a ridge from the basal horncore to the orbital rim. Similar differences separate other taxa in the *Megalovis* group from BOU-1/9, although *M. latifrons* has less raising of the frontals beneath the horncores than *M. broomi* (Gentry 1970a). Also, the basioccipital of BOU-1/9, although it has the general resemblance of narrowing anteriorly, has anterior tuberosities that are more sparated, and each of which is narrower mediolaterally, than in *Makapania*, *Megalovis* and also living *Ovibos*, (Gentry 1970a: Figure 1). *K. ahmadi* (Heintz and Thomas 1981), which Gentry (1990a) considered to be ovibovine, shows several resemblances to BOU-1/9: horncores arising from short pedicels at a very large angle to the braincase roof, lacking keels; with moderate basal divergence and a low angle of the maximum diameter to the midfrontal suture; a high width across the posterior tuberosities of the basioccipital and anterior tuberosities that are not very close posteriorly and converge anteriorly; and perhaps an auditory bulla that is larger than in advanced ovibovines. Differences of *K. ahmadi* from BOU-1/9 include its absolutely lower and narrower yet substantially longer braincase; much larger craniofacial and parietal-occipital angles; absence of basal sinuses; absence of horncore torsion on the holotype; a very slight horncore curvature after the base that results in slight anterolateral concavity and in increasing divergence towards the tips; and horncore bases that are larger and less compressed (with ratio 62/76 = 82% compared with 45.7/61.6 = 74% in BOU-1/9) and less separated. Also, the basioccipital of BOU-1/9 has a slight spine extending backwards from the posterior parts of the anterior tuberosities, followed by a valley that widens posteriorly towards a broad hollow between the posterior tuberosities, and marked longitudinal ridges are absent. In contrast, the *K. ahmadi* holotype lacks the broad posterior hollow and the anterior spine, and instead has longitudinal ridges flanking a narrow groove of nearly even width extending along the entire basioccipital. The differences in braincase shape, horncore course and torsion, and in incidence of basal sinuses are so fundamental that they debar BOU-1/9 from membership of *Kabulicornis*.

There is another group of taxa that have generally been seen as related to each other within Ovibovini (see review in Gentry 1996). This group from Miocene Europe and Asia is centred on *Urmiatherium*, which has highly derived characters such as a prominent united frontal boss and extremely abbreviated horncores, and some of the specialized features related to thickening and strengthening of the posterior basicranium that Bouvrain and Bonis (1984) advanced as ovibovine synapomorphies. This group also includes *Parurmiatherium*, *Criotherium*, *Plesiaddax* and *Tsaidamotherium*. I will not compare these in detail with BOU-1/9 because I consider that their various specialized cranial, frontal and horncore structures place them even further apart from the Bouri species than are the ovibovines that I have discussed.

Tribe Caprini Simpson 1945

1821 Capridae Gray
1866 Caprina Haeckel
1945 Caprini Simpson

Caprine characters include a tendency to high narrow skulls; horncores often with a flat anterior surface, or with an antertior keel that may be produced forward to insert on the forehead, without transverse ridges, very enlarged relative to skull size in males of some advanced forms; inserted above or just behind the orbits, and moderately close together even in most primitive forms and progressively closer in advanced forms with larger horncores; horncores often with torsion; horncore course not an even arc with a large radius of curvature but with a tendency to become more sharply curved towards the tips; not only frontals but also horncores may be hollowed; orbital rims frequently wide; braincase often shortened and in some taxa strongly bent down relative to the facial axis; the level of the frontals between the horncore bases is often raised; there are no strong temporal

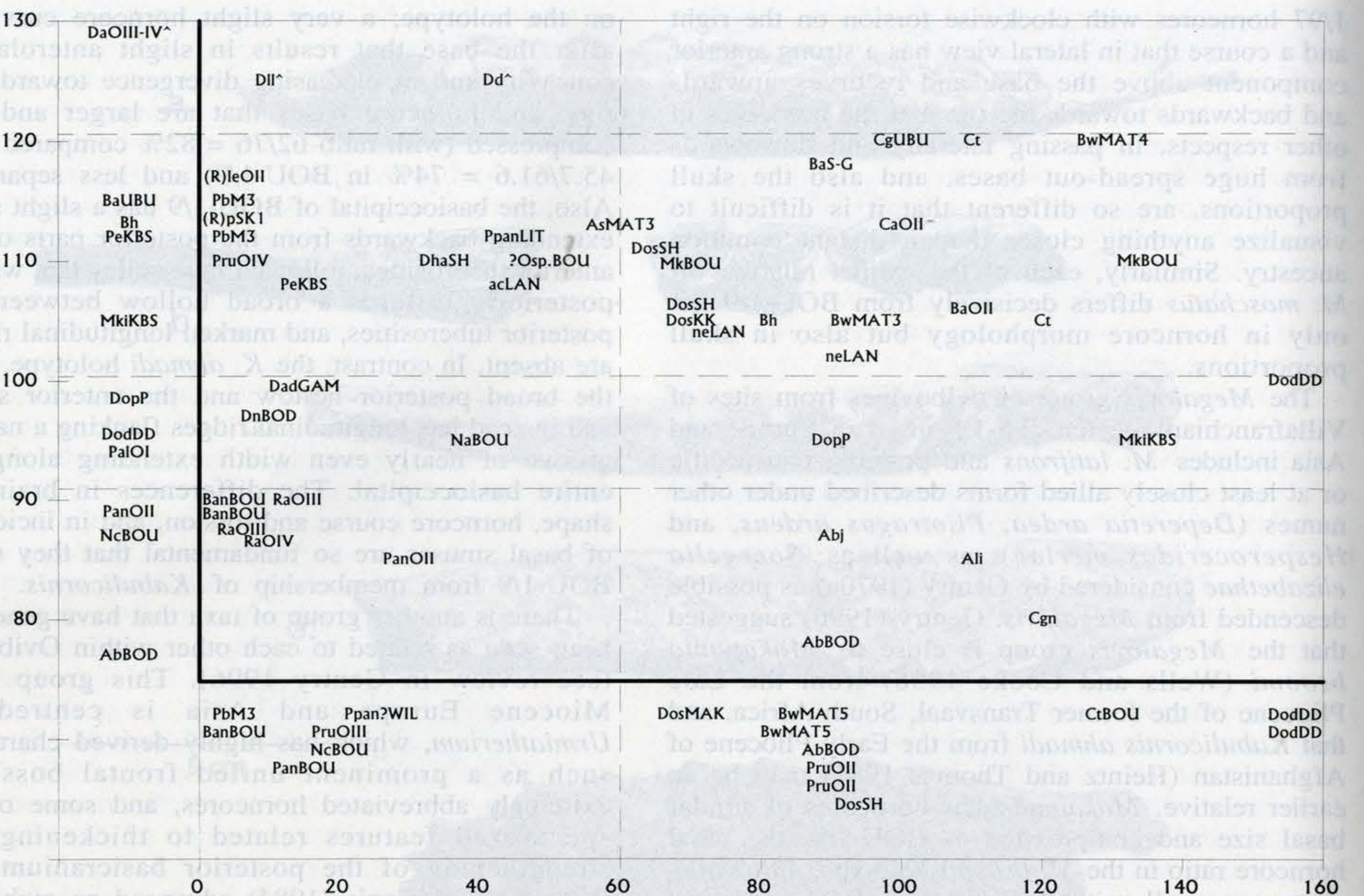

Figure 18. The posterior angle between the maximum horncore diameter and the midfrontal suture (x-axis: the vertical dashed line shows code separation between low = 0, high = 1, character 15 in Tables 13 and 14); and the craniofacial angle (y-axis: the horizontal dashed lines show separations between codes 0-3, character 19 in Tables 13 and 14). The axes are labelled in degrees. The angles were estimated roughly using a mitering gauge. All points represent alcelaphines (codes for taxa from Table 2, followed by codes for sites from Table 1 in the case of extinct taxa) except caprine BanBOU = *Bouria anngettyae*, and ovibovine NaBOU = *Nitidarcus asfawi* both from Bouri 1. For each point plotted below the bold horizontal line, or left of the bold vertical line, only the value along the respective axis is available. All points represent single specimens except those with the symbol ^ which represent means for samples of adult specimens (taxon^: sample size (number of males, number of females), (x-axis range)/(y-axis range): Dd^ = 3 (3, 0), (40°-45°)/(120°-130°); DII^ = 4 (2, 2), (0°-20°)/(120°-130°); DaOIII/IV^ = 3 (1, 2), (unavailable)/(122°-135°).

ridges on the braincase; the braincase in dorsal view is either parallel-sided or narrower towards the rear; small supraorbital pits that in advanced forms like some species of *Capra* are far apart; foramina ovalia small to moderately sized; wide anterior tuberosities of the basioccipital in some advanced later forms; size of auditory bullae small in living forms; posteriorly the ventral edge of the bulla often passes downwards to meet the front edge of the paroccipital process (partly after Lydekker 1898; Pilgrim 1939; Gentry 1970b, 1971).

Genus *Bouria* nov.

Type species *Bouria anngettyae* sp. nov.

Generic diagnosis: The type species is the only one in the genus, and a diagnosis is given under the species.

Bouria anngettyae sp. nov.

Diagnosis: Extinct medium-sized caprines with a new combination of plesiomorphic and advanced features: horncores that are long and large for the skull as in living *Capra*, resembling living *C. ibex* in being basally very close, medially flattened, compressed, but little angled to the midfrontal suture, very upright to the braincase, and strongly backbent with hardly any tendency to torsion; strong raising of frontals between horn bases and elongation of the frontal between the horncore and orbit as in *Hemitragus* and more advanced than in *C. ibex*; braincase roof shorter than in living *Capra* and with a higher angle to the occipital surface; and a longer, narrower basioccipital, less flat and with less widened anterior tuberosities, and larger auditory bullae than in advanced living caprines but resembling the extinct *Tossunnoria* and *Sivacapra*. Horncore bases have a

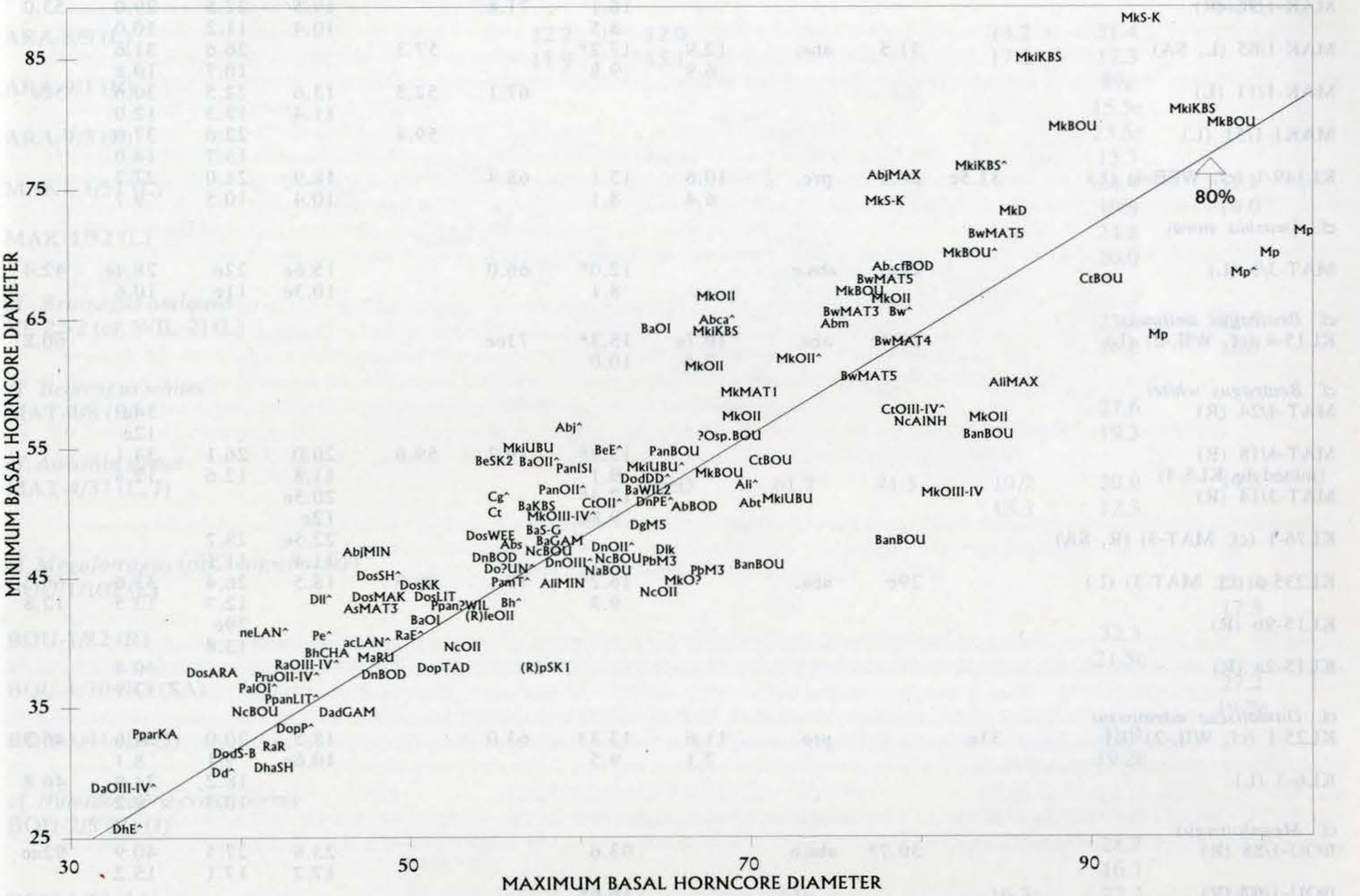

Figure 19. Maximum and minimum horncore diameters in millimeters. All points represent alcelaphines (codes for taxa from Table 2, followed by codes for sites from Table 1 in the case of extinct taxa) except caprine BanBOU = *Bouria anngettyae*, and ovibovine NaBOU = *Nitidarcus asfawi*, both from Bouri 1. The line along which y/x = 80% separates codes 0 and 1 for character 1 (Tables 13 and 14). Points with symbol ^ are means, while others represent single specimens. The entries below represent: Taxon^ = sample size (number of males, number of females, if sex is known), (x-axis range)/(y-axis range).

Abca^ = 5 (3, 2), (51-80)/(49-75);
Abj^ = 12 (3, 3, 6 of unknown sex), ranges given by AbjMIN-AbjMAX in the figure;
acLAN^ = 21, (40.7-53.7)/(31.7-44.3);
Ali^ = 5 (2,3), ranges given by AliMIN-AliMAX in the figure;
BaOII^ = 3, (44.3-67.2)/43.6-65.8);
BeE^ = 4, (52.5-64.0)/(47.5-60.0);
Bh^ = 2 (1, 1), (53.0-59.0)/39.0-47.0);
Cg^ = 6, (53.4-58.9)/46.1-56.7) (from UBU, KBS, OI-II);
CtOII^ = 3, (47.8-75.5)/41.4-55.5);
CtOIII-IV^ = 2, (75.2-84.2)/(53.9-61.9);
DaOIII/IV^ = 4, (29.2-39.2)/(23.6-36.9);
Dd^ = 10 (5, 5), (29.5-44.1)/(23.5-32.3);
DhE^ = 2, (31.5-35.2)/25.0-26.4);
Dll^ = 11 (5, 6), (39.5-52.1)/(36.0-49.0);
DnOII^ = 5, (56.9-67.1)/(43.3-51.6);
DnOIII^ = 4, (55.9-65.7)/(42.5-48.3);
DnPE^ = 2, (63.9-64.2)/(50.9-51.3);
DodDD^ = 3, (60.5-66.0)/(50.0-54.2);
Do?UN^ = 3, (51.0-59.8)/(41.1-47.8);
DopP^ = 3, (39.0-49.0)/(32.0-35.0);
DosSH^ = 3, (44.2-51.0)/(41.8-47.4);
MkOII^ = 4, (67.0-82.6);
MkOIII/IV^ = 4, (48.9-81.9)/(47.6-51.5);
MkiUBU^ = 2, (57.0-72.0)/(52.0-55.0);
MkiKBS^ = 4, (68.0-99.0)/(64.0-85.0);
Mp^ = 3, (94.0-102.5)/(63.7-71.7);
neLAN^ = 17, (36.2-51.3)/(35.6-45.2);
PamT^ = 5, (52.0-59.0)/(41.0-50.0);
Pe^ = 5, (38.0-53.0)/(32.0-46.0) (from KBS, UBU, and OKT);
PpanLIT^ = 4; (39.2-45.1)/(32.8-38.2);
PalOI^ = 5, (30.9-50.3)/(27.4-44.5);
PanOII^ = 10, (46.8-69.3)/(38.4-60.0);
PruOII-IV^ = 7, (31.2-52.9)/(24.3-50.2);
RaE^ = 13, (37.0-58.5)/(29.5-46.5);
RaOIII-IV^ = 3, (37.1-47.5)/(34.0-41.4);
(for acLAN and neLAN see Gentry, 1980; for sites O and PE, Gentry and Gentry, 1978, and personal observation; for UN, Gentry, 1987; for KBS, UBU, and OKT, Harris, 1991, and personal observation; for T, Geraads, 1981).

TABLE 11.

Measurements of alcelaphine mandibular dentitions. Length in mm; * = paraconid and metaconid of P_4 are fused in adult; abs./pre. = P_2 was absent/present in life; D = deciduous, e = estimated; J = juvenile (at least one deciduous tooth present); SA = subadult (deciduous teeth absent, but at least M_3 is not yet in full occlusion); L = left; R = right. In the case of each tooth, the mesio-distal length is given above the bucco-lingual breadth, both measured at the occlusal surface. Ramus = depth of mandibular ramus at a right angle to the occlusal surface at the M_2/M_3 junction. Note that MAK-1/51 also includes right mandibular and left maxillary dentitions.

	P_{2-4}	P_{3-4}	P_2	P_3	P_4	M_{1-3}	M_{2-3}	M_1	M_2	M_3	Ramus
cf. (*Damalops*) "*sidihakomai*"											
ARA-1/36 (R)					13.1* 7.6						
ARA-4/1 (L)								9.5e	19.8 10.7		
MAK-1/76 (R)					16.1 8.5	71.8		19.5 10.4	22.5 11.2	29.0 10.0	53.0
MAK-1/65 (L, SA)		31.5	abs.	12.9 6.9	17.2* 9.8		57.3		26.6 10.7	31.6 10.8	
MAK-1/11 (L)						67.1	52.3	13.6 11.4	22.5 12.3	30.6 12.0	52e
MAK1-1/51 (L)							59.4		22.0 13.7	37.6 14.0	
KL149-1 (cf. WEE-4) (L)	31.5e	24.0	pre.	10.6 6.4	13.1 8.1	68.4		18.9 10.4	21.0 10.5	27.2 9.7	
cf. *Awashia suwai*											
MAT-3/6 (L)		21e	abs.e		12.0* 8.1	66.0		15.6e 10.3e	22e 11e	28.4e 10.6	42.4
cf. *Beatragus antiquus*											
KL15-4 (cf. WIL-2) (L)		27.4e	abs.	10.7e 7.4	15.3* 10.0	73ee					60.8
cf. *Beatragus whitei*											
MAT-4/24 (R)										34e 12e	
MAT-4/18 (R) (joined to KL5-3)					13.3* 9.1	79.2	59.6	20.0 11.8	26.1 12.6	34.1 12.4	
MAT-3/14 (R)					17.4* 9.8e			20.5e 12e			
KL76-1 (cf. MAT-3) (R, SA)								22.5e 11.4	28.2 11.1		
KL235-6 (cf. MAT-3) (L)		29e	abs.		16.2* 9.3	79.1	59.9	18.5	26.4 12.7	33.6 13.5	60.5 12.8
KL15-9b (R)									29e 13.8		
KL15-2a (R)										40.4 13.9	
cf. *Damaliscus ademassui*											
KL25-1 (cf. WIL-2) (L)	31e		pre.	11.6 7.1	13.3* 9.5	63.0		18.5 10.6e	20.0 9.1	24.6 8.1	46.8
KL6-3 (L)									18.2 10.3	24.8 9.2	46.8
cf. *Megalotragus*											
BOU-1/88 (R)		30.7*	abs.e		93.6			23.6 17.2	27.5 17.1	40.9 15.2	92ee
BOU-1/67 (R)					16.6* 12.8						
BOU-3/3 (R) (SA)					95.4			25.1 12.8	31.0 13.3e	39.1 11.1	73.6
BOU-1/101 (R)										40.7 13.7	
cf. *Numidocapra crassicornis*											
BOU-1/49 (L)					75.5e			23.9 12.3e		30.6 11.8	53.2
BOU-1/63 (R) (SA)										30.8 9.8	
Gen. et sp. indet.											
BOU-3/4 (L)					63e			13e 10.5e	19.4 11.3	29.1 10.1	
BOU-5/4 (R)										26.5e 8.8	
GAM-1/12 (L)					16.3*	79.6	62.2	17.4 13.2	28.1 13.9	35.5 13.5	61.8
KL5-1 (cf. MAT-4) (R)					15e			19.2	22.7e		
KL256-4 (R)										28.4 10.3	
KL34-1 (L)										22.7 13.1	
KL188-? (cf. Andelee) (R)			abs.		11.6*			13.5	21.0	32.1	
KL191-51 (R)										11.5	
MAT-6/2 (L) (J)				5eD	27.9D 9.7D			23.1 9.2	26.8 9.0		

TABLE 12.

Measurements of alcelaphine maxillary denitions. Length in mm; D = deciduous, e = estimated; J = juvenile (at least one deciduous tooth present); SA = subadult (deciduous teeth absent, but at least M_3 is not yet in full occlusion); L = left; R = right. In the case of each tooth, the mesio-distal length is given above the bucco-lingual breadth, both measured at the occlusal surface.

	P^3	P^4	M^{1-3}	M^{2-3}	M^1	M^2	M^3
cf. (*Damalops*) "*sidihakomai*"							
ARA-1/418 (R)					22e		
ARA-1/522 (L)					19.0 14.2		
ARA-4/5 (L)							22.7e 14.8e
ARA-8/9 (L)	12.2 11.9	12.0 15.1			14.2 17.2	21.4 17.3	
ARA-9/1 (R)						19e 15.5e	
ARA-9/3 (L)						23.5e 15.3	
MAK1-1/51 (L)						24.4 19.8	37.1 14.0
MAK-1/52 (L)						24.8 20.0	
cf. *Beatragus antiquus*							
KL 22-2 (cf. WIL-2) (L)						25.2 16.2	22.8 13.9
cf. *Beatragus whitei*							
MAT-4/8 (R)						27.6 19.3	
cf. *Awashia suwai*							
MAT-4/37 (L, J)		16eD	61.7	41.5	19.7 13.3	20.9 12.3	19.3
cf. *Megalotragus* (or *Connochaetes*)							
BOU-1/102 (L)							27.1e 17.3
BOU-1/82 (R)						32.3 21.5e	
BOU-1/70 (R) (SA)							27.2 19.2e
BOU-1/41 (L) (J)						31.9 19.2e	
cf. *Numidocapra crassicornis*							
BOU-2/5 (R) (J)						28.7 16.3	
BOU-1/52 (L)			61e		16.3e	22.2 15.6	24.0 16.0
BOU-1/26 (R)							24.9 15.0
Gen. et sp. indet.							
BOU-?1/91 (R)							19.3 13.2
KL15-18 (L)							18.6 12.8
KL2-1 (L)							26.2 15.7
KL6-13 (L)							21.8 14.1
KL15-2B (R)							19.0 12.8
KL283-3 (R) 23.5e							11.7
KL256-7 (L)							21.4 12.7
KL256-5 (R)				63.1			
KL189-52 (R, J)							19.4 11.3

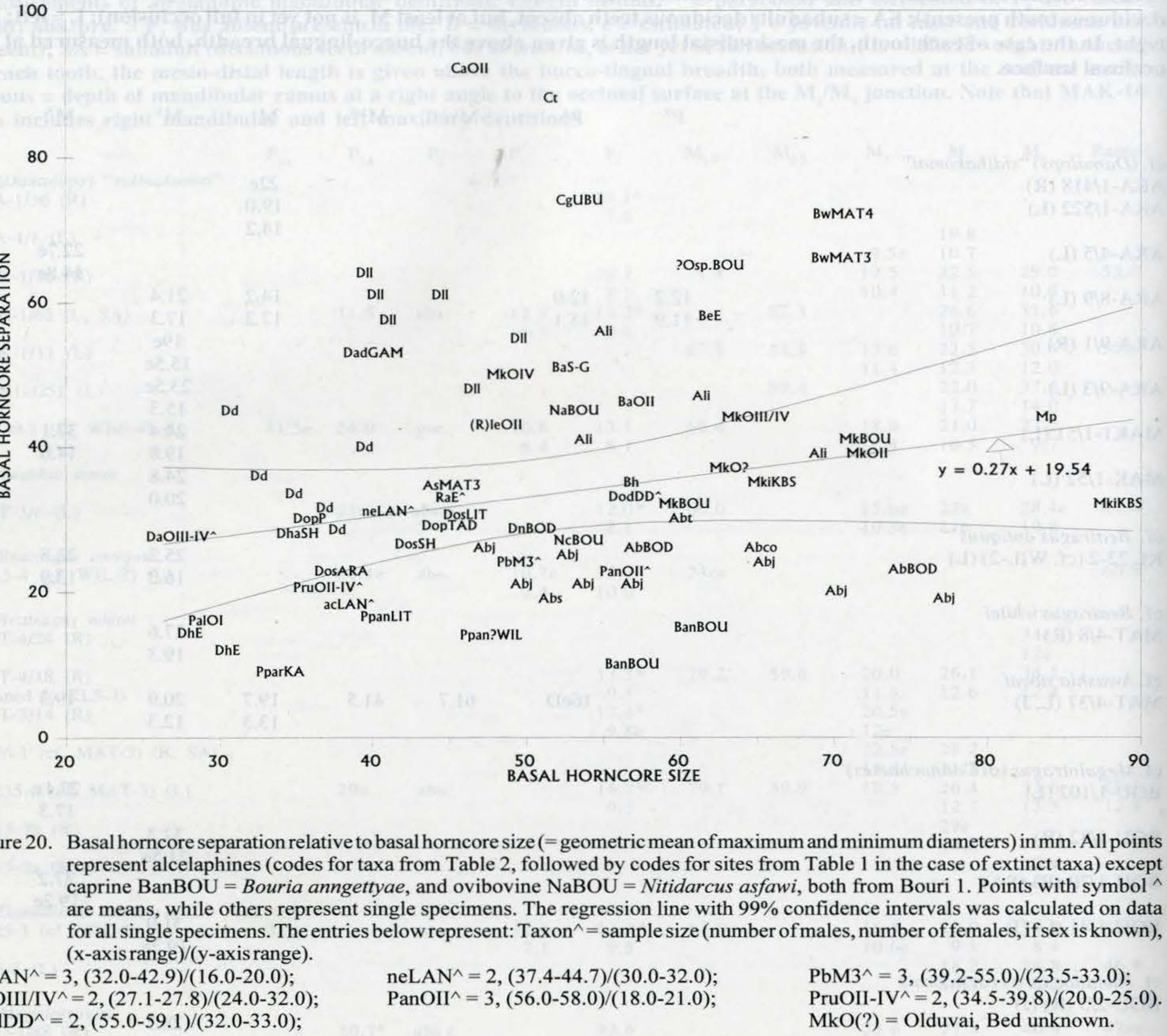

Figure 20. Basal horncore separation relative to basal horncore size (= geometric mean of maximum and minimum diameters) in mm. All points represent alcelaphines (codes for taxa from Table 2, followed by codes for sites from Table 1 in the case of extinct taxa) except caprine BanBOU = *Bouria anngettyae*, and ovibovine NaBOU = *Nitidarcus asfawi*, both from Bouri 1. Points with symbol ^ are means, while others represent single specimens. The regression line with 99% confidence intervals was calculated on data for all single specimens. The entries below represent: Taxon^ = sample size (number of males, number of females, if sex is known), (x-axis range)/(y-axis range).

acLAN^ = 3, (32.0-42.9)/(16.0-20.0);
DaOIII/IV^ = 2, (27.1-27.8)/(24.0-32.0);
DodDD^ = 2, (55.0-59.1)/(32.0-33.0);
neLAN^ = 2, (37.4-44.7)/(30.0-32.0);
PanOII^ = 3, (56.0-58.0)/(18.0-21.0);
PbM3^ = 3, (39.2-55.0)/(23.5-33.0);
PruOII-IV^ = 2, (34.5-39.8)/(20.0-25.0).
MkO(?) = Olduvai, Bed unknown.

greatest mediolateral diameter situated posteriorly, an anteromedial keel that sharpens progressively higher up, and a posterior cross-section that is more rounded basally but also develops a progressively sharper keel towards the horncore tip.

Holotype: BOU-1/44 includes most of a posterior cranium with the base of the right and almost the entire left horncore (Figure 16). The skull is high and narrow; the horncore has no torsion or transverse ridges, smooth backward curvature that is so strong that the tip recurves in a ventral direction with a slight distal increase in curvature, extreme basal compression that increases distally so that 300 mm from the base it is 13.5/33.2 = 41%, widest mediolateral diameter situated posteriorly, strong flattening medially but not laterally, anterior narrowing to form a sharp ridge or keel; there are rugose features on the forehead in front of the anterior keel and, although the anterior basal parts of both horncores are damaged, these rugosities may indicate that the keel in life was produced forward onto the forehead; the posterior horncore margin also sharpens higher up to approach a ridge or keel; horncores inserted very uprightly and closely and with the anteroposterior axis almost parallel to the midfrontal suture, on short pedicels with a well marked pedicel-horncore transition; horncore divergence is basally almost absent but distally substantial; the frontal between the horncore bases is strongly raised and the distance from horncore to orbit is relatively long; some marked longitudinal grooves are present near the anterior and posterior horncore margins; only the inner margin of the right supraorbital foramen is preserved and this indicates substantial separation between the supraorbital foramina; the parietofrontal suture is not centrally indented; on the posterior dorsal cranium the temporal lines show

TABLE 13.

Skull Characters. For anatomical terms and diagrams see Sisson and Grossman (1975). All characters are assessed relative to skull size. Each character's performance in the alcelaphine consensus tree (Figure 21, resulting from application of HENNIG86 options, Farris, 1988, to the codes given below) is shown in brackets as (consistency index/ retention index).

Horncores and pedicels

1 The ratio of basal horncore compression : The minimum basal horncore diameter above the pedicel divided by the maximum basal horncore diameter (low = 0, high = 1); (16/50).
2 The horncore length relative to skull size is low (0), moderate (1) or high (2); (28/61).
3 Basal horncore separation is low (0), moderate (1), high (2), or very high (3); (27/63).
4 Transverse ridges, that are unmistakeable along the entire anterior horncore and that are spaced relatively far apart, are absent (0), present (1), very prominent (2); (66/88).
5 A posterolateral basal swelling of the horncore is absent (0) or (present (1); (100/100).
6 The basal horncore margin is: lower laterally than medially in anterior view but not lower posteriorly than anteriorly in lateral view (0), more or less horizontal in both views (1), or only lower posteriorly than anteriorly in lateral view (2); (100/100).
7 The basal horncore cross-section shows pronounced flattening laterally but not posteriorly (0), neither laterally nor posteriorly (1), or posteriorly but not laterally (2); (100/100).
8 The tendency to a posterolateral keel is absent (0), present (1), pronounced (2); (100/100).
9 The angle between the basal horncores is low (0), moderately high (1), very high (1); (25/66).
10 The horncore in lateral view is: basally markedly concave such that it recurves forward shortly above the base (0), basally straight to slightly convex (1), convex over much of the base (2) or convex over much of the base with slight to marked lyration towards the tip (3) (lyration is anterior-ward recurvature of the tip after basal convexity); (100/100).
11 Marked and localized increase in backward curvature of the horncore shortly above its base in lateral view is absent (0), or present (1); (100/100).
12 Anticlockwise torsion of the right horncore is absent (0), incipient (1), or strong (2); (50/71).
13 Clockwise torsion of the right horncore is absent (0), incipient (1), or strong (2); (50/90).
14 The angle between basal horncores and dorsal cranium is lower (0), or higher (1); (20/20).
15 The posterior angle between the maximum horncore diameter and the midfrontal suture is low (0), or high (1); (25/82).
16 A long straight horncore tip that points upward is absent (0), or present (1); (100/100).
17 The horn pedicels are short (0), at least moderately long (1), long and well-defined by a tendency to parallel sides; (66/95).
18 Horn pedicel fusion into a joint boss is absent (0), incipient (1), or well-developed (2); (66/85).

Skull shape and size

19 The angle of forehead to braincase, or craniofacial angle (between the straight lines from the most dorsal point of the mifdrontal suture to the internasal suture, and from bregma to occiput) is low (0), moderately high (1), high (2), or very high (3); (20/38).
20 Body size, estimated from skull size, is small to medium (0), large (1), very large (2); (66/90).

Posterior cranium

21 Brain width across the parietal-squamosal suture, is low (0), moderate (1), high (2); (20/60).
22 Dorsal braincase length, estimated by the minimum distance between the fronto-parietal suture and occiput is low (0), moderately high (1), high (2), or very high (3); (30/76).
23 The distance across the mastoids of the occipital is low (0), moderate (1), high (2); (33/77).
24 The occipital height from the top of foramen magnum to the top of occiput, is low (0), moderate (1), or high (2); (33/71).
25 A round parietal boss nearly centrally placed on the dorsal braincase is absent or very slight (0), moderately developed (1), or strongly developed (2); (50/87).
26 The braincase roof in lateral view is straight to concave (0), slightly to moderately convex (1), or strongly convex (2); (66/95).
27 The basioccipital has longitudinal ridges behind the anterior tuberosities, with a central groove between the ridges, absent to poorly developed (0) or well-developed (1); (100/100).

Anterior cranium and dentition

28 Maximum distance between supraorbital foramina is low (0), moderate (1), high (2); (22/58).
29 The distance between the supraorbital foramen and the anterior horncore midpoint is low (0), moderately high (1), high (2), very high (3); (37/82).
30 The dorsal orbital width is low (0), or high (1); (33/66).
31 The minimum distance between horncore and orbit is low (0), moderate (1), high (2); (66/93).
32 The preorbital fossae are absent to hardly developed (0), small, localized with a weak upper rim if any (1), medium-sized with a definite upper rim (2), or very large with a strong upper rim such that the naso-maxillary cross section appears compressed (3); (33/71).
33 The frontal anterior to the horncores is not (0) or is (1) convex; (50/85).
34 Posterior suture of nasal bones is not (0) or is markedly centrally indented (1); (100/100).
35 The anterior nasals do not (0) or do (1) extend far beyond the premaxillary contact; (100/100).
36 The face anterior to the orbits is shorter to moderately long (0), or it is markedly elongated with the toothrow far anterior to the orbit (1); (100/100).
37 A steep upward-doming of the anterior part of the nasals and adjacent bones, to form a crest, is absent (0), present (1), strongly developed; (66/75).
38 The P_{2-4} : M_{1-3} ratio is markedly low with P_2 absent and P_3 very reduced (0), moderately low with P_3 less reduced (1), or higher with P_2 present in most specimens (2); (33/76).
39 The frontal sinus in the basal horncores and pedicels is minimally developed with bony intrusions into the sinus (0), or well-developed and smooth-walled (1); (100/100).
40 Marked lateral expansion of the anterior premaxillae to form an anteriorly rectangular biting surface is absent (0), or present (1); (100/ 100).

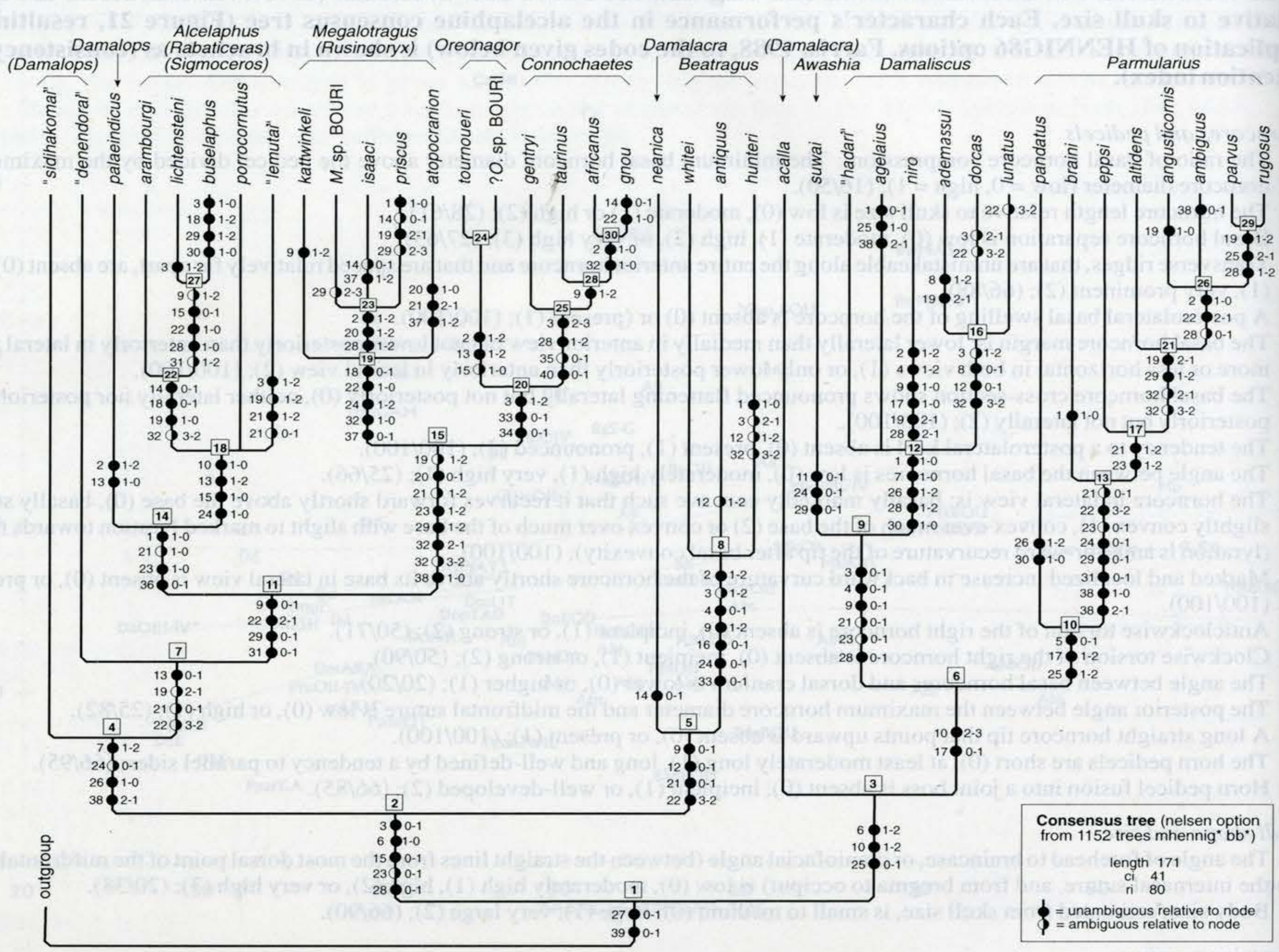

Figure 21. Consensus tree for Alcelaphini based on all character codes (except those labelled Mk* which treats Mk, Mki and MkBOU as a single taxon) in Table 14. See the box in the figure for HENNIG86 options (Farris, 1988) and for tree statistics, consistency index (ci), and retention index (ri). Ambiguous changes could occur either at the node at which they are plotted or equally parsimoniously at an adjacent node. For character numbers see Table 13 which also gives the performance of each character in this consensus tree in terms of the ci and ri of characters.

a conspicuously narrowest approach that nevertheless remains well separated; the dorsal braincase is strongly angled relative to the preserved part of the face; there is no parietal boss; the braincase sides in superior view are near-parallel; the dorsal border of the occipital surface is not evenly and broadly rounded but laterally concave, and there is a median spine with flanking hollows; the basioccipital does not have strongly expanded anterior tuberosities, nor a marked central longitudinal groove flanked by strong longitudinal ridges but is rather flat with only tiny ridges especially anteriorly; the auditory bulla is missing.

Horizon: The holotype comes from Bouri 1 dated ca. 1 m.y. (Figure 1).

Etymology: The genus is named after the source site, and the species after Ann Getty who repaired the holotype and has supported in many ways the field efforts that made these fossils available.

Measurements: The measurements of the holotype and referred specimens are given in Table 10.

Referred specimens: A cranium with nearly complete right and left horncores BOU-1/17 from Bouri 1, and a right frontlet with complete right horncore and part of the cranium BOU-2/18 from Bouri 2, also belong to *B. anngettyae*. There are few aspects in which BOU-1/17 and BOU-2/18 deviate from or add to the features of the holotype. In BOU-1/17, the horncores are basally larger, even more compressed, and were not as long in the complete state; the posterior margin of the right horncore trends laterally towards the tip while the anterior margin keeps a straight course, resulting in a hint of clockwise torsion; on the left can be seen the base of a sinus extending up into the horncore base, although it is unclear how far up and there may be a bony partition in it laterally; the midfrontal suture is large and complex between the horncores; the basioccipital was long and narrow with more of a shallow longitudinal groove between

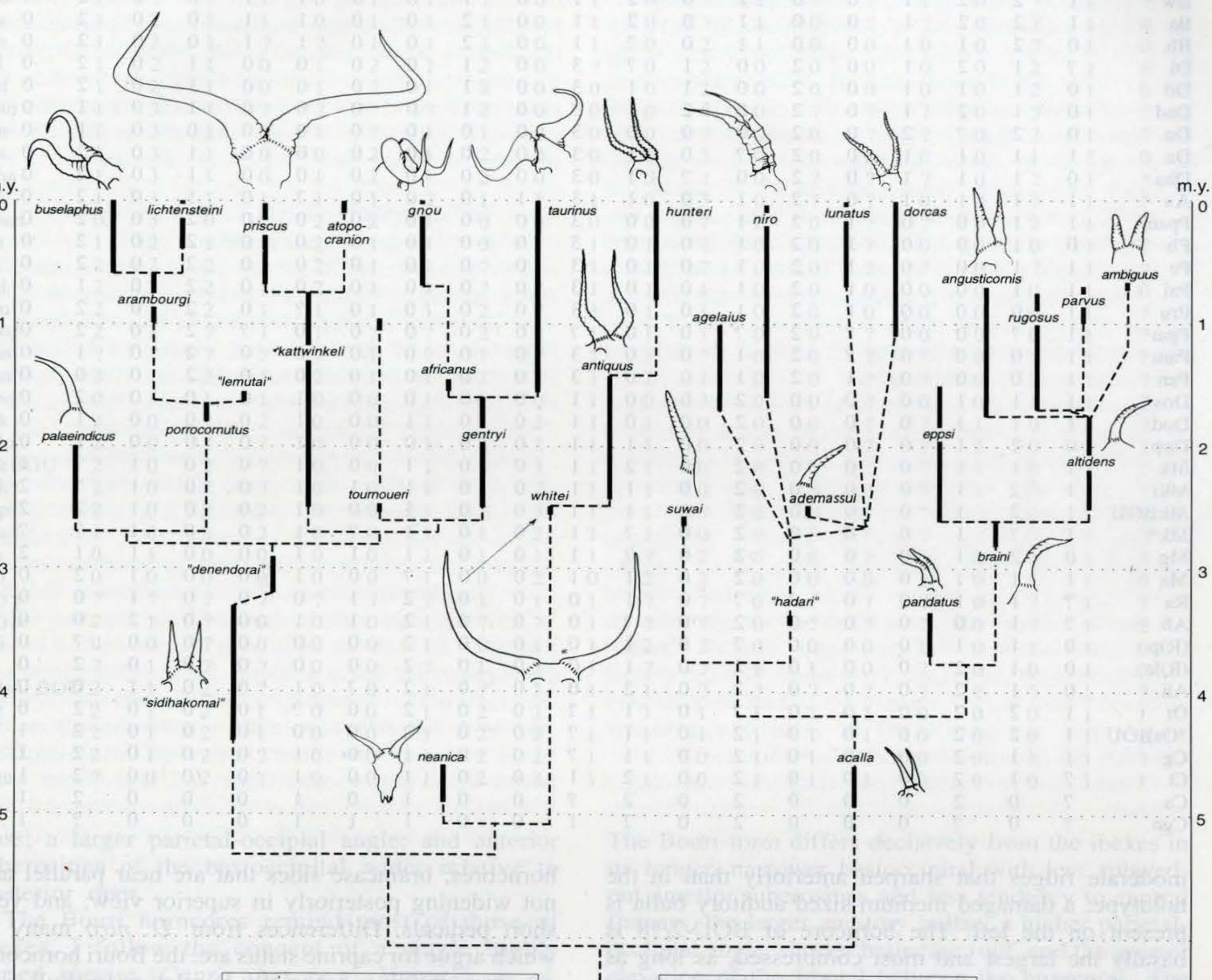

Figure 22. Phylogenetic tree of Alcelaphini, plotted against time, based on the same data (Table 14) as the consensus tree in Figure 21, except that an inclusive *Megalotragus kattwinkeli* was used (Mk* in Table 14, which includes Mk, Mki and MkBOU). The corresponding consensus tree topology is identical to that in Figure 21, except that *M. atopocranion*, *M. priscus* and the inclusive *M. kattwinkeli* formed a trichotomy. In this tree each taxon that has no autapomorphies, and is therefore the hypothetical potential ancestor of its sister-group in terms of the present hypotheses of character distribution, is shown in the appropriate ancestral position. I have here considered that the two apparent autapomorphies of *Beatragus whitei*, shortened dorsal braincase 22, and absence of a parietal boss 25, have been misinterpreted due to its exceptional basal horncore expansion, and shown it as the potential ancestor of *B. antiquus*. Similarly, I have considered that the single autapomorphy of *Parmularius braini*, strong basal horncore compression 1, has been misinterpreted due to its very marked posterolateral swelling on the basal horncore, and shown it as the potential ancestor of its sister-group. Dates for first and last appearances of these taxa are given in Table 2.

TABLE 14.

Cladistic Codes for Skull Characters. For taxon letter-codes see Table 2; for character numbers Table 13. Mk*: Mk, Mki, and MkBOU are treated as one taxon. OG = outgroup states.

a. Characters 1-20.

Taxa	Characters																			
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12•**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
OG	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	2	0
ac	1	1	0	0	0	2	1	0	0	2	0	0	0	0	0	0	0	0	2	0
ne	1	1	1	0	0	0	1	0	1	1	0	1	0	1	1	0	0	0	2	0
Bw	1	2	2	1	0	0	1	0	2	1	0	1	0	0	1	1	0	0	2	?
Ba	1	2	2	1	0	0	1	0	2	1	0	2	0	0	1	1	0	0	2	0
Bh	0	2	1	1	0	0	1	0	?	1	0	2	0	0	1	1	0	0	2	0
Dl	?	1	2	1	0	2	0	1	?	3	0	1	0	0	0	0	1	0	2	0
Dd	0	1	1	1	0	2	0	1	1	3	0	1	0	0	0	0	1	0	2	0
Dad	0	1	2	1	0	2	0	2	1	3	0	1	0	0	0	0	1	0	1	0
Dn	0	2	?	2	0	2	0	0	0	3	0	0	0	0	0	0	0	0	1	0
Da	1	1	1	1	0	2	?	0	1	3	0	0	0	0	0	0	1	0	2	0
Dha	0	1	1	1	0	2	0	?	1	3	0	0	0	0	0	0	1	0	2	0
As	1	1	1	1	0	2	1	0	1	3	1	0	0	0	?	0	1	0	2	0
Ppan	1	1	0	0	1	2	1	0	0	3	0	0	0	0	0	0	2	0	2	0
Pb	0	1	0	0	1	2	1	0	0	3	0	0	0	0	0	0	2	0	2	0
Pe	1	1	0	0	1	2	1	0	0	3	0	0	0	0	0	0	2	0	2	0
Pal	1	1	0	0	1	2	1	0	0	3	0	0	0	0	0	0	2	0	1	0
Pru	1	0	0	0	1	2	1	0	0	3	0	0	0	0	?	0	2	0	2	0
Ppar	1	?	0	0	?	2	?	0	0	?	0	0	0	0	0	?	2	0	2	0
Pam	1	0	0	0	?	2	1	0	0	3	0	0	0	0	0	0	2	0	1	0
Pan	1	0	0	0	1	2	1	0	0	3	0	0	0	0	0	0	2	0	0	0
Dos	1	1	1	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	2	0
Dod	1	1	1	0	0	0	2	0	0	1	0	0	1	0	1	0	0	0	1	0
Dop	0	2	1	0	0	0	2	0	1	1	0	0	0	0	1	0	0	0	1	0
Mk	1	1	1	0	0	0	2	0	2	1	0	0	1	0	1	0	0	1	?	1
Mki	1	2	1	0	0	0	2	0	1	1	0	0	1	1	1	0	0	1	?	2
MkBOU	1	2	1	0	0	0	2	0	1	1	0	0	1	0	1	0	0	1	2	2
Mk*	1	?	1	0	0	0	2	0	?	1	0	0	1	?	1	0	0	1	?	?
Mp	0	2	1	0	0	0	2	0	?	1	0	0	1	1	1	0	0	1	1	2
Ma	1	1	1	0	0	0	2	0	1	1	0	0	?	0	1	0	0	1	2	0
Ra	?	1	1	0	0	?	?	0	1	0	0	0	2	1	0	0	0	1	0	0
Ab	?	1	0	0	0	0	2	0	?	0	0	0	2	1	1	0	0	2	0	0
(R)p	0	1	1	0	0	0	?	0	1	0	0	0	2	0	0	0	0	0	?	0
(R)le	0	1	2	0	0	0	2	0	1	0	0	0	2	0	0	0	0	0	2	0
Ali	0	1	2	0	0	0	2	0	2	0	0	0	2	?	1	0	0	1	0	0
Ot	1	2	2	0	0	0	?	0	1	?	0	0	2	0	?	0	0	0	2	0
?OsBOU	1	2	2	0	0	0	2	0	1	?	0	0	2	0	0	0	0	0	2	1
Cg	1	1	2	0	0	0	2	0	1	?	0	0	1	0	1	0	0	0	2	1
Ct	?	1	2	0	0	0	2	0	2	1	0	0	1	0	1	0	0	0	2	1
Ca	?	0	2	0	0	0	2	0	2	?	0	0	1	0	1	0	0	0	2	1
Cgn	?	0	?	0	0	0	2	0	2	1	0	0	1	1	1	0	0	0	?	1

moderate ridges that sharpen anteriorly than in the holotype; a damaged medium-sized auditory bulla is present on the left. The horncore of BOU-2/18 is basally the largest and most compressed, as long as that of BOU-1/44, and again shows sharp anterior and posterior keels higher up with the anterior keel present also at the base, and has no transverse ridges. *Comparisons*: It is appropriate to explain why I do not regard this Bouri form as close to *Damaliscus niro* which is present at Bodo (Figure 13) and has the closest resemblances to this Bouri form of all the Awash taxa. Similarities are long horncores although the two longest from Bouri are longer than the longest ones of *D. niro* (from Olduvai Bed III, Gentry and Gentry 1978: 398); well separated supraorbital foramina in small pits; low angle of the maximam basal horncore diameter to the midfrontal suture, and strong craniofacial bending although the Bouri form is more extreme (Figure 18); flattened medial horncore surfaces; upright insertion of horncores; braincase sides that are near parallel and not widening posteriorly in superior view; and very short pedicels. Differences from *D. niro* many of which argue for caprine status are: the Bouri horncores are more massive, especially in relation to skull size, have greater basal compression (Figure 19), lower basal divergence, a widest mediolateral diameter situated posteriorly and not anteriorly, substantially lower basal separation (Figure 20), a hint of clockwise torsion in BOU-1/17 which is unknown in *Damaliscus*, absence of transverse ridges, less flattened lateral surfaces, a higher degree of curvature in lateral view, and a narrow sharp anterior ridge or keel that may have connected anteriorly with bony knobs on the face and that I have not seen on any *D. niro* horncores (alcelaphines as a whole generally lack keels, and never have sharp anterior keels); a superior orbital margin that widens more relative to the outer pedicel diameter; a braincase that is much shorter although of comparable width; no parietal

TABLE 14 continued

b. Characters 21-38.

Taxa	Characters																		
	21	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
OG	0	3	0	0	0	1	0	0	0	1	0	3	0	0	0	0	0	2	0	?
ac	0	3	0	0	1	1	1	0	0	1	0	?	0	0	?	0	0	2	1	?
ne	1	2	1	0	0	1	1	1	0	1	0	3	0	0	0	0	0	2	1	?
Bw	1	?	1	1	0	1	1	1	0	1	0	?	1	?	?	?	0	?	1	?
Ba	1	2	1	1	0	1	1	1	0	1	0	?	1	0	?	?	0	?	1	0
Bh	1	2	1	?	?	1	1	1	0	1	0	2	1	0	0	0	0	?	1	0
Dl	1	2	1	0	1	2	1	2	0	?	0	2	0	0	0	0	0	2	1	0
Dd	1	2	1	0	1	2	1	2	0	0	0	2	0	0	0	0	0	2	1	0
Dad	1	3	1	?	?	?	?	2	0	0	0	?	0	?	?	?	0	?	1	?
Dn	1	3	1	0	1	?	1	1	0	0	0	?	0	0	?	?	0	2	1	?
Da	1	3	1	0	0	2	1	2	0	0	0	3	0	0	0	0	0	1	1	0
Dha	1	3	1	0	1	2	1	2	0	0	0	?	0	?	?	?	0	?	1	?
As	1	3	1	1	1	1	?	1	1	1	0	3	0	?	?	0	0	?	1	?
Ppan	0	3	0	0	2	2	1	0	0	0	0	?	0	0	?	?	0	2	1	?
Pb	1	2	1	1	2	1	1	0	1	1	1	?	0	0	?	0	0	0	1	?
Pe	2	2	2	1	2	1	1	?	1	1	1	?	0	0	?	?	0	?	1	?
Pal	2	2	2	1	2	1	1	?	2	1	1	1	0	0	0	0	0	0	1	0
Pru	2	1	2	1	1	1	1	2	?	1	1	1	0	0	0	0	0	0	1	?
Ppar	2	1	?	1	1	?	?	2	2	1	1	1	0	0	?	0	0	0	1	?
Pam	?	?	?	?	?	1	?	1	?	1	1	?	0	0	?	?	0	1	1	?
Pan	2	1	2	1	2	1	1	1	2	1	1	1	0	0	?	?	0	?	1	?
Dos	0	3	1	1	0	0	1	1	0	1	0	3	0	0	?	0	0	1	1	?
Mk	2	0	2	2	0	0	1	1	2	1	1	0	0	0	?	?	1	0	1	?
Mki	2	0	2	?	0	0	1	2	2	1	1	0	0	0	?	?	2	0	1	?
MkBOU	2	0	2	?	0	0	1	2	3	1	1	0	0	0	?	?	1	0	1	?
Mk*	2	0	2	?	0	0	1	?	?	1	1	0	0	0	?	?	1	0	1	?
Mp	2	0	2	2	0	0	1	?	3	1	1	?	0	0	?	?	?	0	1	?
Ma	1	0	2	2	0	0	1	1	2	1	1	0	0	0	?	?	2	?	1	?
Ra	0	1	0	0	0	0	1	1	1	1	?	2	0	0	?	?	0	?	1	?
Ab	0	0	0	0	0	0	1	0	2	0	2	2	0	0	0	1	0	1	1	0
(R) p	?	?	?	?	?	?	?	1	1	1	?	?	0	?	?	?	0	?	1	?
(R) le	2	1	?	0	0	0	1	?	?	1	?	?	0	?	?	?	0	?	1	?
Ali	0	0	?	0	0	0	1	0	1	1	2	2	0	0	0	1	0	1	1	0
Ot	?	1	?	?	0	0	?	1	2	1	?	?	1	1	0	?	0	0	1	0
?Osp. BOU	2	1	2	?	0	0	1	?	2	1	1	?	?	?	?	?	?	?	1	?
Cg	2	1	2	1	0	0	1	2	2	1	1	1	1	1	1	0	0	0	1	1
Ct	2	1	2	1	0	0	1	2	2	1	1	1	1	1	1	0	0	0	1	1
Ca	2	1	2	?	0	0	1	2	2	1	1	0	1	1	?	0	0	?	1	?
Cgn	?	0	2	?	0	0	1	2	2	1	1	0	1	1	1	0	0	0	1	1

boss; a larger parietal-occipial angle; and anterior tuberosities of the basioccipital wider relative to posterior ones.

The Bouri horncores remind most of those of ibexes. I follow the concept of a single highly varied species *Capra ibex* (e.g., Honacki *et al.* 1982) that includes varieties *ibex* (Alpine Ibex), *sibirica* (Asiatic Ibex), and two African forms of especial interest in the present context *nubiana* (the Arabian Ibex), and *walie* (Abyssinian Ibex). *C. i. nubiana* occurs in Africa only east of the Nile, in the hills along the Red Sea coast, from near Cairo south to Eritrea, near the Sudanese border, and in the Sinai Peninsula. Outside Africa this subspecies extends into Arabia, Palestine and Syria. *C. i. walie* is limited to the Simien Mountains in the Ethiopian Highlands. *C. i. walie* is larger than *C. i. nubiana*, with relatively shorter horns. *C. i. walie* also differs in the broad anterior surface of the horn which is also present in *C. i. sibirica*, and a bony boss on the forehead, both of which are absent in *C. i. nubiana*. The Bouri form differs decisively from the ibexes in its longer, narrower basioccipital with less splayed-out anterior tuberosities and less tendency to central flatness, the larger auditory bullae, a higher parietal-occipital angle, shorter braincase roof, and the greater elevation of the frontal between the horncores. The last three features are more advanced, indicating that *B. anngettyae* is not part of the lineage to modern ibexes. Cregut-Bonnoure (1992a, 1992b) argued that in Europe *Capra ibex* and *C. pyrenaica* appeared in the late Middle Pleistocene; before that only the shorter-horned *Hemitragus* was present, casting doubt on whether the finds really belong to *Capra* that were described as *C. alba* from the Early Pleistocene of Venta Micena, Spain (Moya-Sola 1987), and as *C. primaeva* from Late Pliocene Ain Brimba, Algeria (Arambourg 1979).

C. alba resembles the Bouri fossils in having several advanced features including a low craniofacial angle, and high angles between the occipital surface and the dorsal braincase and between the latter and the horncore, and in horncores without torsion and with low basal separation. The horncores of *C. alba* differ in that their bases have smaller maximum diameters, lower compression, larger angles of the maximum diameters to the midfrontal suture, posterior keels, and markedly subdivided basal sinuses. They are also decidedly shorter. The ratio of braincase length (coronal suture to occiput) to width is 58.3/72.4 = 0.81 in the *C. alba* holotype (Moya-Sola, 1987), while in BOU-1/44 it is 44.8/78.7 = 0.57 and in BOU-1/17 it is 42.2/85.0 = 0.50. The basioccipital of *C. alba* appears to be more advanced towards modern caprines than in the later Bouri form, being relatively shorter with markedly wider anterior tuberosities: the ratio of anterior to posterior tuberosities is 37.8/31.8 = 1.2 in the *C. alba* holotype, while it is estimated to be only 29.5/32 = 0.9 in BOU-1/44. This last difference suggests that the two species belong to different lineages. Horncores of *C. primaeva* from Ain Brimba are as compressed as those from Bouri, but of only about half the basal size and 22-33% of the length, and lacking any marked keels.

Similarities of *B. anngettyae* to living *Hemitragus*, tahrs, include a braincase shorter and a forehead more elongated than in living *Capra*, and horncores that are basally very close with medial flattening and anteromedial keels. The horncores in the Bouri species are much more upright than in tahrs, not rising from the skull in the same plane as the face as in tahrs, and much longer. These presumably more advanced features of *B. anngettyae* suggest that it does not belong in *Hemitragus* nor is closely connected with the ancestry of tahrs. Yet the shared advanced features of cranial and frontal morphology leave open the possibility of sister-group status between the Bouri form and *Hemitragus*.

B. anngettyae shares some features with early caprines like *Sivacapra sivalensis*, which Pilgrim (1939) thought came from the Plio-Pleistocene Pinjor Formation of the Siwaliks, and *Tossunnoria pseudibex* from the Late Miocene of Tsaidam, China (Bohlin 1937): all three share a rather long narrow basioccipital that lacks strongly widened anterior tuberosities and retains at least some central longitudinal depressions, and larger auditory bullae, which are all plesiomorphic relative to living caprines. They also share some elongation of the frontal anterior to the horncores, possibly indicating that none of them is on the lineage to living goats but that they may be connected with the ancestry of tahrs. These indications are reinforced for *T. pseudibex* by its relatively short braincase which may be the early harbinger of the even shorter one in *B. anngettyae*.

S. sivalensis differs from the Bouri species in horncores that have a posteromedial keel and torsion and are much shorter and distally less divergent, and in its longer and lower braincase. *T. pseudibex* differs from the Bouri form in an occipital surface that is wider relative to its height, and in shorter, less back-curved horncores that have a larger posterior angle of the basal horncore to the midfrontal suture, higher basal separation and higher divergence. These two taxa resemble each other in horncores that are posteriorly rounded at the base and have an anterior keel that sharpens strongly distally with frontal rugosities just anterior to the basal keel, in the absence of hollows in the horncores themselves as present in many advanced caprines, in temporal lines that converge strongly towards the rear, as well as in the basicranium as mentioned earlier. It is possible that *Tossunnoria* is close to the ancestry of both *Hemitragus* and *Bouria*.

DISCUSSION AND CONCLUSIONS

Systematics

The present results imply some minor and also some major revisions of previous analyses. One new proposal is that Alcelaphini has two ancient, large subtribes that diverged during or before the Mio-Pliocene transition: Alcelaphina (from node 2 in Figure 21) and Damaliscina (from node 3). Each diverged again during the Early Pliocene so that by 3.6 m.y. four major groups had arisen: the *Damalops*-to-*Connochaetes* clade and its sister taxon the *Damalacra-Beatragus* clade in Alcelaphina, and *Parmularius* and its sister-clade containing *Damaliscus* together with their proposed common ancestor (*Damalacra*) *acalla* in Damaliscina. Infertile hybrids between *Alcelaphus* and *Damaliscus*, which diverged at least ca. 4.5 m.y. ago in terms of my cladogram, are known (Gray 1972). Comparison of diverse recent systematic results with chronology and with hybridization data shows that there are many cases of divergence times of this magnitude between living species that are known to have hybridized at least in confined circumstances. For instance, among reduncine antelopes, the living *Kobus kob* forms a sister-group with the clade of waterbuck, *K. ellipsiprymnus*, and lechwes, *K. leche* and *K. megaceros* (Vrba *et al*., 1994). *K. kob* is known by 3.0 m.y. in the fossil record (Gentry 1985) and Gentry (1980) considered a Langebaanweg taxon, ca. 4.5-5 m.y. old, as part of the *K. kob* lineage. A male *K. kob* was successfully mated with a female *K. megaceros* X *K. e. defassa* hybrid. I believe that we need to accept that several millions of years of divergence, as well as considerable phenotypic divergence, can be compatible with the plesiomorphicly retained ability to hybridize (although perhaps that ability only survives at the genetic and embryological levels, such that hybridization may be behaviourally excluded in the wild).

At the end of any large systematic analysis, the author tends to be left with major doubts about the results. One of my main uncertainties concerns the

the cladistic position of the new genus *Awashia*. Its affinities remain unresolved to such an extent that it could either belong as one of the basal branches in Damaliscina (as tentatively shown in Figures 21 and 22), or in a basal position in Alcelaphina close to the *Damalops* group. This new taxon does not share the synapomorphies, and certainly not the diagnosis, of any previously named genus. Other tentative and new systematic proposals are the removal of *Beatragus* from *Damaliscus* (*contra* Ansell 1971, Vrba 1979, and others), the close relationship of *Beatragus* to *Damalacra neanica*, and the sister-group status of *Damalacra-Beatragus* with the *Damalops*-to-*Connochaetes* clade. The present scheme renders *Damalacra* (Gentry 1980) paraphyletic, and suggest that *D. neanica* (as being the first that Gentry, 1980, described) is the sole species in *Damalacra*, while the species *acalla* deserves a new generic name. This proposal could be consistent with Gentry's (1980) argument that the species *neanica* and *acalla* are closely related. After all, all pairs of great clades with a common ancestry were initially founded by sister-species.

Gentry (1981, and elsewhere) has suggested that the Hadar taxa here called (*Damalops*) "*sidihakomai*" and "*denendorai*" are part of one species ?*Damalops* sp. and possibly also conspecific with the emigrant from Africa, *D. palaeindicus* known from the Siwaliks in Tadzhikstan, Pakistan and India. The present analysis agrees that these three temporally successive taxa are closely related, potentially in a direct ancestor-descendant sequence (Figure 22). At the same time, in my result these forms emerge as three distinct taxa, and the genus *Damalops* of Gentry's proposal is paraphyletic such that the species *palaeindicus* remains the only valid species of *Damalops*. The present results tie *D. palaeindicus* more firmly into the cladogram, as the sister-taxon of *Alcelaphus*, than did the previous cladistic hypothesis (Vrba 1979). However, a particularly high level of uncertainty attaches to the placement of this enigmatic taxon in the cladogram in Figure 21: Of the two advanced characters towards this species, horn elongation (2 : 1->2) would be scored as a local autapomorphy in any realistic placement of this species within Alcelaphina, but the other apomorphy is a reversal (13 : ->0 loss of clockwise torsion in the right horncore). The latter suggests that a better branching-off point for this species might be between nodes 4 and 7 in Figure 21, that is, after (*D.*) "*sidihakomai*", before evolution of (*D.*) "*denendorai*" and clockwise torsion that later has to reverse in the present scheme. This difference also has biogeographic implications: emigration of *D. palaeindicus* occurred after 2.9 m.y. ago in the present result, but between 3.4-3.2 m.y. ago given the earlier branching position.

I suggest that a single, long-lasting and variable species, *Megalotragus kattwinkeli*, includes not only the fossils previously called *M. kattwinkeli* (with several synonyms, see Gentry and Gentry 1978; Gentry *et al.* 1995), but also new fossils from Bouri and the fossils assigned to *M. isaaci* by Harris (1991). This implies that both *Rhynotragus semiticus* and *Megalotragus isaaci* are synonyms of *Megalotragus kattwinkeli*. *Megalotragus* constitutes a well-supported clade, in spite of the fact that the branching sequence within it remains unresolved. As *Megalotragus* includes the species *atopocranion*, *Rusingoryx* is a synonym of *Megalotragus* (as suggested by Harris 1991). Similarly, both the *Connochaetes* clade, and its sister-group status with *Oreonagor*, are well supported. An enigmatic new cranium from Bouri is the sister-taxon of the extinct *O. tournoueri* in my cladistic result. While I present this result for discussion, I feel dissatisfied with it and regard it as possible that this new Bouri cranium belongs to *M. kattwinkeli*. My previous alcelaphine cladogram (Vrba 1979) suggested that *Megalotragus* and *Alcelaphus* are a sister-group. In contrast, the present revision suggests that *Megalotragus* is the sister-taxon of the *Oreonagor-Connochaetes* clade.

The affinities of living *Alcelaphus* with taxa previously called *Sigmoceros*, *Rabaticeras*, and *Numidocapra*, and the nomenclature of this group, require further study. The earliest taxon in this clade (from node 18 in Figure 21) is the species *porrocornutus* from Swartkrans Member 1 that I initially described as *Damaliscus porrocornutus* (Vrba 1971) and subsequently included in *Rabaticeras* (Vrba 1976). Just a little later occurs the distinct form here called "*lemutai*" (based on Olduvai Bed II specimen S.208) that Gentry and Gentry (1978) suggested may be ancestral to *A. lichtensteini* or to *R. arambourgi*, with the latter possibly ancestral to the living hartebeest *A. buselaphus*. The cladogram in Vrba (1979) suggested that "*lemutai*" belongs with *lichtensteini* in *Sigmoceros*, and that this genus may be closer to *Connochaetes* than to *Alcelaphus*. In the revised cladogram (Figure 21), the species *porrocornutus* is the potential direct ancestor of "*lemutai*" and *arambourgi*, which in turn is the potential direct ancestor of *buselaphus* (supporting Gentry and Gentry 1978) and its sister-species *lichtensteini*.

The Bodo *A. buselaphus*, the earliest secure record of the living species, confirms its close relationship to *A. lichtensteini*. Also allied to this group is *Numidocapra crassicornis* previously known from the Early Pleistocene of Algeria (Arambourg, 1949) and Djibouti (Bonis *et al.* 1988). Gentry (1978, 1990a) considered it as caprine and Geraads (1981) as alcelaphine. I have now described this species from Bouri based on crania and associated teeth. I confirm that it is alcelaphine and suggest that the *Rabaticeras-Alcelaphus* lineage may have descended from it. If the monophyly of this group is upheld by future studies, it may be appropriate to call it *Alcelaphus* with synonyms *Sigmoceros*, *Rabaticeras* and *Numidocapra*. One hopes that in future additional fossils will be found of the species *porrocornutus* and "*lemutai*" which are so far known only from single specimens, and that a resolution will emerge that improves on the trichotomy at node 18 in Figure 21. I suggest that we defer nomenclatural revisions of this group until then.

In the second basal alcelaphine taxon, Damaliscina, the least certain placement is that of the new taxon *Awashia suwai* as already mentioned. The status of the speciose extinct genus *Parmularius* remains essentially unchanged from Vrba (1979). I regard the monophyly of *Damaliscus* as more problematic than that of *Parmularius*. At least two of the present synapomorphies of *Damaliscus*, 7 : 1->0 horncore bases that are laterally flattened, and 26 : 1->2 a convex dorsal braincase roof, represent tentative hypotheses of synapomorphy. The branching sequence within *Damaliscus* has been revised from Vrba (1979), but remains problematic as indicated by the extensive polytomy (Figures 21, 22). The status of the species here termed "*hadari*" will probably need revision once the matrix attaching to the single known cranium of this species is removed. The precise affinities of *D. niro* and *D. agelaius* remain enigmatic, as shown by the several character state reversals that are required in their cladistic positions in Figure 21. *D. agelaius* may eventually turn out to belong to a more basal stem, one possibly related to *Awashia suwai*.

A new genus and species of Caprini, *Bouria anngettyae,* combines some specialized features of tahrs, *Hemitragus*, as well as advanced features of goats, *Capra*, with primitive caprine features. The affinities of a new genus and species tentatively included in Ovibovini, *Nitidarcus asfawi*, remain elusive. Both new genera appear near 1 m.y. ago at Bouri, probably after immigration from Eurasia.

Chronology and Turnover

Some times of major change in the bovid communities of the Middle Awash are becoming evident. Only some of these can be detected by the alcelaphine record alone. An early change occurred somewhere between 5.0 m.y. and the 4.4 m.y. level of Aramis. By the end of this interval, the earliest secure Alcelaphini appear, while taxa in other bovid tribes had disappeared (Vrba 1995b). The next two changes appear to have occurred in the intervals 4.4-3.8 m.y. and 3.8-3.4 m.y. They are reflected in the Alcelaphini only by evolution within the (*Damalops*) "*sidihakomai*" lineage between Aramis on the one hand and the later Wee-ee 5 and Maka 1.

There is further evidence of evolutionary episodes later in the Pliocene: While earlier stratigraphic evaluations (White, pers. comm.) placed Matabaietu localities 1-6 close in time to each other and to the associated tuff dated 2.5 m.y., the bovid evidence hints that between an earlier Matabaietu 6 and a later Matabaietu 1-5 (Figure 1) significant evolution and turnover occurred. Matabaietu 6 may be the latest Awash stratum that shares reduncine and tragelaphine elements with 2.9 m.y.-old subunits of Shungura B. These elements disappear and new taxa appear elsewhere in Africa between 2.9-2.6 m.y. (Vrba 1995a, b). This change may be reflected in the alcelaphine record by the fact that Matabaietu 6 and all lower strata contain evidence of only one lineage or none, while by Matabaietu 3-5 two new taxa – the global first appearances of the genera *Beatragus* and *Awashia* – are recorded.

Similarly, while current stratigraphic concepts still suggest that all the localities plotted at the 2.5 m.y. level in Figure 1 are indeed ca. 2.5 m.y., the bovid evidence suggests that Matabaietu 3-5 (ca. 2.6 - 2.5 m.y.) predates Wilti Dora 2-3 and Gamedah 1, and perhaps also Matabaietu 1 and 2, which may all be closer to 2 m.y. ago. By the time of these later levels, a number of new taxa appear in the Awash area that are absent from Matabaietu 3-5. These include first Awash records (I give in brackets for each case the earliest radiometrically dated record elsewhere) of *Hippotragus gigas* (2.6 m.y. for referred teeth, 1.9 m.y. for cranial fossils), *Tragelaphus gaudryi* (2.4 m.y.), *Megalotragus kattwinkeli* (2.5 m.y.), and *Beatragus antiquus* (1.9 m.y.), as well as the global first appearance of *Damaliscus ademassui*. A later date than 2.5 m.y. for at least Gamedah 1 and Wilti Dora 2-3 might fit better with the previous first records for *H. gigas* and *B. antiquus*, and with the cladistic inference that *B. antiquus* is the direct descendant of *B. whitei* which is last recorded just below 2.5 m.y.

Even more far-reaching faunal changes occurred in the Awash between the last-mentioned Late Pliocene sites and Bouri at 1 m.y., and between that and Bodo 1 at 0.6 m.y.

Evolution and Biogeography

Phylogenetic results of this kind can provide powerful tests of evolutionary hypotheses. Take for example the notion that physical changes – climatic and tectonic changes – initiate most speciation events (part of the turnover pulse hypothesis, see detailed discussions in Vrba, 1995a, in press). The prediction is that speciation events involving different kinds of organisms should be concentrated nonrandomly in time and in predictable association with the climatic record. In contrast, hypotheses that invoke biotic interactions as the major initiating cause of speciation, like Van Valen's (1973) Red Queen's hypothesis, predict a random pattern of speciation events in time. We need information on the timing of speciation to distinguish between these predictions. The problem is that the times of species' first *appearances* in the record may postdate their *origins* by varying lengths of time. For instance, those species may have remained unseen in previous strata – and appeared in our record when they did – simply because conditions of fossil preservation changed.

This is where cladistic analysis can help because it points out taxa that have no autapomorphies, and that are therefore potential direct ancestors of others. If the last appearance of such a potential ancestor and the first appearance of its descendant are radiometrically dated, good estimates can result for the interval during which speciation occurred. Take for example the two cladogenetic events between potential ancestor (*Damalops*) "*denendorai*", last recorded in Shungura B11 just above tuff B-10 dated 2.95±0.03 (Feibel *et al.* 1989; also known up to the Hadar BKT-2L tuff dated 2.88±0.08, Haileab and Brown, 1992, which gives a similar date), and *Connochaetes gentryi* which is first recorded in unit KU2 of the Upper Lomekwi Member of the Nachkui Formation (Harris 1991) just below a tuff dated 2.52 ± 0.05 (Feibel *et al.* 1989). Thus, the time interval during which these speciation events occurred is quite well delimited to the interval 2.9-2.5 m.y. In Figure 21 there are 14 potential direct ancestors of other taxa. For eight of the cladogenetic events (with more than one descendant) from these 14 ancestors one can estimate a short interval for the occurrence of speciation that is bounded by radiometric dates, four of which occurred between 2.9-2.5 m.y., three between 1.9-1.7 m.y., and one between 0.8-0.6 m.y. For a further three cladogenetic events that can be limited to a short interval, one of the bracketing dates for that short interval is biochronological. For these three events the estimated limits are 2.9-2.6 m.y., 1.8-1.7 m.y., and 0.8-0.6 m.y. This is of course only one clade; and a more convincing assessment of the temporal pattern should be based on a larger number of clades.

I applied a similar approach, including several statistical significance tests, to the entire African record for 147 bovid species. The results pointed out the same three time intervals as marked by high numbers of speciation events (Vrba 1995b). This constitutes some support for the notion that widespread physical changes influence speciation not only in the Alcelaphini but also in other groups.

The lineage from (*D.*) "*sidihakomai*" to (*D.*) "*denendorai*", unbranching over 4.4-2.9 m.y., provides a contrast to the higher evolutionary rates of their descendants over 2.9-2.5 m.y. and also later. Global and African climatic history may have influenced this: The mean of the global climatic cycles stayed more nearly constant over the Pliocene up to 2.9 m.y., from which time onward a series of massive mean cooling trends set in (e.g., Shackleton 1995) including in the African tropics (deMenocal and Bloemendal 1995; Dupont and Leroy 1995).

Alcelaphines in general probably have the potential to be geographically wide-spread as evidenced by the large modern distributions of species such as *A. buselaphus* and *C. taurinus*, and the Middle Pleistocene distribution of *Rabaticeras arambourgi* which is almost literally 'from Cape to Cairo'. One can infer that many alcelaphine species had and still have a predisposition to migrate rapidly once geographic changes of their habitats permit it. This is suggested by observations that species belonging to each of the living genera can undergo seasonal migrations. There are indications of past biogeographic events in the alcelaphine pattern: Between 2.9 m.y. and 2.6 m.y. a descendant of (*Damalops*) "*denendorai*" emigrated to Eurasia where it is first seen in Tadzhikstan as *D. palaeindicus* (Dmitrieva 1977) associated with the Gauss-Matuyama palaeomagnetic anomaly (Lindsay *et al.* 1980) now dated to 2.6 m.y. (Shackleton *et al.* 1990) and also in the Pinjor Formation of the Siwaliks (Pilgrim, 1939). Two hippotragine lineages, an *Oryx* and a *Hippotragus*, also emigrated from Africa to Eurasia ca. 2.7 m.y. (Vrba and Gatesy 1994), as did two species of Reduncini (Vrba 1995b). One antilopine, three ovibovine, and three caprine species appear in Africa 2.7-2.4 m.y. ago as migrants from Eurasia (Vrba 1995b), most and perhaps all as migrants from Eurasia and part of the same intercontinental dispersal event. Within the same interval, ancestral (*Damalops*) populations may have migrated into northern Africa as evidenced by the appearance of the descendant *Oreonagor* in Algeria. Also during this interval, *Beatragus* first appeared in the form of the giant Middle Awash *B. whitei*. The direct ancestry of this lineage remains mysterious as there seems to be nothing very similar in the previous fossil record. I suggest tentatively that the ancestors of *B. whitei* are not seen in northern and eastern African sequences because they evolved until the Late Pliocene in southern Africa. There is a large gap in the southern African fossil record between the Early Pliocene Langebaanweg and the Late Pliocene cave assemblages such as Makapansgat and Sterkfontein. Perhaps the earlier forms related to *Beatragus* remained confined to southern African cooler habitats at higher southern latitudes until global cooling after 3 m.y. spread these habitats across the equator along the eastern highlands of Africa. Support for this comes from the fact that the sister-taxon of *Beatragus*, *Damalacra neanica*, is known from the Cape of Africa, and *Beatragus* is known in southern Africa perhaps from the latest Pliocene Swartkrans Member 1, and certainly from the Pleistocene of Swartkrans Member 2 and Elandsfontein.

The Bouri assemblage is the earliest in the Awash with a high alcelaphine diversity, and it also attests to dispersal events. The new caprine (*B. anngettyae*) and ovibovine (*N. asfawi*) species are probably derived from Eurasian immigrants. They suggest that the previously vicariated steppe habitats at high latitudes in Eurasia and at high altitudes in East Africa became continuous during Bouri times due to climatic cooling and eustatic enlargement of the Eurasian-African landbridge. Two other caprine species appear in the Nariokotome Member (Nachukui Formation, Kenya, Harris *et al.* 1988) probably ca. 1 m.y. and probably also immigrants from Eurasia (Vrba 1995b). The Bouri assemblage, in relation to its total number of bovid fossils not only shows remarkably high diversity among species, but also high morphological diversity within the best represented species, *Megalotragus kattwinkeli*. This could be the result of hybridization between previously separated conspecific subspecies, after they were newly brought into contact by climatically-induced merging of their habitat patches. The increase of variability in hybrid zones is well known in general, and also in Alcelaphini since Ruxton and Schwarz (1929) noted that hybrid hartebeests from the East African Rift Valley were more variable than either of the parent populations, *Alcelaphus buselaphus ?cokei* and *A. b. jacksoni*. Bouri in several ways typifies the special features of the Middle Awash fossil assemblages: they include well-preserved fossils, time levels that are poorly known elsewhere in Africa, and have good chronological control, as well as a geographic situation in an area of high topographic diversity and at the cross-roads between zoogeographic areas. These special features of the Middle Awash fossil record have substantially extended our knowledge of the temporal and geographic ranges of several alcelaphine species, and also of the number of alcelaphine species known, and will probably result in similar extensions in our knowledge of other mammals.

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REFERENCES

ANSELL, W.F.H. 1971. Artiodactyla. **In:** Meester, J. & Setzer, H.W., Eds, *The Mammals of Africa: An Identification Manual*. 1-93. Washington, D.C. Smithsonian Institution Press.

ARAMBOURG, C. 1949. *Numidocapra crassicornis*, nov. gen., nov. sp., un Ovicaprine nouveau du Villafranchien constantinois. *C. r. somm. Séanc. Soc. géol. Fr*, Paris, **13**, 290-291.

-------- 1979. *Vertèbres Villafranchiens d'Afrique du Nord*. Paris, Singer-Polignac.

BOHLIN, B. 1937. Eine Tertiäre Saugetier-fauna aus Tsaidam. *Palaeontologia Sinica* S. C., **14 (1)**, 5-111.

BONIS, L. DE, GERAADS, D., JAEGER, J.-J. & SEN, S. 1988. Vertèbres du Pleistocène de Djibouti. *Bull. Soc. géol. France* (8), **4**, 323-334.

BOUVRAIN, G. & DE BONIS, L. 1984. Le genre *Mesembriacerus* (Bovidae, Artiodactyla, Mammalia) L'un ovibovine primitif du Vallesian (Miocène supérieur) de Macédonie (Grèce). *Palaeovertebrata* Montpellier **14**, 201-223.

BRINK, J.S. 1987. The archaeozoology of Florisbad, Orange Free State. *Memoirs van die Nasionale Museum*, **24**, 1-151.

-------- 1988. The taphonomy and palaeoecology of the Florisbad spring fauna. *Palaeoecology of Africa*, **19**, 169-179.

BROWN, F.H., SARNA-WOJCICKI, A.M., MEYER, C.E., & HAILEAB, B. 1992. Correlation of Pliocene and Pleistocene tephra layers between the Turkana Basin of East Africa and the Gulf of Aden. *Quat. International*, **13/14**, 55-67.

CLARK, J.D., DE HEINZELIN, J., SCHICK, K.D., HART, W.K., WHITE, T.D., WOLDEGABRIEL, G., WALTER, R.C., SUWA, G., ASFAW, B., VRBA, E.S., & HAILE-SELASSIE, Y. 1994. African *Homo erectus*: Old radiometric ages and young Oldowan assemblages in the Middle Awash Valley, Ethiopia. *Nature*, **264**, 1907-1910.

CREGUT-BONNOURE, E. 1992a. Dynamics of bovid migration in western Europe during the Middle and Late Pleistocene. *Courier Forsch.-Inst. Senckenberg* Frankfurt a. M., **153**, 177-185.

-------- 1992b. Les Caprinae (Mammalia, Bovidae) du Pleistocène d'Europe: intérêt biostratigraphique, paléoecologique et archéozoölogique. *Mem. Soc. géol. Fr*. **160**, 85-93.

DEMENOCAL, P., & BLOEMENDAL, J. 1995. Plio-Pleistocene subtropical African climate variability and the paleoenvironment of hominid evolution: a combined data-model approach. **In**: Vrba, E.S., Denton, G.H., Partridge, T.C., & Burckle, L. Eds., *Paleoclimate and Evolution, with Emphasis on Human Origins*, 262-288. New Haven, Connecticut, Yale University Press.

DE QUEIROZ, K., & GAUTHIER, J. 1994. Towards a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution*, **9**, 27-31.

DIETRICH, W.O. 1950. Fossile Antilopen und Rinder Äquatorialafrikas. *Palaeontographica*, **99A**, 1-62.

DMITRIEVA, E.L. 1977. Tajikistan's and India's fossil Alcelaphinae. *J. Palaeont. Soc. India*, **20**, 97-101.

DORST, J. & DANDELOT, P. 1970. *A Field Guide to the larger Mammals of Africa*. London, Collins.

DUPONT, L.M & LEROY, S.A. 1995. Steps towards drier climatic conditions in North-Western Africa during the Upper Pliocene. **In:** Vrba, E.S., Denton, G.H., Partridge, T.C., & Burckle, L. Eds. *Paleoclimate and Evolution, with Emphasis on Human Origins*, 289-298. New Haven, Connecticut, Yale University Press.

FARRIS, J.S. 1988. Hennig 86, Version 1.5. Port Jefferson Station, New York. Distributed by author.

FEIBEL, C.S., BROWN, F.H., & MCDOUGALL, I. 1989. Stratigraphic context of fossil hominids from the Omo Group Deposits: Northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthrop*., **78**, 595-622.

GATESY, J. 1993. *Cows, Sheep, Antelopes, and Molecules*. Unpublished Ph.D. thesis, Yale University, New Haven.

--------, YELON, D., DESALLE, R., & VRBA, E.S. 1992. Phylogeny of the Bovidae (Artiodactyla, Mammalia), based on mitochondrial ribosomal DNA sequences. *Mol. Biol. Evol*., **9**, 433-466.

--------, AMATO, G., VRBA, E.S., SCHALLER, G. & DESALLE, R. in press. A cladistic analysis of mitochondrial ribosomal DNA from the Bovidae. *J. Molec. Evol*.

GEIST, V. 1971. *Mountain Sheep: a Study in Behavior and Evolution*. Chicago. Univ. of Chicago Press.

GENTRY, A.W. 1970a. Revised classification for *Makapania broomi* Wells and Cooke (Bovidae, Mammalia). *Palaeont. afr*., **13**, 63-67.

-------- 1970b. The Bovidae of the Fort Ternan fossil fauna. **In:** Savage, L.S.B., & Savage, R.J.G, Eds., *Fossil Vertebrates of Africa*, 243-323. London, Clarendon.

-------- 1971. The earliest goats and other antelopes from the Samos *Hipparion* fauna. *Bull. Br. Mus. Nat. Hist*. (Geol.). London, **20**. 231-296.

-------- 1978. Bovidae. **In:** Maglio, V.J., & Cooke, H.B.S., Eds. *Evolution of African Mammals*, 540-572. Cambridge, Massachusetts. Harvard University Press.

-------- 1980. Fossil Bovidae from Langebaaweg, South Africa. *Ann. S. Afr. Mus.*, Cape Town, **79,** 213-337.

-------- 1981. Notes on Bovidae from the Hadar Formation, Ethiopia. *Kirtlandia*, **33,** 1-30.

-------- 1985. The Bovidae of the Omo Group deposits, Ethiopia. **In:** *Les Faunes Plio-Pleistocenes de la Basse Valle de l'Omo (Ethiopie), Perissodactyles, Artiodactyles* (Bovidae), **1.** Paris. CNRS. 119-191.

-------- 1987. Pliocene Bovidae from Laetoli. **In:** Leakey, M.D. & Harris, J.M., Eds., *The Pliocene site of Laetoli, northern Tanzania.* Oxford. Clarendon Press.

-------- 1990a. Evolution and Dispersal of African Bovidae. **In:** Bubenik, G.A., & Bubenik, A.B., Eds., *Horns, Pronghorns, and Antlers. Evolution, Morphology, Physiology, and Social Significance*, 195-233. New York, Springer-Verlag.

-------- 1990b. The Semliki fossil bovids. *Virginia Mus. Nat. Hist. Memoir*, **1,** 225-234.

-------- 1992. The subfamilies and tribes of the family Bovidae. *Mammal Rev.*, **22,** 1-32.

-------- 1996. A fossil *Budorcas* (Mammalia, Bovidae) from Africa. **In:** Stewart, K.M. & Seymour, K.L., Eds., *Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals*, 571-587. Toronto, Canada. University of Toronto Press.

--------, & GENTRY, A. 1978. Fossil Bovidae of Olduvai Gorge, Tanzania. *Bull. Br. Mus. Nat. Hist.* (Geol.). London. Part I., **29,** 289-445. Part II. **30.** 1-83.

--------, -------- & MAYR, H. 1995. Rediscovery of fossil antelope holotypes (Mammalia, Bovidae) collected from Olduvai Gorge, Tanzania, in 1913. *Mitt. Bayer. Staatsslg. Palaeont. hist. Geol.*, **35,** 125-135.

GERAADS, D. 1979. La faune des gisements de Melka Kunture (Ethiopie): Artiodactyles, Primates. *Abbay*, Paris. **10,** 21-49.

-------- 1981. Bovidae et Giraffidae (Artiodactyla, Mammalia) du Pleistocène de Ernifine (Algérie). *Bull. Mus. natn. Hist. Nat.*, Paris **3.** 47-86.

GRAY, A.P. 1972. *Mammalian Hybrids*. Edinburgh. Commonwealth Agricultural Bureau.

GROVES, P. 1995. The takin and the muskox: a molecular and ecological evaluation of relationship. Unpublished Ph.D. thesis, University of Alaska, Fairbanks, Alaska, U. S. A.

HAILEAB, B. & BROWN, F.H. 1992. Turkana Basin-Middle Awash Valley correlations and the age of the Sagantole and Hadar Formations. *J. Hum. Evol.*, **22,** 453-368.

HARRIS, J.M. 1991. Family Bovidae. **In:** Harris, J.M., Ed., *Koobi Fora Research Project. The Fossil Ungulates: Geology, Fossil Artiodactyls, And Palaeoenvironments*, **3,** 139-320. Oxford. Clarendon Press.

--------, BROWN, F.H., & LEAKEY, M.G. 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Contributions in Science*. Natural History Museum of Los Angeles County, **399,** 1-128.

HEINTZ, E. & THOMAS, H. 1981. Un nouveau Bovide, *Kabulicornis ahmadi* gen. nov., sp. nov., dans le gisement Pliocene de Pul-e Charkhi, bassin de Kabul, Afghanistan. *Bull. Mus. natn. Hist. nat., Paris*, Series 3, Section C, **1,** 31-44.

HONACKI, J.H., KINMAN, K.E., & KOEPPL, J.W. Eds., 1982. *Mammal Species of the world: a Taxonomic and Geographic Reference*. Lawrence, Kansas: Allen Press.

KIMBEL, W.H. 1995. Hominid speciation and Pliocene climatic change. **In:** Vrba, E.S., Denton, G.H., Partridge, T.C., & Burckle, L. Eds. *Paleoclimate and Evolution, with Emphasis on Human Origins*. 425-437. New Haven, Connecticut, Yale University Press.

KLEIN, R.G. & CRUZ-URIBE, K. 1991. The bovids from Elandsfontein, South Africa, and their implications for age, palaeoenvironment, and origins of the site. *Afr. Archaeol. Rev.*, **9,** 21-79.

LAUBSCHER, N.F., STEFFENS, F.E., & VRBA, E.S., 1972. Statistical evaluation of the taxonomic status of a fossil member of the Bovidae (Mammalia: Artiodactyla). *Ann. Transv. Mus.*, **28,** 17-26.

LEAKEY, M.G., FEIBEL, C.S., MCDOUGALL, I., & WALKER, A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*. **376,** 565-571.

LINDSAY, E.H., OPDYKE, N.D., & JOHNSON, N.M. 1980. Pliocene dispersal of the horse *Equus* and Late Cenozoic mammalian dispersal events. *Nature*, **287,** 135-138.

LYDEKKER, R. 1898. *Wild Oxen, Sheep and Goats of all Lands*. London. Rowland Ward.

LIPSCOMB, D. 1992. Parsimony, homology, and analysis of multistate characters. *Cladistics*, **8,** 45-65.

MOYA-SOLA, S. 1987. Los bovidos (Artiodactyla, Mammalia) del yacimiento del Pleistoceno inferior de Venta Micena (Orce, Granada, Espana). *Paleont. Evoluc.* Sabadell Mem. Esp., **1,** 181-236.

PILGRIM, G.E. 1939. The fossil Bovidae of India. *Mem. geol. Surv. India Palaeont. ind.* (n.s.), **26,** 1-356.

PICKFORD, M. & THOMAS, H. 1984. An aberrant new bovid (Mammalia) in subrecent deposits from Rusinga Island, Kenya. *Proc. Koninjl. Ned. Akad. Wettensch.*, **B87** (4), 441-52.

RECK, H. 1925. Aus der Vorzeit des innerafrikanischen Wildes. *Illustrierte Zeitung*, Leipzig, **164,** 451.

-------- 1935. Neue Genera aus der Oldoway-Fauna. *Zentbl. Miner. Geol. Palaont.*, **B (6).** 215-218.

RUXTON, A.E. & SCHWARZ, E. 1929. On hybrid hartebeests and on the distribution of the *Alcelaphus buselaphus* group, *Proc. Zool. Soc.*, London, **2,** 567-583.

SHACKLETON, N.J. 1995. New data on the evolution of Pliocene climatic variability. **In:** Vrba, E.S., Denton, G.H., Partridge, T.C., & Burckle, L. Eds., *Paleoclimate and Evolution, with Emphasis on Human Origins*, 242-248. New Haven, Connecticut. Yale University Press.

---------, BERGER, A. & PELTIER, A. 1990. An alternative astronomical calibration of the Lower Pleistocene timescale based on ODP Site 677. *Trans. Roy. Soc. Edin. Earth Sci.*, **81,** 251-261.

SCHAUB, S. 1923. Neue und wenig bekannte Cavicornier von Seneze. *Eclog. geol. Helv.*, Basle, **18**, 281-295.

SCHWARZ, E. 1932. Neue diluviale Antilopen aus Ostafrika. *Zentbl. Miner. Geol. Palaont.*n **B (1),** 1-4.

SINCLAIR, A.R.E. 1977. *The African Buffalo.* Chicago, University of Chicago Press.

SISSON, S., & GROSSMAN, J.D. 1975. The anatomy of the domestic animals. **1.** London, W.B. Saunders.

SPINAGE, C.A. 1986. *The Natural History of Antelopes*. New York. Facts on File Publications.

TEILHARD DE CHARDIN, P. & TRASSAERT, 1938. Cavicornia of south-eastern Shansi. *Palaeontologia Sinica* Pekin NS C, **6,** 1-98.

THOMAS, H. 1984. Les origines africaines des Bovidae miocènes des lignites de Grosseto (Toscane, Italie). *Bull. Mus. Nat. Hist.*, Paris, **4,** (6C) 81-101.

THOMAS, P. 1884. Recherches stratigraphiques et paléontologiques sur quelques formations d'eau douce de l'Algérie, *Mem. Soc. géol. Fr.*, Paris. **3,** 2. 1-51.

VAN VALEN, L. 1973. A new evolutionary law. *Evolutionary Theory*, **1.** 1-30.

VRBA, E.S., 1971. A new fossil alcelaphine (Artiodactyla: Bovidae) from Swartkrans. *Ann. Transv. Mus.*, **27**, 59-89.

-------- 1976. *The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. Transv. Mus. Mem.*, Pretoria, **21**, 1-166.

-------- 1977. New species of *Parmularius* Hopwood and *Damaliscus* Sclater and Thomas (Alcelaphini, Bovidae, Mammalia) from Makapansgat, and comments on faunal chronological correlation. *Palaeont. afr.*, **20**, 137-151.

-------- 1979. Phylogenetic analysis and classification of fossil and recent Alcelaphini. *Biol. J. Linn. Soc.*, London, **11**, 207-228.

-------- 1984. Evolutionary pattern and process in the sister-group Alcelaphini-Aepycerotini (Mammalia: Bovidae). **In:** Eldredge, N., & Stanley, S.M., Eds., *Living Fossils*, 62-79. New York, Springer-Verlag.

-------- 1987. A revision of the Bovini (Bovidae) and a preliminary revised checklist of Bovidae from Makapansgat. *Palaeont. afr.*, **26**, 33-46.

-------- 1994. An hypothesis of early hominid heterochrony in response to climatic cooling. **In:** Ciochon, R., & Corruccini, R., Eds., *Integrative Pathways to the Past: Paleoanthropological Advances in Honor of Clark Howell*, 345-376. New York, Prentice Hall.

-------- 1995a. On the connections between paleoclimate and evolution. **In:** Vrba, E.S., Denton, G.H., Partridge, T.C., & Burckle, L. Eds., *Paleoclimate and Evolution, with Emphasis on Human Origins*, 24-45. New Haven, Connecticut, Yale University Press.

-------- 1995b. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. **In:** Vrba, E.S., Denton, G.H., Partridge, T.C., & Burckle, L. Eds., *Paleoclimate and Evolution, with Emphasis on Human Origins*, 385-424. New Haven, Connecticut, Yale University Press.

-------- In press. Habitat theory in relation to the evolution in African Neogene biota and hominids. **In:** Bromage, T.G., & Schrenk, F., Eds., *African Biogeography, Climate Change, and Early Hominid Evolution*. New York, Plenum Press.

-------- & GATESY, J.E. 1994. New fossils of hippotragine antelopes from the Middle Awash deposits, Ethiopia, in the context of a phylogenetic analysis of Hippotragini (Bovidae, Mammalia). *Palaeont. afr.*, **31**, 1-18.

-------- VAISNYS, J.R., GATESY, J.E., DESALLE, R., & WEI, K.Y. 1994. Analysis of paedomorphosis using allometric characters: the example of Reduncini antelopes (Bovidae, Mammalia). *Syst. Biol.*, **43**, 92-116.

WELLS, L.H. & COOKE, H.B.S. 1956. Fossil Bovidae from the Limeworks Quarry, Makapansgat, Potgietersrus. *Palaeont. afr.*, **4**, 1-55.

WHITE, T.W., SUWA, G., HART, W.K., WALTER, R.C., WOLDEGABRIEL, G., DE HEINZELIN, J., CLARK, J.D., ASFAW, B., & VRBA, E.S. 1993. New Pliocene hominids from Maka, Ethiopia. *Nature*, **366**, 261-265.

WHITE, T.D., SUWA, G., & ASFAW, B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, **371**, 306-312.

WOLDEGABRIEL, G., WHITE, T.D., SUWA, G., RENNE, P., DE HEINZELIN, J., HART, W.K. & HEIKEN, G. 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature*, **371**, 330-333.