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NEW ANTELOPE FOSSILS FROM AWASH, ETHIOPIA, AND PHYLOGENETIC ANALYSIS OF HIPPOTRAGINI (BOVIDAE, MAMMALIA)

by

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ABSTRACT

New hippotragine antelope fossils from the Middle Awash, Ethiopia, include a new species *Praedamalis howelli* from Maka, an early species of *Oryx* from Matabaietu, and *Hippotragus gigas* from Gamedah. Our comparisons of these fossils with all other known fossil and Recent Hippotragini includes a cladistic analysis. The results suggest that the two major lineages in the monophyletic Hippotragini are *Hippotragus* including taxa from the Siwaliks previously ascribed to *Sivatragus*, and a *Praedamalis – Oryx* sister-group. Some evolutionary and biogeographic implications of the new fossils from the Middle Awash deposits are discussed.

KEY WORDS: Hippotragini, Awash, *Praedamalis*

INTRODUCTION

The new fossils form part of a large assemblage of Plio-Pleistocene fossil vertebrates, including representatives of Hominidae, that has recently been recovered from sedimentary deposits in eastern Ethiopia's Middle Awash Valley (White *et al.*, 1994). The Awash faunas are of particular interest because their evolution was affected by pervasive tectonism and by the repeated opening and closing of land and habitat bridges between Africa and Eurasia.

This paper focuses on description of a new species, and on the placement of this new species in a cladistic analysis of skull characters of all hippotragines. Additional descriptions of other hippotragine taxa from the Middle Awash await the results of ongoing field work and laboratory analyses. Our more complete cladistic analysis of Hippotragini (Gatesy *et al.*, in preparation) will incorporate mitochondrial DNA sequence data together with skull characters.

Hippotragini contains three living genera: *Hippotragus* Sundevall, 1846; *Oryx* Blainville, 1816; and *Addax* Rafinesque, 1815. There is one recently extinct species, *Hippotragus leucophaeus* (Pallas, 1766) the small South African bluebuck exterminated about 1799. The living species are: *Hippotragus equinus* (Desmarest, 1804) the roan antelope; *Hippotragus niger* (Harris, 1838) the sable antelope; *Oryx gazella* (Linnaeus, 1758) the gemsbuck and beisa; *Oryx leucoryx* (Pallas, 1777) the Arabian oryx; *Oryx dammah* (Cretzschmar, 1826) the scimitar-horned oryx; and *Addax nasomaculatus* (Blainville, 1816) the addax of the Sahara. The extinct taxa in our analysis are introduced in Table 1, which also contains first and last appearance data for all hippotragines.

In a previous survey of Makapansgat Limeworks Hippotragini (Vrba, 1987) it was suggested that *Wellsiana torticornuta* Vrba 1987 and *Brabovus nanincisivus* Gentry 1987 might be hippotragine. Based on these tentative suggestions we included these taxa in the cladistic analysis. In fact, as discussed later in this paper, our cladistic results turned out not to support the hypotheses that these taxa are members of Hippotragini.

MATERIALS AND METHODS

Samples of most of the living hippotragine species were measured (Gatesy, 1993), and the entire fossil record of Hippotragini (Table 1) was surveyed using photographs and measurements for comparison with the new Awash material. Table 2 introduces fossil sites to which we refer. The Awash fossils are shown in Figures 1-4. Their measurements are given in Tables 3 and 4, and shown in relation to those of other hippotragines in Figures 5-9. The skull characters in Table 5 were compared across all hippotragine taxa. Codes for these characters were assessed (Table 6) based on the available measurements in the case of some characters, and based on qualitative comparison in other cases, and then analyzed cladistically. The ie option of the HENNIG86 program (Farris, 1988) which finds all trees of minimal length was used. Cladistic results from mitochondrial DNA sequences of a large bovid sample (Gatesy *et al.*, 1992) suggest that living hippotragines are monophyletic and that Caprini and

TABLE 1.

Living and extinct Hippotragine and Related Taxa.

First and last appearance data (FAD and LAD, given as first and last entries per taxon) and the taxon codes used in figures and Table 3 are given. Selected other fossil sites are cited in some cases. Dates follow Vrba's (in press) review. Literature citations numbered in brackets are: (1) Gentry (1987), (2) Vrba (1987), (3) Vrba (1974, 1976), (4) Klein and Cruz-Uribe (1991), (5) Gentry (1985), (6) Gentry and Gentry (1978), (7) Pilgrim (1939), (8) Lehmann and Thomas (1987), (9) Geraads (1987), Arambourg (1979), (10) Harris (1991), (11) Geraads (1981), (12) Gentry (1981); (13) Smart (1974), personal observation of undescribed fossils including specimen LT188. Millions of years = m.y.; L = Locality; M = Member. LPlio = Late Pliocene. Note on *Hippotragus gigas*: the FAD of this species could be near 2.7 m.y. from Chiwondo, Malawi (Coryndon, 1966; Kaufulu et al., 1981). Concerning its LAD, the tentative Late Pleistocene record for Florisbad by Gentry and Gentry (1978) is not followed here because later studies cast doubt on it (Brink, 1986, 1987). Note on *H. cookei*: the tentative assignment of dentitions from Sterkfontein M4 to this taxon is not reflected here. Note on the date '5.5 m.y. or Late Pliocene' for *H. sp. nov.* from Sahabi: This refers to Geraads's (1989) argument that some of the Sahabi fossils may be datable to the Late Pliocene, which we suspect may be true of this species, and not to the Late Miocene.

Taxon	Site of FAD Site of LAD	FAD date LAD date m.y.	Extinct = † Common name	Taxon code
Taxa possibly related to Hippotragini :				
Brabovus				
nanincisivus	Laetoli (1)	3.6	†	bra
	Laetoli (1)	3.6		
Wellsiana				
torticornuta	Makapansgat M3 (2)	2.7	†	w
	Makapansgat M3 (2)	2.7		
Hippotragini :				
Addax				
nasomaculatus	no fossil record		addax	a
Hippotragus				
equinus	Sterkfontein M4 (3)	2.5	roan antelope	e
niger	Swartkrans M3 (3)	0.7	sable antelope	n
leucophaeus	Elandsfontein (4)	0.6	†, bluebuck	l
	Cape Province	1799 AD		
gigas: all	Shungura C8 (5)	2.6	†	g1
except from	Gamedah L1, Awash	2.5		
Elandsfontein	Olduvai Bed III JK2 (6)	1.0		
gigas: from	Elandsfontein (4)	0.6	†	g2
Elandsfontein				
cookei	Makapansgat M3 (2)	2.8 - 2.6	†	c
	Makapansgat M3 (2)	2.8 - 2.6		
bohlini	Siwaliks, Pinjor (7, 6)	2.6 - 1.6	†	bo
(*Sivatragus*)	Siwaliks, Pinjor (7, 6)	2.6 - 1.6		
brevicornis	Siwaliks, Tatrot (7, 6)	3.1 - 2.6	†	bre
(*Sivatragus*)	Siwaliks, Tatrot (7, 6)	3.1 - 2.6		
sp. nov.	Sahabi (8)	5.5 or LPlio	†	s
	Sahabi (8)	5.5 or LPlio		
Oryx				
gazella	Ain Hanech (9)	1.8 - 1.7	beisa, gemsbuck	og
sp. nov. 1	Shungura C9 (5)	2.6	†	o1
	Matabaietu L4, Awash	2.5		
sp. nov. 2	Olduvai Bed I (6)	1.8	†	o2
	Koobi Fora, KBS (10)	1.7		
sp. from Ternifine	Ternifine (11)	0.7		o3
O. gazella?				
sivalensis	Siwaliks, Pinjor (7, 6)	2.6 - 1.6	†	os
(*Sivoryx*)	Siwaliks, Pinjor (7, 6)	2.6 - 1.6		
Praedamalis				
deturi	Laetoli (1)	3.6	†	d
	Hadar, Denen Dora (12)	3.2		
	Upper Ndolanya (1)	2.6		
howelli sp. nov.	Awash, Maka L1	3.5	†	ho
	Awash, Maka L1	3.5		
Gen. indet.				
sp. nov.	Lothagam I (13)	6.5	†	lo
	Lothagam I (13)	6.5		

TABLE 2

Fossil Sites. The table gives only those fossil sites and their stratigraphic subunits that are referred to in this paper. The stratigraphic subunits are arranged from latest at the top to earliest at the bottom. Table 2 cites sources for the antelope occurrences at these sites, and Vrba (in press) reviews their chronology.

Site	Country	Time period
Ain Hanech	Algeria	Early Pleistocene
Awash, Middle	Ethiopia	Plio-Pleistocene
Gamedah Locality 1		Late Pliocene
Matabaietu Locality 5		Late Pliocene
Maka Locality 1		Middle Pliocene
Chiwondo	Malawi	Plio-Pleistocene
Mwenirondo		Late Pliocene
Elandsfontein	South Africa	Middle Pleistocene
Florisbad	South Africa	Late Pleistocene
Hadar Formation	Ethiopia	Middle Pliocene
Denen Dora Member		
Kanjera	Kenya	Early Pleistocene
Koobi Fora Formation	Kenya	Plio-Pleistocene
KBS Member		
Upper Burgi Member		
Laetoli Beds	Tanzania	Early Middle Pliocene
Lothagam Unit 1	Kenya	Late Miocene
Makapansgat Limeworks	South Africa	Late Pliocene
Member 3		
Nachukui Formation	Kenya	Plio-Pleistocene
Upper Lomekwi Member		
Nelson Bay Cave	South Africa	Late Pleistocene
Olduvai Gorge	Tanzania	Pleistocene
Beds I-IV		
Sahabi	Lybia	Late Miocene
Shungura Formation	Ethiopia	Plio-Pleistocene
Members B to J		
Siwaliks formations	India and Pakistan	Mio-Pleistocene
Pinjor		Late Pliocene to Early Pleistocene
Tatrot	Early-Middle Pliocene	
Swartklip	South Africa	Late Pleistocene
Swartkrans Formation	South Africa	Lower Pleistocene
Members 1 to 3		
Sterkfontein Formation	South Africa	Late Pliocene
Member 4		
Ternifine	Algeria	Middle Pleistocene
Upper Ndolanya Beds	Tanzania	Late Pliocene

Alcelaphini are sequential outgroups of Hippotragini. We used these results together with the cladistic results for skull characters in Vrba (1979) and Gatesy (1993), to hypothesize the general states for the characters in Table 5 and used these as the states in the hypothetical outgroup of the present taxa. The outgroup rooting option of HENNIG86 was then employed. The NELSEN option of HENNIG86 was used to construct a consensus tree. The multistate characters were ordered on the basis of ontogenetic progression and similarity between adjacent states (see Lipscomb, 1992). The nature of these particular characters suggests that ordering is appropriate. Both the genetic and the empirical bases of allometric evolution (e.g., Atchley *et al.*, 1984) suggest change through adjacent states rather than leaps between extreme states at one splitting event.

SYSTEMATIC RESULTS

The cladistic results are represented by the consensus tree in Figure 10. In terms of these results, we suggest that Hippotragini is the monophyletic group from node 1 in Figure 10. That is, Hippotragini includes all living and extinct taxa previously assigned to hippotragines together with a new Lothagam species, and excludes *Brabovus nanincisivus* and *Wellsiana torticornuta* (*contra* Vrba, 1987). Living and fossil species previously assigned to *Oryx*, and including *Addax*, form a monophyletic group which is the sister-taxon of *Praedamalis*. In terms of these results *Addax* should be synonymized with *Oryx*. The Siwaliks taxa that Pilgrim (1939) called *Sivatragus bohlini* and *S. brevicornis* form parts of a monophyletic group with all living and fossil taxa previously

Figure 1. A. Holotype right horncore and frontlet MAK-VP-1/24 of *Praedamalis howelli*, B. right horncore and frontlet MAK-VP-1/113, both in anterior view.

assigned to *Hippotragus*, although the species *brevicornis* could be assigned to a new genus as the sister-taxon of *Hippotragus*. In the diagnoses and descriptions that follow we will refer both to the characters in this cladistic result, by citing Figure 10, as well as to additional characters.

Tribe Hippotragini

Hippotragini are characterized by horncores that are long and of large basal area relative to skull size, by moderately to well-developed basal sinuses in their horn pedicels and extending into the basal horncore, and by bulbous, lingually-extending metaconids on their P_4's (synapomorphies in Figure 10). Their horacores are unkeeled, little divergent, and generally without transverse ridges, and their postcornual fossae are shallow or absent. In terms of the present cladogram, Hippotragini have plesiomorphously retained long braincases which became secondarily reduced in parallel in oryxes and in the clade that includes *Hippotragus bohlini* and *H. gigas*. Hippotragine teeth are large relative to jaw size and have basal pillars on upper and lower molars and goat folds anteriorly on lower molars. Extant hippotragines are large antelopes that mostly graze, and both sexes have horns. Their mastoids appear to face mainly backwards on the occipital surface from early on in ontogeny. Gentry and Gentry (1978) suggested that additional hippotragine characters are a midfrontal suture that is moderately complicated, a straight and moderately complicated parietofrontal suture, temporal lines not approaching very closely, infraorbital foramen high over the P^2-P^3 junction, premaxillae with a short contact along the sides of the nasals, nasals without lateral flanges anteriorly, median indentation at the back of the palate more or less level with the lateral ones, and mastoid exposures that are moderate to large.

Figure 2. A. Holotype right horncore and frontlet MAK-VP-1/24 of *Praedamalis howelli*. B. Juvenile right horncore and frontlet MAK-VP-1/113, both in medial view.

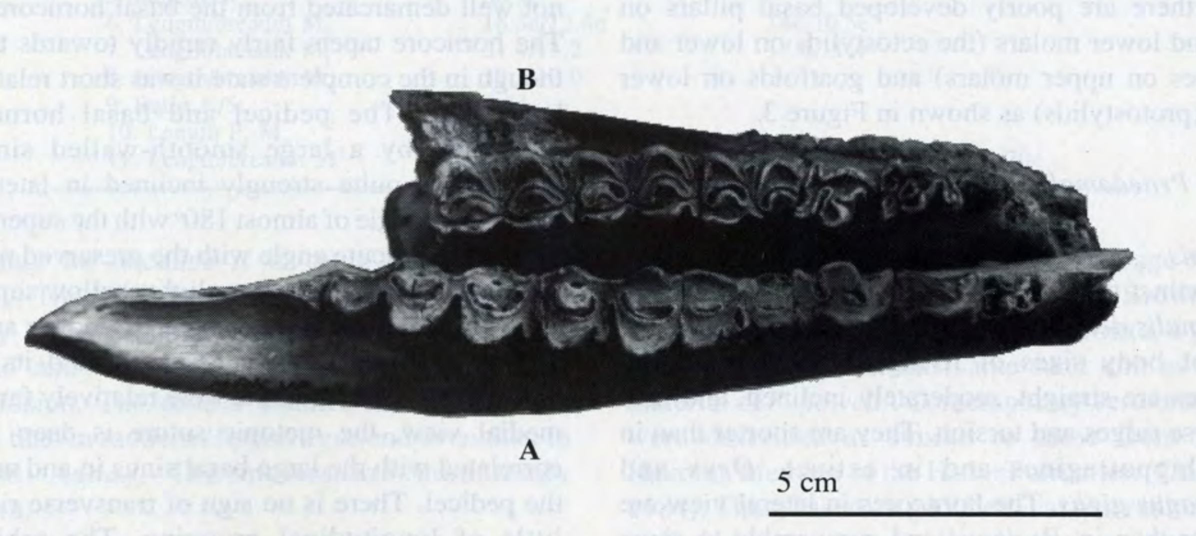

Figure 3 A Paratype right mandible MAK-VP-1/63 of *Praedamalis howelli* from Maka Locality 1, Middle Pliocene. B. Left mandible KL64-2, possibly referable to late Pliocene Matabaietu Locality 5 (T. White, pers. comm.), which may belong to a small hippotragine species but could be reduncine.

Genus *Praedamalis* Dietrich 1950:30.
Type species *Praedamalis deturi* Dietrich 1950.

Generic diagnosis

Gentry (1987) gave a diagnosis for this genus based directly on the only included species *P. deturi* known at that time from Hadar, the Laetoli Beds and the Upper Ndolanya Beds. We augment this diagnosis in the light of the new Awash species. Gentry (1987, p. 387) considered *Praedamalis* to have "long horncores with some mediolateral compression, no flattening of the lateral or medial surface, no keels or transverse ridges, and hardly any backward curvature. The insertions are rather upright above the back of the orbits, not very wide apart and little divergent. The greatest transverse width of the horncores lies near or slightly behind the anteroposterior mid-point. The base of the horncore proper is not well demarcated from the top of the pedicel, the frontals between the horn cores are at about the same level as the dorsal parts of the orbital rims, there is a shallow postcornual fossa, the pedicel and part of the frontals are hollowed internally, there is a tiny rudiment or vestige of a temporal ridge behind the horncores, and a concavity in the surface of the frontals posteromedially to the pedicel". Gentry (1987) also noted that the upright insertion and cross-sectional shape of the horncore resembles *Hippotragus* and the straight course *Oryx*. We add that *Praedamalis* has exceptionally large sinuses in the frontals and pedicel at the base of the horncore and partly extending into the horncore, in comparison with *Oryx* and for hippotragines in general (synapomorphy in Figure 10). It had small skull size relative to other hippotragines, horncores with an angulation of the maximum basal diameter relative to the metopic suture that was intermediate between living oryxes and all described *Hippotragus* species (Figure 8), and widely separated supraorbital foramina as in modern oryxes and addaxes (Figure 6). The genus exhibits a smaller premolar to molar length ratio than in living *Hippotragus* species (Figure 9). The teeth are primitive in being buccolingually narrow relative to antero-posterior length, in their lack of constricted molar lobes and complex central enamel cavities, and in that there are poorly developed basal pillars on upper and lower molars (the ectostylids on lower and entostyles on upper molars) and goatfolds on lower molars (protostylids) as shown in Figure 3.

Species *Praedamalis howelli* sp. nov.

Diagnosis

An extinct species that was averagely smaller than *Praedamalis deturi*, and also at the low extreme of the range of body sizes of living hippotragines. The horncores are straight, moderately inclined, and lack transverse ridges and torsion. They are shorter than in living hippotragines and in extinct *Oryx* and *Hippotragus gigas*. The horncores in lateral view are straighter than in *P. deturi* and comparable to some specimens of *Oryx*. The sinuses in the pedicel are exceptionally large, partly extending into the horncore, and surrounded by relatively thin frontal bone in comparison with *Oryx* and hippotragines in general. In this respect the new species is even more extreme than *P. deturi* although the resemblance to *P. deturi* is closer than to other Hippotragini. The horncores were more compressed than in modern and extinct members of *Oryx*, with the exception of *Oryx sivalensis*, and less compressed than in living *Hippotragus* and in *P. deturi* as known from Laetoli, although they show overlap with this species from the Hadar Denen Dora Member. The angle of the maximum basal horncore diameter to the midfrontal suture was much smaller than in any living *Oryx* and *Addax* species, yet larger than in all living and extinct *Hippotragus* species and in *P. deturi*. The angle of horncore inclination relative to the dorsal braincase was much smaller than in any living and extinct *Hippotragus* species and also smaller than in *P. deturi*, but larger than in living *Oryx* and *Addax* species, comparable to that in *Oryx sivalensis* from the Pinjor Formation. The supraorbital foramina were relatively far apart resembling modern oryxes and addaxes, and further apart than in living and extinct *Hippotragus* species. The premolar row length was as reduced relative to molar length as in oryxes and in *Hippotragus gigas* from Olduvai Bed I. The dental occlusal morphology is more advanced that in dentitions tentatively assigned by Gentry (1987) to *Praedamalis deturi* from the Laetoli Beds, yet less advanced than in all living hippotragines, being closest to that in *Oryx* species.

Holotype

MAK-VP-1/24 is the right half of a frontlet with approximately two thirds of the horn core. The frontal anterior to the horncore is preserved from the anterior orbital rim to the metopic suture including the supraorbital pit and foramen (Figures 1a and 2a). The pedicel is moderately long with sloping sides, and it is not well demarcated from the basal horncore margin. The horncore tapers fairly rapidly towards the tip as though in the complete state it was short relative to its basal size. The pedicel and basal horncore are excavated by a large smooth-walled sinus. The horncore is quite strongly inclined in lateral view, forming an angle of almost 180° with the superior facial plane and an acute angle with the preserved part of the dorsal braincase. There is a slight shallow supraorbital pit with a shallow wide groove extending anteriorly. The supraorbital foramen is small, and its position indicates that the foramina were relatively far apart. In medial view, the metopic suture is deep which is correlated with the large basal sinus in and anterior to the pedicel. There is no sign of transverse ridges and little of longitudinal grooving. The orbit is not prominent. There is a slight indication of the depression in the frontal postero-medially to each horncore found in *Praedamalis deturi*.

Paratype

Partial right mandible MAK-VP-1/63 with P_3-M_3 in medium adult wear (Figure 3a). The socket and roots of a relatively reduced P_2 are also preserved. There is a large laterally-directed metastylid, a small basal pillar and a slim anterior goatfold on the M_3. The M_2 has a moderately developed basal pillar protruding from the posterior lobe of the tooth. No goatfold is evident on M_2

TABLE 3: Measurements of Hippotragine Frontlets from the Middle Awash

Length measurements in millimeters; e = estimated; HMAX = horncore maximum diameter; HMIN = horncore minimum diameter; HRAT = horncore ratio of HMIN/HMAX; SOF = width across lateral margins of supraorbital foramina; AHMET = angle of HMAX to metopic suture; AHCBR = angle of horncore to braincase in lateral view; HLEN = estimated length of complete horncore.

Taxon	*Praedamalis howelli*			*Oryx* sp.	*Hippotragus gigas*
Catalogue number	MAK-VP-1/24	MAK-VP-1/113	MAK-VP-1/62	MAT-VP-4/21	GAM-VP-1/14
HMAX	39.80	39.50	40.50	45e	72.80
HMIN	31.83		32.50	42.5e	55.80
HRAT	0.80		0.80	0.94e	0.77
SOF	64e			82e	
AHMET	38°e	40°e			15°e
AHCBR	65°e	65°e			
HLEN	270e	210e			

TABLE 4. Measurements of Dentitions from Middle Awash.

MAK-VP-1/63 is the paratype right mandible of *Praedamalis howelli* from Maka. The left mandible KL64-2 of unknown provenence, probably from Matabaietu Locality 5, may belong to a small hippotragine or to a large reduncine species. The left upper molar GAM-VP-1/4 from Gamedah Locality 1 is referred to cf. *Hippotragus gigas*. Length measurements in millimeters; e = estimated.

	MAK-VP-1/63	KL64-2	GAM-VP-1/4
1. Length P_{2-4}	36e	32.3	
2. Length/breadth P_2	7.8/5.8		
3. Length/breadth P_3	12.9/8.0	12.0/9.6	
4. Length/breadth P_4	14.9/10.0	12.5e/9.9	
5. Length M_{1-3}	66.5e		
6. Length/breadth M_1	16.3e/12.4e	14e/10.5e	
7. Length/breadth M_2	21.4/13.2	17.6/11.4	
8. Length/breadth M_3	30.3/13.0		
9. Ratio 1./5.	0.54		
10. Length P_2-M_3	104e		
11. Length/breadth M^2			31.02/20e

which may be because it is quite heavily worn anteriorly. The M_1 is broken anteriorly. The P_4 has a markedly bulbous and projecting metaconid, and its paraconid and metaconid are touching but without enamel fusion. The central enamel cavities are less complex than in modern *Hippotragus* and even than in *Oryx* and *Addax*. The molars are moderately hypsodont.

Horizon

The holotype and paratype were collected as surface finds associated with a fossiliferous sand unit, the Maka sands at Maka Locality 1, and without doubt derive from the Maka sands.

In this paper each specimen is referred to by its field and locality number, which for Maka Locality 1 is MAK-VP-1/number. White *et al.* (1994) report that within these sands is the tuff MA 90-16 for which no direct age estimate is available to date, but which correlates in several chemical aspects with the SHT tuff at the base of the Hadar Formation and with the Tulu Bor beta tuff in the Turkana Basin with age estimates very close to 3.4 million years (m.y.) (Brown *et al.*, 1992). The first hominid fossil from Maka, a proximal femur, derived from this same sand unit as the type material of *P. howelli*. Contemporary vertebrate fossils were described as similar to those from the Sidi Hakoma Member of the Hadar Formation (Clark *et al.*, 1984). Thus, based on geochemical and radiometric as well as biochronological and stratigraphic data, the fossils from Maka Locality 1 are about 3.4 m.y. old (White *et al.*, 1994).

Name

The new species is named after F. Clark Howell in recognition of his great contributions to mammal palaeontology.

Measurements

Measurements on the holotype and paratype are given in Tables 3 and 4.

Figure 4. A. Right and left horncores MAK-VP-1/62a of *Praedamalis howelli* from Maka unit 1, Middle Pliocene. **B**. Frontlet MAT-VP-4/21 of *Oryx* sp. from Matabaietu Locality 5, Late Pliocene. Both are shown in anterior view.

Referred specimens

Two additional skull fragments were also found in the Maka Locality 1: the right horncore and frontlet MAK-VP-1/113 (Figures 1b and 2b), and the frontlet with both separated horncores and other associated fragments MAK-VP-1/62a and b (Figure 4). Table 3 gives measurements for these fossils. MAK-VP-1/113 differs from the holotype by relatively shorter horncores and higher basal horncore separation. These differences are consistent with subadult status of this specimen. MAK-VP-1/62 is slightly larger than the holotype individual, with horncores that are closer to the orbital margin and have a slightly lower diminution rate from the base upwards. Fragments associated with this specimen include a damaged, abraded basioccipital. It shows anterior narrowing of the somewhat flat surface between the posterior tuberosities, about 32 mm wide, and the anterior tuberosities that measure about 20.5 mm across. Both MAK-VP-1/113 and MAK-VP-1/62 have the same large sinus in the pedicel and horncore base, surrounded by relatively thin bone, that is present in the holotype. Both specimens are very comparable with the holotype in other visible respects.

Comparisons

The new species is clearly closely related to *Praedamalis deturi* from Laetoli and Hadar. However, our result that *deturi* and *howelli* form a sister-group (Figure 10) depends on the current hypothesis that these taxa share a more extensive sinus in the frontal, pedicel and basal horncore than have other hippotragines. If this character is omitted from the analysis, then in several of the most parsimonious trees *howelli* is positioned as the next branch after *P. deturi* and before the diversification of the clade that is here called *Oryx*. The chief differences of *howelli* from *deturi* are the relatively less backbent horncores in the Maka form, its higher angle between the maximum horncore diameter and the midfrontal suture (Figure 8), its less upright (Figure 8) and probably less divergent horncores, and the lesser expression in *howelli* of the depression on the frontal postero-medially to the horncores. The main difference from all oryxes are *howelli*'s shorter horncores relative to skull size (although this character could not be assessed on *O. sivalensis*), the averagely more compressed horncores, and the greater angle between the forehead and the dorsal cranium. Differences between the new

Maka species and *Hippotragus* species are much more far-reaching and numerous (see Figure 10).

We compared the paratype mandible with hippotragine fragmentary dentitions from Shungura Member C unit 6, Member E unit 3, and Member G unit 5, and with dentitions that Gentry (1987) attributed tentatively to *P. deturi* from Laetoli. The Maka specimen is a little smaller than the Shungura dentitions, and less advanced in the degree of outbowing of the lingual molar walls and pinching of the buccal molar lobes, but quite comparable in the low degree of development of basal pillars and goatfolds relative to later hippotragines. As it is not clear to which taxon the Shungura specimens belong, we will not pursue this comparison further. Several of the Laetoli *P. deturi* dentitions look very comparable in the mentioned respects to the Maka paratype, while others are more primitive.

Genus *Oryx* Blainville 1816
Type species *Oryx gazella* (Linnaeus) 1758.

Generic diagnosis

We here construe *Oryx* in terms of the outcome of our cladistic analysis to include *Addax* and the fossil taxa cited under *Oryx* in Table 2. The genus is characterized unambiguously by relatively long horncores and a reduced angle between the face and the dorsal braincase, and ambiguously by reduced braincase length (Figure 10). The genus also shares with *Praedamalis* and *Hippotragus gigas* a reduced premolar/molar ratio (Figure 9), and shares with *Praedamalis* reduced backbending of the horncore, horncore insertion further posteriorly than directly above the orbit, reduced degree of basal horncore compression, and increased distance between the supraorbital foramina.

Oryx sp. from Matabaietu, Middle Awash

The deposits at Matabaietu have yielded abundant and diverse vertebrate fossils including hominids (White, pers. comm.). Matabaietu Localities 1 to 6 (MAT-VP-1 to MAT-VP-6) are associated with tuff MA 90-42 dated 2.52 m.y., with MAT-VP-1 and MAT-VP-2 above this tuff and MAT-VP-3 to MAT-VP-6 below it (White, pers. comm.). Thus, this new *Oryx* sp. from Matabaietu Locality 4 is slightly older than 2.5 m.y..

A broken frontlet, MAT-VP-4/21, apparently belonged to an adult (Figure 4; measurements in Table 3). It includes the basal part of the right horncore and the pedicel of the left horncore. It belonged to an oryx about the size of larger individuals of *O. gazella* and larger than the new species *P. howelli*. The horncores were only slightly compressed (Figure 5). The right horncore base suggests that they were relatively longer than in either of the *Praedamalis* species yet shorter than in living oryxes (Figure 4). The frontal anterior to the horncores is damaged, but the remaining pieces suggest that the supraorbital foramina were far apart as is typical of oryxes, the addax, and the new species *P. howelli* (Figure 6).

In oryx evolution, the horncore length has increased. Also, in the less advanced condition the basal horncore separation was lower and the pedicels and basal horncores were less parallel-sided with a greater tendency for their medial surfaces to slope basally towards the mid-plane and towards each other. The Matabaietu specimen shares this less advanced condition with *Oryx sivalensis* of the Pinjor stage in the Siwaliks, and is more plesiomorphic in this respect than is the juvenile *Oryx* frontlet, Omo 78 69-2731G from upper member G in the Shungura Formation (Gentry, 1985: Plate VII: Figure 4). A relatively high basal horncore separation is characteristic of earlier ontogenetic stages in antelopes, and the very high separation in the Shungura specimen is undoubtedly partly due to its juvenile status. However, the combination of this feature together with longer horncores already in the juvenile state is advanced in the Shungura *Oryx* species relative to that from Matabaietu. Similarly, the *Oryx* sp. reported by Harris (1991) from the KBS and Upper Burgi Members in the Koobi Fora Formation, Kenya, appears to more advanced in this combination of features than the Siwaliks and Matabaietu forms.

The single *Oryx* horncore from Shungura Member C8 (Gentry, 1985) may be a juvenile of the same species as the Matabaietu form. In the cladistic analysis they are treated as such and referred to as *Oryx* sp. 1. The more advanced forms from upper member G in the Shungura Formation (Gentry, 1985), from Olduvai Bed I (Gentry and Gentry, 1978), and the *Oryx* sp. reported by Harris (1991) from the KBS and Upper Burgi Members in the Koobi Fora Formation, and from the Upper Lomekwi Member in the Nachukui Formation (Harris *et al.*, 1988) are tentatively suggested to belong to the same species, called *Oryx* sp. 2 in our cladistic analysis. The *Oryx* from Ternifine, Algeria (Geraads, 1981) is included as *Oryx* sp. 3. On the few available characters, *Oryx* sp. 1 from Matabaietu is less advanced than the later species, and most closely comparable to *Oryx sivalensis* from the Siwaliks. Thus, no difference between them is reflected in our conservative cladistic coding (Table 5). Among possible more subtle differences are that the Matabaietu oryx is larger with less compressed horncores.

A horncore midpiece KL234-48 belongs to an oryx, and a left mandible KL64-2 (Figure 3, Table 3) might

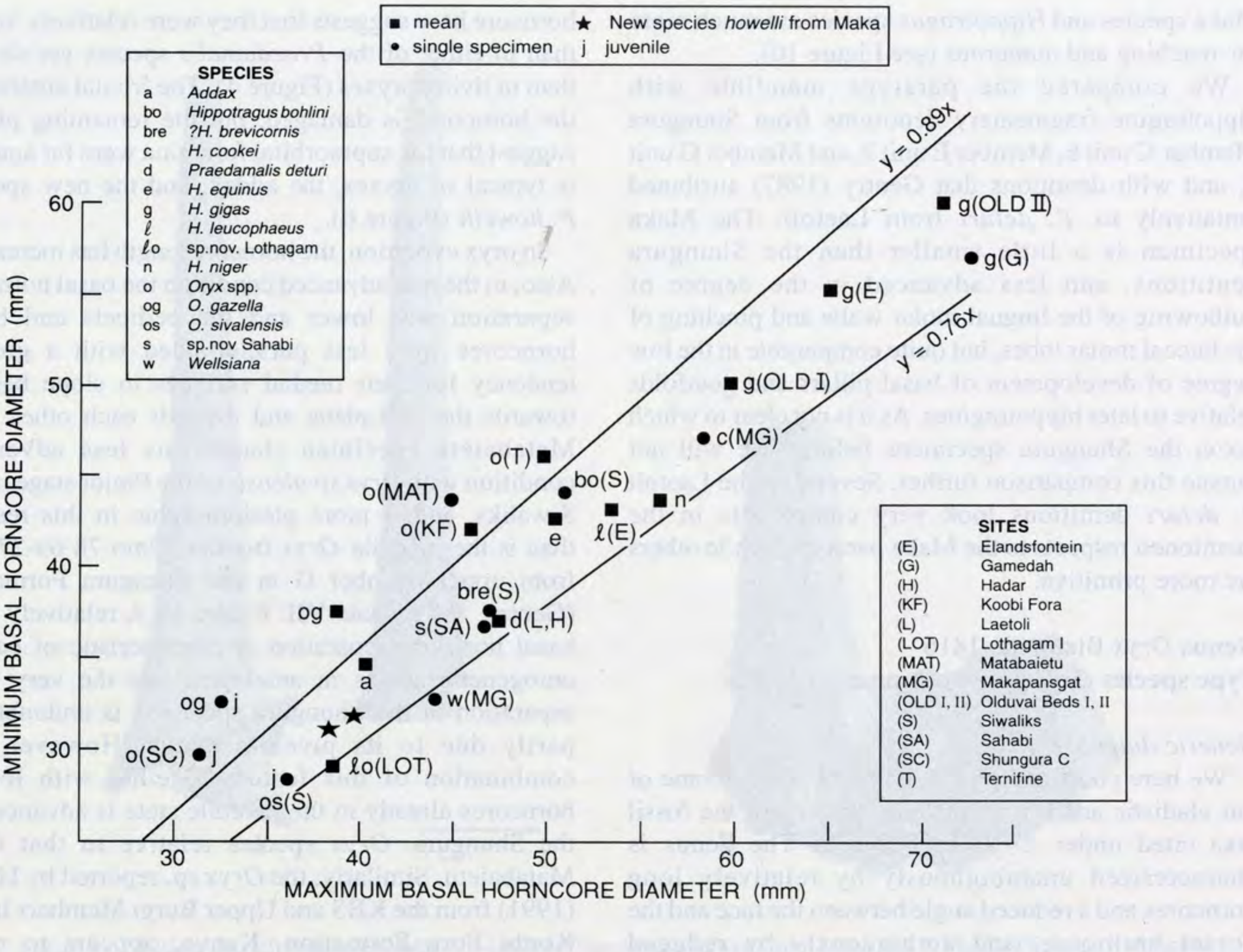

Figure 5. Minimum and maximum basal horncore diameters in some recent and fossil hippotragine taxa. The following sources for measurements apply to Figures 5-9. We have also seen and measured all these specimens ourselves. Numbers in brackets are sample sizes greater than one. Fossil taxa: **solid star** = *Praedamalis howelli* from Awash Maka Locality 1 (Table 3); **d(L)** = *P. deturi* from the Laetoli Beds (Gentry, 1987); **d(H)** = *P. deturi* from Hadar (Gentry, 1981); **d(L, H)** = mean of 4 Laetoli and 2 Hadar *P deturi*, (6); **o(MAT)** = *Oryx* sp. from Awash Matabaietu Locality 4 (Table 3); **o(SC)** = *Oryx* sp. 1 from Shungura Member C (Gentry, 1985); **o(KF)** = *Oryx* sp. 2 from the Upper Burgi and KBS Members, Koobi Fora Formation (Harris, 1991), (5); **o(OLD I)** = *Oryx* sp. 2 from Olduvai Bed I (Gentry and Gentry, 1978), (2); **o(T)** = *Oryx* sp. 3 (cf. *gazella*) from Ternifine (Geraads, 1981), (3); **os(S)** = *Oryx sivalensis* from the Siwaliks Pinjor stage (Pilgrim, 1939); **g(E)** = *Hippotragus gigas* from Elandsfontein (Klein, 1974), (3); **g(OLD I, II)** = *H. gigas* from Olduvai Bed I (3) and Bed II (8) (Gentry and Gentry, 1978), (3); **g(G)** = *H. gigas* from Awash Gamedah Locality 1; **c(MG)** = *H. cookei* from Makapansgat Member 3 (Vrba, 1986); **s(SA)** = *Hippotragus* sp. nov. from Sahabi (Gentry and Gentry, 1978; Lehmann and Thomas, 1987); **bo(S)** = *H. bohlini* from the Siwaliks Pinjor stage (Pilgrim, 1939); **bre(S)** = *?H. brevicornis* from the Siwaliks Tatrot stage (Pilgrim, 1939); **l(E)** = *H. leucophaeus* from Elandsfontein (Klein, 1974), (7); **w(MG)** = *Wellsiana torticornuta* from Makapansgat Member 3 (Vrba, 1986); **bra(L)** = *Brabovus nanincisivus* from the Laetoli Beds (Gentry, 1987); **lo(LOT)** = nov. sp. from Lothagam (measurements by us; see also Smart, 1976) (4); Extant taxa: **a** = *Addax nasomaculatus*, (3, sex unknown); **g** = *Oryx gazella*, (2, sex unknown); *H. niger* and *H. equinus* after Klein (1974) who gives sample size (N), mean (m), and standard deviation (s), for each sample: **n** = pooled mean for *Hippotragus niger* (♂ anteroposterior diameter, ♀apd: N = 11, m = 68.11, s = 8.76; apd: N = 17, m = 48.11, s = 4.77; ♂ mediolateral diameter, mld: N = 11, m = 49.42, s = 5.15; ♀mld: N = 17, m = 39.64, s = 3.85); **e** = *H. equinus*, (♂ apd: N = 4, m = 59.38, s = 8.96; ♀apd: N = 6, m = 44.40, s = 4.32; ♂mld: N = 4, m = 49.05, s = 5.61; ♀ mld: N = 6, m = 38.35, s = 3.04).

do although it could also belong to a large reduncine. Both are of unknown provenience but possibly referable to Matabaietu Localities 3 and 5 respectively (T. White, pers. comm.). The mandible shows a projecting metaconid on P_4 as found in hippotragines, but less so than in the *P. howelli* paratype mandible (Figure 3), and more extensive development of the goatfolds and basal pillars than in *Praedamalis*.

Genus *Hippotragus* Sundevall 1846
Type species *Hippotragus leucophaeus* (Pallas) 1766

Generic diagnosis

We here construe *Hippotragus* in terms of the outcome of our cladistic analysis to include *Sivatragus* (Pilgrim, 1939). The genus is characterized unambiguously by

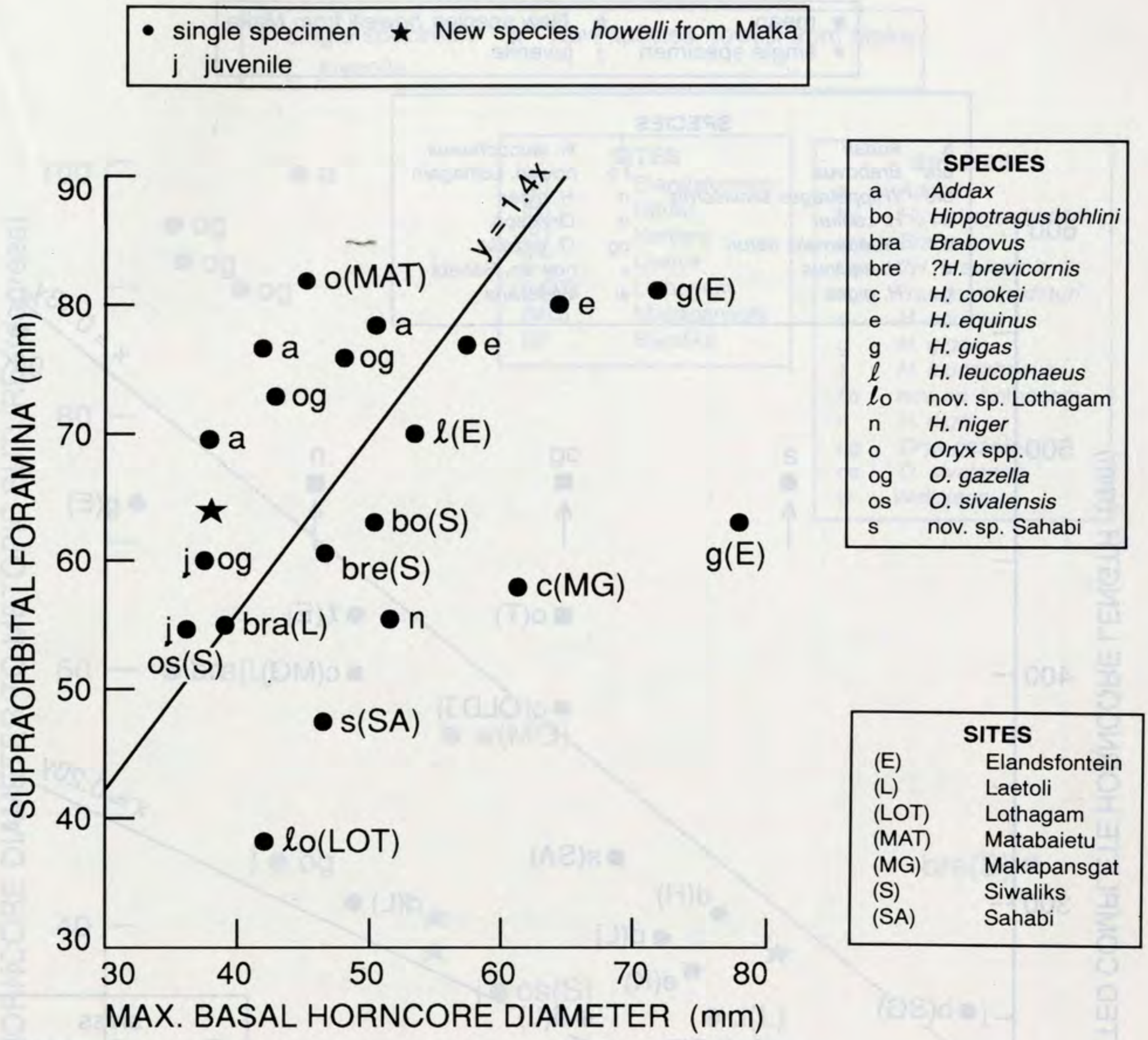

Figure 6. Maximum separation of supraorbital foramina relative to maximum basal horncore diameter in hippotragine taxa. For *Brabovus* see Gentry (1987). See Figure 5 for other sources.

prominently jutting dorsal orbital rims, and by very upright horncores that form a large angle with the dorsal braincase and are inserted right above the orbit and close together. Characters that could characterize the entire clade but that are not preserved on all component species, include relatively narrow premaxillae, an ethmoidal fissure that is largely or totally occluded by bone from the inside or by extension of the frontal, more developed goatfolds on lower molars than in *Oryx*, and relatively compressed horncores. Additional diagnostic features mentioned by Gentry and Gentry (1978) are nasals that are more domed than in *Oryx*, and stronger longitudinal ridges behind the anterior tuberosities of the basioccipital than in *Oryx*.

Hippotragus gigas from Gamedah, Middle Awash

The Gamedah Locality 1 (GAM-VP-1) is not yet directly associated with physical dates. However, according to White (pers. comm.), the Matabaietu Localities 1 to 6 (MAT-VP-1 to MAT-VP-6), associated with tuff MA 90-42 dated 2.52 m.y., on stratigraphic grounds represent the same part of the column as GAM-VP-1. These Matabaietu fossil assemblages share many species with those from GAM-VP-1. Thus, the Gamedah Locality 1 fossils are estimated to be about 2.5 m.y. old although it remains possible that they will turn out to be closer to 2.0 m.y. than to 2.5 m.y..

GAM-VP-1/14 is a right horncore of preserved length 290 mm. The original length was near 560 mm. Additional measurements are given in Table 3. It belonged to a large animal, as large as the *Hippotragus gigas* from Olduvai Bed II, Kanjera and Elandsfontein, and larger than means for *H. gigas* from Olduvai Bed I (Figure 5). Its basal horncore compression is low relative to means from the other assemblages of this species (Figure 5). It had only very slight flattening of the lateral horncore surface, very low horncore separation,

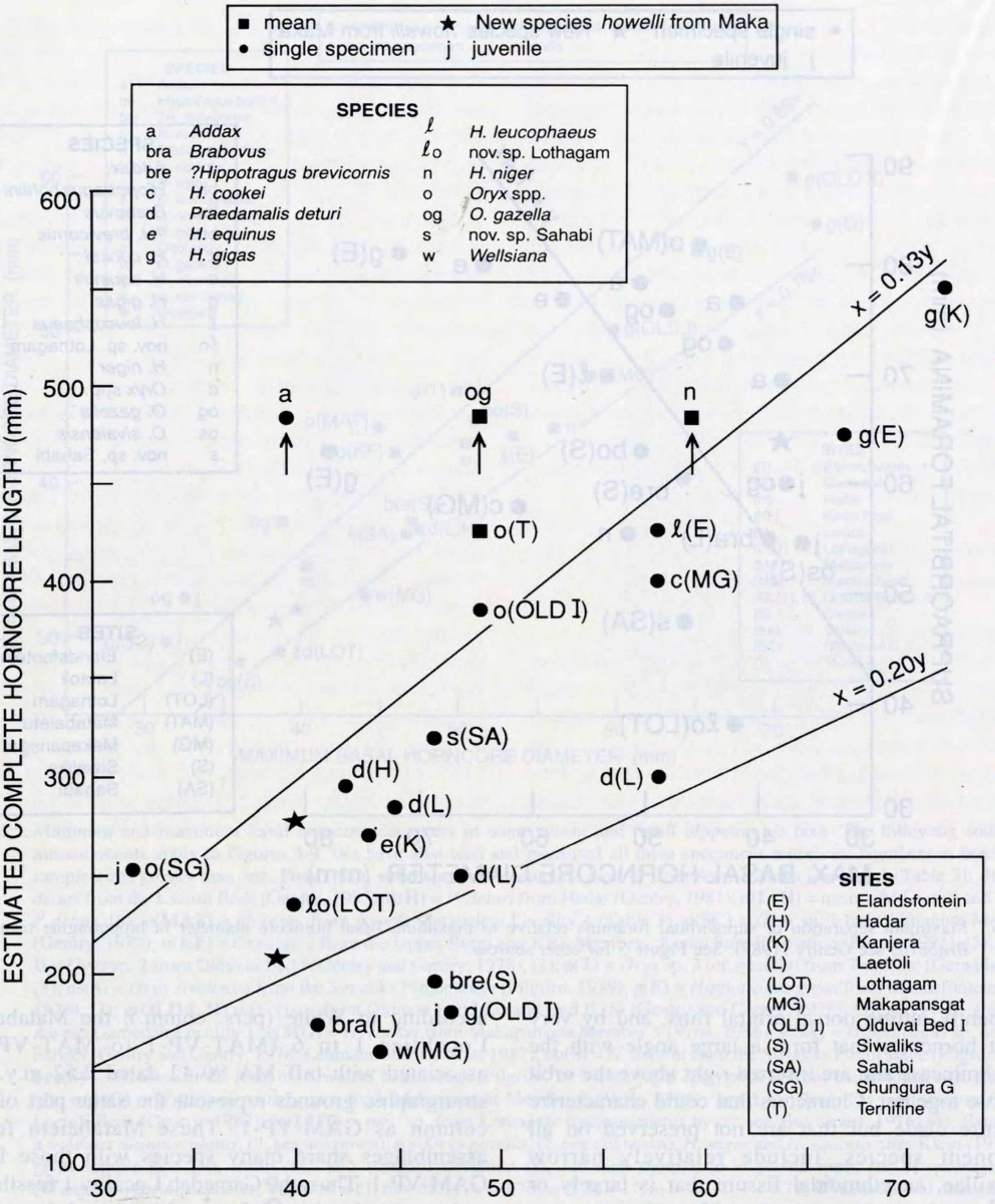

Figure 7. Estimated complete horncore length relative to maximum basal horncore diameter in hippotragine taxa. See Figures 5 and 6 for sources.

a very short pedicel, and a large basal sinus extending into the horncore base. In these respects, as also in size, strong backbending in lateral view, and lack of transverse ridges, the Gamedah horncore is typical of other *H. gigas* specimens, and there is little doubt that it belongs to this taxon. A right upper second molar, GAM-VP-1/4 (Table 4), also belongs to this species.

CONCLUSIONS

The main systematic conclusion is that the new species *howelli* is closely related to taxa previously assigned to *Praedamalis* and *Oryx*. Our assignation of the new species to *Praedamalis* is tentative and awaits additional fossil finds. However, the conclusion that *Praedamalis* and *Oryx* are more closely related to each

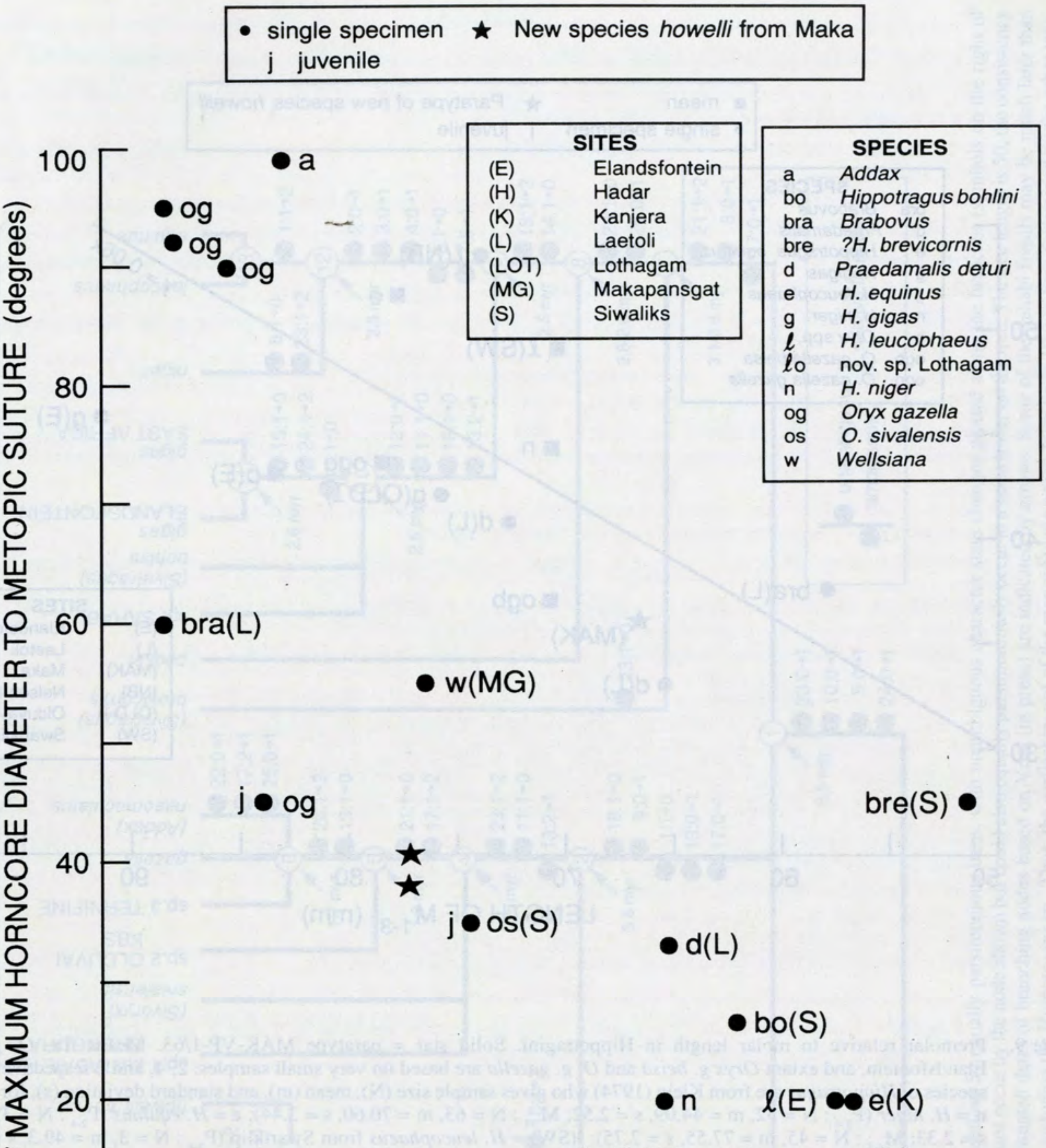

Figure 8. Angle of the maximum basal horncore diameter to the metopic (midfrontal) suture relative to the angle between the basal horncore and the dorsal braincase in lateral view in hippotragine taxa. See Figures 5 and 6 for sources.

other than either is to any taxon previously assigned to *Hippotragus*, and that the new species *P. howelli* belongs in this *Praedamalis-Oryx* clade, is firmly based in terms of our cladogram of skull characters.

In terms of the present cladistic results, we suggest that Hippotragini is the monophyletic group from node 1 in Figure 10, including all living and extinct taxa previously assigned to hippotragines together with the undescribed taxon from Lothagam (Table 1), and excluding *Brabovus nanincisivus* and *Wellsiana*

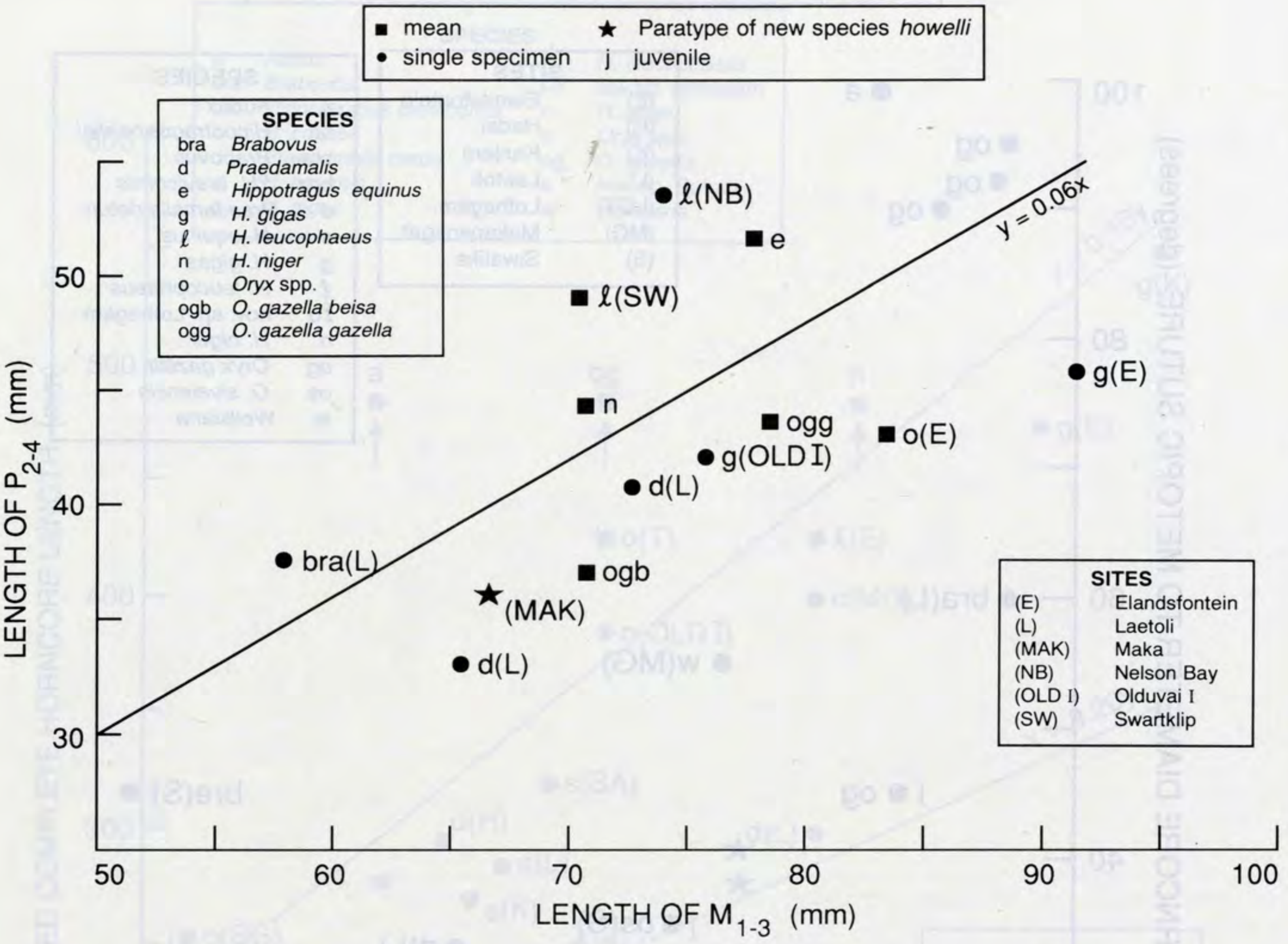

Figure 9. Premolar relative to molar length in Hippotragini. Solid star = paratype MAK-VP-1/63. Means for *O. gazella* from Elandsfontein, and extant *Oryx g. beisa* and *O. g. gazella* are based on very small samples: 2, 4, and 2 respectively. Means for species of *Hippotragus* are from Klein (1974) who gives sample size (N), mean (m), and standard deviation (s), for each sample: **n** = *H. niger* (P_{2-4} : N = 52, m = 44.09, s = 2.52; M_{1-3} : N = 63, m = 70.60, s = 3.44); **e** = *H. equinus* (P_{2-4} : N = 31, m = 51.02, s = 2.33; M_{1-3} : N = 45, m = 77.55, s = 2.75); **l**(SW) = *H. leucophaeus* from Swartklip (P_{2-4} : N = 3, m = 49.3, s = 3.53; M_{1-3} : N = 4, m = 71.15, s = 1.17). See Figures 5 and 6 for other information on sample sources.

torticornuta (*contra* Vrba, 1987). Hippotragine fossils are relatively rare throughout the fossil record, and in view of this their known species diversity is surprisingly high. The main proliferation of species occurred from the Middle to Late Pliocene onwards. Two major monophyletic lineages diversified in Africa with excursions into Eurasia. According to our cladogram (Figure 10) in comparison with detailed chronological information on all the taxa (Vrba, in press), the *Praedamalis-Oryx* lineage diversified and remained in Africa until between 2.7 and 2.0 m.y. ago when an early *Oryx* species, *O. sivalensis*, appeared in the Siwaliks Pinjor stage. Vrba (in press) suggested that this excursion dates to a period close after 2.7 m.y. ago when two conditions coincided: due to sea-level lowering, a landbridge was present between Africa and eastern Asia across Arabia, and the previously vicariated steppe habitats at high altitudes in East Africa and at high latitudes in Asia became continuous across the landbridge due to climatic cooling.

The *Hippotragus* lineage gave rise to two migrants to Eurasia. The later migration is evidenced by the presence of *H. bohlini* (previously *Sivatragus bohlini*) in the Siwaliks Pinjor stage. According to our data this emigration from Africa also occurred close to 2.7 million years ago. (We here took note of Geraads's, 1989, argument that some of the Sahabi fossils may not be datable to the Late Miocene but to the Late Pliocene. Thus, we let the minimum date of the divergence node 10 in Figure 10 be determined only by *Hippotragus gigas* and *H. bohlini*.) This was possibly coeval with the emigration of *Oryx* that culminated in *O. sivalensis*,

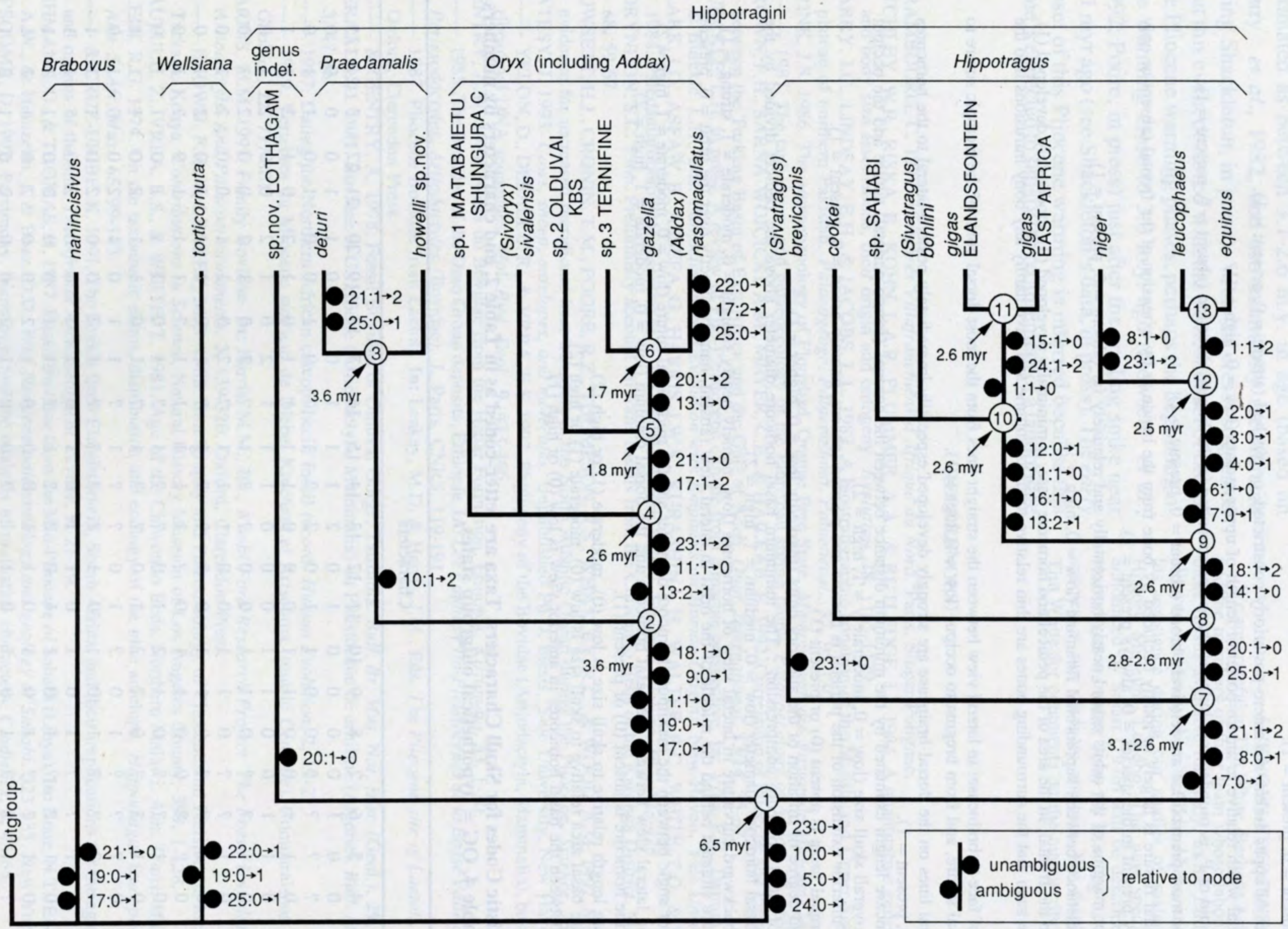

Figure 10. Consensus tree for hippotragine and related taxa, based on 54 equally parsimonious trees, with unambiguous character state changes plotted along the branches (symbols on the right of branches). Ambiguous changes (to left of branches) must occur by the node shown but could also equally parsimoniously occur at a node lower on the tree. The tree length is 50, the consistency index is 68 and the retention index 86. Minimum estimated dates of branching nodes based on Vrba (in press) are indicated by arrows. Some of the Sahabi fossils may be much later than the main Late Miocene assemblage (Geraads, 1989), including the *Hippotragus* sp.. Thus, the earliest record of the monophyletic group from node 10 was here determined by the other taxa. For character numbers see Table 5.

TABLE 5.

Skull Characters. For anatomical terms and diagrams see Sisson and Grossman (1975).

1 The $P_{2\text{-}4} : M_{1\text{-}3}$ ratio; that is, the maximum lingual length of the lower premolars divided by the maximum lingual length of the lower molars (low = 0, medium = 1, high = 2).

2: Basal pillars (prominent ectostylids on lower and entostyles on upper molars) strongly developed so as to form a Y-shaped structure (absent = 0, present = 1).

3 Medial lobes of upper molars are antero-posteriorly constricted, or pinched (absent = 0, present = 1).

4 Bucco-lingual width relative to antero-posterior length of upper molars (low = 0, high = 1).

5 The metaconid of P_4 is rounded into bulbous shape and extended in the lingual direction (absent = 0, present = 1).

6 The anterior-most premaxillae are relatively broad (absent = 0, present = 1).

7 The ethmoidal fissure is largely or totally occluded by bone from the inside or by extension of the frontal (absent or only occasionally present in the species = 0, always present = 1).

8 The superior margins of the orbits extend nearly horizontally and relatively far (absent = 0, present = 1).

9 Maximum distance between supraorbital foramina (low = 0, high = 1).

10 The sinus in the frontal, in the area of the pedicel and horncore base, is minimally developed (0), moderately developed (1), or extensive such that the surrounding bones are thin relative to sinus volume and have hardly any bony intrusions into the sinus (2).

11 The angle of face to braincase: in lateral view between the straight lines from the most dorsal point of the metopic suture to the internasal suture, and from bregma to occiput (low = 0, high = 1).

12 The temporal lines on the dorsal braincase are strongly developed especially immediately postero-lateral to the horncores (absent = 0, present = 1).

13 Dorsal braincase length estimated by the minimum distance between the coronal (fronto-parietal) suture and the occiput relative to overall skull size (low = 0, moderately = 1, high = 2).

14 The antero-inferior extension of the parietal is narrow and pointed (absent, namely broad = 0, present = 1).

15 The postcornual fossa is absent (0) or present (1).

16 The size and degree of inflation of the auditory bulla (markedly low = 0, higher = 1).

17 The ratio of basal horncore compression : The minimum basal horncore diameter above the pedicel divided by the maximum basal horncore diameter (low = 0, medium = 1, high = 2).

18 Degree of backward curvature in lateral view of horncores (low, namely nearly straight = 0, moderate = 1, strong = 1).

19 Horncores are situated behind the middle of the orbit in lateral view (absent, namely directly over the orbit = 0, present = 1).

20 The posterior angle between the maximum horncore diameter and the midfrontal suture (low = 0, moderate = 1, high = 2).

21 The angle in lateral view between the basal horncore and the dorsal cranium (low = 0, moderate = 1, high = 2).

22 Torsion of the horncore is absent (0) or present (1).

23 The horncore length relative to skull size is low (0), moderate (1) or high (2).

24 The horncore basal area relative to skull size is low (0), moderate (1) or high (2).

25 The angle between the basal horncores in anterior view is low (0) or high (1).

TABLE 6. Cladistic Codes for Skull Characters. Taxa are letter-coded as in Table 2, and characters by numbers as in Table 4. OG = hypothetical outgroup states.

Taxa	Characters																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	3	24	25
OG	1	0	0	0	0	1	0	0	0	0	1	0	2	1	1	1	0	1	0	1	1	0	0	0	0
lo	?	?	?	?	?	?	?	0	0	1	1	0	2	?	1	?	0	1	0	0	1	0	1	1	0
a	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	1	0	1	2	0	1	2	1	1
og	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	2	0	1	2	0	0	2	1	0
o3	?	?	?	0	1	?	?	0	1	1	0	0	?	?	1	?	2	0	1	2	0	0	2	1	0
o2	?	?	?	0	1	?	?	0	1	1	0	0	1	1	1	?	2	0	1	1	0	0	2	1	0
o1	?	?	?	0	1	?	?	0	1	1	0	0	?	?	1	?	1	0	1	1	1	0	2	1	0
os	?	0	0	0	?	?	0	0	1	1	0	?	1	1	1	1	1	?	1	1	1	0	?	1	0
ho	0	0	0	0	1	?	?	0	1	2	1	0	?	?	1	?	1	0	1	1	1	0	1	1	0
d	0	0	0	0	1	?	?	0	?	2	1	0	?	?	1	?	1	0	1	1	2	0	1	1	1
bre	?	?	?	0	?	?	?	1	0	?	1	0	?	?	1	?	1	1	0	1	2	0	0	1	0
s	?	?	?	?	?	?	?	1	0	1	0	1	?	?	?	?	1	2	0	0	2	0	1	1	1
bo	?	?	?	?	1	?	?	1	0	1	0	1	1	0	1	0	1	?	0	0	2	0	?	1	1
c	?	0	0	0	1	?	?	1	0	1	1	0	?	?	1	?	1	1	0	0	2	0	1	1	1
g2	0	0	0	0	1	?	?	1	0	1	0	1	1	0	0	0	1	2	0	0	2	0	1	2	1
g1	0	?	?	?	1	?	?	1	0	1	0	1	1	?	0	0	1	2	0	0	2	0	1	2	1
e	2	1	1	1	1	0	1	1	0	1	1	0	2	0	1	1	1	2	0	0	2	0	1	1	1
n	1	1	1	1	1	0	1	0	0	1	1	0	2	0	1	1	1	2	0	0	2	0	2	1	1
l	2	1	1	1	1	?	?	1	0	1	1	0	2	?	1	?	1	2	0	0	2	0	1	1	1
w	?	?	?	?	?	?	?	?	?	0	1	0	?	?	?	?	0	1	1	1	1	1	0	0	1
bra	1	0	0	0	0	1	0	0	0	0	1	0	2	?	1	?	1	1	1	1	0	0	0	0	0

and also with emigration of one species of Alcelaphini and two of Reduncini (Vrba, in press). The earlier Eurasian immigrant from the *Hippotragus* lineage, *H. brevicornis* (previously *Sivatragus brevicornis*), appeared during the Tatrot stage in the Siwaliks estimated as between 3.1-2.6 m.y. in age (based on Barry *et al.*, 1982, and astronomically recalibrated using Shackleton, in press). Vrba (in press) suggested that this event occurred with the earliest onset of one of the Pliocene warming phases, perhaps the beginning of the warming close to 3.0 m.y. ago (Dowsett *et al.*, 1992; Poore, in press) just after the cooling spike near 3.1 myr ago (see Shackleton's data, in press). The *early* onset of this Pliocene warming is inferred because this time is expected to satisfy the requirement of a landbridge that was still available as melting of polar ice had not yet progressed sufficiently to flood the landbridge, and the requirement that the mesic wooded savanna habitats inferred for *Hippotragus* would have already extended to higher latitudes due to global warming.

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