

Original article

The Pleistocene fauna (other than Primates) from Asbole, lower Awash Valley, Ethiopia, and its environmental and biochronological implications

La faune pléistocène (sauf Primates) d'Asbole, basse vallée de l'Awash, Éthiopie: implications environnementales et biochronologiques

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Abstract

The Asbole area in the Lower Awash Valley yielded a diverse fauna of large and small mammals, associated with an Acheulean industry. The most notable forms are a potentially new species of herpestid, a large collection of *Kolpochoerus majus*, and the earliest known *Bos* in Africa. Biochronologically, this fauna belongs to the earliest Middle Pleistocene, and is roughly contemporaneous with the Bodo site further south. Paleoenvironmentally, the fauna suggests a mosaic of landscapes among which humid environments, grasslands and forests, are predominant.

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Résumé

La région d'Asbole dans la basse vallée de l'Awash a livré une faune diversifiée de grands et petits Mammifères associée à une industrie acheuléenne. Les formes les plus remarquables sont une mangouste d'une espèce probablement nouvelle, une importante collection de *Kolpochoerus majus*, et le plus ancien *Bos* connu en Afrique. La biochronologie permet de la placer au tout début du Pléistocène moyen, et elle serait donc à peu près contemporaine du site de Bodo un peu plus au sud. Cette faune témoigne d'une mosaïque de milieux parmi lesquels les environnements humides, prairies et forêts, semblent dominer.

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Keywords: Mammalian fauna; Pleistocene; Ethiopia; Environment

Mots clés : Faune de Mammifères ; Pléistocène ; Éthiopie ; Environnement

1. Introduction

The Asbole area is located on the left bank of the Awash river, about 11.0° N, 40.5° E, and roughly 20 km SSW of

Hadar. The first detailed survey of the area was led by one of us (Z.A.) in 1999. More extensive field work was undertaken in 2000 and 2002, and is still in progress, mainly examining the taphonomic and environmental aspects of the site. This paper focuses on the systematics and biochronology of the mammalian fauna (excluding Primates, which are being studied separately). It is therefore a modified and expanded version of the preliminary report (Alemseged and Geraads,

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2000) with greater emphasis on extinct forms. Systematic paleontological collection awaits final resolution of the geology and taphonomy. Most of the materials presented here are from surface collection without screening and are thus biased toward larger mammals.

All fossils are housed in the National Museum of Ethiopia in Addis Ababa. In the following descriptions, lowercase denotes lower teeth, and uppercase denotes upper teeth. The use of cf. and aff. follows Matthews (1973) and Lucas (1986). Abbreviations are as follows: ASB: Asbole; LZMO: Laboratoire de Zoologie (Mammifères et Oiseaux), Muséum National d’Histoire Naturelle, Paris; KNM: National Museums of Kenya, Nairobi. All measurements are given in millimeters unless otherwise noted and the abbreviations “W, L” indicate width and length measurements, respectively.

2. Stratigraphic context

Sediments containing the fossils described here are exposed along Bironita Duma ridge, a broad, gravel-capped

ridge between the Awash River and Asbole Rivers, south of the large Busidima channel (Fig. 1). Our regional mapping and geological studies of this area have demonstrated a need for a revised lithostratigraphy for the Awash Group to successfully ascribe the Asbole sediments to a formal nomenclature. A small portion of the lower sequence may be attributed to the “upper” Kada Hadar Member of Hadar Formation as was mapped by Kalb (1993), although the definition of its upper boundary is not well defined, and most of the strata shown here cannot be attributed to this formation. Some of the lower strata are similar to what was called the “unconformable post-Hadar Deposits” at Gona, and the sedimentology of the lower sections are broadly similar to those described in Semaw et al. (1997). The upper part of the sequence is similar to those from various sites throughout the Awash region, which have been ascribed to the lower Wehaitu Formation. However, because terminology for the Awash Group has not made use of information derived from tephra, this framework is cumbersome and non-applicable at Asbole. Accordingly, our current geological focus is on a tephros-

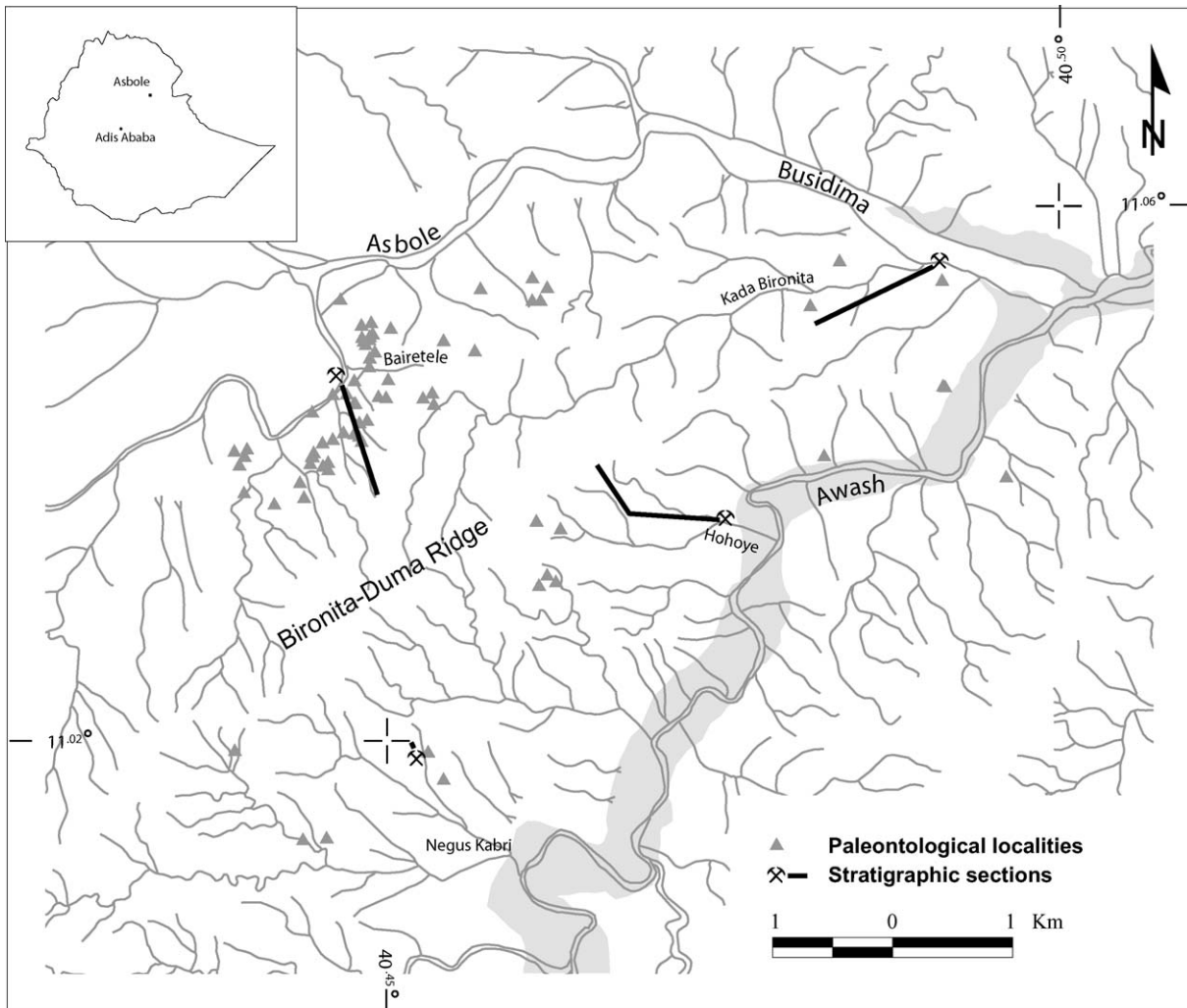


Fig. 1. Map of the Asbole Research Area showing location of fossil specimens and stratigraphic sections in Fig. 2. Carte de la région d’Asbole indiquant l’emplacement des points fossilifères et des coupes stratigraphiques de la Fig. 2.

stratigraphic framework to tie the Asbole strata with adjacent strata throughout the lower and middle Awash regions.

Despite the lack of an applicable lithostratigraphy, what we call the “Asbole fauna” can be constrained between two widespread and mappable stratigraphic markers (Fig. 2). It derives from levels above a series of thick carbonate cemented conglomerates, the uppermost of which is mappable

throughout the boundaries of the research area, and is observable across the Awash River, and into the Gona area to the north. We informally designate the uppermost conglomerate in this series the “top conglomerate”. All fossils also derive from within or below a prominent unlithified gravel unit capping the broad ridge, informally referred to here as the “plateau-forming gravels”. Kalb (1993) attributed these to

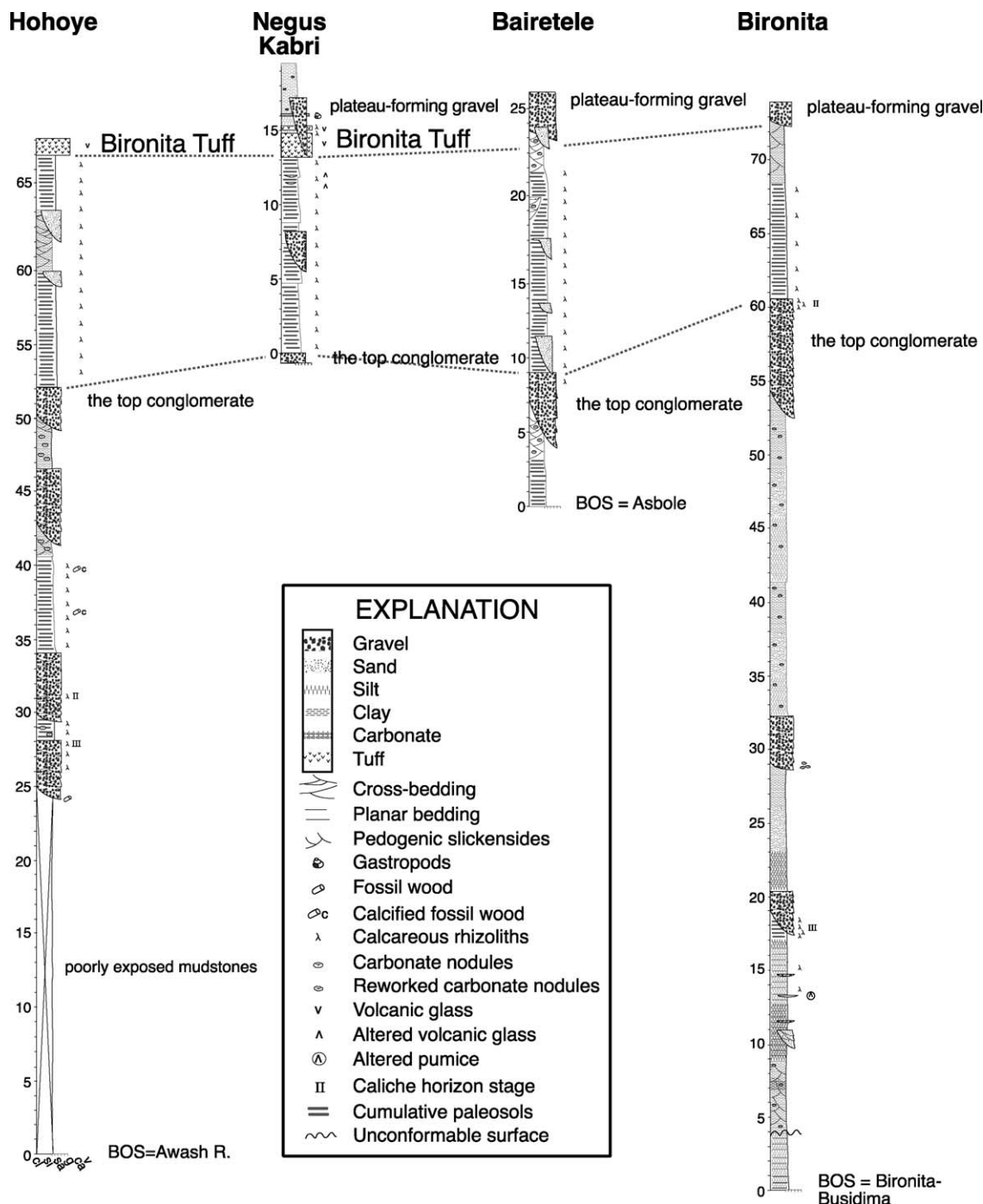


Fig. 2. Stratigraphic sections containing the Asbole fauna in Hohoye, Negus Kabri, Bairetele, and lower Bironita (locations in Fig. 1). BOS indicates the vertical location of the base of section. Particle sizes are indicated at the base of the first section. Cl = clay, si = silt, sa = sand, g = gravel (conglomerate), ca = carbonate, v = volcanic.

Coupes stratigraphiques incluant la faune d’Asbole fauna à Hohoye, Negus Kabri, Bairetele, et Bironita inférieur (localisation, cf. Fig. 1). BOS indique le niveau de la base de la coupe. La taille des particules est indiquée à la base de la première section. cl = argile, si = silt, sa = sable, g = gravier (conglomérat), ca = carbonate, v = volcanique.

the Middle Pleistocene Awash, or MPA gravels, which were mapped as a single stratigraphic unit throughout the entire Awash region. In Negus Kabri, these gravels form a down-cutting fluvial channel lateral to a prominent vitreous tephra cropping out along the southern crest of the ridge, here designated the Bironita Tuff. We are of the opinion that tephrostratigraphic correlation of the Bironita Tuff, among others in the region will provide much better control than the more problematic lithostratigraphic correlation invoked for the MPA gravels. Chemical analysis of glass shards from the Bironita Tuff (Table 1) demonstrate a correlation to samples from a tuff in the middle Awash Valley area which have dates of 0.55 ± 0.03 to 0.74 ± 0.03 (Samples MA90-23, MA90-20; Clark et al., 1994).

The sediments below the top conglomerate have also yielded some fossils, described separately in this paper. These sediments consist of a series of fining upwards sequences of thick conglomerates interspersed with thick well developed fossil Vertisols containing well formed carbonate nodules and calcareous rhizoliths and displaying abundant pedogenic slickensides. Several of the conglomerates have well developed stage II and stage III caliche horizons indicating formation in an evaporative regime over extended periods of non-deposition (Terminology of Gile et al., 1966). A prominent angular unconformity in the base of the section at Bironita also indicates a major gap in time, and can likely be traced to the unconformity, or one of the unconformities in the upper Kada Hadar Member of the Hadar Formation, first recognized by Kimbel et al. (1996). The well formed calcic paleosol on the top conglomerate, and subsequent change in the nature of sedimentation also likely indicates an extended period of non-deposition.

The Asbole fauna derives from the strata overlying the “top conglomerate”, which have a different sedimentological character from those below. Strata above the top conglomerate consist of a sequence of cumulative paleosols formed on

yellowish brown (10YR 5/4) poorly consolidated silty clay floodplain deposits with fine calcareous rhizoliths and fine ped structure, generally lacking the Vertic features noted in the underlying floodplain sediments except within isolated lenticular clay units near the top of the sections. Several channel-form deposits of medium to coarse grained trough cross-bedded sand with or without fine gravel bases can be mapped through this sequence, especially in the Bairetele area. Occasional large lenticular dark grayish brown (10YR 4/2) clay deposits occur near the top of the sequence. This sequence is capped by either the unconsolidated plateau-forming gravel or Bironita Tuff, which can be considered roughly contemporaneous. In Negus Kabri, above the Bironita Tuff, lies a short sequence of very loose, poorly consolidated and often laminated silts and clays, and a thin gastropod bearing clay.

3. Systematic study of the Asbole fauna

Order RODENTIA Bowdich, 1821

Family THRYONOMYIDAE Pocock, 1922

Genus *Thryonomys* Fitzinger, 1867

Thryonomys cf. *swinderianus* (Temminck, 1827).

No systematic screening has been undertaken yet, it is not surprising that the large, marsh cane-rat is relatively abundant among rodents, with several more or less complete crania and mandibles. The Asbole specimens are larger (length P4-M3 = 17–18 mm) than the extant species *T. gregorianus* and match the size of *T. swinderianus*. *Thryonomys* is indigenous to Africa though a related genus, *Paraulacodus*, is reported from the Middle Miocene Siwaliks of Pakistan (Flynn and Winkler, 1994). An indeterminate species of *Thryonomys* is reported from the Miocene–Pliocene at Manonga (Winkler, 1997) and the extant species are seemingly very old, with *T. gregorianus* dating back to Omo

Table 1
Chemical analyses of samples identified as the Bironita Tuff
Analyses chimiques sur des échantillons du Bironita Tuff

Sample	Location	SiO ₂	TiO ₂	Al ₂ O ₃	Fe ₂ O ₃	MnO	MgO	CaO	Na ₂ O	K ₂ O	Total
Normalized electron microprobe data (percent)											
E02-1111	Hohoye	72.48	0.38	12.69	6.44	0.22	0.02	0.61	3.87	3.29	100
E02-1126	Nogus Kaberie	71.57	0.45	12.02	6.42	0.25	0.02	0.57	5.08	3.62	100
E02-1127	Nogus Kaberie	71.77	0.36	12.52	6.36	0.22	0.02	0.59	4.38	3.79	100
E02-1151	Elamuïta	73.89	0.37	12.88	5.97	0.25	0.02	0.58	3.06	2.97	100
X-ray fluorescence data (ppm)											
		Ba	Rb	Zn	Zr	Sc	Sr				
E02-1111	Hohoye	950	80	198	713	n/d	50.8				
E02-1127	Nogus Kaberie	965	82	197	714	2	55.1				
E02-1151	Elamuïta	875	76.9	188	695	4	71.2				
ICP-MS data (ppm)											
		Ce	Nb	Y	Eu	Hf	La	Lu	Nd	Sm	Ta
E02-1111	Hohoye	162.3	117	92.2	3.83	16.7	80.99	1.66	77.87	15.57	8.1
E02-1127	Nogus Kaberie	162.7	120.5	94.2	3.72	16.4	80.80	1.62	77.75	15.44	8.1
E02-1151	Elamuïta	156.3	111.7	85.4	3.61	16.6	77.85	1.54	73.84	15.37	8.2

Member B and *T. swinderianus* from Omo Member J (Wesselman, 1984). Living thryonomids are sympatric though *T. gregorianus* occupies a more restricted range (Kingdon, 1974), and both inhabit mesic grass or reed environments with the slightly smaller *T. gregorianus* occupying better drained moist grasslands and the larger *T. swinderianus* having a semi-aquatic habit along river and lake margins. The presence of *T. swinderianus* at Asbole is a positive indication of moist grassed habitats adjacent to persistent water.

Family RHIZOMYIDAE Miller and Gidley, 1918

Genus *Tachyoryctes* Rüppel, 1835

Tachyoryctes sp.

An incomplete skull and a few maxillary and mandibular tooth-rows do not differ from the living *T. splendens*, nor from *T. pliocaenicus* Sabatier, 1978, from Hadar, and an unpublished new species described by Sabatier (1979), from Melka Kunturé. The Asbole specimens are intermediate in size between the two fossil species. According to Sabatier (1979), the distinction between these species rests mainly upon hypsodonty and the correlative height of the bridges linking the enamel plates. A greater sample of teeth at various wear stages is necessary for a positive identification.

Measurements: m1 ASB-93: L = 3.0; m2 ASB-122: 2.67 × 3.04; m3 ASB-122: 2.72 × 3.04.

Family HYSTRICIDAE Fischer, 1817

Genus *Hystrix* L.

Hystrix cristata L.

A mandible with heavily worn teeth is smaller than that of other Plio-Pleistocene species of this genus, and must belong to the modern species, which is of comparable size. The length p4-m3 is 33.5, and the log (L × W) of p4 is close to 1.84, as in *H. cristata* (Sabatier, 1979: Tab. 20; Denys, 1987a: Fig. 6.20).

Family MURIDAE Illiger, 1815

Genus *Otomys* Cuvier, 1824

Otomys sp.

A cranial fragment with M2–M3 is very large (width of M3 = 2.7 mm). No fossil species has such a broad M3, which can be found only in the living *O. angoniensis* (Denys, 2004). The Asbole *Otomys* is much larger than those of Isenya, Olduvai Bed IV, and even than that of Kapthurin.

Genus *Arvicanthis* Lesson, 1842

Arvicanthis cf. *niloticus* (Desmarest, 1822)

A maxilla with three molars (L M1–M3 = 6.22) is more like the modern *A. niloticus* than *A. primaevus* Jaeger, 1976, from Oldvai, in the following features:

- on M1 t3 is a little more posterior than t2, and t9 is a little more anterior than t8. However, the *A. primaevus* from Lake Natron (Denys, 1987b) is also closer to the recent *A. niloticus* than is the Olduvai population in these features;
- on M2, the main loph is only slightly chevron (V)-shaped, with its three tubercles almost in a line. Both *A. primaevus*

populations (and still more *A. arambourgi* Jaeger, 1975 from Tighenif, Algeria) have a more V-shaped main loph on M2;

- M3 is also more similar to the modern species in that t8 and t9 are fused to form a transverse loph.

A mandible ASB-298 (L m1–m3 = 6.4) looks identical to that of *A. niloticus*. In contrast, to *A. arambourgi* Jaeger, 1975, from Tighenif, the longitudinal crest is completely absent. It is also lacking in *A. primaevus*, but this species is smaller (L m1–m3 = 5.23–5.44 according to Jaeger, 1976).

Order CARNIVORA Bowdich, 1821

Family HERPESTIDAE Gill, 1811

Genus *Ichneumia* Geoffroy, 1837

Ichneumia aff. *albicauda* (Cuvier, 1829)

ASB-107 is the anterior part of a cranium, rather crushed and with deeply worn teeth. It can be readily referred to *Ichneumia*, which is an extant monospecific genus (*I. albicauda*, the white-tailed mongoose). The orbit is completely encircled by a bony ring, a feature found only, among herpestids, in *Ichneumia*, *Herpestes* and *Atilax*. ASB-107 cannot be referred to either of the latter two genera, because the molars are large relative to P4, and M2 is not much smaller than M1.

The P4 of ASB-107 differs from that of *I. albicauda* by its small protocone (see measurements), which leaves a concavity on the postero-lingual side of the tooth. In the living form, the protocone is large, and this side is straight or convex. Furthermore, the teeth of ASB-107 are larger, and the muzzle is much longer than in *I. albicauda*, as illustrated in the following comparison using the largest specimens of *I. albicauda* that we could find in the LZMO:

	ASB-107	<i>I. albicauda</i> range (N = 6)
Length from C/to posterior border of orbit	53	40.3–45.5
Length from C/to front of P4	ca. 27.5	17.7–19.5
Length P4-M2	19.2	16.8–18.5
Teeth dimensions (W perpendicular to labial side)		
P4	9.4 × 6.9	7.2–9.2 × 7.0–8.3
M1	7.0 × 8.2	6.2–6.7 × 8.0–8.9
M2	5.4 × 7.2	4.4–5.5 × 6.1–7.6

Undoubtedly the Asbole *Ichneumia* is a new species, but the cranium is too crushed and the teeth are too worn for it to be named at present.

Genus *Herpestes* Illiger, 1811

Herpestes cf. *ichneumon* (L.).

A maxilla in connection with the lower jaw, and associated with a few post-cranial elements (ASB-226), belongs to *Herpestes*. It ranks among the largest *H. ichneumon*, but in shape is nearly identical to living forms, except perhaps that the internal cusps of P2–P3 are slightly stronger. Its main dimensions are: length p2–m2 = 30.5; length P2–M2 = 26.2

Family HYAENIDAE Gray, 1869

Genus *Hyaena* Brisson, 1762

Hyaena hyaena (L.).

ASB-85 is a partial cranium of a striped hyena. Neither the individual measurements of the skull and teeth, nor the PCA (Fig. 3) permit its distinction from the modern form, although it is smaller, and has especially shorter premolars than most representatives of the living species, which first appears in Shungura Member C at Omo and Upper Lomekwi at West Turkana.

Measurements

Maximum width above auditory foramen	76.8	Length from P4 to post-glenoid tubercle	60
Minimum post-orbital width	35	Length from P4 to occipital condyle	109

P2 = 14.7 × 10.2; P3 = 19.4 × 13.4; P4 = 29 × 18.5.

Genus *Crocota* Kaup, 1828

Crocota crocuta (Erxleben, 1777)

A lower jaw fragment with p4 and m1, ASB-125, is the only specimen of the spotted hyena. All its dimensions (W p4 = 12.8; m1 = 29.2 × 11.6, trigonid length = 24.5) fall within the range of both modern and fossil *Crocota* from Africa (*C. crocuta* and its lower Pleistocene relatives *C. ultra*, etc.) but its relatively narrow m1 brings it closer to the extant forms than to the fossil ones from the lower Pleistocene of Africa (Fig. 4). Although the differences are not major, they clearly point to an increase of robustness of this tooth in the Middle Pleistocene.

Family FELIDAE Gray, 1821

Genus *Felis* L.

Felis cf. *libyca* Forster, 1780

A few specimens belong to a small felid, which cannot be distinguished, neither by its dimensions nor by its morphology, from the recent *Felis libyca*, the only wild cat living in the area today, and this is the most likely identification. The best specimen is ASB-84, a left maxillary fragment with only

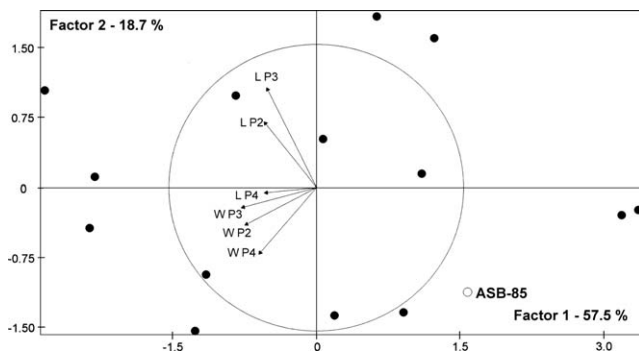


Fig. 3. Principal component analysis on upper teeth of ASB-85 and a sample of recent specimens of *Hyaena hyaena*. Axis 1 mainly reflects size, axis 2 reflects the L/W ratio of premolars.

Analyse en composantes principales sur les dents supérieures de ASB-85 et sur un échantillon de spécimens actuels de *Hyaena hyaena*. L'axe 1 reflète surtout la taille, l'axe 2 reflète le rapport longueur/largeur des prémolaires.

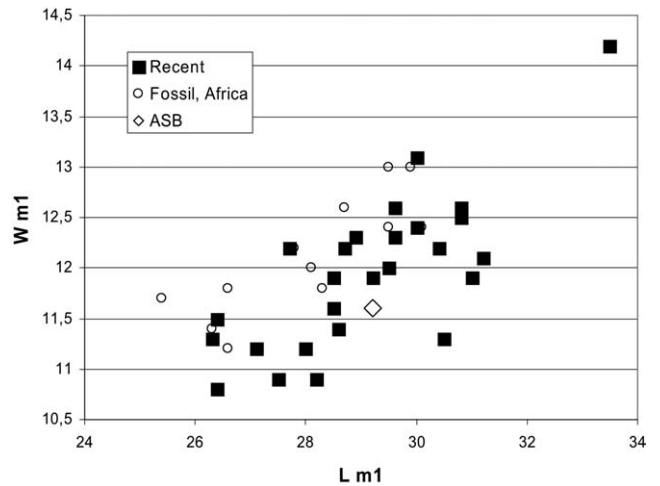


Fig. 4. Length × width scatter plot of *C. crocuta* m1. Graphique longueur/largeur des m1 de *C. crocuta*.

the canine crown missing, but there are also several mandibular pieces. Their dimensions, given below, fall within the range of the modern wild cat.

	P3/p3	P4/p4	M1/m1	
ASB-84 (upper)	7.8 × 3.7	12.2 × 6.2	2.2 × 4.1	
ASB-108 (lower)	5.5 (alv.) × -	6.0 (alv.) × -	8.8 (alv.) × -	L p2-m3 = ±22
ASB-106 (lower)		8.3 × 3.4	± 9.2 × -	
ASB-51 (lower)			9 × -	

Measurements of a distal humerus, ASB-207, are: width = 19.3; maximum depth = 12.3.

Genus *Panthera* Oken, 1816

Panthera cf. *leo* (L.).

A fragment of upper carnassial is the only remain of a large *Panthera*, the size of *P. leo*.

Family CANIDAE Gray, 1821

Genus *Canis* L.

Canis cf. *aureus* L.

A cranial fragment, with mandible and elements of the post-cranial skeleton, ASB-20, is the size of a large *Vulpes* or small *Canis*, but all African *Vulpes* are small, and the frontal seems to lack the supra-orbital depressions of this genus. Its tooth proportions and morphology are similar to those of the living *C. aureus* of Ethiopia (nine specimens examined in LZMO), but it plots near the lower limit of their size range (Fig. 5). We believe it is best assigned to this species.

Measurements: P3 = 9.8 × 3.8; P4 = 14.1 × 7.8; M1 = ca. 9.9 × 12.2.

Family MUSTELIDAE Swainson, 1835

Genus *Mellivora* Storr, 1780

Mellivora capensis (Schreber 1776)

An almost complete and well-preserved cranium and associated mandible, ASB-240 (Fig. 6(3)), belongs to a honey badger very similar to the recent form, widespread in Africa

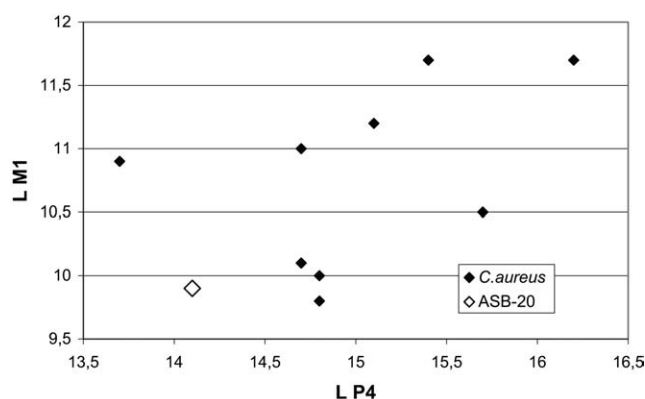


Fig. 5. Scatter plot of L M1 vs. L P4 in *Canis aureus* from Ethiopia.
Graphique des longueurs de M1 et P4 chez des *Canis aureus* d'Éthiopie.

and also extending to Southern Asia. It is a rather large specimen, larger than most living individuals from the tropics, but not than the Southern African forms (Fig. 7), and also larger than the fossil forms from the late Pliocene of Ahl al Oughlam in Morocco (Geraads, 1997) and the Mio-Pliocene of Langebaanweg (Hendey, 1974). This early origin of *Melivora capensis* probably explains why the Asbole form does not display any morphological difference with the living form.

Measurements

Condylal-basal length	138.5
Min. post-orbital width	34.5
L from front of orbit to post-glenoid apophysis	54.5
Bi-mastoid width	± 80
Occipital height (from basion)	47.5
Length P2–M1	32.5

Order PROBOSCIDEA Illiger, 1811

Family ELEPHANTIDAE Gray, 1821

Genus *Elephas* L.

Elephas recki recki Dietrich, 1915

A fragment of a mandible, ASB-199, bears a slightly worn molar. Eleven plates remain, but one is probably missing anteriorly. Only slightly worn, the plates consist of numerous isolated islands that fuse with wear into forwardly concave plates, with only minor median expansion, and without any tendency towards loxodont shape. The number of plates, together with the width (73 mm), fit m2 rather than m3, and its height (ca. 130 mm) is the maximum value reported by Beden (1979) for *E. recki recki*. This subspecies is known from the lower Pleistocene onwards, the last and most evolved subspecies of the *E. recki* lineage. Thus, we refer it to this taxon.

Order PERISSODACTYLA Owen, 1848

Family RHINOCEROTIDAE Gray, 1821

Genus *Diceros* Gray, 1821

Diceros cf. *bicornis* (L.).

A maxillary fragment with M2 and M3, ASB-139, is the most definite evidence of *Diceros*. The teeth are badly dam-

aged, but the transverse orientation of the lophes and absence of crista on M2 are very clear. It certainly belongs to *Diceros*, but specific identification is impossible. Several other fragmentary remains may belong to *Diceros*. The dimensions of an astragalus, ASB-167, fall within the range of variation of the living *D. bicornis* (Guérin, 1980, mean and range in brackets):

Maximum width = 85 (84; 78–90); distal articular width = 72 (68; 60–73).

Ceratotherium may also be present in the Asbole fauna, but definite evidence is still lacking, because distinction of the two living African genera is difficult on fragmentary remains.

Family EQUIDAE Gray, 1821

Genus *Equus* L.

Equus sp.

Two incisors and a half-molar are the only Equid (probably zebra) remains. The molar has a stenoian double-knot, and the incisors have cones, but specific identification is impossible.

Order ARTIODACTYLA Owen, 1848

Family HIPPOPOTAMIDAE Gray, 1821

Genus *Hippopotamus* L.

Hippopotamus cf. *amphibius* L.

Hippopotamids are quite rare in Asbole. The best specimen is a maxilla, ASB-9 (L M1–M3 = 141.5). It is indistinguishable from the living *H. amphibius*, but no diagnostic feature allows a specific identification.

Family SUIDAE Gray, 1821

Genus *Metridiochoerus* Hopwood, 1926

Metridiochoerus modestus (van Hoepen and van Hoepen, 1932)

Two m3s, ASB-45 and ASB-246, plus a third one in a mandible fragment (unnumbered), and an M3, ASB-233-20 (Fig. 8) strongly resemble those of warthog, but are smaller. The pillars of the anterior pair have a poorly formed T-shape pattern, which is still less clear on the second pair, and all other pillars are oval or circular in section. Teeth of *Metridiochoerus/Phacochoerus* are not easy to measure, because of their trapezoidal shape, but those from Asbole are clearly smaller than those of *Phacochoerus* s.str., as shown by the measurements of the m3s in Table 2.

So, the size of these teeth impedes their assignment to the living species, but their morphology is more simplified in the direction of the warthog than those of *M. modestus* from the Lower Pleistocene of Koobi Fora (Harris and White, 1979: Fig. 115), Olduvai Bed I (Cooke, 1982) or Sterkfontein Member 5 (Cooke, 1994), and they resemble perhaps more the specimen of the late Lower Pleistocene of Olduvai Bed IV; unfortunately Leakey (1958: Pl. 18) illustrated only upper teeth.

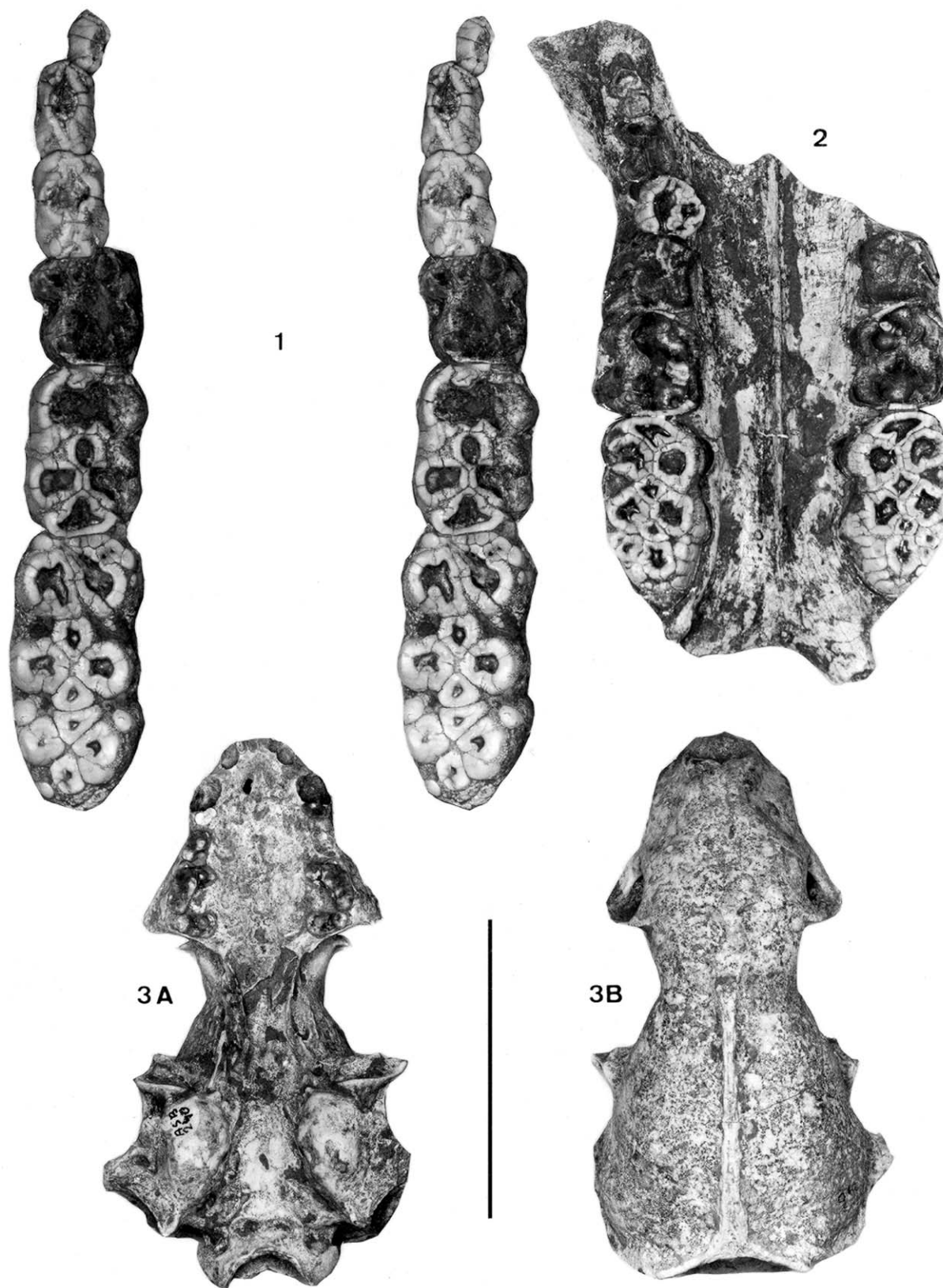


Fig. 6. (1) *Kolpochoerus majus*, ASB-257-1, stereo view of lower tooth-row. (2). *K. majus*, ASB-169, maxilla. (3) *M. capensis*, skull ASB-240, A: ventral and B: dorsal views. Scale = 50 mm for Fig. 6(1), 75 mm for Fig. 6(2,3).

(1) *Kolpochoerus majus*, ASB-257-1, vue stéréo de la série dentaire inférieure. (2) *K. majus*, ASB-169, maxillaire. (3) *M. capensis*, crâne ASB-240, A : vue ventrale ; B : vue dorsale. Échelle = 50 mm pour la Fig. 6(1), 75 mm pour la Fig. 6(2,3).

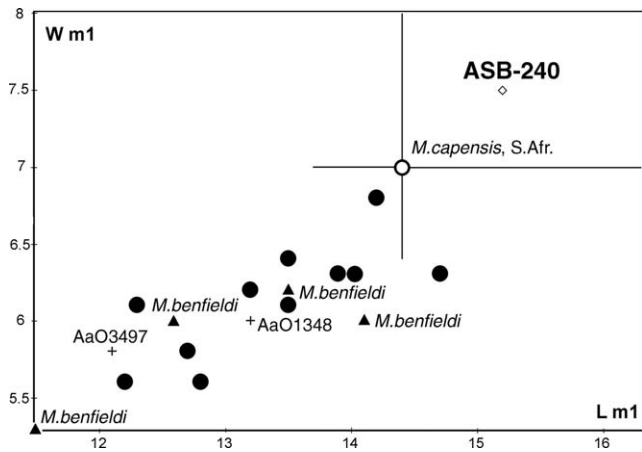


Fig. 7. Length × width scatter plot of *Mellivora* m1. Dots = Recent *M. capensis*, central and East Africa; mean and range of South African specimens after Henedy (1974).

Graphique longueur/largeur des m1 de *Mellivora*. Points = *M. capensis* actuel, d’Afrique centrale et orientale ; moyenne et intervalle de variation des spécimens sud-africains d’après Henedy (1974).

Genus *Kolpochoerus* van Hoepen and van Hoepen, 1932
Kolpochoerus majus (Hopwood, 1934).

This is by far the most common suid in Asbole, as in other Ethiopian sites of similar age (Bodo, Bouri-Daka). We recovered several mandibles, maxillary fragments (Fig. 6(1,2)) and isolated teeth but, as is usually the case for pigs, post-cranial elements are relatively rare. The best specimen is a nearly complete female cranium, ASB-198-2 (Fig. 9(2)), from the top of the top conglomerate. Its dimensions, compared with those of the Bodo skull L6-10, collected by J. Kalb and his team, are:

	ASB-198-2	L6-10
Length M1-M3 (basal)	78	76
L from front of I1 to back of M3	232	231
L condyle-Pmx	390	365
L condyle-back of M3	152	146
Minimum occipital width	108	100+
Maximum occipital width	155	132
Occipital height (from opisthion)	135	122
L from orbit to front of canine	195	198

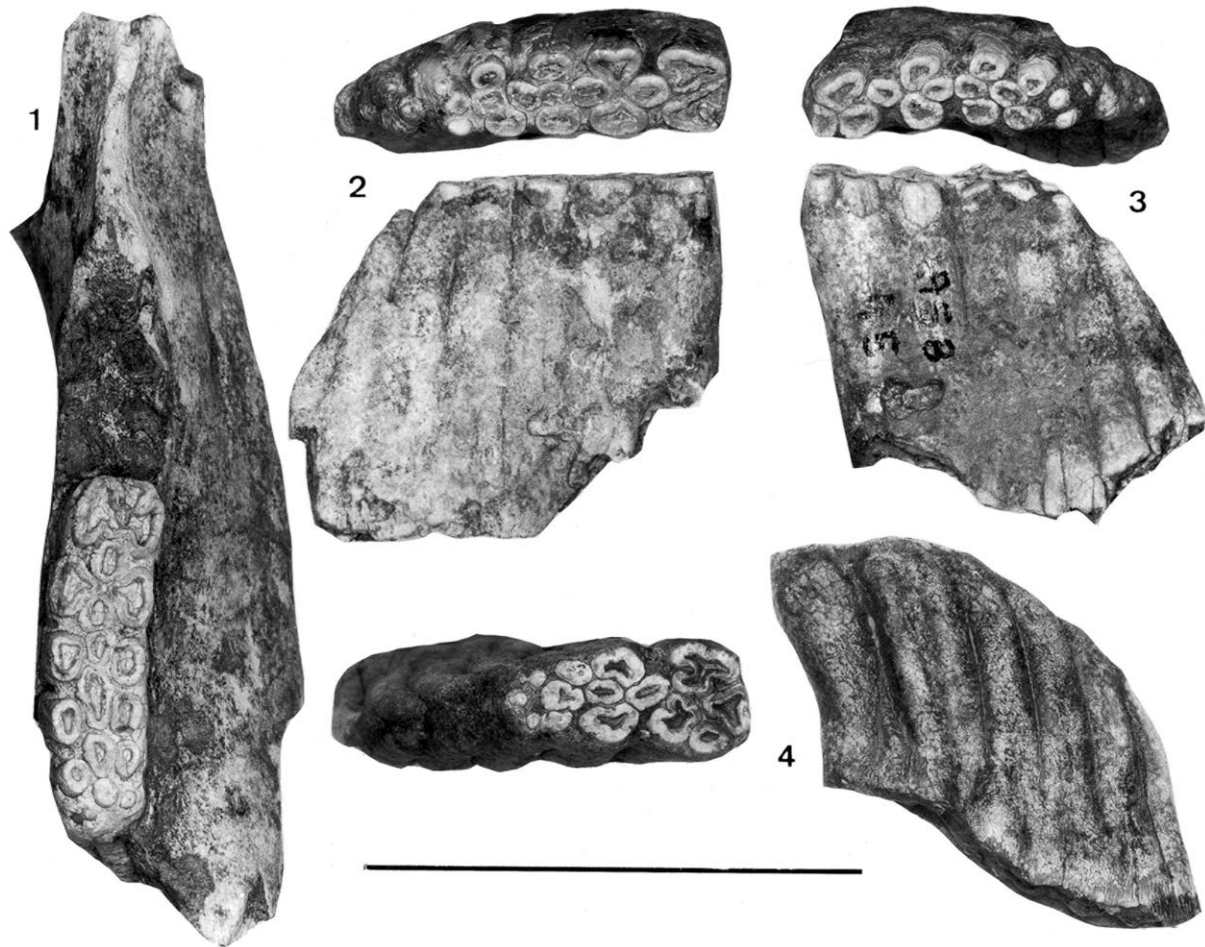


Fig. 8. *Metridiochoerus modestus*. (1) Lower jaw, no number. (2) ASB-246-5, m3, occlusal and labial views. (3) ASB-45, m3, occlusal and labial views. (4) ASB-233-20, M3, occlusal and lingual views. Scale = 50 mm.

Metridiochoerus modestus. (1) Mandibule, sans numéro. (2) ASB-246-5, m3, vues occlusale et labiale. (3) ASB-45, m3, vues occlusale et labiale. (4) ASB-233-20, M3, vues occlusale et linguale. Échelle = 50 mm.

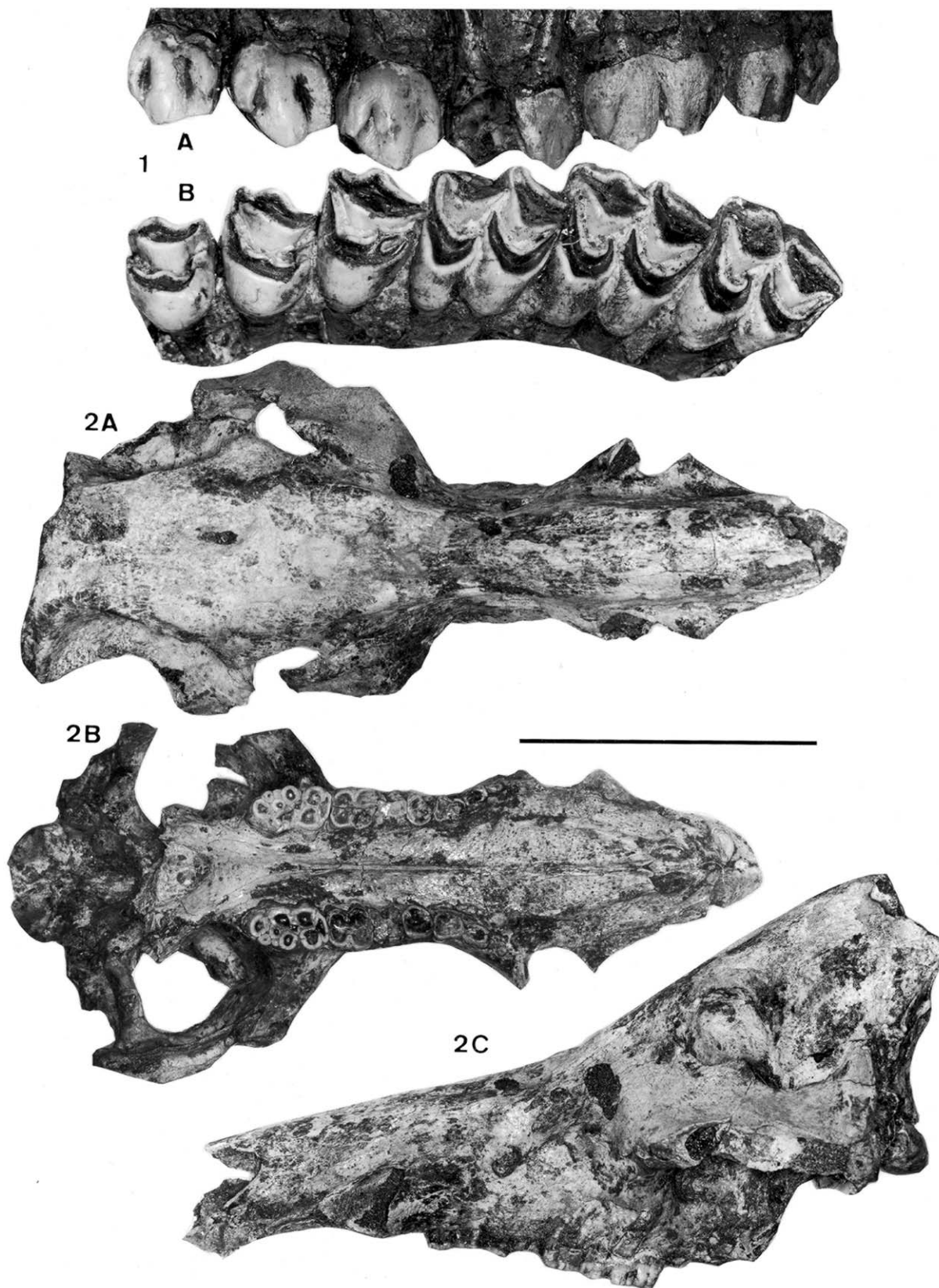


Fig. 9. (1) Aff. *Giraffa pygmaea*, upper tooth-row from below the "top conglomerate", A: labial and B: occlusal views. (2) *Kolpochoerus majus*, skull ASB-198-2 in A: dorsal, B: ventral and C: lateral views. Scale = 50 mm for Fig. 9(1), 150 mm for Fig. 9(2).

(1). Aff. *Giraffa pygmaea*, série dentaire supérieure récoltée sous le « top conglomerate », A : vue labiale, B : vue occlusale. (2). *Kolpochoerus majus*, crâne ASB-198-2, A : vue dorsale, B : vue ventrale, C : vue latérale. Échelle = 50 mm pour la Fig. 9(1), 150 mm pour la Fig. 9(2).

Table 2
Length of lower m3s of *M. modestus* and *Phacochoerus*
Longueurs des m3 de *M. modestus* et *Phacochoerus*

	<i>M. modestus</i>				<i>P. aethiopicus</i>	<i>P. africanus</i>		
	Asbole			No	Old Bed I	Swartkrans	MSA	Recent
	246-5	45	242		Cooke (1982)	Cooke (1993)	Ewer (1957)	Ewer (1957)
Overall length	45	ca. 40	48	ca. 43	50.5		48–63.8	55–65
Length at mid-height, perpendicular to pillars	43.5			41				
“Length”						52		

Because of recent discoveries of additional material belonging to two *Kolpochoerus* species (*K. majus* and *K. phacochoeroides*) that were previously poorly known, a taxonomic revision of the genus might be necessary. Pending such revision, we will only mention the major features of the Asbole *K. majus*:

- the skull is rather short. The muzzle is antero-posteriorly shorter than in advanced forms of *K. limnetes*, such as those from Peninj, although less so than that of *K. phacochoeroides* from North Africa (Geraads, 1993);
- the mandibular symphysis is shorter and broader than that of *K. limnetes*. The difference also holds for the *K. majus* mandible from Bodo in Addis Ababa, but differs from the description of a specimen from Kapthurin by Harris and White (1979: 41);
- the parieto-occipital region is not stretched backwards, resulting in an occipital plane which is nearly vertical and both low and broad, the width over the occipital crest being greater than the occipital height, in contrast to most *K. limnetes* (Harris, 1983: Tab. 6.15);
- although the zygomatic arches of the Asbole cranium are not completely preserved, it is clear that they were less laterally inflated than in the Peninj specimen. In vertical view, the anterior root is more strongly oblique with respect to the sagittal plane;
- in the available sample, M3 is more variable than m3. The M3s in the Asbole cranium (and that of the Bodo cranium: L6–10) consist of two pairs of pillars, plus a talon consisting of a large postero-medial pillar and five smaller ones buccal to it. In other specimens, the talon may consist of more than 10 tubercles. The M3 of *K. limnetes* may have the same number of pillars, but they are less closely packed, and the tooth is, on average, longer relative to its breadth. The m3 usually consists of three well-defined pairs of pillars plus a median distal pillar, but smaller pillars may be present around it, and between the second and third pairs. Some *K. limnetes* M3/m3s from the Shungura Fm, especially from members C and D, do not have additional pillars, but the teeth are longer and the pillars themselves are not simple.
- *K. majus* has never been described in detail, but has been reported from several Early and early Middle Pleistocene East African sites: Olduvai upper Bed II–IV, Kapthurin, Olorgesailie, latest Omo Shungura, Konso-Gardula, Bouri-Daka, Garba IV (Harris and White, 1979; Asfaw et

al., 1992; Gilbert et al., 2000; Geraads et al., [in press]). Its earliest record might be the Nyabusosi Fm of Uganda (Pickford, 1994). It probably branched off from the *K. limnetes* lineage around the time of Shungura Members C–D, before the latter acquired its specialized morphology (*Kolpochoerus* “olduvaiensis” morph).

Family GIRAFFIDAE Gray, 1821

Genus *Giraffa* Brisson, 1762

Giraffa cf. *camelopardalis* L.

ASB-224 is a fragment of upper tooth-row with P2–P4. Its size (Length P2–P4 = 66) is similar to that of the recent giraffe (Length P2–P4 = 64–71 on five specimens) and it is clear that the teeth had the typical bulbous appearance of those of *G. camelopardalis*, the living species. It cannot be ruled out, however, that they belong instead to the extinct form, *Giraffa jumae* Leakey, which is of similar size, and can be distinguished only by its skull morphology.

Family BOVIDAE Gray, 1821

Genus *Tragelaphus* Blainville, 1816

Tragelaphus scriptus (Pallas, 1766)

A frontlet consisting of the two horn-cores ASB-219 and ASB-48 is the best specimen. The horn-cores are triangular in cross-section, with a sharp postero-lateral keel, a flattened posterior surface, and they are clearly twisted. Another horn-core ASB-252-7 is very similar. Their size and degree of antero-posterior compression (index: 26×36.4 for ASB-219/48, 26.2×37 for ASB-252-7) is almost identical with the mean of the recent *T. scriptus* (27.1×35.7 according to Gentry, 1985: 132). A juvenile horn-core ASB-119 can be referred to the same species, as well as two mandibular pieces, although the molar row is slightly shorter than that of the living form:

	p2–p4	m1–m3
ASB-52	24.5	
ASB-77		36.7
Recent <i>T. scriptus</i> : mean (minimum–maximum), $N = 9$	26.4 (22.8–29.5)	40.2 (37.5–44)

Genus *Taurotragus* Wagner, 1855

Taurotragus sp.

ASB-142 is a short piece of a rather large horn-core, lacking the base. Its cross-section is almost round ($49+ \times 55$) except for a conspicuous keel and a hint of another one, with

a flattened surface in between. These features indicate a Tragelaphini. The tight spiraling points to *Taurotragus*, the eland, rather than to *Tragelaphus*, from which genus it arose probably in the late Lower Pleistocene. No horn-core of eland type is definitely known in the early Pleistocene (Gentry and Gentry, 1978; Gentry et al., 1995).

Three mandibular fragments, ASB-70 (m1–m3 = 85.5), ASB-252-1 (L m3 = 41) and ASB-108 (L p2–p4 = ±52) are most probably of the same species.

Genus *Bos* L.

Bos sp.

The most remarkable fossil found from Asbole is the Bovine fragmentary skull ASB-198-1 (Fig. 10(1)), excavated in situ at the same stratigraphic level as the *Kolpochoerus* cranium, on top of the top conglomerate. Therefore, its stratigraphic origin is not in doubt. It consists mainly of the frontal bones, with the right orbit, part of the left one, the whole forehead and the upper part of the occipital area, but the horn-cores are missing. It may be that the back of the skull is slightly compressed dorso-ventrally, but not much, because no conspicuous crack is visible, and the orbit has retained its normal, circular shape.

The very large size and overall morphology of the specimen shows that it belongs to Bovini. It can readily be distinguished from *Syncerus* (the living African buffalo), "*Pelorovis*" *antiquus* (= *Bathyleptodon*, *Homoioceras*) and also from Asian buffaloes by the extreme backward shift of the horn-core insertions, which are set far behind the orbits. The only African Pleistocene Bovini bearing resemblance to the Asbole cranium are *Pelorovis oldowayensis* Reck, best known from Bed II to IV at Olduvai (Gentry, 1967), and its close relative *P. turkanensis* Harris from Koobi Fora and Melka Kunturé. However, the Asbole skull can be clearly distinguished from them by the following features:

- the orbits are much more salient, and directed partly forwards, instead of facing laterally as in *Pelorovis*;
- the root of the zygomatic arch, below the orbit, is not particularly strong (Fig. 10(1B)), in contrast to *Pelorovis*, in which it is very deep anteriorly (Gentry, 1967: Fig. 2; Pl. 6, Fig. 1; Harris, 1991b: Fig. 5.10.B);
- the small supra-orbital foramina open wide apart on the forehead. They are much closer in *Pelorovis*;
- the post-orbital constriction is much stronger than in *Pelorovis*, in which the minimum breadth of the braincase is but slightly smaller than the maximum bi-orbital width;
- although nothing is preserved of the horn-cores themselves, there is no doubt that they were inserted wider apart than in *P. oldowayensis*, but perhaps not so much as in *P. turkanensis*;
- last, there is a strong ridge connecting the bases of the horn-cores and overhanging the occipital surface, of which only the upper part is preserved. This ridge is absent in *P. oldowayensis* and present, but much less developed, in *P. turkanensis*.

All the above-mentioned features of the Asbole skull match those of *Bos* s.str., and its assignment to this genus would be straightforward in Eurasia. Therefore, even though no *Bos* of this age has ever been reported from East Africa, we refer it to this genus, rather than to *Pelorovis*, which would imply convergent evolution of several characters from a species like *P. turkanensis*. In Eurasia, *Bos* is best known by the species *B. primigenius*, which appears to be only slightly distinct from the Indian *B. namadicus*, *B. acutifrons* and *B. planifrons*. One of the features said to distinguish *B. namadicus* is the strong extension of the supra-occipital inter-cornual ridge (Lydekker, 1878; Pilgrim, 1939); this is a feature also found in Asbole. The sagittal crest of the forehead of *B. acutifrons* is absent on ASB-198-1, but the rather close approximation of the horn-cores above the occipital is a similarity between these forms, that we regard as more important. The Asbole *Bos* might therefore be closer to *Bos* cf. *acutifrons*, but no revision of these Asian forms has been undertaken recently; as a result differences between them are not well established, and we prefer to keep the specific identification open.

Measurements

Length from back of orbit to top of occipital (sagittal)	237
Width over posterior supra-orbital foramina	155
Minimum post-orbital width	190
Maximum bi-orbital width	257
Length from orbit to horn-core/pedicle limit	ca. 140

Among a few limb-bones, a metacarpal ASB-173 and an uncollected metatarsal can be compared to other taxa. Both are longer than those of the extant *S. caffer* or *S. acoelotus* from Olduvai (Gentry and Gentry, 1978), and are intermediate in length and robustness between the two *Pelorovis* species. They fit better the upper Pleistocene *B. "opisthonomus"* Pomel, from Algeria, an extinct variety of *B. primigenius* (Fig. 11).

Syncerus/Pelorovis sp.

The mandible ASB-3 is of a large Bovine, which is distinct from *Bos*. The p4 is strongly molarized, with an elongated metaconid closing the anterior valley, a feature not encountered in *Bos*. It would fit an African Bovine of the *Syncerus/Pelorovis* group, but the specimen (L m1–m3 = 96; p2–p4 = 57) is certainly too small for *P. oldowayensis* (Gentry and Gentry, 1978: Fig. 8; Gentry, 1980: Fig. 16). It can provisionally be referred to a buffalo close to *S. caffer* or *P. turkanensis*.

Genus *Oryx* Blainville, 1816

Oryx sp.

ASB-28 and ASB-260-1 are two horn-core fragments, straight and almost cylindrical in their upper part, slightly compressed (38 × 33.5 and 43.5 × 39, respectively) lower down, but they cannot be oriented. Specific identification is impossible.

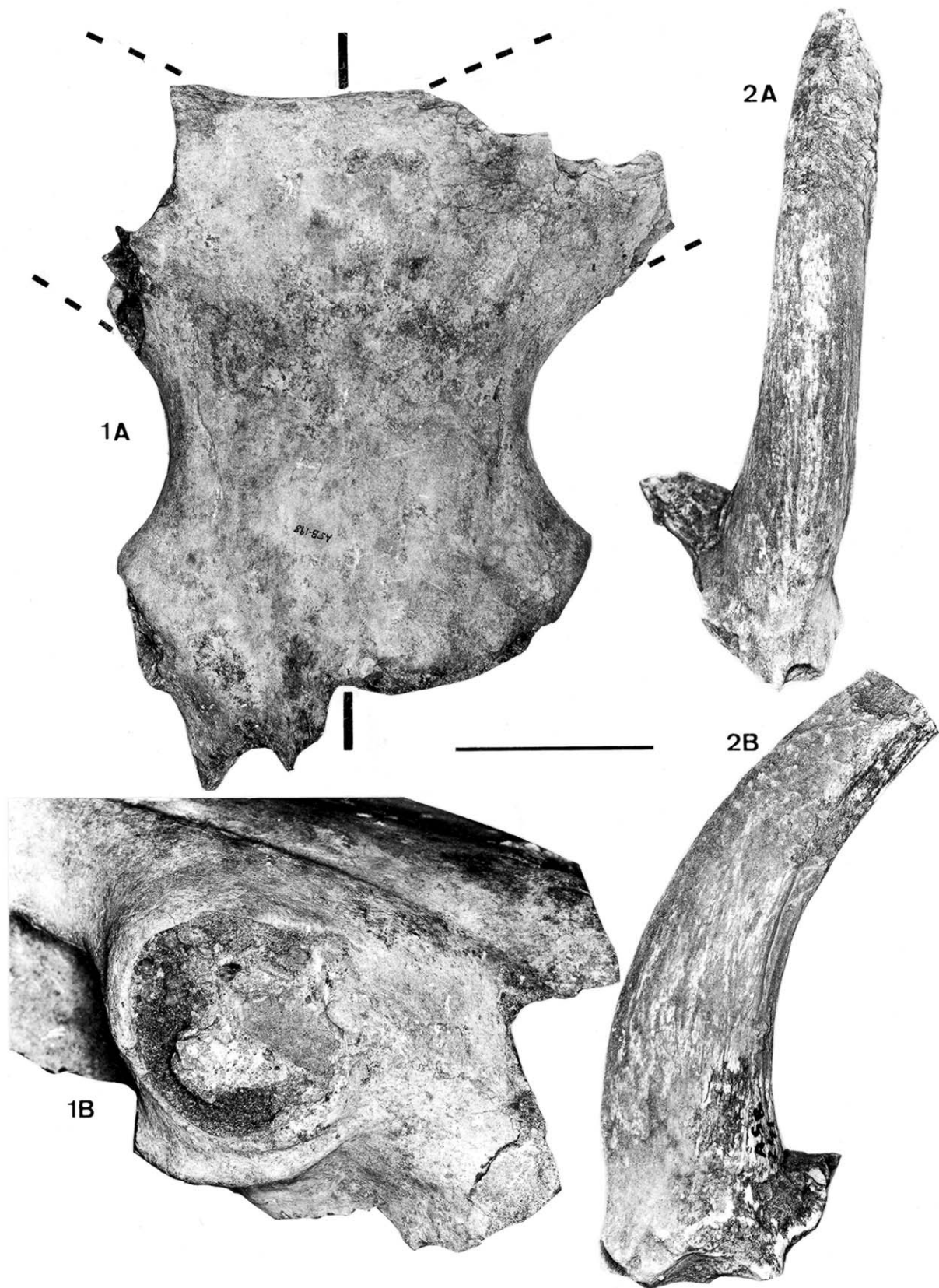


Fig. 10. (1) *Bos* sp., ASB-198-1, skull fragment. A: dorsal view (thick line: sagittal plane; broken lines: approximate outline of horn-cores); B: detail of right orbit. (2) *Gazella* aff. *granti*, ASB-241, left horn-core in A: anterior and B: lateral views. Scale = 100 mm for Fig. 10(1A), 50 mm for Fig. 10(1B, 2).
 (1) *Bos* sp., ASB-198-1, crâne incomplet. A : vue dorsale (trait épais : plan sagitta ; tireté : contour approximatif des chevilles osseuses) ; B : détail de l'orbite droite. (2) *Gazella* aff. *granti*, ASB-241, cheville gauche, A : vue antérieure B : vue latérale. Échelle = 100 mm pour la Fig. 10(1 A), 50 mm pour la Fig. 10(1B, 2).

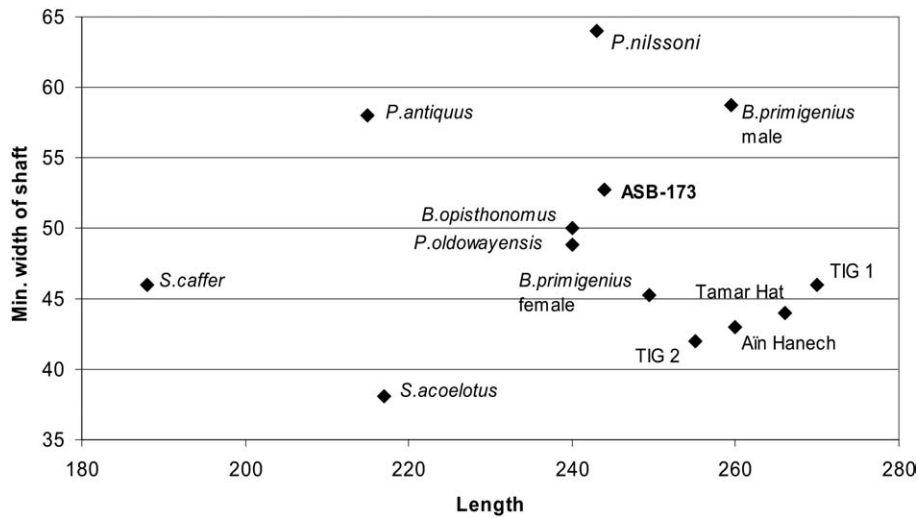


Fig. 11. Plot of length vs. minimum width of shaft of Bovine metacarpals. Measurements from Brugal (1985), Gentry (1967, 1980), Geraads (1981). Graphique longueur/largeur minimum de la diaphyse des métarpes de Bovini. Mesures d'après Brugal (1985), Gentry (1967, 1980), Geraads (1981).

Genus *Kobus* A. Smith, 1840

Kobus kob (Erxleben, 1777)

This is the most common large mammal in Asbole. We collected about 20 horn-cores, a braincase (ASB-248) and a complete skull (ASB-249). The horn-cores have the same size and morphology as in the living species, in contrast to those of the *Kobus kob* from the lower Pleistocene of Olduvai Beds II–III and Omo Members J–L, which are larger and/or more compressed (Fig. 12). The only difference from the modern form is the greater size of the occipital, which is also relatively higher, but this might be an allometric effect.

Measurements of the most complete specimens are:

	ASB-249	ASB-248
Length from occipital condyle to P2	ca. 215	
P2-M3	72	
Width over ant. tuberosities of basi-occipital	36	
Minimum post-orbital width		70
Width over pedicles	105	2 × 53
Basal horn-core diameters (A-P × transverse)	50.5 × 40	47 × 42.5
Width over base of paroccipital processes	ca. 95	93
Occipital height (from opisthion)	51	50

Genus *Redunca* H. Smith, 1827

Redunca sp.

A single horn-core with part of the frontal, ASB-243, belongs to *Redunca*. It is antero-posteriorly compressed, almost straight in anterior view, slightly curved backwards at the base and then forwards, and more strongly divergent than those of the kob. The orbital rim is very prominent.

Two mandibular fragments probably belong to the same species. The p4 differs from that of *Kobus* by the narrowness and greater length of the talonid, and more transverse orientation of the metaconid, which does not grow forwards.

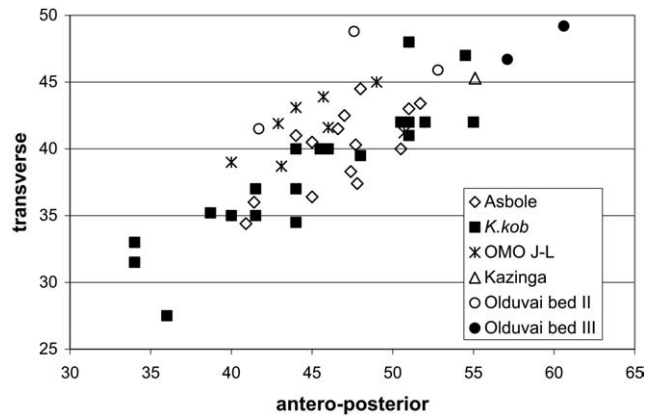


Fig. 12. Basal horn-cores dimensions of living and fossil *Kobus kob*. Mainly from Gentry and Gentry (1978) and Gentry (1985). Dimensions basales de chevilles osseuses de cornes de *Kobus kob* fossiles et actuels. Surtout d'après Gentry et Gentry (1978) et Gentry (1985).

Measurements of Reduncine lower teeth:

	P2–p4	m1–m3
<i>Kobus kob</i>		
ASB-12	24.7	–
ASB-18	29.4	51.7
ASB-50	–	51
ASB-73	–	49.7
ASB-75	25.4	49.8
ASB-125	–	49.5
ASB-164	–	48.3
<i>Redunca</i> sp.		
ASB-72	ca. 22.5	42.2
ASB-163	–	41.4

Genus *Connochaetes* Lichtenstein, 1814

cf. *Connochaetes* sp.

Alcelaphine remains are uncommon, but at least two taxa are present. ASB-149 is a horn-core fragment, probably the

middle part, of a *Connochaetes* of rather small size (diameters 35×39). The teeth are large, however, and it is possible that a larger taxon, perhaps *Rhynotragus* (= *Megalotragus*) is also present. These teeth are ASB-197, a slightly worn upper molar (25.4×18.4) and ASB-242, an M2 (30×20).

Genus *Damaliscus* Sclater and Thomas, 1894

Damaliscus niro (Hopwood, 1936)

The right part of a brain case with most of the attached horn-core, ASB-152, provides definite evidence for the occurrence of this extinct species, known from Olduvai Middle Bed II onwards in East Africa, possibly lingering until the late Pleistocene in South Africa.

The horn-core bears weak transverse ridges and is rather strongly curved backwards and uprightly inserted. Its cross-section is almost symmetrical but not very compressed (59.5×51.5) with little flattening of the lateral side. There is a large sinus in the pedicle. The poorly preserved brain case is long for an Alcelaphine (length from occipital crest to front of horn-core = 153). There is no parietal boss; the paroccipital process is inclined backwards.

Genus *Gazella* Blainville, 1816

Gazella cf. thomsoni Günther, 1884

A gazelle of medium size is represented by a horn-core, a brain case and two teeth. The brain case (ASB-256-1) has strong temporal ridges anteriorly that quickly fade out posteriorly, the frontals extend posteriorly beyond the (missing) horn-cores, and the *foramen ovale* is small. The horn-core (ASB-61) is strongly inclined backwards, but slightly curved, not twisted, very compressed (31.5×20.3) with a flat external surface and a regularly convex medial one, and the maximum transverse diameter is rather posterior. This last feature is reminiscent of *G. praethomsoni* Arambourg (Gentry, 1985) but the first one is more like the living species, to which we shall tentatively refer it.

Two m3s, ASB-183 and ASB-184, probably from the same individual, are about 18.5 mm long; their third lobe is but slightly shorter than the first two.

Gazella aff. granti Brooke, 1872

A large left horn-core with part of the frontal, ASB-241 (Fig. 10(2)), belongs to a large gazelle (index 44.6×28.6) noticeable by its conspicuous anti-clockwise torsion, and medial side more flattened than the lateral one, in contrast to other gazelles. Another specimen (ASB-150) has a similar cross-section, but is slightly smaller (39.6×24.4) and is not twisted. The large size of these specimens recalls *G. granti*,

the horn-cores of which are also strongly compressed and sometimes have a hint of homonymous torsion, especially in those varieties with very divergent tips, but have a more or less symmetrical cross-section. Thus, although they are probably closely related to *G. granti*, the Asbole specimens might belong to a new extinct variety.

ASB-117, a lower jaw with almost complete dentition (p2 missing) is probably of the same species. The lingual valley of p4 is wide open, m2 has an incipient goat fold, and the third lobe of m3 is long, and its internal valley is still visible. The premolars look more reduced than in the living form, but the loss of p2 prevents any quantifying of the difference. Its dimensions are:

p2–p4 = ca. 28; m1–m3 = 59; p2–m3 = ca. 88.3; L m3 = 24.7.

4. Fossils from below the “top conglomerate”

We have not included in the “Asbole fauna” those fossils that come from below the “top conglomerate”. As it seems that there are several sedimentary gaps in this lower part of the section, these fossils may be significantly older. Indeed, although they consist only of a limited sample, their composition is distinct from the Asbole fauna, and their value is enhanced by the occurrence of at least one new species, and of a Giraffid maxilla which raises questions about a poorly known species. We will describe only the most important specimens.

Family HERPESTIDAE Gill, 1811

Genus *Crossarchus* Cuvier, 1825

Crossarchus nov. sp.

ASB-206-3 is a fragment of a lower jaw with m1–m2 (m1 = 6.0×4.2 ; m2 = 5.0×3.6), which shows the following features (Fig. 13):

- the trigonid of m1 is short, with a paraconid wing not much longer than the metaconid, and high, with the metaconid slightly lower than the paraconid and protoconid;
- the talonid is narrower than the trigonid, and bears a high hypoconid much more anterior than the postero-lingual crest;
- m2 is not much shorter and not much narrower than m1.

The paraconid is not distinct from the metaconid, but the trigonid valley is closed distally.

The living species *Mungos mungo* and *M. gambianus* resemble the Asbole herpestid, but are smaller. The lingual

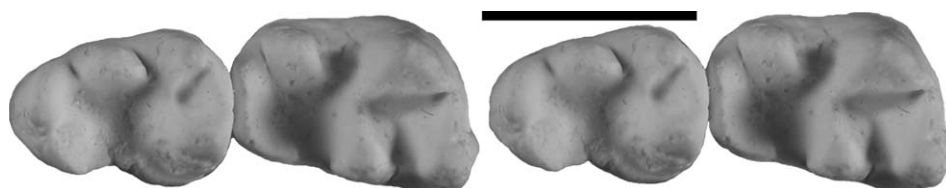


Fig. 13. *Crossarchus* n. sp. ASB-206-3, from below the top conglomerate, occlusal view of m1 and m2 (cast); stereopair. Scale = 5 mm.
Crossarchus n. sp. ASB-206-3, récolté sous le « top conglomerate », vue occlusale stéréo de m1 et m2 (moulage). Échelle = 5 mm.

tubercles of the trigonid of m1 are closer to each other, and may even fuse on some specimens, as on m2. On this tooth, the talonid is narrow, and the trigonid valley is not blocked distally.

The fossil species *M. dietrichi* Petter, 1963, from Laetoli and Olduvai Bed I (Petter, 1963, 1973) is close to ASB-206-3 in size, but the trigonid of m1 is shortened, as in the living forms, and m2 is much narrower than m1.

In *Crossarchus obscurus* the lingual tubercles of the m1 trigonid are situated wide apart, thus more like those of ASB-206-3, but both molars, and especially m2, are narrow.

Cynictis penicillata is almost as large as ASB-206-3, but it differs from it in several features. On the fossil, the talonids of m1 and m2 are similar, while in *Cynictis* the hypoconid of m1 is much stronger than that of m2, the reverse being true of the entoconid–hypoconulid complex. In *Cynictis*, the m1 is narrow, its trigonid is much less symmetrical than on the fossil, with a long paraconid wing, and the paraconid of m2 is still distinct from the metaconid. These latter differences are obviously primitive.

Definite specific identification is probably not possible with such a fragmentary specimen, but it cannot be referred to a living species. Its m1 trigonid is intermediate between those of *Cynictis* and *Mungos*, and more like that of *Crossarchus*, so we refer it provisionally to this genus.

Family SUIDAE Gray, 1821

Genus *Metridiochoerus* Hopwood, 1926

M. hopwoodi (Leakey, 1958) or *M. andrewsi* Hopwood, 1926

ASB-234, a lower jaw fragment with a damaged m1 and slightly worn m2 is the only specimen that can be referred to this genus. The m2 consists of two pairs of pillars plus a very strong talonid bulging backwards distal of the roots. The four main pillars are almost H-shaped, thus less simplified in morphology than those of *M. modestus* or *M. compactus*, and the tooth is also larger (basal length = ca. 27; maximum length = 35; width = 18) than in these species. On the other hand, it falls within the size ranges of *M. hopwoodi* and *M. andrewsi* (cf. Harris and White, 1979). With a single tooth, the choice between the two species is problematic. The latter is known as early as Omo Shungura B, while the former has been tentatively reported as late as Isenya (Brugal and Denys, 1989).

Family GIRAFFIDAE Gray, 1821

Genus *Sivatherium* Falconer and Cautley, 1836

Sivatherium maurusium (Pomel, 1893)

ASB-227-2 is one of the few remains coming from the right bank of the Awash. It consists of a mandibular fragment with most of p4, m1 and a piece of m2, all well-worn, of much larger size than *Giraffa* (L p4–m1 = ±90). The p4 is particularly broad and probably had, like all Giraffids, a long metaconid completely closing the lingual valley. The species has a long chronological range, from the early Pliocene until the early Middle Pleistocene, at least.

Giraffidae indet. aff. *Giraffa pygmaea* Harris, 1976.

A left maxilla with complete dentition ASB-231 (Fig. 9(1)) belongs to a small Giraffid the size of “*Giraffa*” *pygmaea* from the African Plio-Pleistocene, or of *Palaeotragus rouenii* from the upper Miocene of the Eastern Mediterranean. What is preserved of the maxilla shows that the infra-orbital foramen was more anteriorly placed than P2, in contrast to *Giraffa*. The diagnostic importance of the molars is low, but the premolars are more characteristic. They differ from those of *G. camelopardalis* (and of ASB-224) by the following features:

- their smaller size relative to the molars (length P2–P4 = ±51; L M1–M3 = 73; giving an index Pm/M of about 70, a conservative value for Giraffids);
- the shape and narrowness of P4. This tooth is more triangular than in *Giraffa*. It is also clearly narrower than M1, whereas the difference is weak in *Giraffa*;
- their brachydonty, which is only moderate, remembering more the Miocene *Palaeotragus*, than the strongly brachydont *Giraffa*;
- the weakness of the labial ribs and folds, are quite different from the high ridges and deep folds of the labial walls of *Giraffa* premolars.

They differ from those of *Okapia* by their weak styles, and by the anterior closure of the valley of P2 and P3. Fossil representatives of this genus are still unknown.

Had this specimen been found in the Upper Miocene of the Eastern Mediterranean, we might have referred it to *Palaeotragus*, a widespread super-genus at that time, but its provenance from the Plio-Pleistocene of East Africa make it more difficult to identify, because all East African Plio-Pleistocene small and medium Giraffids seem to be referable to *Giraffa*.

According to Harris (1991a), there are two species of small size, *G. pygmaea* Harris and the slightly larger *G. stillei* (Dietrich, 1942) (= *G. gracilis* Arambourg, 1945). Upper premolars of the former species are unknown, or at least undescribed. However, the holotype (Harris, 1991a: Fig. 4.6), a mandible, has a very large p4, suggesting that the upper premolars were also of large size. The dentition of *G. stillei* is better known. Upper dentitions from Omo, the holotype of *G. gracilis* (Arambourg, 1948: Pl. 22, Fig. 1) and undescribed specimens in the National Museum, Addis Ababa, have large premolars with broad P4s, a synapomorphy with the living species. This seems to be also true of most of the material from Laetoli (Dietrich, 1942: Pl. 21) although its significance is weakened by the composite nature of some of the sets of teeth illustrated as tooth-rows by Dietrich, which have an average index of about 75 (estimated from Dietrich's figures), thus certainly higher than ASB-231. Anyway, all of the teeth from Laetoli that we have seen in the KNM are typical of *Giraffa*.

It can be said, therefore, that the small Giraffid from Asbole is probably distinct from the small species previously reported from the Plio-Pleistocene of East Africa. Its primitive premolars make a close phyletic relationship with *Gi-*

raffa unlikely. It could in turn be related to one of the few African “Palaeotragines”, such as the ones from Langebaanweg (Harris, 1976: Fig. 1) and Toros-Menalla in Chad (Likius, 2002), which are, however, of much earlier age.

5. Paleocology of the Asbole fauna

Carnivores are not usually good ecological indicators, but it should be noted here that the closest living relatives of the Asbole mongooses prefer rather closed biotopes, usually not far from water, and that both the inhabitants of open country (hunting dog, cheetah) and of the forest (panther) are missing in our assemblage. Overall, carnivores from Asbole suggest humid bushy landscape near a water source.

No screening has been undertaken yet, so the resulting proportions of rodents are strongly biased towards large forms. However, the rodents that are present chiefly represent mesic environments with ubiquitous herbaceous growth. As mentioned above, *Thryonomys* is a mesic adapted genus, and *T. swinderianus* is especially adapted to moist or swamp-like conditions. *Otomys* is another mesic adapted, specialized herbivore and in conjunction with *A. niloticus* further indicate a moist habitat with abundant herbaceous vegetation. The large size of the Asbole *Otomys* might suggest a more favorable (less arid) environment than at Isenya, Olduvai Bed IV, or Kapthurin, but additional material is needed before its precise relationships can be determined. *Tachyoryctes* is a burrowing rodent that feeds on grass leaves and roots in moist open country, though usually at high altitudes.

Among ungulates the most dominant group are the reduncines, especially *Kobus*, and the suid *Kolpochoerus*. This abundance of reduncines, which are well-known to live in edaphic humid grasslands, and of *Kolpochoerus*, which was also water-dependent (Harris and Cerling, 2000), show that this kind of environment was well represented in Asbole. According to Bishop et al. (1999), both *K. majus* and *M. modestus* preferred closed habitats. Among bovines, antilopines, alcelaphines, tragelaphines, bovines, and *Oryx* are less common, but not rare, and there are two other suid species. Taxonomic and ecological diversity is rather high despite the relatively poor number of collected specimens, suggesting a mosaic landscape. The tragelaphines, *Diceros*, perhaps the Suidae, and especially the abundance of colonies, show that a significant part of the area must have been occupied by more forested areas, but drier biotopes were present also, as shown by alcelaphines, antilopines, and *Oryx*. Pending detailed sedimentological and taphonomic analysis, we may surmise that the wooded environments were gallery forests along the main river, and derive from the near-channel deposits.

6. Biochronology

To augment the temporal interpretations of the Asbole fauna (excluding the fossils from below the “top conglomer-

ate”) we compared it against seven other late Early Pleistocene/Middle Pleistocene East African faunas: Kanjera, Olorgesailie, Isenya, Bodo, Bouri-Daka, Olduvai Bed IV, and Lainyamok. Insectivores are excluded as they are absent from the Asbole fauna (Table 3). For the sake of completeness, we have also included a preliminary list of the Primates (Alemseged and Geraads, 2000), not studied here.

The faunal list of Kanjera North is a composite (Ditchfield et al., 1999) from several levels. It has not been radiometrically dated, but a part of the section at least is earlier than the Brunhes/Matuyama boundary, and could encompass the Jaramillo subchron as well. Faunal evidence might suggest that it is the earliest of the sites considered here, because it still lacks *Pelorovis antiquus* and *Kolpochoerus majus*, but has *Loxodonta*, unlike all other localities, and *Parmularius angusticornis*, best known from Olduvai Bed II. This evidence is weak, however, because the latter species is also present at Bouri-Daka, and because *K. majus* is already present at the earlier site of Konso-Gardula (Asfaw et al., 1992). Bouri-Daka (Gilbert et al., 2000; Asfaw et al., 2002), dated to ca. 1 Ma, could be slightly younger. *Pachycrocuta* aff. *brevirostris* and *Kobus sigmoidalis*, in addition to *P. angusticornis*, suggest a lower Pleistocene age.

The Olorgesailie fauna is mostly known through faunal lists. The lack of *K. olduvaiensis* suggests that it post-dates the extinction of this species, but the fauna is otherwise similar to those of Kanjera, Konso-Gardula and Bouri-Daka.

The fauna from Isenya is poor and fragmentary (Brugal and Denys, 1989). The occurrence of *Hipparion* shows that it should not be placed very high in the Middle Pleistocene, but it is hard to be more assertive.

Several extinctions seem to occur afterwards, and both Bodo and Asbole lack evidence of *Hipparion*, *M. hopwoodi* and *M. compactus*. They also lack *Megalotragus* (although some teeth from Asbole might belong to it), but the genus lingered until the late Pleistocene (Pickford and Thomas, 1984, as *Rusingoryx*).

Details of the vertical distribution of *M. compactus* at Kanjera North have been provided by Behrensmeyer et al. (1995) and Ditchfield et al. (1999). This suid is present up to bed KN-4. The normal polarity recorded at the top of this bed was correlated with Jaramillo by Behrensmeyer et al. (1995) on the basis of a correlation with Kanjera South, which is now known to be incorrect (Ditchfield et al., 1999). In fact, bed KN-4 probably covers the Matuyama/Brunhes boundary, thus providing an approximate extinction date for this species.

Hipparion is another useful biochronological indicator. It is already absent in Tighenif in Algeria, although this site has *M. compactus* (Geraads et al., 1986), but it is present at Isenya and in the Acheulean level of Gomboré II at Melka Kunturé, close in age to the Matuyama/Brunhes boundary (Cressier, 1980). Its absence from Bodo and Asbole suggest a later date for these sites.

The definite occurrence of the living genus *Alcelaphus* at Bodo, but not at Asbole, points to a later age for Bodo, the

Table 3

Faunal lists of East African Pleistocene sites, used for the correspondence analysis

Listes fauniques des sites du Pléistocène est-africain utilisées dans l'analyse factorielle

Bouri-Daka	Kanjera N	Olduvai IV	Ologesailie	Asbole	Bodo	Isenya	Lainyamok	Living
Primates								
cf. Colobus sp. gen. sp. indet.	Colobus sp.			Colobus sp. Cercopithecus sp.				Colobus sp. Cercopithecus sp.
Theropithecus oswaldi	Th. oswaldi	Papio sp. Th. oswaldi	Th. oswaldi	Papio sp. Th. oswaldi	Papio sp. Th. Oswaldi		Papio sp.	Papio sp.
Homo erectus				Homo sp.	Homo erectus	Homo sp.	Homo sp.	
Rodentia								
cf. Thryonomys sp.				T. cf. swinderianus Tachyoryctes sp. H. cristata Otomys sp.	Thryonomys sp.	Thryonomys sp.	Thryonomys sp.	Thryonomys sp. Tachyoryctes sp.
		O. petteri Dasymys sp. A. niloticus Aethomys sp.		A. cf. niloticus		H. cf. africae australis Otomys sp. A. niloticus Aethomys sp. Thamnomys sp.		Hystrix sp. Otomys sp. Dasymys sp. A. niloticus Aethomys sp. Thamnomys sp.
		Zelotomys sp. Thallomys sp.				Mus sp. Praomys sp.		Zelotomys sp. Thallomys sp. Mus sp. Praomys sp.
		Mastomys natalensis S.? cf. campestris Steatomys sp. Tatera gentryi Heteroceph. sp.				S. cf. mearnsi Tatera sp.		Mastomys natalensis Saccostomus sp. Steatomys sp. Tatera sp. Heteroceph. sp.
						Pedetes surdaster	Pedetes sp.	Pedetes sp.
Lagomorpha						L. cf. capensis	Lepus capensis	Lepus capensis
Carnivora								
				I. aff. albicauda Herpestes cf. ichneumon Hyaena hyaena C. crocuta			I. albicauda	I. albicauda Herpestes ichneumon
cf. Pachyrocata aff. Brevirostris		Hyaena sp.					Hyaena hyaena C. crocuta	Hyaena hyaena C. crocuta
		F. libyca P. leo P. pardus		Felis cf. libyca P. cf. leo			L. caracal F. libyca P. leo P. pardus	L. caracal F. libyca P. leo P. pardus
Panthera cf. leo		C. mesomelas ?		Canis cf. aureus		cf. Acin. jubatus C. aff. mesomelas	C. mesomelas C. adustus Lycaon pictus Otocyon sp. M. capensis	Acinonyx jubatus C. mesomelas C. adustus Lycaon pictus Otocyon sp. M. capensis
Proboscidea								
Elephas recki recki	E. recki L. africana	E. recki recki	E. recki recki	E. recki recki	E. recki	E. recki recki		L. africana
Tubulidentata								
							Oryct. afer	Oryct. afer

(continued on next page)

Table 3
(continued)

Bouri-Daka	Kanjera N	Olduvai IV	Olorgesailie	Asbole	Bodo	Isenya	Lainyamok	Living
Perissodactyla								
	Diceros bicornis			D. cf. bicornis				D. bicornis
Cerath. sp.	C. simum	C. simum	C. simum	C. simum?		Rhinocerotidae		C. simum
Hipparion sp.	Hipparion sp.	H. ethiopicum	H. albertense			Hipparion sp.		
Equus sp.	Equus sp.		E. aff. grevyi	Equus sp.	Equus sp.	Equus sp.	E. grevyi E. burchelli	E. grevyi E. burchelli
		E. burchelli E. oldowayensis	E. oldowayensis					
Artiodactyla								
Hippop. gorgops	H. cf. gorgops H. cf. amphibus	H. gorgops	H. gorgops		Hippop. sp.			
				H. cf. amphibus		H. cf. amphibus M. cf. hopwoodi	H. amphibus	H. amphibus
Metridiochoerus cf. hopwoodi	M. hopwoodi	M. hopwoodi	M. hopwoodi			M. cf. compactus		
M. compactus	M. compactus	M. compactus	M. compactus					
M. modestus	“Phacochoerus”	M. modestus		M. modestus			P. aethiopicus	P. aethiopicus
K. majus		K. majus	K. majus	K. majus	K. majus	Kolpochoerus sp.		
K. olduvaiensis	K. olduvaiensis	K. olduvaiensis					Potam. porcus G. camelopardalis	Potam. porcus G. camelopardalis
Giraffa cf. camelopardalis		G. jumae	G. camelopardalis Giraffa gracilis ?	G. cf. camelopardalis	Giraffa sp.			
Sivatherium cf. maurusium		S. maurusium						
	Tragelaphini	T. scriptus T. strepsiceros T. arkelli	Tragelaphus sp.	T. scriptus	Tragelaphus sp.			T. scriptus T. strepsiceros T. oryx
T. cf. strepsiceros			Taurotragus sp.	Taurotragus sp.		Taurotragus sp.	T. oryx	
	P. oldowayensis	P. oldowayensis		Bos sp.				
Pel. cf. antiquus	S. acoelotus Hippotragini	P. antiquus S. acoelotus	P. antiquus ?	Pelorovis sp.? Syncerus sp.? Oryx sp.	P. cf. antiquus S. acoelotus	Bovini	Bovini	Oryx gazella Hippotr. equinus Kobus sp.
Kobus kob K. sigmoidalis K. ellipsiprymnus	Kobus sp.		Kobus sp.	Kobus kob	Kobus sp.			K. ellipsiprymnus Redunca sp. C. taurinus
			Redunca sp.	Redunca sp.		cf. Redunca sp.		
C. taurinus		C. taurinus	Connochaetes sp.	cf. Connoch. sp.		Connochaetes sp.	C. taurinus	C. taurinus
M. kattwinkeli	Megalotragus sp.	M. kattwinkeli	M. cf. kattwinkeli			M. cf. kattwinkeli		
Numidocapra crassicornis								
Rabaticeras sp.		R. arambourgi						
P. angusticornis	P. angusticornis	P. rugosus				Parmularius sp.?		
		Damaliscus niro		D. niro	Alc. Buselaphus D. niro	Damaliscus sp.	D. lunatus D. cf. dorcas Beatr. hunteri	Alc. buselaphus D. lunatus D. dorcas Beatragus hunteri
Nitidarcus asfawi Bouria angettyae cf. Aepyceros sp.					A. cf. melampus	Aepyceros sp.	A. melampus Madoqua sp.	A. melampus Madoqua sp.
Gazella sp.	Gazella sp.			G. cf. thomsoni G. aff. granti		G. thomsoni G. cf. granti	G. thomsoni G. granti Litocranius walleri Antidorcas sp.	G. thomsoni G. granti Litocranius walleri Antidorcas sp.
	Antidorcas recki	A. recki	Antidorcas ?					

Table 4
Composition of the Asbole fauna
Composition de la faune d'Asbole

Recent species	Probably living	Probably extinct	Extinct
<i>H. cristata</i>	<i>Colobus</i> sp.	<i>Otomys</i> sp.	<i>Th. oswaldi</i>
<i>Hyaena hyaena</i>	<i>Cercopithecus</i> sp.	<i>Gazella</i> aff. <i>granti</i>	<i>I. aff. albicauda</i>
<i>C. crocuta</i>	<i>Papio</i> sp.		<i>E. recki recki</i>
<i>M. capensis</i>	<i>Homo</i> sp.		<i>M. modestus</i>
<i>T. scriptus</i>	<i>T. cf. swinderianus</i>		<i>K. majus</i>
<i>Kobus kob</i>	<i>Tachyoryctes</i> sp.		<i>Bos</i> sp.
	<i>A. cf. niloticus</i>		<i>Damaliscus niro</i>
	<i>Herpestes</i> cf. <i>ichneumon</i>		
	<i>Felis</i> cf. <i>libyca</i>		
	<i>P. cf. leo</i>		
	<i>Canis</i> cf. <i>aureus</i>		
	<i>D. cf. bicornis</i>		
	<i>Equus</i> sp.		
	<i>H. cf. amphibius</i>		
	<i>G. cf. camelopardalis</i>		
	<i>Taurotragus</i> sp.		
	<i>Syncerus</i> sp.?		
	<i>Oryx</i> sp.		
	<i>Redunca</i> sp.		
	cf. <i>Connochaetes</i> sp.		
	<i>G. cf. thomsoni</i>		

dating of which to 0.65 Ma needs confirmation (Renne, 2000).

The fauna from the Kapthurin Formation is only known through a faunal list with most identifications at the genus level. It includes *Theropithecus* and *K. majus*, but lacks *Elephas* and *Metridiochoerus*, suggesting that it is somewhat younger than that of Asbole. Assuming that it is roughly the same age as the Kapthurin Hominids, which have recently been dated to about 0.51 Ma (Deino and McBrearty, 2002), this provides a minimum age for Asbole.

Lainyamok has only recent species, and is undoubtedly the youngest of all these sites. It is perhaps not much older than the minimum age provided for the fossiliferous layers (0.34–0.41 Ma; Potts et al., 1988).

M. modestus is not known in the Middle Pleistocene, and its occurrence at Asbole indicates an earlier age.

As a whole, the Asbole fauna has a significant proportion of extinct taxa: the total number of extinct forms is at least seven, and probably nine, out of 36 (Table 4). Although they do not provide definite indications as to the age, they tend to push the Asbole fauna downwards in time.

Correspondence analysis can provide a graphic display of the relationships between these various sites. Fig. 14 shows the results of the analysis on presence/absence matrix of the various species (and genera when there are several species). They roughly confirm the previous conclusions, but not too much weight should be given to them, because this analysis is very sensitive to the completeness of the faunal lists. The distance between Asbole and Bodo, for instance, mainly stems from the recovery, in the former site, of a rich collection of rodents and carnivores, most of them similar to recent forms. Bodo, instead, has almost none, and this brings it

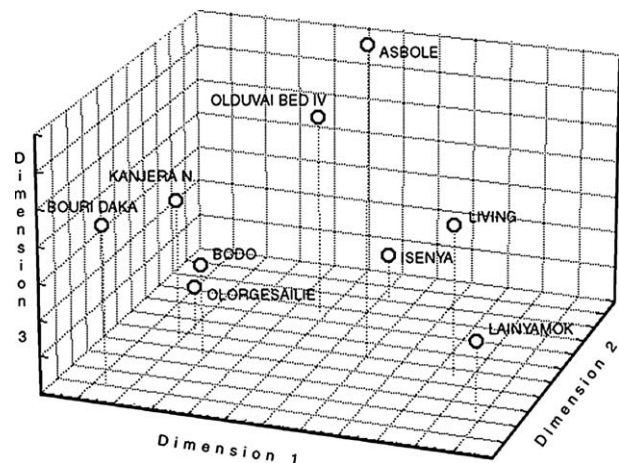


Fig. 14. Correspondence analysis on presence/absence of taxa of Pleistocene East African sites (data = Table 1). Inertias: Dimension 1: 29.5%; Dimension 2: 14.4%; Dimension 3: 13.1%.

Analyse factorielle sur la présence/absence de taxons de sites pléistocènes est-africains (données = Tableau 1). Inerties : axe 1 : 29,5 % ; axe 2 : 14,4 % ; axe 3 : 13,1 %.

closer to Kanjera North, Ologesailie and Bouri-Daka, which also have very few rodents and carnivores.

Taken together, these data constrain the age of Asbole between 0.8 and 0.6 Ma. Of course, the discovery of *Hippa- rion*, or of *Alcelaphus*, would alter this conclusion, but it can be taken as the most reasonable estimate at the present time.

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