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Editors



Earliest Man and Environments in the Lake Rudolf Basin

Stratigraphy, Paleoecology,
and Evolution

Edited by

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20. EQUIDAE FROM THE SHUNGURA FORMATION

V. Eisenmann

Material

The Omo collections of Equidae discussed here comprise those from the missions of Bourg de Bozas (1900-1903) and the late C. Arambourg (1932-33) and from the recent Omo Research Expedition, the last collected under the direction of C. Arambourg and Y. Coppens (collections of 1967, 1968, 1972, and 1973). The collections made after 1967 have precise provenance data. The specimens and their stratigraphic situations (where known) in the Shungura Formation are listed in table 1.

Hipparion

Members A and B

The lower members of the Shungura Formation have afforded fossil remains indicating the existence at this level of a large form of *Hipparion*. Its lower cheek teeth probably lacked an ectostylid. A rather damaged astragalus is evidently *Hipparion*, to judge from the junction of internal and posterior surfaces at a right angle, the proportion and form of the lower articular surface, the distance between that surface and the external lip, and the curvature of the internal lip (Gromova 1952, pp. 125 ff.). It is longer than the largest hipparionid astragali known--those of *H. longipes* Gromova of Pavlodar (table 2).

A lingual portion of a lower premolar appears distinctly larger than those from the upper part of the Shungura Formation. The double knot (conjoined metaconid-metastylid) and the entoconid are similar in size to a specimen from Ain Brimba which is 30 mm long (Arambourg 1970, plate XVIII, fig. 4). If a broadly similar size for the Member B specimen is assumed, it approaches in size remains from Langebaanweg and Laetolil (Boné and Singer 1965). It is larger than the P_4 from the earlier Kaiso (North Nyabrogo) (Cooke and Coryndon 1970). An M_1 or M_2 from Member B is also larger than those from the upper Shungura members but is smaller than those from Laetolil and Langebaanweg. A P_2 also from Member B is smaller than the aforementioned specimens, falling in the range of specimens from the upper Shungura.

The only intact lower molar, an M_1 or M_2 from Member B, lacks an ectostylid. In this respect it resembles some specimens from Laetolil, Langebaanweg, and earlier Kaiso and differs from those of Ichkeul and Ain Brimba, although the latter are of comparable size.

A damaged calcaneum and a phalanx are also known from Member A. The proximal phalanx, also damaged, has an estimated length of not more than 65 mm. It is therefore much smaller

Table 1

Stratigraphic Locations of Specimens from the Shungura Formation

Members	Localities	Hipparion	Equus
J	K 20		2 upper cheek teeth 1 fragment of metacarpal 3
H	11.2		1 astragalus
G	29 and 210, 35, 47, 113, 150, 187, 195 214, 215, 233, 235, 248, 252, 253, 256, VEO	4 upper cheek teeth 6 lower cheek teeth, 1 lower fragment 1 lower cheek tooth series 2 astragali, 1 incomplete tibia	5 upper cheek teeth 1 lower cheek tooth series 5 lower cheek teeth 1 fragment of radius 4 fragments of metacarpal 3 2 tibia fragments 1 astragalus 1 fragment of metatarsal 3 3 phalanges 1 2 phalanges 2
F	1 C, 76, 118, 130	2 upper cheek teeth, 1 upper incisor 1 lower cheek tooth series, 2 lower cheek teeth 1 metacarpal 3	
E	38, 108	1 upper cheek tooth, 1 upper fragment	
D	18 bis, 153, 216	1 upper cheek tooth 2 fragments metacarpal and metatarsal 3	
C	3.1, 18, 30, 53	1 upper cheek tooth 9 lower cheek teeth and fragments 1 fragment of metacarpal 3	
B	3, 28, 41	1 upper milk tooth, 1 upper fragment 3 lower cheek teeth, 1 cup	
A	127, 128	astragalus, calcaneum, phalanx 1	
Expeditions of Bourg de Bozas and Arambourg		1 upper incisor 3 upper cheek teeth and 2 fragments 7 lower cheek teeth	1 upper incisor 2 upper cheek teeth 3 lower cheek teeth 1/2 distal radius 1 fragment of metacarpal 3 1 phalanx 1 2 phalanges 2
Dental series		2	1
Isolated teeth and fragments		47	18
Postcranials		3	9
Fragments of postcranials		8	12
Total		60	40

Table 2

Dimensions (mm) of *Hipparion Astragali*

Source	Specimen	Internal Height
Pavlodar	n = 9	59 to 63
Omo Member A	128-1972-12	69
Omo Member B	41-1973-991	56

than those described and figured by Boné and Singer (1965), the shortest of which is 70.2 mm. (According to their illustrations, phalanges L 1462 B and C come from an *Equus* and L 1462 A from a *Hipparion*, as does, possibly, L 1456.) On the other hand, the phalanx from Omo is much more gracile; but this might merely reflect the immaturity of the animal.

Members C through G

An ectostylid is present on all *Hipparion* lower premolars and molars from Member C upward. An exception is an M_3 which is a part of a dentition from Member F. The crown length of these teeth (tables 3 and 4) and the size of the postcranials (tables 2 and 5) are in general smaller.

The height (buccally, in mm) of a series of lower teeth of a young adult from Member F affords an indication of the degree of hypsodonty.

P_2	P_3	P_4^*	M_1	M_2	M_3
46	54	68	61	68.5	69

* Height slightly reduced by wear

The buccal half of a P_4 (Member E) already in wear, has a height of 71 mm. An unworn M_3 from the same horizon has a height of 59 mm.

Table 3

Length (mm) of Mandibular Cheek Teeth in *Hipparion*

Character	Source	P_2	P_3 and P_4	M_1 and M_2
Lacking ectostylids	Langebaanweg	33.5	28.3 to 32 (n=5)	26.5 to 29.3 (n=6)
	Laetolil	33	28.5; 29.5	27; 27
	Earlier Kaiso		26	18-20
	Shungura B	29	30?	25.5
Having ectostylids	Shungura G	28.5	25 to 26.5 (n=4)	20 to 24 (n=5)
	Shungura F	27.5	22; 23	20.5 to 22 (n=4)
	Shungura C	29; 29.5	24 (very worn)	25.5
	Ichkeul		28	
	Ain Brimba	33.5	30	28; 26

Discussion

An astragalus (from Member A) and two lower cheek teeth (from Member B) attest to the presence of a large *Hipparion* species in the lowest part of the Shungura Formation. The only intact lower tooth lacks an ectostylid. These remains are provisionally assigned to *Hipparion* cf. *albertense* Hopwood, a large form lacking an ectostylid.

Table 4

Length (mm) of Maxillary Cheek Teeth in *Hipparion*

Character	Source	P ²	P ³ and P ⁴	M ¹ and M ²	M ³
Lacking ectostylids	Langebaanweg		27.5 to 30 (n=8)	20.5 to 27.8 (n=10)	23.6
	Laetolil	39	31; 31	27.3; 25	24.2
	Earlier Kaiso	(29)	29.5; (28.5)	21.5; 24	(20)
?	Later Kaiso		24.5		27.5
Having ectostylids	Shungura G		26; (26)	21; 23	
	Shungura F		23; 24		
	Shungura E		25		21
	Shungura D				22
	Shungura C			23	
	Ichkeul		26.5; 27	24 to 26 (n=4)	(24)
	Ain Brimba	41	28 to 32 (n=5)	27	28

The P₂ and first phalanx from members A and B are of more modest size. The P₂ is ~~worn~~ ^{damaged} on the buccal side, and it is thus impossible to discern whether an ectostylid was present. Additional material is necessary to determine whether these remains can also be assigned to *Hipparion* cf. *albertense* or whether they might represent the *Hipparion* found from Member C upward. Hooijer (this symposium) regards the latter as *Hipparion* cf. *ethiopicum* (Joleaud), a generally more gracile form with lower cheek teeth, almost invariably having ectostylids.

Equus

The genus *Equus* appears for the first time at the base of Member G in the Shungura Formation.

The first phalanges (table 6) and the lower cheek teeth (table 8) from the Shungura Formation are near the upper limits of variability of *Equus grevyi*. However, an astragalus (113-1972-42) from Member G falls at the lower limits of the size range of *Equus grevyi* (table 7). The astragali of *Equus numidicus* from North Africa are also relatively small, a feature in common with the specimen from the Omo. Most remains indicate the presence of an *Equus* larger than most modern zebras, including possibly *Equus grevyi*. Its size was comparable to that of *Equus numidicus* Pomel from Ain Boucherit and Ain el Bey.

A distal metacarpal 3 from the lower units of Member G represents a very large species of *Equus*. This might well be the large *Equus* sp. nov. A, present in the Lower and Upper members of the Koobi Fora Formation, East Rudolf (see following chapter). Aside from the large species of *Equus* there are also some specimens collected by Arambourg (1947) and an astragalus recently collected from Member H which indicate the presence of an *Equus* similar in size to *Equus burcheilli granti*. A left astragalus (1967-726), though damaged, clearly represents *Equus*. Its maximum height could not have exceeded 56 mm, and is well within the range of variability of *E. burcheilli granti*, but not of *Equus grevyi* (table 7).

We cannot exclude the possibility that the specimen represents a young individual. (One newborn *Equus grevyi* had an astragalus height less than 60 mm, and an eight-month old individual had an astragalus height of 61 mm, larger than that of any *E. burcheilli granti*.)

Arambourg (1947, p. 306, pl. X, fig. 4) collected an M₁ or M₂ (1933-9-397) which he hesitated to attribute to *Hipparion* or to *Equus*. It is in fact a small *Equus*, approximating

Table 5
Dimensions (mm) of *Hipparion* Metapodials

Source	Maximum Length	Proximal, Anterior-Posterior		Proximal Transverse	Mid-Shaft Transverse	Distal Anterior-Posterior	Distal Transverse	
		Articular Surface	Maximum				Articular Surface	Supra-articular Surface
Metacarpal 3								
Olduvai Bed II	206; 217; 223	36; 37; 37		44; 45; 46		33; 34; 36	42; (45); 48	
Shungura F	219	27.5	32	40.5	24.5	31	34	36.5
Shungura D						34	39.5	38
Shungura C		(30)		44	31.5			
Ichkeul	267	(33)		54	34	>37.5	>40.5	>45
Metatarsal 3								
Laetolil ^a						35	37	42
Olduvai Bed II ^a	242 to 266 (n=5)	37 to 41 (n=5)		45 to 48 (n=5)		32 to 38 (n=7)	43 to 48 (n=7)	
Shungura D					(31)	34.5	40	(42.5)
Ichkeul	267.5	>38		47	34.5	>33.5	>42	>44.5

^aThe transverse diameters of metatarsal 3 from Laetolil are from measured photographs published by Dietrich (1942), and the anterior-posterior diameter of this specimen, as well as those of the Olduvai Bed II specimens, are those given by Boné and Singer (1965).

the size of *Equus burchelli granti*. In figure 1 it is compared with a large specimen (252-1967-414) from Member G. The length of *Equus* lower premolars and molars from the Shungura Formation, as well as those from Ain Boucherit (Arambourg 1970) and those of modern *Equus grevyi* and *Equus burchelli granti*, are given in table 8.

Discussion

The size of phalanges, astragali, and lower cheek teeth of the large *Equus* from the upper Shungura Formation compare favorably with *Equus numidicus* Pomel from Ain Boucherit. A more interesting comparison might be made with *Equus* remains from eastern Africa, particularly Olduvai and East Rudolph. However, the collections from these localities have still to be studied in detail. Hooijer (this symposium) considers *Equus* teeth from Shungura Formation members G-I to be similar to those of Olduvai Bed II. Following this assumption, this large *Equus* is provisionally attributed to *Equus* cf. *oldowayensis* Hopwood. Another very large species of *Equus* is also represented in lower Member G.

The small form of *Equus* is too poorly known to identify at this point, but its presence is worth mentioning.

Coexistence of *Hipparion* and *Equus*

Equus and *Hipparion* coexisted in Member G of Shungura Formation and are found together at four localities:

Table 6
 Maximum Length (mm) of First Phalanges of Equus

Specimen	Forelimb			Hind Limb		
	n	Mean	Range	n	Mean	Range
<i>Equus burchelli granti</i>	18	75.76	69.4-82.4	17	71.59	66.7-77.3
<i>Equus zebra</i>	7	79.74	75.8-83.4	7	75.51	71.2-79.6
<i>Equus grevyi</i>	9	86.33	82.0-91.1	9	81.33	76.4-87.0
<i>Shungura G</i>						
215-1973-2547			87.1			
253-1973-5116			86.2			
113-1972-42			> 84.3			
<i>Omo</i>						
1933-9-741			84.2			
<i>Equus numidicus</i>						
(after Arambourg 1970)			85			78-81

NOTE: The minimum length of the phalanges varies between 70 and 73 mm, whereas the length of those from Olduvai varies between 64 and 69 mm (cf. Hopwood 1937 and his use of these measures).

Table 7
 Maximum Height (mm) of *Equus Astragali*

Specimen	n	Mean	Range
<i>Equus burchelli granti</i>	26	56.44	52.2-60.0
<i>Equus grevyi</i>	10	63.60	60.5-67.5
Shungura H 1967-762			(56)
Shungura G 113-72-4			>61
Ain Boucherit <i>Equus numidicus</i> (Arambourg 1970)	4	61.25	57-64

- 29-- *Equus* 1 upper cheek tooth, 1 lower cheek tooth
Hipparion 1 upper cheek tooth
- 215-- *Equus* 6 postcranial fragments, 1 upper cheek tooth
Hipparion 1 astragalus
- 233-- *Equus* 1 lower cheek tooth
Hipparion 1 lower cheek tooth
- VEO-- *Equus* 1 upper cheek tooth and some teeth fragments, 1 proximal metatarsal 3,
 1 tibia fragment
Hipparion 1 tibia fragment

The coexistence of *Equus* and *Hipparion* has repeatedly been noted. The evidence from Europe and the Middle East bearing on this problem has recently been discussed elsewhere

Table 8
Mesiodistal Lengths (mm) of Equus Lower Cheek Teeth

Specimen	n	P ₃ and P ₄		n	M ₁ and M ₂		n	M ₃	
		Mean	Range		Mean	Range		Mean	Range
<i>Equus grevyi</i>	12	28.55	25.8-31.0	15	26.38	23.1-31.0	6	30.53	26.8-33.8
<i>Equus burchelli granti</i>	108	23.78	20.1-26.1	110	21.72	18.5-25.7	52	24.21	21.5-28.0
<i>Shungura Fm.</i>									
252-1967-414			>31.3						
29-1968-1823			31.5						
195-1973-1353			>31.3						
233-1973-4129					28				
214-1973-4163								34	
113-1972-40 (mandible)			31.5-32		28			33	
1951-4-121			31						
1933-9-367			30						
1933-9-397					22				
<i>Equus numidicus</i> (after Arambourg 1970)									
			32		28-33.7			33.5-35	

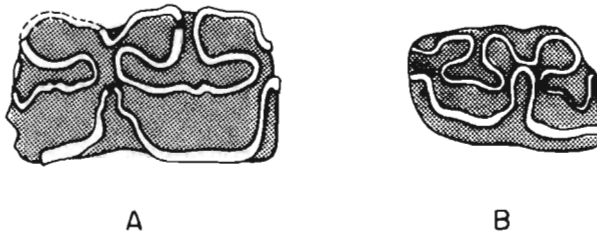


Figure 1. Lower molars of (B) a small species of *Equus* (1933-9-397) collected by Arambourg and (A) a large species from Member G, Shungura Formation (Omo locality 252-1967-414).

(Eisenmann and Brunet 1973). The collections from Ain Boucherit, Ain Hanech, and Ichkeul do not confirm such coexistence in North Africa, at least. In East Africa there is clear evidence that *Equus* and *Hipparion* coexisted at Olduvai Beds I and II (Leakey 1971, p. 293), at Koobi Fora and Ileret (Maglio 1972, and personal observations), and in the upper Shungura Formation, lower Omo basin.

Conclusions

Equids are present throughout the Shungura Formation. *Hipparion* occurs from Member A through Member G, and *Equus* appears from the base of Member G upward. *Hipparion* cf. *albertense* is present in members A and B. It is large, with lower cheek teeth probably almost invariably lacking an ectostylid, as in the samples from Laetolil and Langebaanweg. The large *Hipparion* from Ain Brimba and Ichkeul, Tunisia, is distinct in that an ectostylid is always present. From Member C upward, *Hipparion* cf. *ethiopicum* is the species commonly represented. It is smaller than the earlier species and almost always has an ectostylid.

For the moment the relationships of these two forms are unclear. It is thus impossible to know now whether *H. cf. ethiopicum* is a derivative of *H. cf. albertense* or if it is a new immigrant species, and it is also uncertain whether the two hipparionids may have coexisted before *H. cf. ethiopicum* ultimately replaced *H. cf. albertense*.

Equus cf. oldowayensis appears at the base of Member G about 1.9 m.y. (Bonnefille et al. 1973), or in the upper part of Zone IV as defined by Coppens (1972). In North Africa, the most ancient *Equus* known is *E. numidicus* from Ain Boucherit. According to J. J. Jaeger (pers. comm.) this occurrence is equivalent to Coppens's Zone III and probably to Olduvai Bed I. The findings from Omo, Olduvai, and Ain Boucherit are in agreement, showing that the genus *Equus* was already widespread in Africa about 1.9 m.y. in the upper part of Zone IV or Zone III. The first African appearance of *Equus* could be even older.

At Koobi Fora the skull of a large *Equus* has been recovered from below the KBS Tuff, which has a radiometric age of about 2.61 m.y. (Fitch and Miller 1970). This same very large species may also be present in lower Member G. In Europe *Equus* appears for the first time in localities which are dated at least 2.5 m.y.--including Roccaneyra (Eisenmann and Brunet 1973), and probably also Montopoli, Beresti, Malusteni, Grauceanu, and Moldavia (De Giuli 1972).

Besides *Equus cf. oldowayensis*, a small form of *Equus* is present in Member G. However, the paucity of material available does not permit us to determine its affinities or its biostratigraphic significance.

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