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The systematic position of *Equus hydruntinus*, an extinct species of Pleistocene equid☆

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Abstract

Palaeolithic people commonly hunted *Equus hydruntinus*, an extinct species of equid whose cursorial body proportions suggest an adaptation to semi-arid conditions. Despite the frequency with which it is encountered in fossil deposits, only partial cranial remains have been reported until now. As a result, the systematic affiliation of the species remains a subject of controversy. Two nearly complete *E. hydruntinus* crania are presented here for the first time. These skulls show that *E. hydruntinus* is a distinct species, more closely related to the hemiones (Asiatic asses) than to any other equid. This suggests that the social organisation of *E. hydruntinus* followed one of two known equid sociotypes: resource defense territoriality.

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There are six species of wild equid in existence today—*E. przewalskii* (wild horse), *E. africanus* (the African ass, or ass), *E. hemionus* (Asiatic asses, or hemiones), and three species of zebra: *E. grevyi*, *E. zebra*, and *E. burchelli* (Eisenman, 1980; Groves and Willoughby, 1981)—seven species if the Tibetan kiang (*E. kiang*) is accepted as a species (Groves, 1986) and eight if one adds the recently extinct *E. quagga* (Cape quagga). The horse, *E. caballus*, is a domestic form related to *E. przewalskii*. The donkey, *E. asinus*, is the domesticated form of *E. africanus*. Morphologically, the hemiones occupy an intermediary systematic position between the true, or caballoid horses (*E. przewalskii* and *E. caballus*) and the African ass (*E. africanus*). But the consensus stops there and the phylogeny of the genus *Equus* is still unresolved.

While it is generally accepted that the horse diverged first and that zebras likely diverged from a lineage comprising the asses, the branching orders and timing of the divergences of

hemiones, asses, and zebras are still unresolved (George and Ryder, 1986; Eisenmann and Baylac, 2000; Oakenfull et al., 2000). Monodactyl equids with dental patterns similar to those of modern zebras appear in the palaeontological record of North America during the Pliocene, around 3.4 myr. These early equid forms are referred to as *Plesippines*. More or less similar forms, the *Stenonids*, are known in the Old World from about 2.5 myr. Until recently, modern equid species were thought to have diverged directly from these Pliocene forms. However, recent craniological studies (Eisenmann and Baylac, 2000) suggest that there is no direct link between *Plesippines*, or *Stenonids*, and extant equid species. These observations are supported by recent genetic research (Oakenfull et al., 2000) that indicates that the common ancestor of modern equids is a species that probably existed around 2.3 myr ago.

Equid systematics: genetic data

“Metaphorically the genome projects represent as extensive an archeological excavation as has ever been attempted” (O’Brien et al., 1993, p. 103).

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Genetic mapping is used as a tool for the management of economically important domesticated species (Lindgren et al., 1998; Caetano et al., 1999) and of endangered species, such as the Asiatic wild ass (Ryder and Chemnick, 1990) and Przewalski's horse (Ryder, 1994). Curiously, mapping of the horse genome has lagged somewhat behind other domesticates, but is now being addressed (Xu and Arnason, 1994; Xu et al. 1996; Lindgren et al., 1998; Caetano et al., 1999; Guérin et al., 1999; Shiue et al., 1999; Swinburn et al., 2000; Vila et al., 2002; Jansen et al., 2002).

Although genetic mapping is recognized as a potentially powerful tool for establishing phylogenies (O'Brien et al., 1993) comparatively few studies of equid systematics have made use of genetic data (Oakenfull and Clegg, 1998). Existing studies offer equivocal information (contrast the proposed equid phylogenies in Oakenfull and Clegg (1998), Ishida et al. (1995), and Xu et al. (1996)). For example, estimates of the divergence time of the horse from other equid lineages vary from as long ago as 8–10 myr (Xu et al., 1996) to 3.9 myr (George and Ryder, 1986) or as recently as 2.4 myr (Oakenfull and Clegg, 1998). The timing of the divergence of the zebra lineage is even more problematic since the relative systematic positions of the hemiones, asses (including donkeys), and various zebra species are still unresolved.

The proposed equid phylogenies only agree on a few points, namely:

- (1) the divergence of *E. caballus* from a lineage that includes both zebras and asses (George and Ryder, 1986; Ishida et al., 1995; Xu et al., 1996; Oakenfull and Clegg, 1998)—this point is in agreement with paleontological data (Eisenmann and Baylac, 2000),
- (2) the probable divergence of the zebra lineage from a lineage comprising donkeys and asses.

Sources of disagreement between the phylogenetic trees that have been proposed and different estimates for divergence times include:

- (1) the difficulties inherent with genetic research involving *E. caballus*, a species whose breeding programs require a reliance on half-sib families (Lindgren et al., 1998), although a first study of full-sib families has recently been published (Swinburn et al., 2000);
- (2) uncertainty of molecular clock estimates and selection of a divergence rate (Xu et al., 1996; Oakenfull and Clegg, 1998);
- (3) uncertainty regarding the phylogenetic polarity of molecular markers (Schreiber et al., 2000);
- (4) choice of mode of comparison in pairwise comparisons, compounded with the knowledge that the same gene has different evolutionary rates in different species pairs—in other words, the choice of external reference matters (Xu et al., 1996);
- (5) choice of method for producing phylogenetic trees (e.g., parsimony, neighbor-joining, or maximum

likelihood), given that different methods produce differing results (Oakenfull and Clegg, 1998);

- (6) use of mitochondrial (mtDNA) versus nuclear DNA for genetic mapping.

With the exception of the first point (above), these problems are not unique to the study of equids. Differences between estimates of divergence times obtained using mtDNA and those obtained using nuclear DNA could indicate that mtDNA genealogy differs from nuclear DNA genealogy (Ishida et al., 1995, p. 187) and may be more suited to establishing long-range evolutionary trends, through comparisons between *distantly* related taxa (Xu et al., 1996, p. 439; compare Oakenfull et al., 2000).

Attempts to reconcile genetic data with paleontological evidence heighten the uncertainties highlighted above (e.g., Eisenmann and Baylac, 2000) though more recent studies show that DNA data, used in conjunction with paleontological analyses, hold considerable promise for resolving equid phylogeny (e.g., Higuchi et al., 1984, 1987; Orlando et al., in press; Vila et al., 2001; Sica et al., 2002). Unfortunately, although great strides have been made in DNA amplification from fossil bone, the conditions required for optimum conservation of genetic information (Smith et al., 2001; Hofreiter et al., 2001) are rarely met. Until large-scale genome maps for the extant equids are available, and until DNA amplification from fossil bone has yielded consistently robust data, we will continue to rely on paleontological data when attempting to resolve equid systematics, particularly for fossil species.

Palaeontology of *E. hydruntinus*

Judging from the distribution of fossil remains, *E. hydruntinus* flourished during the late Pleistocene throughout Eurasia. *E. hydruntinus* is characterized by slender limbs, cursorial proportions, relatively small teeth, short protocones on the upper cheek teeth, and primitive enamel patterning in the lower cheek teeth. Its limb bones resemble those of the hemiones; its upper teeth show an affinity with the asses (and share some traits with the zebras) whereas the lower teeth resemble those of *E. stenorhinus*. In other words, *E. hydruntinus* shares morphological traits with numerous other known species of Old World Pleistocene equid, aside from horses (Eisenmann and Mashkour, 1999; Forsten, 1999). As a result, it is sometimes classed as a zebra (Davis, 1980), sometimes as an ass (Stehlin and Graziosi, 1935; Gromova, 1949), and sometimes as a stenonid (Forsten, 1986, 1999; Forsten and Ziegler, 1995). It appears in the fossil record around 0.3 myr and its range extended from the Middle East to Europe throughout the middle and late Pleistocene. It is still encountered in some locations during the Holocene (Willms, 1989).

Prior to this research only two fragments of *E. hydruntinus* skull were known, from the middle Pleistocene site of



Fig. 1. *E. hydruntinus* from Kabazi II, the more complete of two skulls recovered in 1995, during excavations directed by V. P. Chabai. Left, side view. Photograph taken in the Crimea, in 1995 (Burke).

Lunel-Viel (France). The Lunel-Viel equid is smaller than normal, however; hence its designation as *E. hydruntinus minor* (Bonifay, 1991). The relatively old dates for the Lunel-Viel equid, as well as its smaller size, led Azzaroli (1990) to question its assignment to *E. hydruntinus*.

Materials : the Kabazi II skulls

The discovery of two *E. hydruntinus* skulls, one nearly complete (Fig. 1), in the Upper Pleistocene site of Kabazi II, in Western Crimea (Ukraine)—well inside the classic chrono-geographic range of the species—provides us with a unique opportunity to reconsider its systematic position relative to other equids.

The archaeological site of Kabazi II is a middle Palaeolithic kill and butchering locality situated at the foot of a limestone escarpment on the western margins of the second Crimean mountain chain (Chabai, 1999; Patou Mathis, 1999). The regional landscape of Crimea is dominated by open grassland and intersected by river valleys where, during the milder phases of oxygen isotope stage 3 (OIS 3), a mosaic of meadows, shrubs, and limited tree cover may have existed (Burke et al., 1998, 1999). Generally, the region was well suited to equids, particularly *E. hydruntinus*, during the late Pleistocene based on the abundance of bones recovered from archaeological contexts.

Methods

We use standard cranial measurements (cf. Eisenmann, 1980) from the two Kabazi skulls (Fig. 2) to establish the relationship between *E. hydruntinus* and other equid species (extant and fossil) by means of a principal components analysis (PCA) and a mixture discriminant analysis (MDA). MDA (Hastie and Tibshirani, 1996) is a generalisation of linear discriminant analysis that assumes that populations come from a mixture of multivariate normal distributions. Bivariate plots are then used to explore differences in cranial proportions between *E. hydruntinus*, asses, hemiones, plesippines, and stenorid equids as an aid to the taxonomic

identification of fragmentary archaeological and palaeontological remains.

Measurements used in the PCA and MDA analyses are length of the narial opening (31), cheek length (32), postvomerine cranial length (4), muzzle length (5) and palatal length *sensu stricto* (2-5), and muzzle breadth behind the third incisor (17). Measurements used for the bivariate plots include those used above, plus overall palatal length (2). The measurements used in this research (Table 1) were deemed unaffected by deformation of the skulls, which occurs on the vertical plane as a result of burial. Tooth row measurements (Table 2 : 7, 7bis, and 8) are not used for two reasons: (a) intra-specific variability in these data is considerable, and (b) most of the data available for donkeys was obtained from very worn series. Additional cranial measurements for *E. hydruntinus* from Kabazi II are provided in Table 2. We also plotted the following measurements for maxillary third and fourth premolars (P3/P4) and first and second molars (M1/M2): length of the protocone and occlusal dimension corrected for wear. Because occlusal dimensions change as the tooth wears (from a relatively long and narrow surface to a relatively short and broad surface), we calculate occlusal dimension as the average of occlusal length plus occlusal width.

Comparative data were collected by Eisenmann. The Plesippine sample comprises *Equus (Plesippus) shoshonensis* (Hagerman Quarry, Idaho, USA). The stenorid equid sample includes data collected from *E. sanmeniensis* (China) and *E. stenonis* (France, Spain). Additional published data on primitive horses used in this research include *E. cf. sanmeniensis*, Loc 32, China, M 1324 (Zdansky, 1935); *E. (Plesippus) qingyangensis*, Bajiazui, China (Deng, 1997; Deng and Xue, 1999a, 1999b; Eisenmann and Deng, in press); and *E. stenonis mygdoniensis*, Gerakarou, Greece (Koufos, 1992).

Results

The PCA (Fig. 3a) shows that *E. hydruntinus* can be discriminated from the “primitive” (Plesippine and stenorid) equids and the zebras by plotting the first two com-

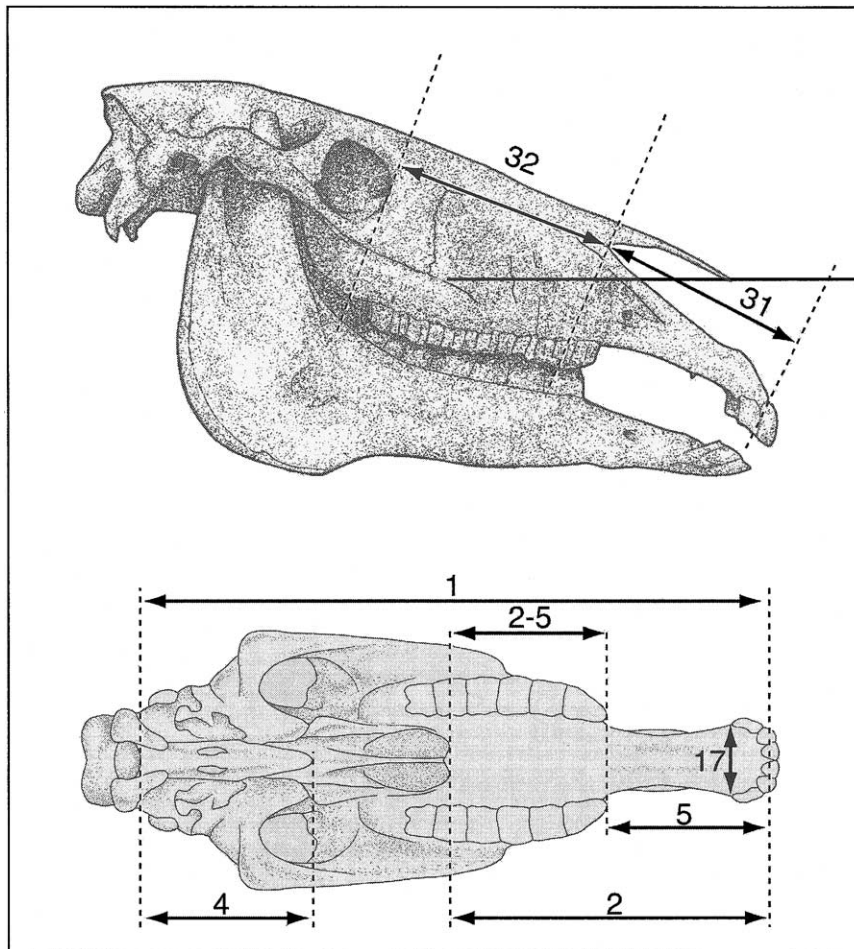


Fig. 2. Cranial measurements used in this research (numbering system after Eisenmann, 1980).

ponents, but cannot easily be discriminated from the asses and hemionies. All of the measurements were centered and scaled to have a mean of 0 and a variance of 1 prior to performing PCA. This was done so that naturally larger or more variable measurements would not carry a disproportionate amount of weight in the analysis. The first principal component (Table 3) explains 77% of the total variation but size is clearly the single most important factor in this com-

ponent. Since we want to prevent allometric variability from interfering with the discriminant analysis, we base the MDA on the remaining five principal components. The second principal component (Table 3) explains 9.55% of the total variation and is primarily influenced by palatal length *sensu stricto* (2–5) and postvomerine cranial length (4). The third component (Table 3) explains 4.9% of the total variation and is largely influenced by cheek length (32) and palatal

Table 1a
Cranial measurements used in this research, *E. hydruntinus* Kabazi II

Measurements	Skull 92	Skull 91
2 (Overall palatal length)	220*	n/a
4 (Postvomerine cranial length)	n/a	96.5
5 (Muzzle length)	102.8*	n/a
2-5 (Palatal length)	117.8	n/a
17 (Muzzle breadth at 13)	59.8	n/a
31 (Length of narial opening)	100.2	n/a
32 (Cheek length)	156*	n/a

Notes. Measurements are in millimeters (mm). Numbering corresponds to Fig. 2 (after Eisenmann, 1980). Asterisks (*) indicated estimates derived from digital images of the skulls.

Table 1b
Dental measurements for *E. hydruntinus*, Kabazi II

P3/4 L protocone	P3/4 Occlusal surface	M1/2 L protocone	M1/2 Occlusal surface
8.12	24.465	22.21	7.64
7.82	24.285	22.3	8.05
9.6	24.59	20.575	7.81
8.54	23.775	21.925	9.91
8.34	23.9	21.82	9.29
10.35	23.265	21.31	9.91

Notes. Dental measurements for upper premolars and upper molars including length (L) of the protocone (after Eisenmann, 1980). Occlusal surface: average of occlusal length plus occlusal width (refer to text).

Table 2
Cranial measurements, *E. hydruntinus* Kabazi II and *E. hydruntinus minor* (Lunel Viel), supplemental data

	Measurement	# 92	# 91	Lunel-Viel
1	Basilar length	358.3 ^a		
2	Overall Palatal length	220 ^a		197
2–5	Palatal length, s.s.	117.2		99
3	Vomerine length			85.5
4	Postvomerine length		96.5	
5	Muzzle length	102.8 ^a		87
6	Diastema	82.8 ^a		58
7	Length of P2-P4	83.0	78.4	81.5
7bis	Length of M1M2	66.1	65.4	62.5
8	Upper cheek teeth length	149.3	143.9	145
9	Choanal length	60 ^a		56
10	Maximum choanal breadth	41.2		41.5
10bis	Minimum choanal breadth	29.1		32
11	Breadth, anterior ends of facial crests			136
12	Distance between Basion and P2	255.4 ^a		
13	Frontal breadth		67.5 ^b	180 ^a
14	Bizygomatic breadth			
15	Cranial breadth			95 ^a
16	Breadth of the supra-occipital crest			
17	Muzzle B. at posterior borders of 13	59.8		50 ^a
n/a	Minimum muzzle breadth			
17bis	Muzzle Breadth, inter-alveolar borders	39.6		36.5
18	Vertex length			
19	Infra-orbital height			11.2
20	Height of external auditory meatus		16 ^b	
21	Antero-posterior diameter of the orbit	52.3 ^b		
22	Dorso-ventral diameter of the orbit	44.4 ^b		53
23	Anterior ocular line	370 ^a		
24	Posterior ocular line			
25	Facial height in front of P2			
26	Facial height between P4 and M1	80.7 ^b	119.2 ^a	110
27	Facial height behind M3			113
28	Cranial height behind the orbits	76.6 ^b	93.0 ^a	84
29	Breadth of the occipital condyles			
30	Breadth of the foramen magnum		29.8 ^b	
31	Length of narial opening	100.2		101
32	Cheek length	156 ^a		

Notes. Measurements are numbered according to Eisenmann (1980). Data on the Lunel Viel specimen collected by Eisenmann.

^a Estimates generated from digital images.

^b Estimates generated from damaged regions.

length *sensu stricto* (2–5). The fourth component explains 4.7% of the total variation and is primarily influenced by muzzle proportions (5, 17). The fifth component explains 3.1% of the total variation and is influenced by most of the measurements. The sixth component only explains 0.89% of the total variation.

When performing MDA, it is necessary to run the analysis several times and average the results, as the algorithm is not exact. The analysis was run 20 times and standard errors for the classification probabilities are given based on these 20 sample runs. We initially grouped the equids into four broad categories: asses, zebras, hemiones, and primitive equids (including Plesippines and stenorids). A plot of the first two mixture discriminants from a representative run is shown in Figure 3b. On the basis of this plot it seems clear that *E. hydruntinus* is most closely related to the hemiones. This is borne out in the classification probabilities, which

are $65 \pm 2.7\%$ hemione, $33 \pm 2.7\%$ ass, and $2 \pm 0.7\%$ zebra, with only a miniscule probability ($\sim 10^{-10}$) that it is a Plesippine or stenorid equid. We performed full leave-one-out cross-validation to assess the robustness of the results and achieved a classification error rate of 18%.

We then split the hemiones into their respective subspecies and reran the analysis with only the hemiones in an attempt to determine which subspecies *E. hydruntinus* was closest to. This turned out to be a much harder classification problem, with a leave-one-out cross-validation error rate of 42%. This is to be expected, as differences between subspecies are appreciably smaller than those between species. This classification difficulty can be seen clearly in Figure 3c, which shows the first two mixture discriminants. With this caveat in mind, the classification probabilities are $80 \pm 1.2\%$ *E. h. hemionus*, $17 \pm 1.1\%$ *E. h. khur*, and $3 \pm 0.1\%$ *E. h. onager*. The remaining classification probabilities are very small.

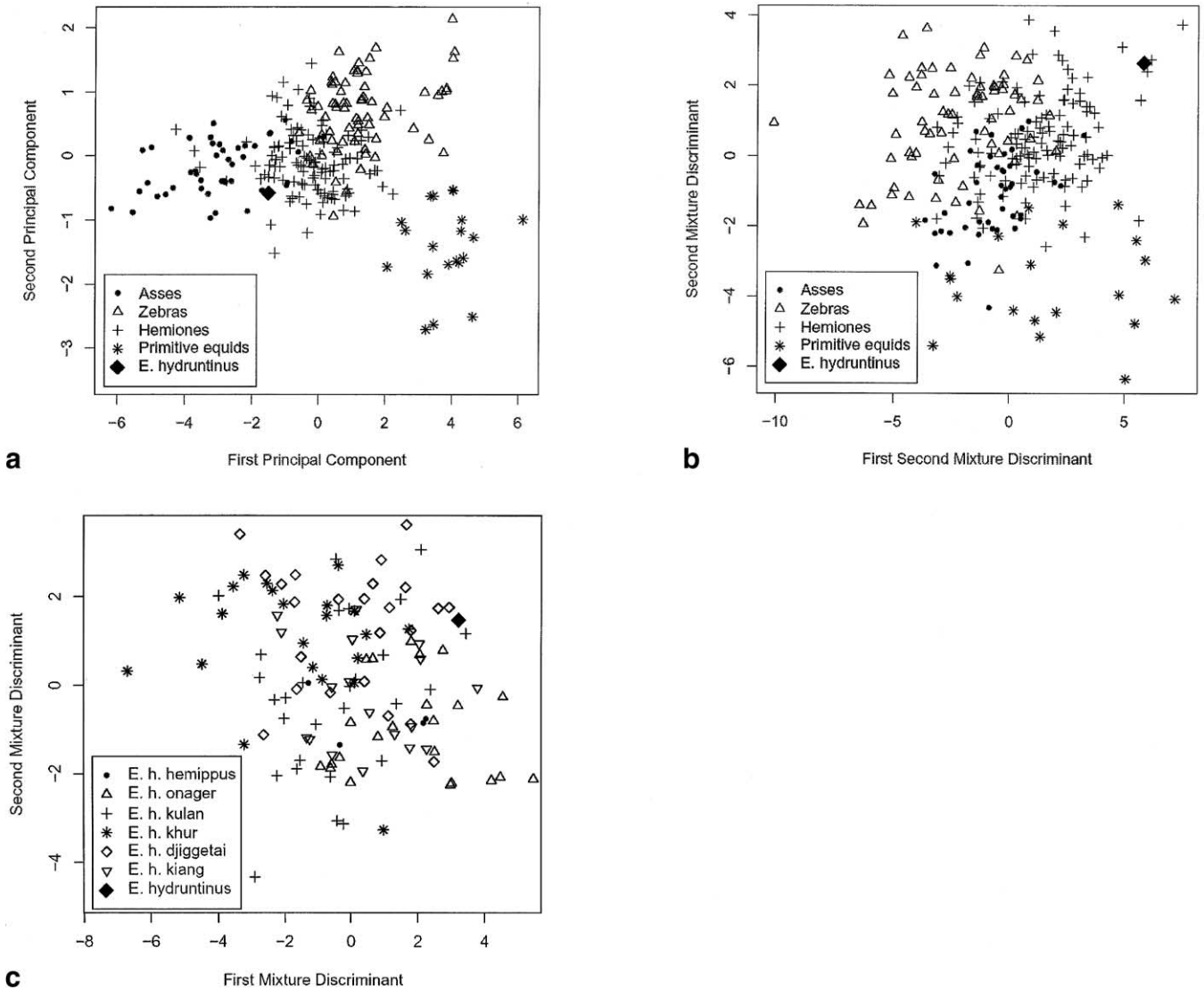


Fig. 3. From upper left: (a) Plot of first two principal components; (b) plot of first two mixture discriminants comparing *E. hydruntinus* with asses, zebras, hemiones, and fossil (Plesippine and Stenonid) equids; (c) plot of first two mixture discriminants comparing *E. hydruntinus* with Hemione subspecies.

Figures 4a (narial opening versus cheek length), 4b (narial opening versus overall palatal length), and 4c (overall palatal length by cranial length) compare cranial proportions of *E. hydruntinus* to species (extant and fossil) with which they share dental sympleisomorphies that distinguish

them from the caballoids. These include extant asses, hemiones, and zebras; primitive, Pliocene equids; as well as *E. hydruntinus minor* (where data are available). Note that *E. hydruntinus minor* is not included in Figure 4a since its cheek length is not known, but it does have a short narial

Table 3
Table of principal components

Measurement	Principal component					
	1	2	3	4	5	6
4 (postvomerine cranial length)	0.35	0.80	0.34	0.28	0.20	0.05
5 (muzzle length)	0.43	0.13	-0.12	-0.46	-0.55	0.52
2–5 (palatal length)	0.40	-0.52	0.48	0.02	0.43	0.39
17 (muzzle breadth at 13)	0.41	-0.21	-0.40	0.75	-0.24	0.04
31 (length of narial opening)	0.44	-0.16	0.35	-0.16	-0.32	-0.72
32 (cheek length)	0.42	0.05	-0.59	-0.34	0.56	-0.22

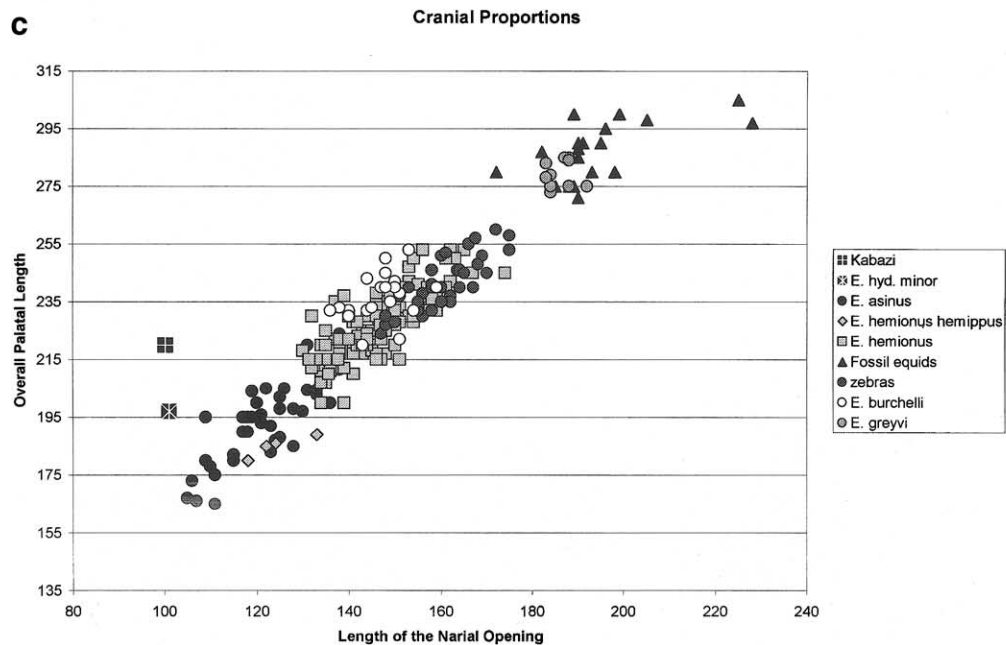
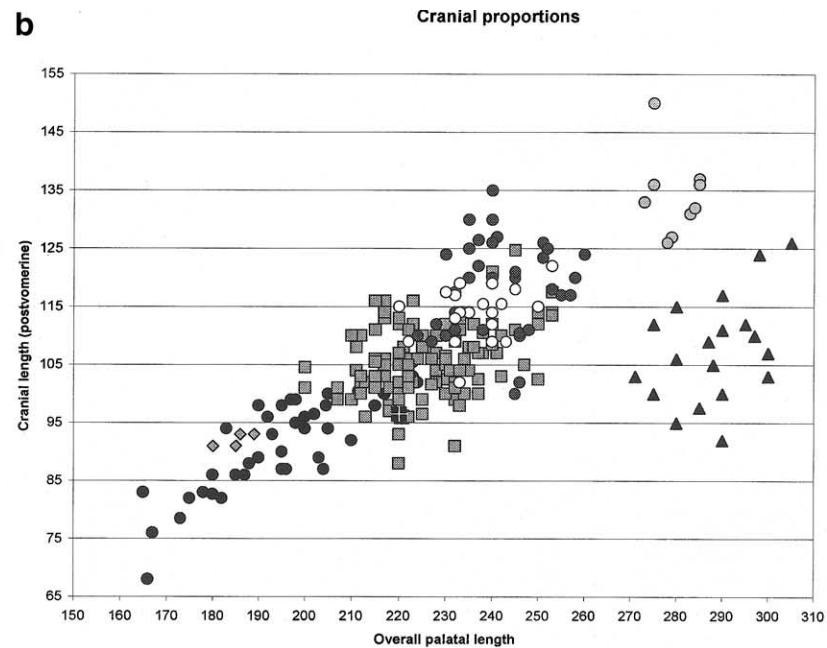
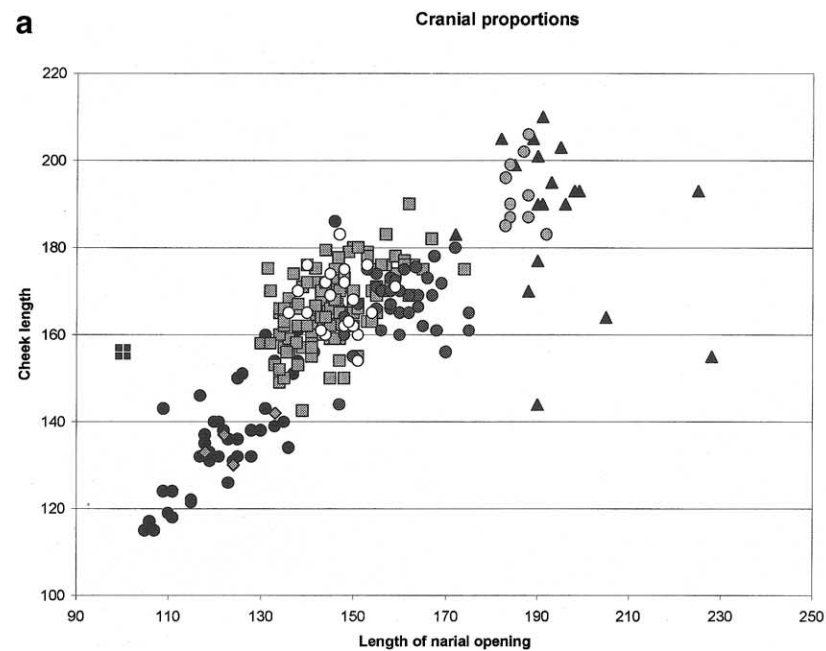


Fig. 4. Cranial proportions. (a) Bivariate plot of narial opening by cheek length; (b) bivariate plot of narial opening by overall palatal length; (c) bivariate plot of overall palatal length by cranial length.

opening (101.0 mm, compared to 100.2 mm for the Kabazi sample).

Figures 4a and 4b indicate that *E. hydruntinus* is distinguished from the other equids on the basis of its short nares (relative to both cheek and palatal length). Figure 4c indicates that primitive, Pliocene equids have relatively short crania and are easily distinguishable from *E. hydruntinus* and modern equid forms.

Figures 5a and 5b compare muzzle proportions of *E. hydruntinus* to those of extant asses, hemiones, zebras, and primitive (Plesippine and Stenonid) equids. Results show that *E. hydruntinus* has a wide muzzle relative to muzzle length (Fig. 5a) and to the length of the palate *sensu stricto* (Fig. 5b), which distinguishes it from most of the asses and zebras as well as the Plesippines and Stenonids.

Tooth dimensions of *E. hydruntinus* were compared to those of extant asses and hemiones and overlapped equally with both species for the premolars (P3 and P4) and the molars (M1 and M2); results are not shown here.

Discussion

We conclude, on the basis of PCA and MDA results, that *E. hydruntinus* is not related to any known Pliocene or Plio-Pleistocene monodactyl equid and is clearly not a Stenonid. In terms of its affiliation with extant equids, both PCA and MDA show that *E. hydruntinus* is distinct from the zebras. The PCA could not establish whether *E. hydruntinus* was more closely related to African asses or hemiones (Fig. 3a). The MDA showed that *E. hydruntinus* was more closely related to hemiones (Fig. 3b), but could not reliably establish which hemione subspecies in particular (Fig. 3c).

On the basis of cranial proportions (Figs. 4a and 4b) it is clear that *E. hydruntinus* can be distinguished from both asses and hemiones by its relatively short nares (length of the narial opening) as well as by deep ectoflexids on the lower molars (suggested elsewhere). Figure 5a shows that *E. hydruntinus* has a wider muzzle (muzzle breadth at 13), relative to muzzle length, than most asses, zebras, or Plesippine and Stenonid horses—a feature it shares with fossil zebras *E. mauritanicus*, *E. capensis*, and the Cape quagga (not shown). Figure 5b shows *E. hydruntinus* from Kabazi has a shorter muzzle relative to the length of the palate *sensu stricto* than the zebras and that its muzzle proportions present clear affinities with the hemiones.

In summary, we consider *E. hydruntinus* to be a distinct species of equid, more closely related to the hemiones than to any other equid species, characterised by a relatively wide muzzle and relatively short nares. This, in turn, leads us to assign *E. hydruntinus* to equid sociotype II—resource defense territoriality (see below).

Equid ethology and human predation patterns

Since *E. hydruntinus* is an extinct species, we cannot observe its social behavior. However, equids in the wild today have remarkably similar ecological niches, as well as similar morphologies (Groves, 1974; Willoughby, 1974), suggesting a degree of ecological stability through time. Since the behavior of prey species must have affected the strategies employed by Paleolithic people to hunt them, it is worth considering how we might reconstruct the ethology of *E. hydruntinus*.

Extant equid species can be grouped into two basic sociotypes: type I (a harem system) characterizes the social organisation of feral horses, *E. burchelli*, *E. zebra*, and *E. przewalski* (Berger, 1986; Klingel, 1975; Linklater, 2000); type II (resource defense territoriality) characterizes the social organisation of *E. hemionus*, *E. africanus*, feral asses, and *E. greyvi* (Klingel, 1974, 1998; Linklater, 2000; Salz and Rubenstein, 2000). The close relationship between *E. hydruntinus* and *E. hemionus* (this paper) suggests that *E. hydruntinus* would have exhibited type II social structure.

Whereas sociotype I equids form small, socially cohesive bands with relatively large territories (Berger, 1986; Klingel, 1975, 1998), sociotype II equids form relatively unstable groups and herds of variable composition (Denzau and Denzau, 1999; Klingel, 1998) and make relatively predictable use of smaller territories. Male dominance and aggression is usually considered a key feature of territoriality and dominant, territorial males generally do not tolerate other males within their core territories—which can overlap with other male core territories, however (see Klingel, 1998). Intraspecific variation in social structure among type II equids is reported and has been linked to ecological factors such as differences in habitat (e.g., Moehلمان, 1998; Rudman, 1998) and pressure from social predators (Feh et al., 2001). Socioecological explanations of variation in the social organization of equids have been criticized, however, since they are not supported across their geographical range (Linklater, 2000) and this issue remains a subject of debate among equid ethologists. Since there remains a possibility that ecological factors may condition the social structure of type II equids (and hemiones in particular) it seems prudent to suggest that modern hemione populations may serve as models for the social organization of *E. hydruntinus*, but only if their habitats can be considered similar in terms of the distribution of resources and the presence or absence of social predators.

Equids belonging to sociotype II form unpredictable social groupings that disperse easily. Their lack of social cohesion and unpredictable herd sizes would not make them amenable to being exploited by humans using communal hunting tactics such as drives at most times of the year. These hunting tactics require that a relatively large number of people coordinate their actions and rely on predictable returns to sustain the group. While *E. hydruntinus* dispersed in their winter or summer ranges, the most likely method of

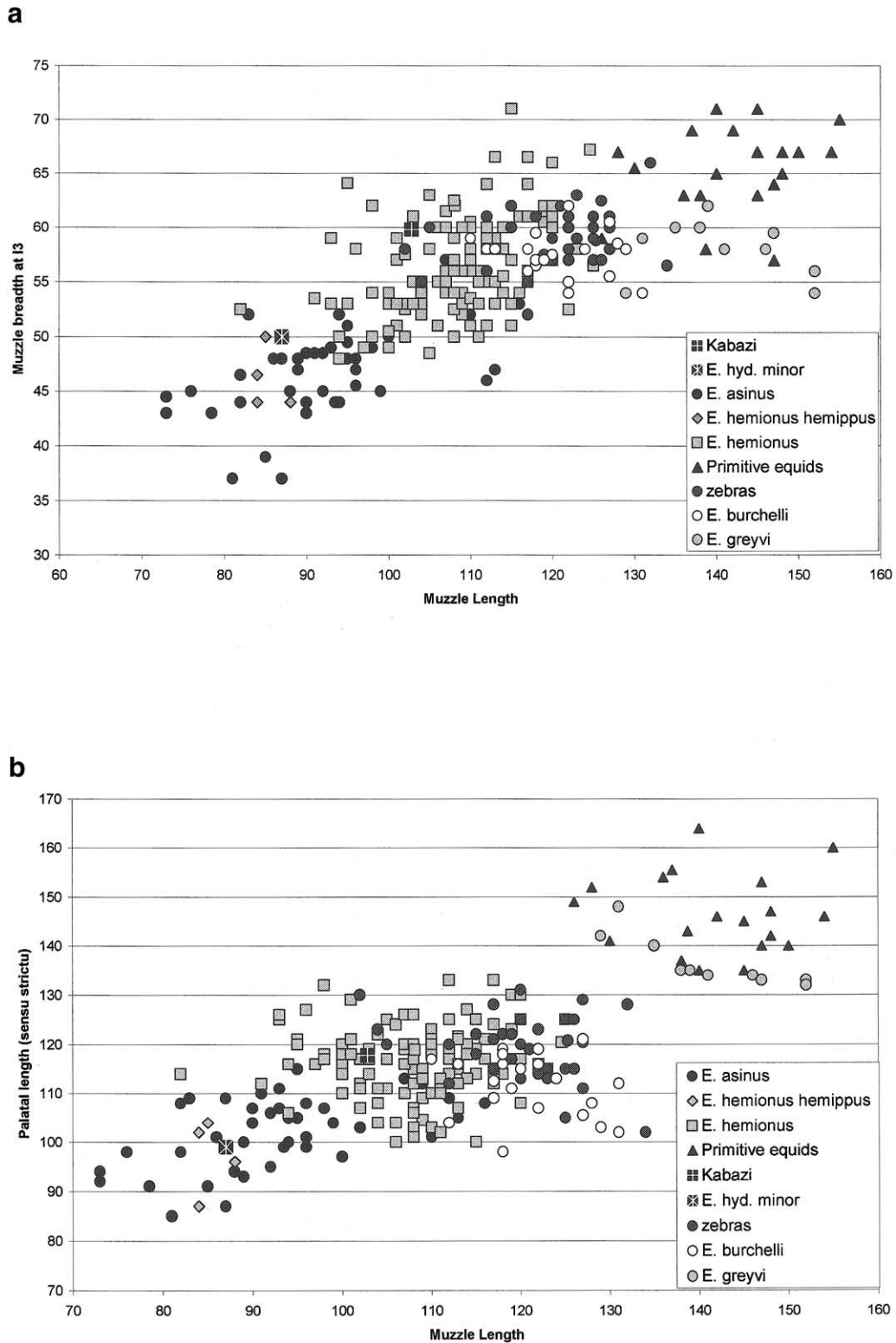


Fig. 5. Muzzle dimensions: (a) bivariate plot of muzzle breadth at 13 by muzzle length; (b) bivariate plot of length of the palate *sensu strictu* by muzzle length.

hunting would have been the stalking and killing of individual animals, which may not have been difficult to locate due to the stallion's attachment to a relatively small, core territory and the need to visit water sources (Denzau and

Denzau, 1999). *E. hydruntinus* herds moving between winter and summer ranges may have been larger and more predictable—making them more attractive to communal hunters (who rely on large yields to sustain their group size)

at these times of year—but the relative lack of social cohesiveness of these equids will still have meant that hunters intercepting the herds would have found it difficult to channel their movements. Ambush tactics, rather than drives, would have been the likely hunting strategy for the better part of the year.

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