Paleoecology of the Akkaşdağı hipparions (Mammalia, Equidae), late Miocene of Turkey

Robert S. SCOTT

Paleoanthropology Laboratory and Neogene Paleoecology Working Group,
Department of Anthropology, Old Main 330, University of Arkansas,
Fayetteville, AR 72701 (USA)
rscott@uark.edu

Murat MAGA

Department of Geological Sciences, The University of Texas at Austin,
1 University Station C1100, Austin, TX 78712-0254 (USA)
maga@mail.utexas.edu

ABSTRACT

KEY WORDS
Mammalia,
Equidae,
Hipparion,
ecomorphology,
paleoecology,
paleoenvironment,
metapodials,
morphometrics,
Akkaşdağı,
Central Anatolia,
Turkey.

Akkaşdağı is an abundant and diverse Turolian mammalian locality from Central Anatolia. Our paper reports the findings of our investigation of the paleoenvironment using an ecomorphological approach on the metapodials of hipparionine horses from Akkaşdağı. First, a detailed description of the underlying theoretical model is given, and a habitat score is described. Then the model developed here and initially applied to the Bovidae is applied to Akkaşdağı and other hipparion localities of Turolian and Vallesian age. Our results confirm the presence of four species of hipparionines in Akkaşdağı. The morphology of the metapodials suggests habitat diversity towards the open end of the spectrum. Forested conditions are ruled out.

RÉSUMÉ

Paléoécologie des hipparions (Mammalia, Equidae) d'Akkaşdağı, Miocène supérieur de Turquie.

MOTS CLÉS
Mammalia,
Equidae,
Hipparion,
écomorphologie,
paléoécologie,
paléoenvironnement,
métapodes,
morphométrie,
Akkaşdağı,
Anatolie Centrale,
Turquie.

Le gisement d'Akkaşdağı (Anatolie Centrale) a livré une faune de mammifères turolienne riche et diverse. Cette note présente les résultats sur le paléo-environnement de ce site à partir d'une approche écomorphologique sur les métapodes d'hipparions. Après une vue détaillée sur la méthodologie, la nature des habitats de ce groupe est discutée. Le modèle développé ici, initialement à partir des Bovidae, est appliqué aux hipparions d'Akkaşdağı, ainsi qu'à ceux d'autres gisements d'âge vallésien et turolien. Nos résultats confirment la reconnaissance de quatre espèces d'hipparions à Akkaşdağı. La morphologie des métapodes suggère des habitats plutôt ouverts ; rien n'indique l'existence d'un contexte forestier.

INTRODUCTION

Four species of hipparion have been recognized from Akkaşdağı on the basis of both cranial and postcranial skeletal material (Koufos & Vlachou 2005). The Akkaşdağı hipparions also clearly dominate the fauna in terms of overall abundance and each of the hipparion species recognized was represented by relatively large samples of third metapodials. The abundance and diversity of Akkaşdağı hipparions suggest that the paleoenvironment of Akkaşdağı can be best understood in the context of hipparion adaptations and the relatively large samples of third metapodials represent an opportunity to quantify key locomotor adaptations relevant to habitat preference.

Paleoecological reconstructions have often relied on taxonomic identifications as paleoecological data. The presence of taxonomic groups whose extant representatives tend to be associated with a particular habitat would be viewed as evidence for that habitat. This approach is limited by the possibility that fossil representatives of extant taxa may well have used different habitats (see Solounias & Dawson-Saunders 1988). More recently, habitat preferences have been reconstructed based on functional morphology (e.g., Kappelman 1988). This taxon-free (no species level identifications of fossil elements are required) approach, sometimes termed ecomorphology, infers paleohabitats based on morphological characters with functional advantages in a specific habitat. Thus, for fossil sites habitat-specific adaptations can fill the role of indicator species in extant settings.

This approach has been applied to bovids from Neogene sites and has focused on both locomotor (Kappelman 1988, 1991; Köhler 1993; Plummer & Bishop 1994; Kappelman *et al.* 1997; Scott *et al.* 1999) and dietary adaptations (Solounias & Dawson-Saunders 1988; Spencer 1995; Fortelius & Solounias 2000). The large extant radiation of bovids with known habitat preferences has made possible the development of discriminant models distinguishing bovids of different habitats on the basis of morphology. A more narrow radiation of extant equids and the

presence of accessory metapodials in hipparionines greatly complicate the application of a similar approach to Neogene hipparionines. However, the great abundance and diversity of hipparionines at Neogene localities such as Akkaşdağı combined with frequent good preservation of hipparionine third metapodials make a framework for interpreting the adaptive significance of hipparionine metapodials desirable.

The abundant bovid radiation makes available a purely empirical approach (e.g., discriminant analysis) for sorting bovid elements by habitat. However, the taxonomic composition of extant comparative sample can have an impact on results (DeGusta & Vrba 2003). When empirical models for sorting specimens to habitat also integrate functional morphological hypotheses, any biases resulting from comparative sample composition may be minimized. The importance of functional morphology is magnified in the case of extinct and tridactyl hipparionines given that the nearest extant group available for comparison is the more narrow radiation of extant monodactyl equines.

Various hypotheses based on the relationship between functional morphology and habitat have been suggested as explanations for variation in hipparionine third metapodial morphology. For instance, elongated metapodials suggest cursorial locomotion, which in turn may suggest more open habitat types (Gromova 1952; Eisenmann 1995). A similar interpretation has been offered for metapodial diaphysis shape. According to this explanation, third metapodials that are craniocaudally expanded are adapted to resist greater loads in the sagittal plane such as those that might be generated by cursorial locomotion. One prediction of this model is that hipparionines living in open environments and engaging in cursorial locomotion would have craniocaudally expanded cannon and shannon bones, while forest dwelling species would have mediolaterally expanded cannon and shannon bones (Gromova 1952; Eisenmann 1995). Sondaar (1968) suggested that craniocaudally expanded equid metapodials could reflect dry as opposed to wet habitats. These hypotheses suggest that the
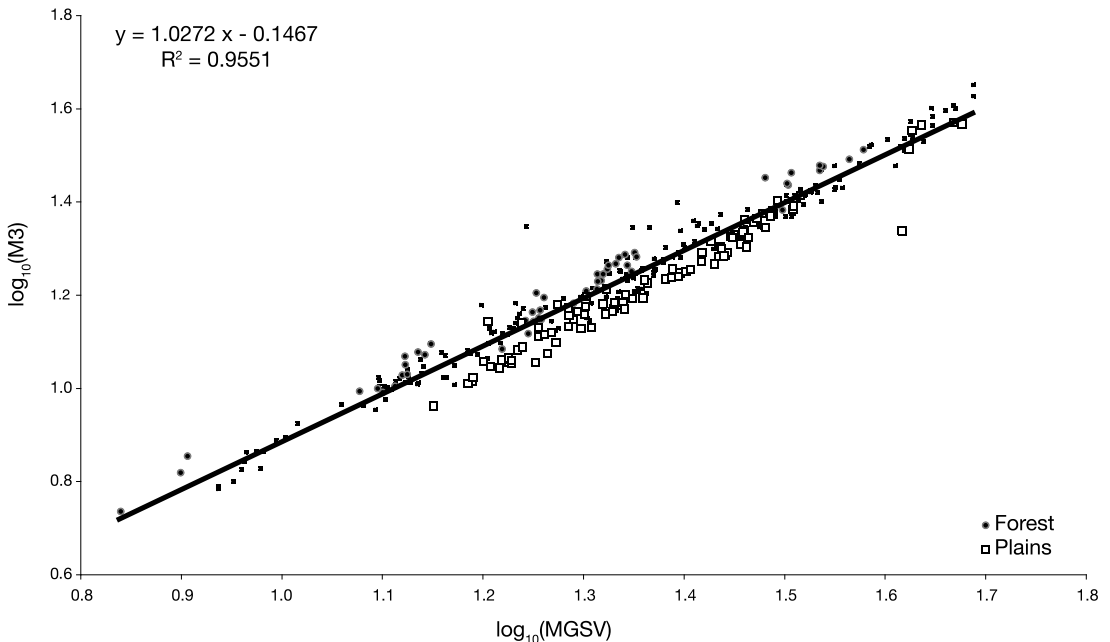
Fig. 1. — Plot of M3 (midshaft width) versus MGSV (a proxy variable for body size) for a sample of 329 bovid and antilocaprid metatarsals. The least squares regression line based on the complete sample is shown. Plains habitat specimens are shown as open squares (□) and forest bovids are shown as filled circles (●). All other specimens including those using intermediate and mountainous habitats are shown as small square dots (■).

degrees of relative elongation and slenderness in hipparionine metapodials are the most relevant metapodial morphological axes for understanding habitat.

Bernor *et al.* (2003) (see also Bernor *et al.* 1999) conducted a principal components analysis (PCA) of hipparionine third metapodials which confirmed the predictions of these models. Total variation (combined within and between group variation) in third metapodial morphology seemed to correspond to axes predicted by functional hypotheses related to habitat conditions and the first two principal components appeared to express relative slenderness and relative elongation.

Most significantly, these two principal components distinguish the large sample of metapodials from Höwenegg, Germany, thought to belong to a single species, *Hippotherium primigenium* von Meyer, 1829 (Bernor *et al.* 1997), from other late Miocene hipparionines. Generally, in the case of the Höwenegg sample, third metapodials had low values for principal component 1 (decreased relative length) and relatively high values for principal component 2 (increased mediolateral expansion) (Bernor *et al.* 2003). These PCA scores correspond to those that would be predicted for a forest living hipparionine by the models discussed above linking habitat and metapodial morphology (Gromova 1952; Sondaar 1968; Eisenmann 1995). Prior interpretations regarding the habitat of *Hippotherium primigenium* from Höwenegg (Bernor *et al.* 1988, 1997) suggested a hipparionine well adapted to subtropical forested habitats. These results confirm that the PCA scores of Bernor *et al.* (2003) can be interpreted to provide evidence regarding habitat.

The key measurements identified in Bernor *et al.* (2003) for paleoenvironmental reconstruction were those relating to diaphysis shape and metapodial length. These measurements were
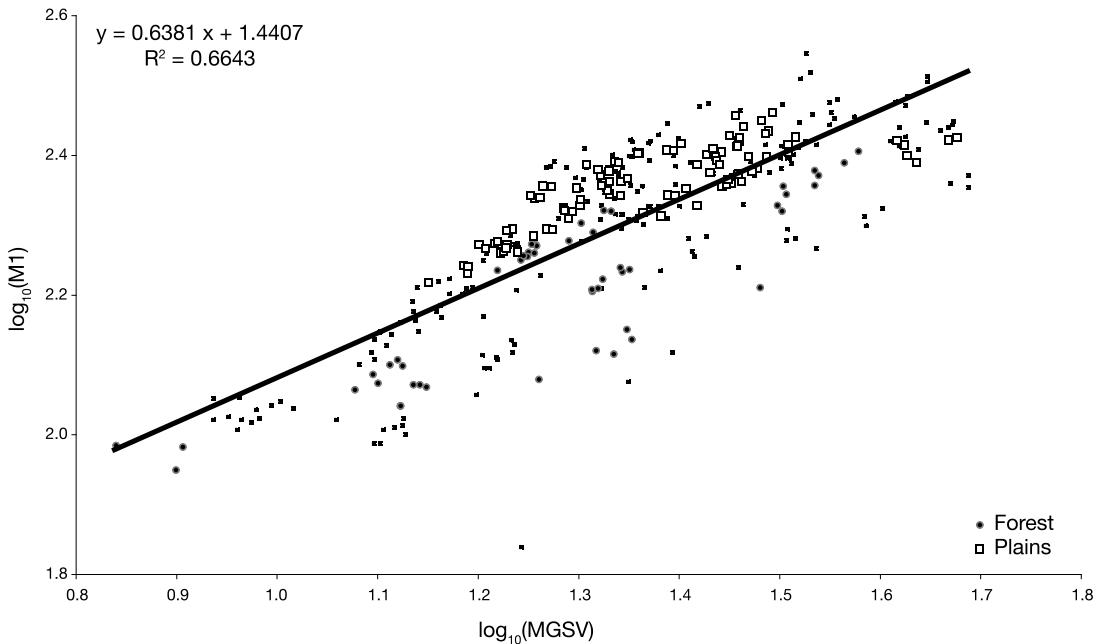
FIG. 2. — Plot of M1 (length) versus MGSV (a proxy variable for body size) for a sample of 329 bovid and antilocaprid metatarsals. The least squares regression line based on the complete sample is shown. Plains habitat specimens are shown as open squares (☐) and forest bovids are shown as filled circles (●). All other specimens including those using intermediate and mountainous habitats are shown as small square dots (■).

subsequently used in paleoecological interpretations regarding fossil hipparionines from Sahabi, Libya (Bernor & Scott 2003), and appear broadly applicable to fossil hipparionines. The use of these metrics for paleoecological interpretations is complicated by the fact that there are no living tridactyl equids with known habitat preferences to be used as a comparative sample. Living equids are monodactyl and occupy a narrow range of habitats, which makes them poor analogs for fossil hipparionines. On the contrary, the radiation of living Bovidae Linnaeus, 1758 is broad and occupies a wide range of habitats. Therefore, bovid metapodials may be useful as a functional analog for hipparionine metapodials. Although, distal metapodials of bovids differ fundamentally from hipparionine metapodials, the diaphysis and overall length of bovid metapodials appear analogous to equine and hipparionine metapodials. Thus, further empirical confirmation regarding the importance of M1 (maximum length)

and M3 (mediolateral dimension at midshaft) with respect to habitat can be looked for in the Bovidae. Scott (2004) analyzed 27 metrics taken on 329 metacarpals and 329 metatarsals from 72 bovid species and *Antilocapra americana* Ord, 1818. Discriminant analyses identified variables most useful in distinguishing between bovids of different habitats. This analysis suggested that mediolateral dimension at midshaft (analogous to the hipparionine metric M3), and maximum length (analogous to the hipparionine metric M1) were among the most informative measurements with respect to habitat. Figure 1 plots M3 versus a proxy for body size for the sample of 329 bovid and antilocaprid metatarsals. Similar to hipparionines (Bernor *et al.* 1999, 2003; Bernor & Scott 2003), forest living bovids appear to have elevated M3 dimensions for their body size. Figure 2 plots M1 versus a proxy for body size for the same sample and forest living forms have reduced M1 dimensions for their body size.

The fact that bovids with known habitat preferences display the same morphological trends across different habitats expected for hipparionines provides a strong confirmation that hipparionine habitats may at least be understood in relative terms based on these morphological axes. The combination of previous PCA analyses on hipparionines and discriminant analyses on bovids suggests that habitat cover may be modeled as a continuous variable derived from morphological variables of the metapodial. Such a variable would be an extremely valuable heuristic for paleontologists and would work much like a hypsodonty index (Janis 1988). As part of our quantification of Akkaşdağı hipparionine locomotor adaptation and likely habitat preference, we propose such a variable and apply it specifically to the large sample of Akkaşdağı metapodials. The goal for this habitat score is that it should have the following properties: 1) it should separate bovids of known habitats; 2) it should separate equines of known habitats; 3) it should separate fossil hipparionines where robust habitat interpretations have already been made; 4) the separation of forms from different habitats should occur in conformity with the biomechanical predictions made regarding morphology and habitat; and 5) the separation of bovids, hipparionines, and equines by habitat should be such that if closed habitat bovids have low scores relative to open habitat bovids then more closed habitat hipparionines should have low scores relative to more open habitat hipparionines. Closed habitat bovids need not necessarily have equivalent scores to closed habitat hipparionines but within taxonomic groups the trend from open to closed habitat should always be in the same direction as it is for other taxonomic groups.

MATERIALS AND METHODS

The Akkaşdağı material used in the present study has been collected during the excavations led under the leadership of Sevket Sen between 1997 and 2001, and it is housed at the Natural History Museum in Ankara.

Ten standard metapodial measurements described by Eisenmann *et al.* (1988) and Bernor *et al.* (1997) were taken on a large sample of hipparionine metapodial IIIs including specimens from Akkaşdağı. These measurements were M1, M3, M4, M5, M6, M10, M11, M12, M13 and M14. These measurements are relatively simple and were well diagrammed by Eisenmann *et al.* (1988) for the explicit purpose of allowing comparisons of measurements taken by different researchers and minimizing the impact of interobserver errors.

The comparative sample used here includes 126 metacarpal IIIs (hereafter MC IIIs) and 160 metatarsal IIIs (MT IIIs). These include 48 MT IIIs from Akkaşdağı (25 measured by M. Maga [shown in Appendix 2] and 23 measured by Koufos & Vlachou [2005]), three MT IIIs from La Gloria, Kalmakpai, and Layna (Eisenmann & Mein 1996), nine MT IIIs from Höwenegg (courtesy of Ray Bernor), and 100 MT IIIs measured by R. Scott from Afghanistan (Molayan [5]), Germany (Höwenegg [11]), Greece (Pikermi [11], Samos [9]), Iran (Maragha [13]), Spain (Ballestar [1], Can Llobateres [3], Concud [6], El Lugarejo [1], La Roma 2 [16], Los Valles de Fuentidueñes [4], Piera [2], Santiga [4], Venta del Moro [1]), Turkey (Çalta [3], Sinap [7]), and the USA (Xmas Quarry [2], Niobrara River [1]). The MC III sample includes 33 specimens from Akkaşdağı (13 measured by M. Maga [shown in Appendix 2] and 20 measured by Koufos & Vlachou [2005]), three specimens from Höwenegg (courtesy of Ray Bernor), and 90 specimens measured by R. Scott from Germany (Höwenegg [11]), Greece (Pikermi [5], Samos [4]), Iran (Maragha [19]), Spain (Can Llobateres [4], Concud [7], El Lugarejo [2], La Roma 2 [7], La Tarumba [1], Los Valles de Fuentidueñes [1], Piera [6], Polinya [1], Santiga [4], Venta del Moro [2]), Turkey (Çalta [5], Sinap [5]), and USA (Xmas Quarry [6]).

Bernor & Scott (2003) noted that description of hipparionine metapodials can be confounded by issues of scaling and concluded that a proxy measure for body size was necessary to understand the scaling of key morphological axes such

as relative elongation and relative slenderness. We follow Bernor & Scott (2003) and constructed a proxy variable for body size (called MGSV for Metapodial Global Size Variable) by taking the geometric mean (Jungers *et al.* 1995) of nine non-length metapodial III measurements (M3, M4, M5, M6, M10, M11, M12, M13, and M14). This size variable is analogous to the Metapodial Global Size Variable (MGSV) computed by Scott (2004) for a large sample of extant bovids based on the geometric mean of 10 non-length bovid metapodial measurements. The use of an analogous size variable for equids and bovids facilitates the comparison of morphological trends associated with habitat preference in these two families and is necessary for any discussion of general morphological trends associated with habitat.

To understand the relationship between morphology and habitat independent of body size, all 10 measurements were transformed to be independent of body size. This allows statements to be made concerning morphology such as relative elongation and relative slenderness. The transformation employed here is a refined version of the transformation used by Bernor & Scott (2003) developed by Scott (2004) and is described in full detail in Appendix 3. The resulting size independent variables are identified with the prefix "si" (for size independent). Thus, when transformed, measurement "M1" becomes the variable "siM1" and expresses maximum metapodial length relative to body size. Larger values for siM1 express greater relative elongation.

Previous principal components analyses (PCA) of Sümeg (Bernor *et al.* 1999), Sinap (Bernor *et al.* 2003) and Dorn Dürkheim (Kaiser *et al.* 2003) have successfully sorted hipparionine MP IIIs into biologically significant groups. Accordingly, we conducted PCAs using SAS of hipparionine MT IIIs and MC IIIs using all 10 size independent variables (siM1, siM3, siM4, siM5, siM6, siM10, siM11, siM12, siM13, siM14). The resulting principal components reflect total variation in metapodial shape for the sample considered here. Inspection of PCA plots is a powerful heuristic for identifying clusters of similarly

shaped metapodials and the eigenvectors for specific components can be interpreted with respect to *a priori* predictions regarding possible morphological associations with habitat. The Höwenegg (Germany) sample has been used in the past as an analytical standard for the interpretation of PCAs (Bernor & Scott 2003; Bernor *et al.* 1999, 2003; Kaiser *et al.* 2003) because it is well sampled and from a single species and a single site. In this study, Höwenegg is again used as an analytical standard and a second sample of Vallesian third metapodials from La Roma 2 (Spain) is added as an analytical standard. Like the Höwenegg sample, the La Roma 2 sample appears to include only a single species. La Roma 2 is also better sampled than most hipparionine localities (16 complete MT IIIs and seven complete MC IIIs).

Koufos & Vlachou (2005) have sorted the Akkaşdağı metapodials into four species groups (*Hipparion moldavicum* Gromova, 1952, "*Hipparion*" *dietrichi* Wehrli, 1941, *Hippotherium brachypus* Hensel, 1862, and *Hipparion longipes* Gromova, 1952). In general, these species-level sortings are adopted here. M. Maga measured a few specimens not measured by Koufos & Vlachou (2005) and these specimens were assigned to the existing groups with linear discriminant function analyses of Akkaşdağı specimens using the variables $\log_{10}$(MGSV) and siM1 in SAS (SAS Institute, Cary, NC). These analyses reclassified a few specimens already assigned by Koufos & Vlachou (2005) and these reclassifications are adopted here and are shown in Appendix 2.

As already noted (see Introduction), metapodial length (M1) and mediolateral dimension at midshaft (M3) appear to be likely correlates of habitat cover. Therefore, simple bivariate plots of siM1 and siM3 were constructed to further clarify morphological variation most likely to be habitat related.

To derive a general habitat score linking metapodial morphology and habitat, an empirical approach was adopted to create a linear combination of variables reflecting habitat variability within bovids, equines, and hipparionines. Since

the extant bovid radiation encompasses species with known and divergent habitat preferences, a bovid model was used to generate such a linear combination of variables. The bovid analogs of the variables siM1 and siM3 appear strongly associated with habitat and these variables are likely the best hipparionine habitat indicators as well (see Introduction). Therefore, siM1 and siM3 were chosen as the morphological basis for a "habitat score". A canonical variable (a linear combination of the quantitative variables that summarizes between-class variation in much the same way that principal components summarizes total variation) was derived using SAS based on bovid analogs of siM1 and siM3 for those bovids categorized in the plains and forest habitat groups (Scott *et al.* 1999; Scott 2004). The coefficients derived for this canonical variable were then applied to values for siM1 and siM3 for the fossil hipparionines in this study and selected extant equines (see also Appendix 3). The resulting scores are discussed for the Akkaşdağı hipparionines and evaluated with respect to the criteria outlined in the Introduction for an appropriate and heuristic habitat score.

RESULTS

METATARSAL III

PCA of hipparionine MT IIIs resulted in four principal components that each accounted for greater than 10% of the total variance. Cumulatively, these four components explained 73.5% of the variance (Appendix 1: Table 1). Of these four components, principal component 1 (PC1) explained 30.1% of the variance and summarized variability mainly in siM1 and siM3 (Appendix 1: Table 2). Increased scores on PC1 corresponded to increased length relative to size as indicated by a positive eigenvector of 0.68 with siM1 and to a decreased mediolateral dimension of the diaphysis as indicated by a negative eigenvector of - 0.53. The next highest eigenvector for PC1 was with siM12 suggesting that elongate, slender specimens tended to also have a craniocaudal expansion of the crista sagittalis (Appendix 1: Table 2).

PC2, PC3 and PC4 appear to describe the morphological axes of general diaphyseal robusticity, expansion of medio-lateral articular dimensions, and the relative reduction of distal dimensions (particularly the crista sagittalis compared to the proximal craniocaudal dimension). PC2 explained 16.5% of the total variance and appears to describe overall diaphyseal robusticity. The two highest eigenvectors for PC2 are positive and are with siM3 and siM4. All other non-length variables have negative eigenvectors with PC2 (Appendix 1: Table 2).

PC3 explained 13.7% of the variance and had positive eigenvectors with the medio-lateral dimensions siM11, siM5, and siM10. Thus, PC3 appears to be greatest when the medio-lateral dimensions of the epiphysis are relatively large and in particular when the distal and proximal medio-lateral articular dimensions are great. The variable, siM11, the medio-lateral, distal articular dimension, and siM5, the medio-lateral proximal articular dimension, had the two greatest eigenvectors with PC3 (Appendix 1: Table 2).

PC4 explains 13.3% of the variance and appears to contrast the distal and proximal metapodial dimensions and is high when siM6, the craniocaudal proximal variable, is large and siM12, the craniocaudal variable for the crista sagittalis, is small (Appendix 1: Table 2).

Figure 3 shows the means, 95% confidence interval, and range of the Höwenegg standard, the La Roma standard, and the four species from Akkaşdağı designated by Koufos & Vlachou (2005). PC1 clearly captures the greatest amount of between species group variation. The Höwenegg and La Roma groups have non-overlapping ranges. The differences between the four Akkaşdağı species for PC1 also appear significant (p < 0.0001, Kruskal-Wallis test). *H. longipes* has clearly elevated scores for PC1 comparable to those from La Roma and *H. brachypus* has the lowest scores for PC1 of all four Akkaşdağı species. All Akkaşdağı species had means for PC1 that were above the 95% confidence interval for the Höwenegg mean.

PC2 may capture more intraspecific variation as opposed to interspecific variation than PC1. The
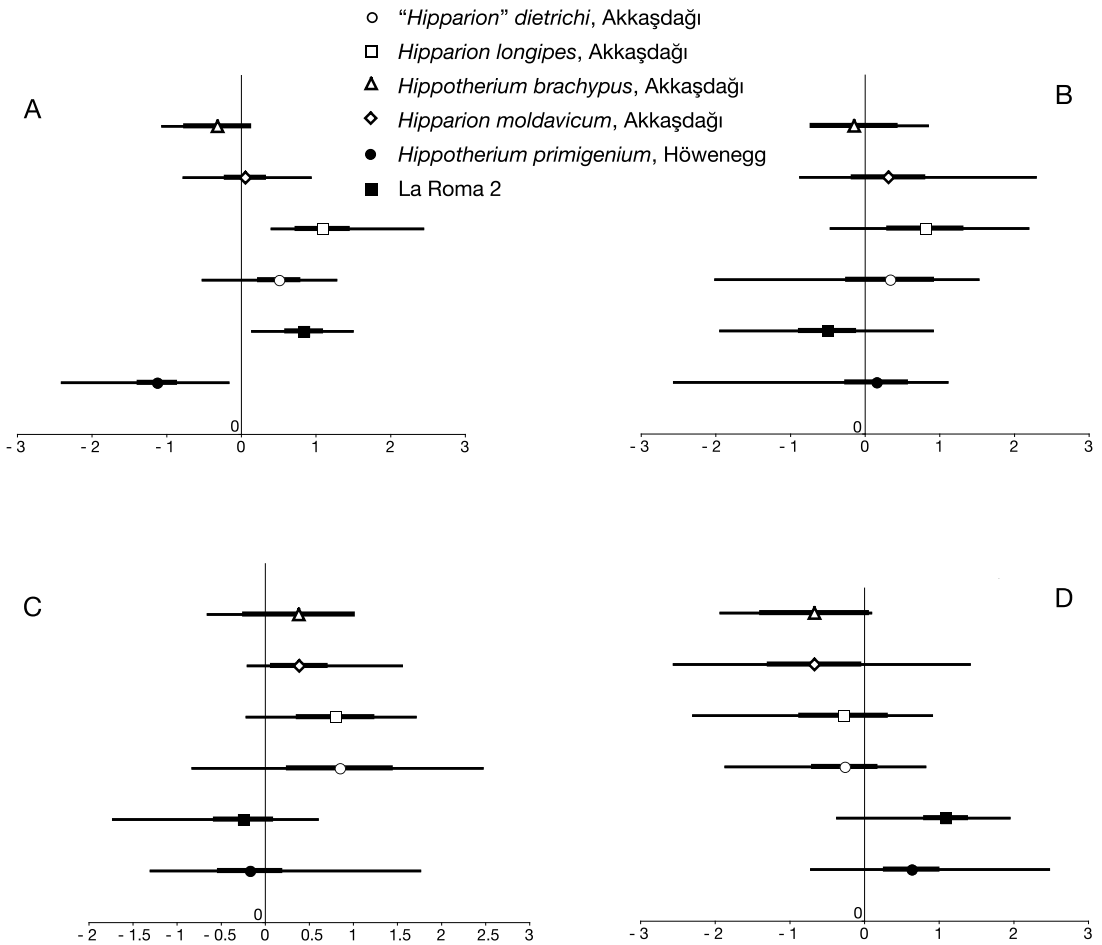
FIG. 3. — Summary plots of principal components 1-4 (PC1, PC2, PC3, and PC4) for hipparion MT IIIs from Höwenegg, La Roma 2, and Akkaşdağı; **A**, PC1 corresponding to MT III elongation and slenderness; **B**, PC2 corresponding to MT III diaphysis robusticity; **C**, PC3 corresponding to MT III mediolateral articular expansion; **D**, PC4 corresponding to MT III proximal craniocaudal expansion and crista sagittalis reduction. Mean principal component scores are shown. The 95% confidence intervals are denoted by thick lines and ranges are shown as thin lines.

ranges for the four Akkaşdağı species and the two standards (Höwenegg and La Roma) are larger for PC2 than they are for PC1. *H. longipes* has maximal values for PC2 while the La Roma hipparionines had minimal values for PC2. These two groups did not have distinct means for PC1 (Fig. 3A) but clearly differ with respect to PC2 (Fig. 3B).

Like PC2, PC3 and PC4 both may capture intraspecific variation as the ranges for these variables are large compared to those for PC1. Both

PC3 and PC4 primarily distinguish the Vallesian standards (Höwenegg and La Roma) from the younger Akkaşdağı forms. Altogether, the Akkaşdağı specimens have larger values for PC3 and smaller values for PC4. Differences among the Akkaşdağı species appear marginal but "*H.*" *dietrichi* and *H. longipes* could be slightly elevated for both PC3 and PC4.

Figure 4A plots siM1 and siM3, the major determinants of PC1. The Höwenegg and La Roma standards are plotted as 95% confidence ellipses
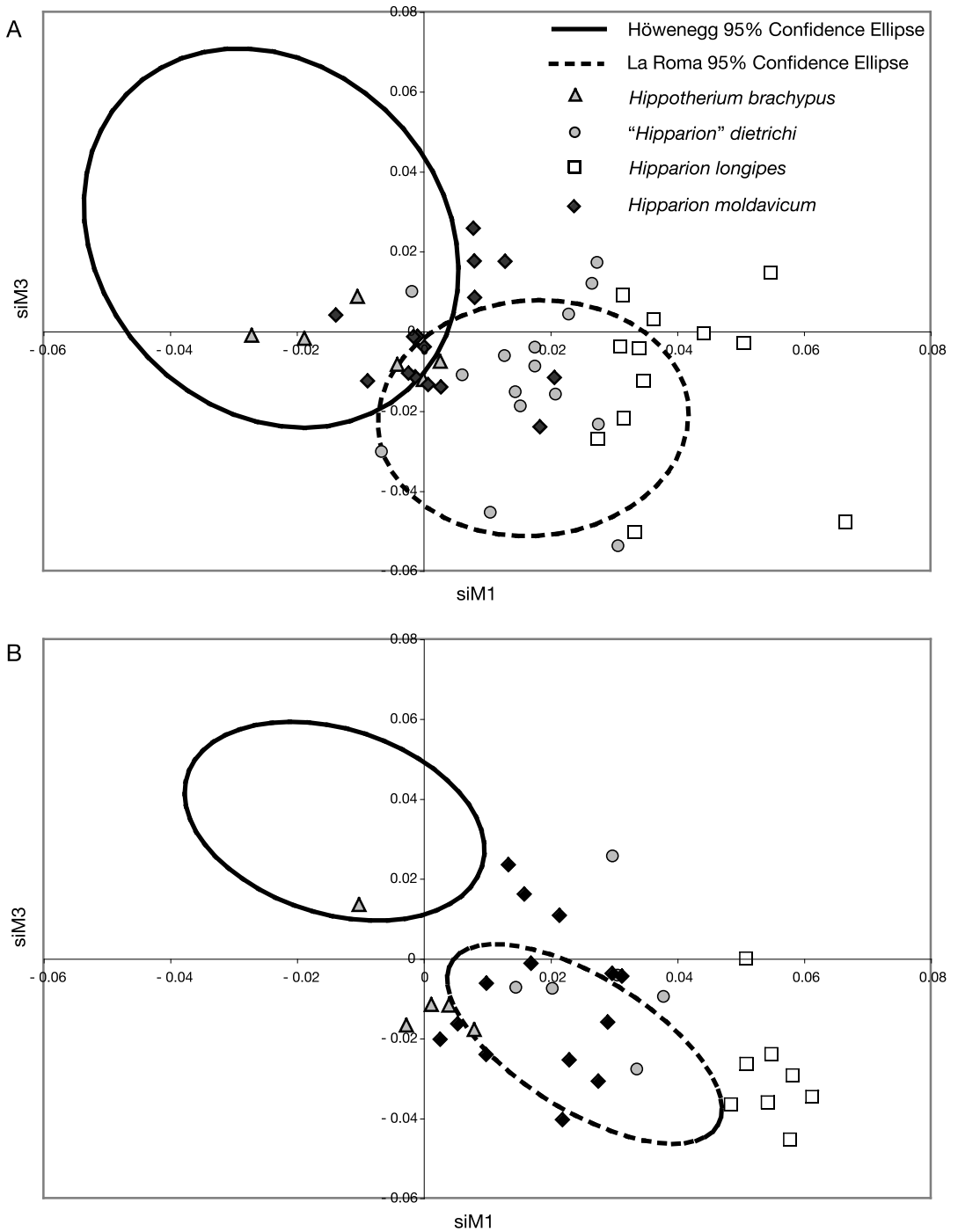
FIG. 4. — Plot of siM3 and siM1 for Akkaşdağı specimens shown with 95% confidence ellipses for Höwenegg (solid line) and La Roma 2 (dashed line); **A**, MT IIIs; **B**, MC IIIs.

and have a very narrow range of overlap. The Höwenegg specimens generally have negative scores for siM1 and positive scores siM3. The La Roma specimens contrast with the Höwenegg sample on both of these axes and generally have positive values for siM1 and negative values for siM3. MT IIIs attributed to *H. brachypus* plot in the lower right portion of the Höwenegg ellipse. *H. moldavicum* specimens cluster towards the border of the Höwenegg and La Roma ellipses. A few of these specimens appear to have values for siM1 like the La Roma sample and values for siM3 like the Höwenegg sample. Specimens of "*H.*" *dietrichi* and *H. longipes* both compare most favorably with the La Roma sample. The values of siM3 for "*H.*" *dietrichi* and *H. longipes* appear slightly elevated compared to the La Roma sample. *H. longipes* differs from "*H.*" *dietrichi* by having the most positive values for siM1. In general, the Akkaşdağı hipparion species fill a gradient in terms of relative elongation and slenderness from *H. brachypus* to *H. moldavicum* to "*H.*" *dietrichi* to *H. longipes*. All four species appear somewhat relatively elongate (measured by siM1) and relatively slender (measured by siM3) compared to the mean for the Höwenegg sample. *H. longipes* appears relatively elongate compared to La Roma. A habitat score for metatarsals based on siM1 and siM3 is calculated as follows: HS = (8.06 × siM1) + (- 30.46 × siM3) (See Appendix 3 for details on this formula). Thus, high values for the habitat score result from reduced values for siM3 (increased slenderness) and increased values for siM1 (increased elongation).

Forest bovids have negative habitat scores while plains habitat bovids have positive habitat scores. Similarly, intermediate habitat bovids which were not part of the sample used to determine the habitat score coefficients appear to differ in terms of habitat score according to the same trend. Heavy cover habitat bovids have lower habitat scores than light cover bovids (p < 0.05, Kruskal-Wallis test). Thus, bovids had habitat scores that appear to increase with increasing habitat cover (Fig. 5A). This trend also appears evident within subfamilies of bovids when comparisons between species of differing habitats are possible (Fig. 6A).

The equines, *Equus burchelli* Gray, 1824 (N = 30) and *Equus grevyi* Oustalet, 1882 (N = 15), are also included in Figure 5A. *Equus burchelli* had a mean habitat score of - 0.67 while *E. grevyi* had a mean habitat score of 0.25. These differences appear significant (p < 0.001, Kruskal-Wallis test).

The Höwenegg standard, previously interpreted as a forest dwelling hipparionine, had a mean habitat score of - 0.90 while the La Roma standard had a mean habitat score of 0.81. The four Akkaşdağı species had positive mean habitat scores as follows: *H. brachypus* (0.03), *H. moldavicum* (0.09), "*H.*" *dietrichi* (0.51), and *H. longipes* (0.68). Other hipparionines included for comparison include *H. brachypus* from Pikermi (- 0.70) *H. mediterraneum* Roth & Wagner, 1855 from Pikermi (0.14), a hipparionine from the Sinap Formation previously interpreted as a cursorial form (- 0.20) (Bernor *et al.* 2003), and non-cursorial (possibly goat-like) species, "*Hipparion*" *kecigibi* Bernor, Scott, Fortelius, Kappelman & Sen, 2003, from Sinap (- 1.25) (Fig. 5A).

METACARPAL III

For the PCA of hipparionine MC IIIs, we obtained three principal components that each explained more than 10% of the sample variance. The eigenvalues and eigenvectors for the MC III PCA are detailed in Tables 1 and 2 (Appendix 1). PC1 for the MC III explained 40% of the variance and, as can be seen in Figure 7A, much of this variation appears interspecific. Much like PC1 in the MT III analysis, PC1 for the MC III appears to describe elongation and slenderness. PC1 had a positive eigenvector of 0.66 with siM1 and a positive eigenvector of 0.46 with siM4. PC1 had a negative eigenvector of - 0.48 with the mediolateral variable siM3.

PC2 explained 19.5% of the variance in the MC III sample and as in the case of MT III had strong positive eigenvectors with both siM3 (0.43) and siM4 (0.63). PC2 also had a strong negative eigenvector with siM13 of - 0.49. Thus, PC2 for the MC III does not appear to depend as much on diaphyseal robusticity as is the case for
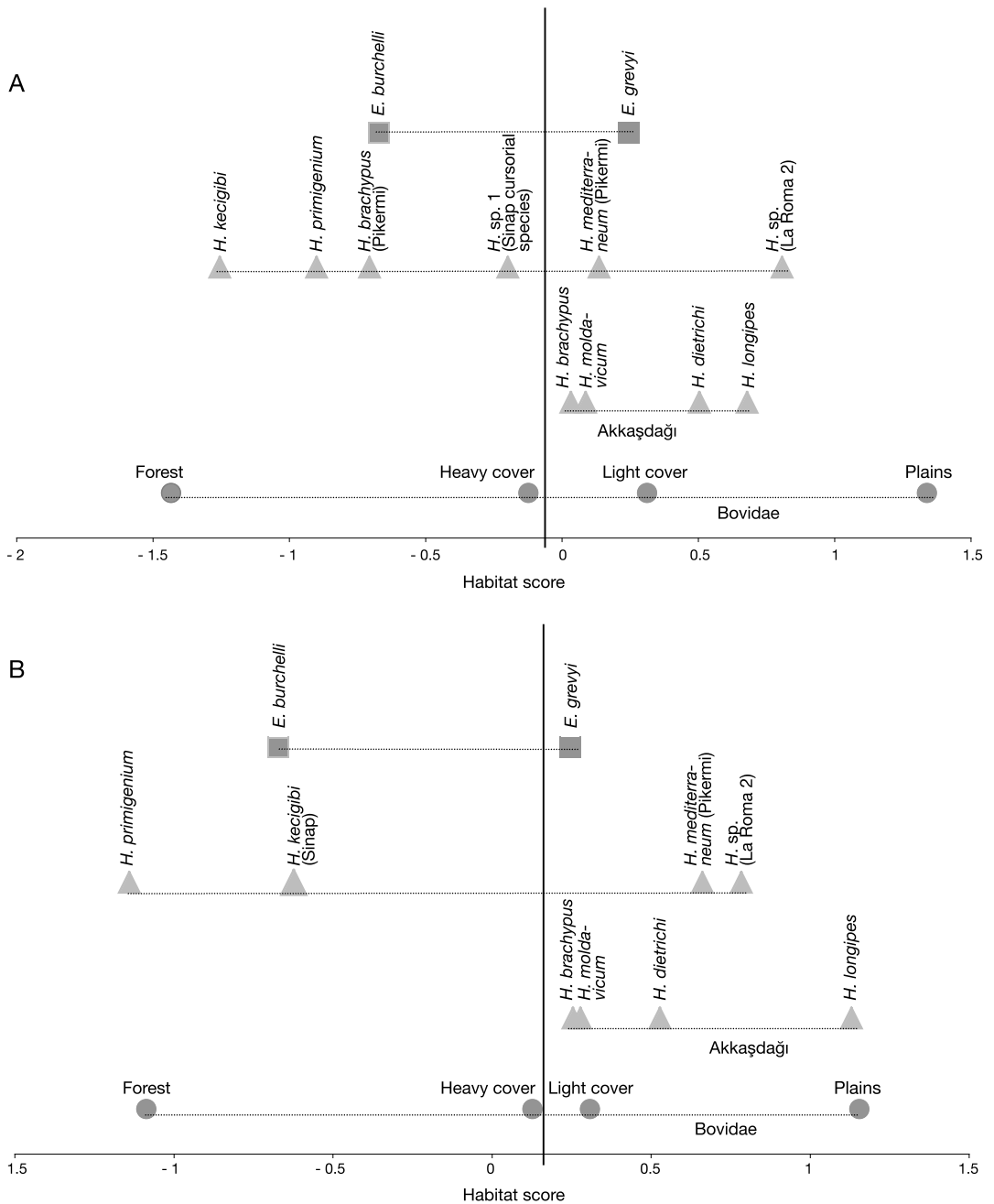
FIG. 5. — Summary of habitat scores for bovids assigned to four habitat categories (plains, light cover, heavy cover, and forest), *Equus burchelli*, *Equus grevyi*, and selected hipparions; **A**, metatarsals; **B**, metacarpals. The horizontal axis is habitat score (based on size, metapodial length, and metapodial width at midshaft – see Appendix 3) and the vertical axis divides bovids, equines, and hipparions. Abbreviations: ***E.***, *Equus*; ***H.***, *Hipparion* or *Hippotherium*.
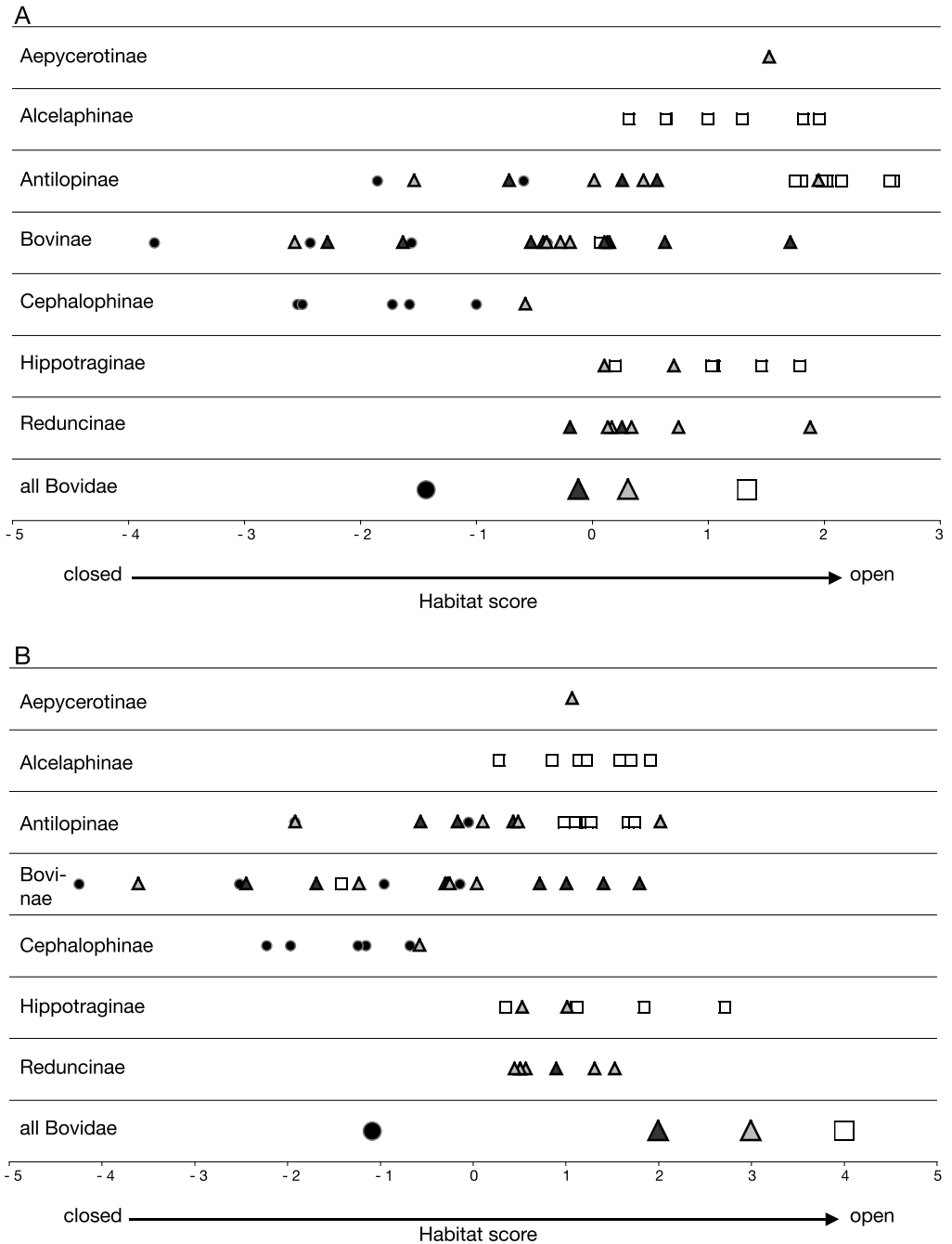
FIG. 6. — Summary of habitat scores for bovids by subfamily and habitat category; **A**, metatarsals; **B**, metacarpals. The horizontal axis is habitat score (based on size, metapodial length, and metapodial width at midshaft – see Appendix 3) and the vertical axis divides bovids by subfamily. The symbols further represent species according to habitat category. Closed circles (●) are forest species, dark triangles (▲) are heavy cover species, light triangles (△) are light cover species, and open squares (□) are plains dwellers. Mean habitat scores for all specimens in each habitat category are shown in the row corresponding to all Bovidae.

the MT III. For PC2 of the MC III, a negative eigenvector with siM13 and negative eigenvectors with siM12 and siM14 indicate distal articular reduction as a second morphological trend tied to PC2.

PC3 explained 10.6% of the MC III sample variance and had strong eigenvectors with siM3 (0.54) and siM13 (0.56). The morphological trends expressed are thus mediolateral expansion of the diaphysis and craniocaudal expansion of distal articular surfaces.

According to Figure 7A, the MC IIIs of the four Akkaşdağı species and Höwenegg and La Roma standards fit the same pattern as that seen for PC1 in the MT III analysis. The La Roma and Höwenegg standards appear even more distinct from each other. The four Akkaşdağı species appear to differ significantly in terms of PC1 (p < 0.0001, Kruskal-Wallis test). *H. brachypus* and *H. moldavicum* from Akkaşdağı appear intermediate between La Roma and Höwenegg. "*H.*" *dietrichi* appears comparable to the La Roma standard on PC1 and *H. longipes* has elevated scores for PC1 compared to La Roma.

PC2 appears to reflect differences between the Höwenegg and La Roma standards (Fig. 7B) but no significant differences can be found between the Akkaşdağı species for PC2. PC3 however appears to possibly divide *H. brachypus* and *H. moldavicum* from "*H.*" *dietrichi* and *H. longipes* (Fig. 7C).

The morphological trend reflected by PC1 can also be seen in the plot of siM1 versus siM3 shown in Figure 4B. The 95% confidence ellipses for Höwenegg and La Roma do not overlap and plot in contrasting quadrants in Figure 4B. Höwenegg tends to have negative values for siM1 and positive values for siM3 while La Roma has positive values for siM1 and negative values for siM3. These results closely parallel those seen in the MT III. *H. moldavicum* and "*H.*" *dietrichi* appear comparable to the La Roma standard in Figure 4B. *H. brachypus* appears comparable to Höwenegg in terms of siM1 and to La Roma in terms of siM3. *H. longipes* appears both more elongate and more slender than La Roma.

The metacarpal habitat score was equal to: (4.01 × siM1) + (- 31.65 × siM3). As with metatarsals, high values for the habitat score result from reduced values for siM3 and increased values for siM1. The metacarpal habitat score gave siM3 a slightly greater weight than in the metatarsal habitat score.

As with the metatarsal habitat score, forest bovids have negative habitat scores while plains habitat bovids have positive habitat scores (Fig. 6B). Intermediate habitat bovids which were not part of the sample used to determine the habitat score coefficients had mean habitat scores that appear fit the same trend (Figs 5B; 6B) but that do not differ significantly (n.s., Kruskal-Wallis test).

MC IIIs of *Equus burchelli* (N = 30) and *E. grevyi* (N = 15) are also included in Figure 5B and yielded results very similar to those for the MT III. *Equus burchelli* had a mean habitat score of - 0.34 while *E. grevyi* had a mean habitat score of 0.26. These differences appear significant (p < 0.01, Kruskal-Wallis test).

The Höwenegg standard, previously interpreted as a forest dwelling hipparionine, had a mean habitat score of - 1.14 while the La Roma standard had a mean habitat score of 0.79. The four Akkaşdağı species had positive mean habitat scores as follows: *H. brachypus* (0.28), *H. moldavicum* (0.39), "*H.*" *dietrichi* (0.27), and *H. longipes* (1.13). Other hipparionines included for comparison include *H. mediterraneum* from Pikermi (0.66), and a non-cursorial (possibly goat like) species, "*H.*" *kecigibi*, from Sinap (- 0.62) (Bernor *et al.* 2003) (Fig. 5B).

DISCUSSION

Our analyses of MT IIIs and MC IIIs from Akkaşdağı are largely congruent and suggest that a range of habitats were used by different Akkaşdağı hipparionine species. We concur with the finding of Koufos & Vlachou (2005) of four distinct species of hipparionine at Akkaşdağı. The plots of PC1 which summarize relative elongation and slenderness (Figs 3A; 7A) show that the four Akkaşdağı species can largely be separated by
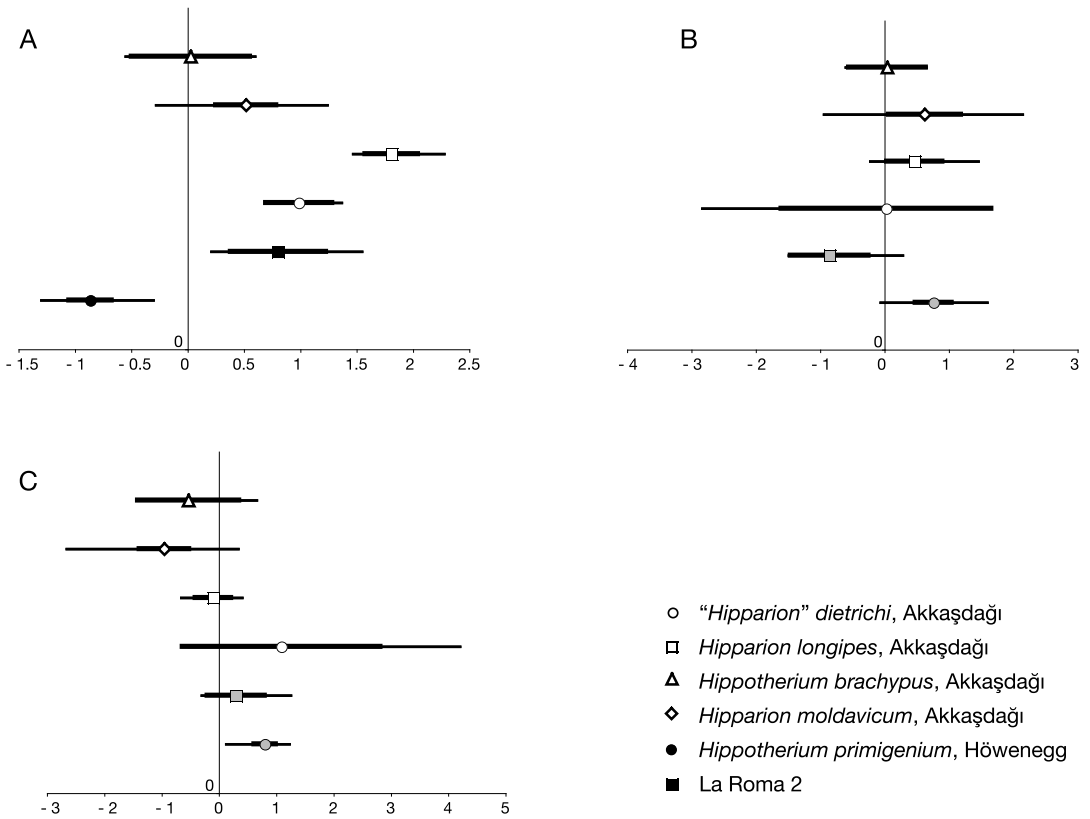
FIG. 7. — Summary plots of principal components 1-3 (PC1, PC2, and PC3) for hipparion MC IIIs from Höwenegg, La Roma 2, and Akkaşdağı; **A**, PC1 corresponding to MC III elongation and slenderness; **B**, PC2 corresponding to MC III diaphysis robusticity and distal craniocaudal reduction; **C**, PC3 corresponding to MC III mediolateral diaphyseal and distal craniocaudal expansion. Mean principal component scores are shown. The 95% confidence intervals are denoted by thick lines and ranges are shown as thin lines.

degree of elongation and slenderness. This appears to be especially true for MC IIIs. The Akkaşdağı species range from the least elongate and slender (*H. brachypus*) to the most elongate and slender (*H. longipes*).

The morphological trends of elongation and slenderness are likely most pronounced in taxa dwelling in more open and/or dry habitats (Gromova 1952; Sondaar 1968; Eisenmann 1995). On this basis, *H. longipes* would appear more open habitat adapted than *H. brachypus*. To further place the Akkaşdağı forms in the context of a habitat spectrum, all four species from Akkaşdağı were compared to two Vallesian age standards. All four species would appear on the basis of PC1 to be more open habitat adapted

than the Höwenegg standard which is thought to represent a forest dwelling hipparionine (Bernor *et al.* 1988, 1997). The La Roma standard clearly differs from Höwenegg in the direction of greater elongation and slenderness. We suggest that the La Roma hipparion was clearly not a forest adapted form and probably made use of habitats that were only lightly wooded. Similarly, the four Akkaşdağı species do not appear like the Höwenegg standard and are unlikely to have lived in forests. Rather, on the basis of their metapodials, they appear to have occupied a range of niches from some cover to at the most lightly wooded areas. *H. brachypus* and *H. moldavicum* may have occupied intermediate habitats while "*H.*" *dietrichi* and especially *H. longipes*

are quite likely to have preferred open and/or dry areas.

PC3 and PC4 from the MT III analysis are interesting in that they appear to distinguish the two older Vallesian standards from the younger Turolian Akkaşdağı species. The older Vallesian MT IIIs have reduced scores on PC3 and elevated scores on PC4. This corresponds to: 1) a reduction of the mediolateral articular surfaces; and 2) an increase in the proximal craniocaudal articular surfaces with a concomitant reduction in the crista sagittalis.

One explanation for these morphological trends would be that a greater proportion of ground reaction forces were absorbed by accessory metatarsals in older Vallesian forms. In uncommon cases where proximal accessory metatarsals are preserved with MT IIIs, it appears that they serve largely to increase the mediolateral component of the total proximal articular surface (pers. obs., RSS). More of the craniocaudal component of the total proximal articular surface would be made up by the MT III. Thus, craniocaudally expanded MT IIIs may correlate with expanded accessory metatarsals. As the accessory metatarsals course distally, they appear less closely articulated with the MT III at their distal extremity and are medial and lateral to the MT III (pers. obs., RSS). An overall decrease in the accessory metatarsals thus may also accord with a relative increase in MT III distal mediolateral articular surface.

Increased accessory metatarsals implied by MT III proportions would indicate their greater likelihood of more frequent or prolonged loading and more contact between the accessory hooves and the ground. Thus, the apparent contrast in morphology on PC3 and PC4 between both of Vallesian standards and the younger Akkaşdağı species suggests that the Akkaşdağı species may have been functionally more monodactyl than earlier Vallesian forms. This is in accord with observations of hipparionine trackways at Laetoli (Renders 1984). The accessory hooves appear to have contacted the ground during strides where one leg was slipping on the wet Laetoli ashfall. Thus, the function of accessory metatarsals may be linked to more or less frequent ground contact depending on substrate features. The distinctions between the Vallesian standards and Akkaşdağı species seen in PC3 and PC4 potentially imply less ground contact with the accessory hooves (or greater functional monodactyly) for all four Akkaşdağı species. This is potentially related to drier substrates at Akkaşdağı compared even to more open habitats such as those likely occupied by the La Roma hipparionine.

Figure 4 clearly shows the separation between the two standards in terms of relative elongation as measured by siM1 and in terms of relative slenderness as measured by siM1. All four Akkaşdağı species appear somewhat more extreme in terms of elongation (siM1) as opposed to slenderness (siM3) and tend to plot to the right of or in the right portion of the La Roma 95% confidence ellipse. If Sondaar (1968) is correct that diaphyseal slenderness tracks habitat dryness, then the Akkaşdağı metapodials could reflect a wet season. The fact that the Akkaşdağı metapodials tend to be as elongate or more elongate than the La Roma standard but not as slender could suggest an adaptation to mediolateral bending during locomotion over a seasonally wet and unpredictable substrate. Alternatively, as already discussed, if the Akkaşdağı species were functionally more monodactyl than earlier Vallesian forms, greater diaphyseal dimensions might potentially compensate for reduced accessory metapodials.

The habitat scores generated here based on both the MT III and MC III appear likely to track the spectrum from open to closed habitats quite generally and appear applicable to bovids, equines, and hipparionines. The habitat score appears to meet all five criteria suggested *a priori* for such a variable.

First, it clearly separates bovids of known habitats. This includes separating forest and plains bovids which were used to generate the habitat score coefficients and, at least in the case of the metatarsal, the habitat score also separates heavy cover and light cover bovids which were not used to generate the habitat score coefficients (Figs 5; 6). Heavy cover bovids plot to the left of light cover bovids and, in the case of the metatarsals, this

difference was significant. This result is supportive of the utility of the habitat score since the light cover and heavy cover species were not included in the generation of the formula for habitat score.

Second, the habitat score separates *E. burchelli* and *E grevyi*. While both species are tied to open habitats, *E. grevyi* is more constrained to arid and very open habitats (Estes 1991). In contrast, *E. burchelli* is more like a light cover bovid using open woodlands and requiring wetter habitats (Estes 1991). The most important result here is where *E. burchelli* and *E. grevyi* plot relative to each other and not what their absolute scores are compared to bovids. *E. burchelli* plots to the left of *E. grevyi* in terms of habitat score (Fig. 5) as would be predicted based on what differences there are in habitat usage for these two species. An extant forest dwelling equine would be expected to plot to the left of *E. burchelli*.

Third, the habitat score separates the Höwenegg sample from other hipparionines such as the La Roma hipparionine. The interpretation of the Höwenegg hipparion as a forest dweller is robust (Bernor *et al.* 1988, 1997) and La Roma hipparion would appear to be more open adapted. Once again, the more closed form (the Höwenegg hipparion) appears to plot to the left in terms of habitat score (Fig. 5).

Fourth, the separation of bovids, equines, and hipparionines from different habitats is in conformity with the biomechanical predictions made regarding morphology and habitat. Scores for open habitat forms result from elongation and slenderness of the metapodials.

Finally, the separation of bovids, hipparionines, and equines by habitat is such that closed forms all have low scores relative to open forms for all three groups. While grade shifts are possible and even likely between the taxonomic groups shown in Figure 5, within each group the more closed forms have lower habitat scores and plot to the left of more open adapted species. This same pattern can be seen within the Bovidae when species are grouped by subfamily (Fig. 6). It would appear that there is a strong case for the validity of the habitat score described here

for distinguishing between species that are relatively more open habitat or closed habitat adapted.

Based on their habitat scores (Fig. 5) none of the Akkaşdağı species would appear likely to have been forest dwelling like *Hippotherium primigenium* from Höwenegg. Each of the four Akkaşdağı species appears likely to have specialized on a different portion of a habitat spectrum likely ranging from less open to more open environments (Fig. 5). The larger bodied *H. brachypus* and smaller bodied *H. moldavicum* likely occupied the least open habitats of the Akkaşdağı hipparionines while "*H.*" *dietrichi* and *H. longipes* appear to have occupied more open habitats. *H. longipes* also appears to have been more extreme than *H. dietrichi*. The spectrum of habitat scores for the four Akkaşdağı species suggests that hipparionine species diversity mirrors habitat diversity at Akkaşdağı. The MT III habitat scores for *H. moldavicum* and *H. brachypus* are quite close to each other suggesting the possibility that they used the same habitat. The very different body size for these two species may suggest niche diversification along body size lines.

The habitat scores for "*H.*" *dietrichi* and *H. moldavicum* are reversed in the MC III analysis compared to the MT III analysis (compare Figure 5A and B). However, Figures 3A and 7A showing PC1 which also expresses relative slenderness and elongation presents a congruent picture for MC IIIs (Fig. 7A) and MT IIIs (Fig. 3A) in which "*H.*" *dietrichi* appears relatively elongate and slender compared to *H. moldavicum*. PC1 for MC III had a high eigenvector with siM4 which was not the case for the PC1 for the MT III. Thus, MC III slenderness may be driven in part by craniocaudal diaphyseal expansion in conjunction with mediolateral diaphyseal reduction while MT III slenderness may be mainly caused by mediolateral diaphyseal reduction. The consequence of this may be that the habitat score derived here based on analogy with the Bovidae is more valid for MT IIIs. Since siM4 was not included in the MC III habitat score, it would seem likely that some of the relative slenderness

for hipparionine MC IIIs would be undescribed by the metacarpal habitat score. This would account for the lower habitat score for "*H.*" *dietrichi* MC IIIs.

CONCLUSIONS

Our analyses confirm those of Koufos & Vlachou (2005) suggesting four species of hipparionine from Akkaşdağı. Morphological differences between Akkaşdağı metapodials appear to reflect habitat diversity at Akkaşdağı towards the open end of a habitat spectrum. Forested conditions are ruled out on the basis of a comparison with *H. primigenium* from Höwenegg. Increased seasonality is considered a possibility. The specific morphological axes relevant to habitat appear to be relative elongation and relative slenderness of third metapodials. Critically, these morphological axes are relative to body size and an accounting of metapodial scaling with respect to body size makes possible more robust interpretations. The validity of the habitat link with the specific morphological complex of elongation and slenderness in hipparionines appears strengthened by the closely analogous situation found for extant bovids where habitats are known and the correspondence of habitat with relative elongation and slenderness appears close. Similarly, *E. burchelli* and *E. grevyi* are also distinguishable on the basis of this morphology. The habitat score proposed here summarizes the habitat relationship with elongation and slenderness in a single heuristic variable which we propose may be used much as hypsodonty indices have been used to make inferences about diet based on crown height. We offer the habitat score for inclusion as a variable in paleontological databases (e.g., NOW database 2003).

Our results for PCA of MT IIIs (specifically PC3 and PC4) also suggest an intriguing possibility whereby an increase in the relative size of the distal mediolateral articular surfaces and reduction in the relative size of the proximal craniocaudal articular surfaces of the third metatarsals may be related to an increase in functional monodactyly among tridactyl equids. These changes may be related to substrate and specifically to drier conditions and appear to distinguish all four younger Akkaşdağı species from the two diverse Vallesian standards employed here. Better resolution perhaps can be obtained by incorporating more well sampled Turolian sites in future analyses. Further testing of this hypothesis is required but it potentially offers a framework for interpreting differences between tridactyl hipparionines and monodactyl equines.

REFERENCES

BERNOR R. L. & SCOTT R. S. 2003. — New interpretations of the systematics, biogeography and paleoecology of the Sahabi hipparions (latest Miocene) (Libya). *Geodiversitas* 25 (2): 297-319.

BERNOR R. L., KAISER T., KORDOS L. & SCOTT R. S. 1999. — Stratigraphic context, systematic position and paleoecology of *Hippotherium sumegense* Kretzoi, 1984 from MN10 (Late Vallesian) of the Pannonian Basin. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 39: 1-35.

BERNOR R. L., KOVAR-EDER J., LIPSCOMB D., RÖGL F., SEN S. & TOBIEN H. 1988. — Systematics, stratigraphic and paleoenvironmental contexts of first-appearing *Hipparion* in the Vienna Basin, Austria. *Journal of Vertebrate Paleontology* 8: 427-452.

BERNOR R. L., SCOTT R. S., FORTELIUS M., KAPPELMAN J. & SEN S. 2003. — Equidae (Perissodactyla), *in* FORTELIUS M., KAPPELMAN J., SEN S. & BERNOR R. L. (eds), *The Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York: 220-281.

BERNOR R. L., TOBIEN H., HAYEK L.-A. & MITTMANN H.-W. 1997. — The Höwenegg Hipparionine horses: systematics stratigraphy, taphonomy and paleoenvironmental context. *Andrias* 10: 1-230.

DEGUSTA D. & VRBA E. 2003. — A method for inferring paleohabitats from the functional morphology of bovid astragali. *Journal of Archaeological Science* 30 (8): 1009-1022.

ESTES R. D. 1991. — *The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores, Primates*. University of California Press, Berkeley, 611 p.

EISENMANN V. & MEIN P. 1996. — Revision of the fauna and study of *Hipparion* (Equidae, Perissodactyla, Mammalia) of the Pliocene locality of La Gloria 4 (Spain). *Acta Zoologica Cracoviensia* 39 (1): 121-130.

EISENMANN V. 1995. — What metapodial morphometry has to say about some Miocene hipparions, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven: 148-163.

EISENMANN V., ALBERDI M.-T., GIULI C. DE & STAESCHE U. 1988. — Studying fossil horses. Volume I: methodology, *in* WOODBURNE M. O. & SONDAAR P. Y. (eds), *Collected Papers after the "New York International Hipparion Conference, 1981"*. Brill, Leiden, 71 p.

FORTELIUS M. & SOLOUNIAS N. 2000. — Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* 3301: 1-36.

GORDON A. D. 2003. — Size matters – does body mass? *American Journal of Physical Anthropology* Supplement 36: 102.

GORDON A. D. 2002. — Increasing population sample sizes using global skeletal size variables. *American Journal of Physical Anthropology* Supplement 34: 77.

GROMOVA V. 1952. — *Le genre* Hipparion. BRGM, CEDP, Orléans 12, 288 p.

JANIS C. M. 1988. — An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference, *in* RUSSELL D. E., SANTORO J.-P. & SIGOGNEAU-RUSSELL D. (eds), Teeth revisited. *Mémoires du Muséum national d'Histoire naturelle* sér. C, 53: 367-387.

JUNGERS W. L., FALSETTI A. B. & WALL C. E. 1995. — Shape, relative size, and size-adjustments in morphometrics. *Yearbook of Physical Anthropology* 38: 137-161.

KAPPELMAN J. 1988. — Morphology and locomotor adaptations of the bovid femur in relation to habitat. *Journal of Morphology* 198: 119-130.

KAPPELMAN J. 1991. — The paleoenvironment of *Kenyapithecus* at Fort Ternan. *Journal of Human Evolution* 20: 95-129.

KAPPELMAN J., PLUMMER T., BISHOP L. C., DUNCAN A. & APPLETON S. 1997. — Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *Journal of Human Evolution* 32 (2-3): 229-256.

KAISER T. M., BERNOR R. L., FRANZEN J. L., SCOTT R. S. & SOLOUNIAS N. 2003. — New interpretations of the systematics and palaeoecology of the Dorn-Dürkheim 1 Hipparions (Late Miocene, Turolian Age [MN11]), Rheinhessen, Germany. *Senckenbergiana Lethaea* 83 (1/2): 103-133.

KOUFOS G. D. & VLACHOU T. D. 2005. — Equidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey, *in* SEN S. (ed.), Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas* 27 (4): 633-705 (this volume).

KÖHLER M. 1993. — Skeleton and habitat of recent fossil ruminants. *Münchner Geowissenschaftliche Abhandlungen.* Reihe A. Geologie und Paläontologie: 1-88.

NOW DATABASE 2003. — Neogene of the Old World. Database of fossil mammals: www.helsinki.fi/science/now

PLUMMER T. & BISHOP L. 1994. — Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *Journal of Human Evolution* 27: 47-75.

RENDERS E. 1984. — The gait of *Hipparion* sp. from fossil footprints in Laetoli, Tanzania. *Nature* 308 (5955): 179-181.

SCOTT K. M. 1990. — Postcranial dimensions of ungulates as predictors of body mass, *in* DAMUTH J. & MACFADDEN B. J. (eds), *Body Size in*

Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge: 301-336.

SCOTT R. S. 2004. — *The Comparative Paleoecology of Late Miocene Eurasian Hominoids*. Ph.D. Dissertation thesis, The University of Texas at Austin, USA.

SCOTT R. S., KAPPELMAN J. & KELLEY J. 1999. — The paleoenvironment of *Sivapithecus parvada. Journal of Human Evolution* 36 (3): 245-274.

SOLOUNIAS N. & DAWSON-SAUNDERS B. 1988. — Dietary adaptations and paleoecology of the late Miocene ruminants of Pikermi and Samos in Greece. *Palaeogeography Palaeoclimatology Palaeoecology* 65: 149-172.

SONDAAR P. Y. 1968. — The osteology of the manus of fossil and recent Equidae, with special reference to phylogeny and function. *Koninklijke Nederlandse Akademie Van Weteschappen* 25 (1): 1-76.

SPENCER L. M. 1995. — Morphological correlates of dietary resource partitioning in the African Bovidae. *Journal of Mammalogy* 76 (2): 448-471.

APPENDIX 1

TABLE 1. — Eigenvalues for Principal Components Analysis (PCA) of MT III and MC III.

Element	Principal Component	Eigenvalue	% Variance Explained
MT III	1	0.00120	30.1%
MT III	2	0.00066	16.5%
MT III	3	0.00054	13.7%
MT III	4	0.00053	13.3%
MT III	5	0.00033	8.2%
MT III	6	0.00026	6.5%
MT III	7	0.00020	5.1%
MT III	8	0.00015	3.8%
MT III	9	0.00011	2.8%
MT III	10	0.00000	0.0%
MC III	1	0.00158	40.0%
MC III	2	0.00077	19.5%
MC III	3	0.00042	10.6%
MC III	4	0.00035	8.8%
MC III	5	0.00024	6.2%
MC III	6	0.00021	5.4%
MC III	7	0.00015	3.8%
MC III	8	0.00013	3.4%
MC III	9	0.00009	2.3%
MC III	10	0.00000	0.0%

TABLE 2. — Eigenvectors for Principal Components Analysis (PCA) of MT III.

Element	Variable	Eigenvector			
		PC1	PC2	PC3	PC4
MT III	siM1	0.683	0.419	0.283	0.165
MT III	siM3	− 0.540	0.470	− 0.221	− 0.058
MT III	siM4	0.204	0.598	− 0.255	− 0.133
MT III	siM5	− 0.027	− 0.094	0.451	0.279
MT III	siM6	0.092	− 0.170	− 0.375	0.774
MT III	siM10	− 0.220	− 0.018	0.359	0.016
MT III	siM11	− 0.119	− 0.028	0.470	− 0.036
MT III	siM12	0.260	− 0.162	0.001	− 0.405
MT III	siM13	0.193	− 0.330	− 0.315	− 0.157
MT III	siM14	0.157	− 0.269	− 0.116	− 0.289
MC III	siM1	0.660	0.075	0.204	
MC III	siM3	− 0.479	0.425	0.536	
MC III	siM4	0.459	0.634	− 0.016	
MC III	siM5	0.040	− 0.061	− 0.222	
MC III	siM6	0.043	− 0.013	− 0.129	
MC III	siM10	− 0.208	0.093	− 0.265	
MC III	siM11	− 0.177	− 0.027	− 0.354	
MC III	siM12	0.176	− 0.305	− 0.264	
MC III	siM13	0.122	− 0.488	0.563	
MC III	siM14	0.023	− 0.258	0.151	

APPENDIX 2

Raw measurements (in mm) taken by M. Maga. An executable file for calculation of HS based on the sample and methods used in this study is available at: http://www.eskeletons.org

Specimen	Element	Species	M1	M3	M4	M5	M6	M10	M11	M12	M13	M14
AK2-242	MT III	*H. longipes*	278	29.05	30.68	43.70	29.21	38.88	38.04	33.95	25.26	28.30
AK2-267H	MT III	*H. moldavicum*	246	24.82	26.85	35.96	26.35	35.51	33.14	28.81	22.96	26.58
AK2-268B	MT III	*"H." dietrichi*	271	24.40	24.84	39.76	30.72	38.96	38.43	31.63	24.90	28.60
AK2-269	MT III	*H. moldavicum*	254	23.30	25.81	34.77	27.51	31.93	30.42	27.95	21.24	23.63
AK3-86	MT III	*H. longipes*	279	28.70	28.75	45.70	32.55	40.20	37.74	33.13	24.40	28.70
AK3-87*	MT III	*"H." dietrichi*	252	26.96	27.30	44.20	31.45	41.30	39.14	32.17	23.20	29.25
AK4-162	MT III	*H. moldavicum*	244	23.25	26.47	34.31	26.53	33.36	30.87	27.67	21.00	24.02
AK4-163	MT III	*H. moldavicum*	245	24.33	24.30	34.97	26.29	32.77	29.10	26.95	20.87	22.14
AK4-165*	MT III	*"H." dietrichi*	272	29.86	28.80	39.88	33.16	38.95	37.92	32.02	22.82	27.82
AK4-35*	MT III	*"H." dietrichi*	271	29.65	31.53	38.74	32.46	39.10	37.65	32.41	25.40	28.82
AK4-95	MT III	*H. brachypus*	266	32.04	31.51	44.76	36.53	48.12	43.23	36.45	27.35	30.68
AK5-153	MT III	*H. longipes*	288	29.10	29.65	42.92	29.92	37.08	35.47	31.30	23.82	26.73
AK5-154	MT III	*H. moldavicum*	242	23.96	23.80	33.80	26.58	33.63	31.23	28.80	21.10	24.80
AK5-408	MT III	*"H." dietrichi*	270	26.49	27.95	42.46	31.08	38.81	38.14	31.93	21.97	27.13
AK5-409	MT III	*"H." dietrichi*	270	28.95	28.50	42.19	31.93	36.55	38.26	31.61	22.02	27.08
AK5-74	MT III	*"H." dietrichi*	253	28.85	28.95	42.15	30.80	38.70	37.43	30.00	22.53	27.88
AK6-108	MT III	*"H." dietrichi*	261	26.65	27.75	42.35	28.45	36.95	36.22	31.93	22.95	28.43
AK6-180	MT III	*H. moldavicum*	251	26.96	27.46	36.13	27.09	37.94	33.46	28.15	19.70	24.98
AK6-181	MT III	*"H." dietrichi*	258	25.25	27.30	35.61	32.56	35.38	36.27	29.93	20.89	26.72
AK6-182	MT III	*"H." dietrichi*	262	26.74	27.35	39.26	32.22	36.15	36.10	30.25	23.01	26.94
AK7-135	MT III	*H. brachypus*	245	30.72	29.00	41.11	34.70	45.80	41.69	33.03	25.13	30.10
AKK-10	MT III	*H. brachypus*	256	32.00	31.66	41.20	33.38	43.70	42.30	35.08	25.54	30.53
AKK124	MT III	*H. moldavicum*	246	24.15	23.60	32.20	27.70	33.90	31.01	27.28	21.04	23.50
AKK145	MT III	*H. moldavicum*	237	25.00	25.80	35.30	27.20	34.05	32.00	28.80	21.03	25.36
AKK149	MT III	*H. longipes*	286	28.20	29.10	42.60	29.55	38.65	35.67	33.01	23.52	28.30
AK2-243	MC III	*H. moldavicum*	212	22.88	19.34	30.96	20.88	30.28	28.96	22.15	18.75	22.31
AK3-1	MC III	*H. longipes*	252	27.35	24.40	41.85	27.75	39.55	34.91	31.37	23.23	27.81
AK3-140	MC III	*"H." dietrichi*	239	27.84	22.25	41.97	28.97	37.44	34.68	28.75	33.51	25.73
AK5-394	MC III	*"H." dietrichi*	236	28.78	24.46	41.18	26.83	38.75	37.79	29.53	23.23	26.27
AK5-5A	MC III	*H. brachypus*	226	31.65	25.10	44.60	30.90	46.15	41.62	31.91	26.45	30.88
AK5-6	MC III	*H. moldavicum*	230	25.20	25.05	38.80	26.45	37.45	34.71	27.71	19.90	25.20
AK5-75	MC III	*H. brachypus*	228	32.00	26.00	46.40	29.95	46.65	40.86	32.47	25.07	30.35
AK5-76	MC III	*H. moldavicum*	219	24.60	21.05	36.10	21.80	34.85	32.24	26.17	20.09	23.46
AK6-107	MC III	*H. longipes*	254	27.10	24.85	42.25	28.90	38.15	34.87	30.65	24.00	27.65
AK6-195	MC III	*H. moldavicum*	211	23.18	20.40	34.10	24.13	33.70	30.96	25.94	19.92	23.83
AKA43	MC III	*H. moldavicum*	216	25.50	21.00	34.12	22.43	35.85	30.00	24.56	19.01	23.26
AKA55	MC III	*H. moldavicum*	220	24.75	20.35	35.00	23.30	32.85	30.70	25.90	19.23	23.10
AKK116	MC III	*"H." dietrichi*	230	28.35	24.65	41.85	25.80	36.80	36.06	29.73	24.07	27.00

APPENDIX 3

Methodological notes.

PROXY BODY SIZE VARIABLE

Jungers *et al*. (1995) recommended geometric means as size variables in morphometric studies while K. M. Scott (1990) used non-length variables of metapodials to estimate equid body masses. Bernor & Scott (2003) note that the regression formulae of K. M. Scott (1990) tend to give differing body mass estimates for MC IIIs and MT IIIs. Gordon (2002, 2003) argued that geometric mean size variables termed Global Size Variables (GSVs) are more stable measures of general body size than body mass estimates and can be measured without prediction errors. Scott (2004) uses a GSV of non-length metapodial dimensions (Metapodial Global Size Variable or MGSV) to investigate scaling of bovid metapodials. This bovid MGSV is precisely analogous to the geometric mean of nine non-length metapodial dimensions used by Bernor & Scott (2003) which they termed "GEOMEAN Size". Here, we use the same geometric mean size variable which for general consistency with other studies (e.g., Scott 2004) we have termed MGSV. MGSV is calculated as follows:

$$MGSV = (M3 \times M4 \times M5 \times M6 \times M10 \times M11 \times M12 \times M13 \times M14)^{(1/9)}$$

SIZE INDEPENDENT MEASURES OF SHAPE

Ratio measures of shape are often correlated with body size and may indicate changes in either the denominator or numerator. This complicates interpretations of shape differences between taxa. For instance, the measurement of diaphyseal shape with a ratio of M3:M4 may be: 1) correlated with body size; and 2) could be driven by M3, M4 or both. Therefore, we prefer to measure relative dimensions with a ratio of a measurement to a linear measure of body size (e.g., M3:MGSV). Thus, in the case of diaphysis shape, the contributions of M3 and M4 may be isolated.

To account for shape differences driven by scaling, tests for correlation between ratio measurements and body size may be performed. Cases where ratios remain correlated with body size can be transformed to variables uncorrelated with body size by calculating residuals. We followed this procedure here.

To generate shape variables uncorrelated with body size and to thus summarize shape differences that are not the result of scaling, all 10 measurements used in this study were first divided by MGSV and the resulting ratios were logged. These ratios were tested for a correlation with the log of MGSV using the entire hipparionine sample in SAS (SAS Institute, Cary, NC). In cases where a significant correlation was found ($p > 0.05$) the residual of the logged ratios was computed. The result was 10 variables uncorrelated with MGSV (our proxy for body size) that were either the log of a simple ratio or the residual of that simple ratio. Each of these variables was designated with the prefix "si" for "size independent". For MT IIIs, residual measures were computed for M1, M3, M4, M10, M11, and M14 and are referred to respectively as siM1, siM3, siM4, siM10, siM11, and siM14. The logged ratios for M5, M6, M12, and M13 over MGSV were not significantly correlated with MGSV and these ratios were retained for the remainder of the MT III analysis. They are referred to as siM5, siM6, siM12, and cM13. In the case of MC IIIs, residual measures were computed for all measures with the exception of M6.

HABITAT SCORE COMPUTATION

Canonical variables are similar to principal components with the key distinction that they summarize between group variance and can only be applied in cases where group membership is known. Thus, canonical variables can be computed for bovids of known habitat. The coefficients of these canonical variables may potentially be applicable to other taxa where precisely analogous variables are known. This appears likely in the case of bovids and equids.

Here we determined a canonical variable based on siM1 and siM3 that maximized the variance explained between plains and forest bovids (as classified in Scott *et al*. 1999; Scott 2004). This canonical variable is potentially a valuable habitat indicator for bovids and is used as the basis of our habitat score (HS). The coefficients by which siM1 and siM3 were multiplied to determine HS for bovids were then applied to siM1 and siM3 for hipparionine and equine specimens.

The logged ratio of M3 to MGSV was not significantly correlated with the log of MGSV for a sample 109 extant equine MT IIIs and 101 extant equine MC IIIs and therefore the logged ratio of M3 to MGSV was standardized to the mean in the case of equine MC IIIs and MT IIIs. Thus, the habitat score for equines was generated using the standardized values for the logged ratio of M3 to MGSV and the variable siM1 generated based on the same equine sample. An executable file for calculation of HS based on the sample and methods used in this study is available at: http://www.eskeletons.org.