Characterizing adaptive morphological patterns related to habitat use and body mass in Bovidae（Mammalia： Artiodactyla）*

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Abstract　A multivariate analysis of the postcranial skeleton of extant bovids reveals patterns of osteological features indicative of ecological adaptations for habitat use and body size. The morphological patterns that characterize the postcranial anatomy of bovid species from each habitat type were identified with stepwise canonical discriminant analysis and decision trees，a technique based on machine learning. The analyses were carried out using 43 measurements from 110 extant bovid species. The discriminant functions and decision trees obtained allow a perfect discrimination among bovids adapted to open plains，forests and mountainous areas（100% of correct reclassifications obtained in all comparisons），using sets of variables measured in all major limb bones as well as combinations of variables derived exclusively from single limb elements. Given that the adjusted algorithms involve small sets of postcranial measurements，they can also be applied to non-complete specimens preserved in archaeological and paleontological assemblages，thus being useful for estimating the locomotor performances of ancient taxa. These algorithms，indicative of ecological adaptations for habitat use，combined with those adjusted with craniodental measurements for estimating the dietary preferences of bovid species，have the potential for characterizing the paleoautecology of extinct taxa and may be used in paleoenvironmental reconstruction. We also analyze if multiple regression equations show higher predictive ability for estimating body mass than simple regression equations，and propose the best algorithms obtained from postcranial morphological variables measured in each single major limb bone［*Acta Zoologica Sinica* 52（6）：971－987，2006］.

Key words　Bovidae，Ecomorphology，Habitat use，Body mass，Discriminant analysis，Decision trees

牛科（哺乳纲：偶蹄目）动物与生境利用有关的适应形态模式 *

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摘　要　对广义牛科动物颅后骨骼的多元变量分析揭示了牛科生境利用和体型之间的骨学特征。利用逐步分辨分析方法和一个基于机器学习的决策树方法鉴别了每种生境中牛科动物颅后解剖结构的形态特征。从 110 个 广义牛科动物测量了 43 个指标进行了这项分析。利用所有主要肢骨测量值和以单根肢骨测量为主的测量值获得的分辨函数和决策树可以完美地区分适应开阔生境、森林和山地的牛科动物（在所有分析中得到了 100% 正确的再分类）。由于调整的函数仅涉及到很小的颅后骨骼测量集，这些函数可以应用于研究考古学和古生物学发掘物中保存的不完整标本。这些表征生境利用的生态适应函数与那些用颅齿部性状建立、用于推测牛科动物食物选择的函数结合，具有刻画已灭绝的分类类群的古个体生态学和重建古环境的潜力。我们还分析了多元回归是否较单一因子回归表现出较高的预测能力，并提出了从每一种单根主要肢骨测量的颅后形态变量得到的最好代数函数［动物学报 52（6）：971－987，2006］。

关键词　牛科　生态形态学　生境利用　体重　分辨分析　决策树

　　Associations of postcranial structure in extant bovids related to locomotor performances are identified in order to characterize morphological adaptations to gross habitat types（flat grasslands，forests，and

hilly and mountainous areas） using a multivariate approach. These associations may be used to reconstruct the locomotor behavior and habitat preferences of ancient bovids preserved in fossil assemblages, and thus allow their autecology to be estimated (e.g., Palmqvist et al., 2003; Mendoza et al., 2005). In addition, the body size of extant bovids is correlated to the dimensions of the postcranial skeleton and multiple regression functions are provided for predicting the mass of ancient species (e.g., Mendoza et al., 2006).

Postcranial features correlated with habitat type and locomotor adaptations include the shape of major limb bones (Scott, 1985; Kappelman et al., 1997; Plummer and Bishop, 1994) and of the ankle and foot (Köhler and Moyà-Solà, 2001; DeGusta and Vrba, 2003, 2005a, b). This study on postcranial adaptations of bovids differs from previous ones in the use of a multivariate analysis to evaluate a broad set of measurements from different limb elements of various extant bovids to identify morphological correlates for habitat.

Many authors have used simple log-transformed bivariate least squares regression equations to estimate the body mass of extinct species based on single anatomical measurements, such as the area of the first lower molar (e.g., Beard et al., 1996; Gagnon, 1997; Kay et al., 1998), the volume of the femoral head (Cartelle and Hartwig, 1996; Kappelman et al., 1997), or the area of the eye orbit (Kordos and Begun, 2001). As might be expected, no single morphological variable shows a perfect correlation with body mass, hence reducing the precision and reliability of predictions derived from them, apparent in the large standard errors and wide confidence intervals around such estimates. A relatively common strategy for avoiding such problems is to combine predictions from several allometric equations, based on different anatomical structures, to calculate the average body mass for extinct taxa (e.g., MacFadden, 1986; Gingerich, 1990; Anyonge, 1993, 1996; Walker et al., 1993; McCrossin, 1994; Viranta, 1994; Flynn et al., 1995; Gebo et al., 1997; Fariña et al., 1998; Christiansen, 1999; Delson et al., 2000; Köhler and Moyà-Solà, 2004; Christiansen and Harris, 2005). Because multiple regression exploits the complementary information contained in the morphological variables studied, it is probably the best suited methodology to compensate for the influence of the phylogeny or specific functional adaptations (Anderson et al., 1985; Damuth, 1990; Jungers, 1990; Hammer and Foley, 1996; Biknevicius, 1999; Palmqvist et al., 1999, 2002; Payseur et al., 1999; Mendoza et al., 2006).

For the study of locomotor behavior, deviations from the expectations of geometric scaling are used to infer the ecological adaptations of species in terms of locomotor performance and habitat choice (e.g., more cursorially adapted bovids living in plains and savanna have proportionally longer distal elements, those specialized for climbing in mountainous country have shorter metapodials, whereas those living in partly open woodland or hilly country tend to have bones of intermediate lengths). For the study of body mass, however, the effects of these deviations have to be minimized and the best estimators of body mass are the dimensions of the proximal limb segments (Kappelman et al., 1997).

1 Materials and methods

A multivariate approach is used to analyze morphological features in the postcranial skeleton of extant bovids, features which are seen to be indicative of body size and ecological adaptations for habitat use. The analyses are performed using 43 measurements taken from 110 extant species in Scott's (1985) database. These measurements are described in Appendix Ⅰ and represented in Fig.1. For details on the specimens used for calculating the species means, see Scott (1985).

1.1 Habitat adaptations

Associations of morphological features related with habitat adaptations in bovids were identified based on 42 size-adjusted variables. These size-transformed variables are obtained by dividing each measurement by the width of the proximal articular surface of the radius (Rd_2), a variable that scales isometrically with body size and is highly correlated with mass ($r^2 = 0.98$). Obviously, Rd_2 was not size-adjusted and it was not directly used as a variable.

The species were divided into three discrete groups for the analysis, corresponding to three general types of habitat: flat grasslands, forests, and hilly and mountainous areas. According to the information available, only 71 out of the 110 bovid species could be unequivocally classified as characteristic of one of these gross habitat types (see Appendix Ⅱ): 46 species are associated with open plains, 13 are typical of forested areas, and the other 12 species are adapted to mountainous terrain. These general types of habitat represent a rather heterogeneous mosaic of habitat and locomotor adaptations in bovids. However, if the habitat types were further subdivided, this would result in a decrease of the number of species associated with each of them, which would lead to a higher probability of obtaining a good discrimination either by chance or by close phylogenetic relationship (see below). There are 39 bovid species which have uncertain habitat preferences or that live in more than one habitat type that were not included in the statisti-

cal analyses. The species of the genus *Oryx* are a good example of those bovids that could not be unequivocally assigned to one habitat category: the fringe-eared oryx （*O. gazella*） lives in arid grasslands, forested savannas, semi-desert plains, thick brush, and near rocky hillsides. Therefore, *O. gazella* could be classified in any of the three types of habitat compared （i.e., open plains, forest and mountainous areas）. Similarly, the former habitat of the Arabian's oryx （*O. leucoryx*） was the flat and undulating gravel plains intersected by shallow wadis and depressions, and the dunes edging sand deserts, with a diverse vegetation of trees, shrubs, herbs, and grasses. Finally, the scimitar-horned oryx （*O. tao*） inhabits the sub-desert lands and is found in rolling dunes, grassy steppes and wooded inter-dunal depressions. The discriminant functions, however, were employed for predicting the habitat preferences of the 39 species not used in their adjustment.

Associations of morphological features characteristic of each type of habitat were identified using stepwise canonical discriminant analysis （SCDA）（Mendoza and Palmqvist, 2006） rather than principal components analysis （PCA） because the latter technique is not appropriate for identifying particular morphological patterns in discrete groupings of species. In contrast, SCDA is specifically designed to identify those variables involved in the differences between the groups compared and it permits the identification of combinations of measurements that have greater potential for specific applications （e.g., in the analysis of bone remains from archaeological and paleontological assemblages） than PCA.

Although the analysis was conducted on complete elements, the algorithms can also be applied to incomplete specimens, given that they involve small sets of postcranial variables （see below）. Species means were used rather than values for individual specimens, because although there are morphological differences related to intraspecific variability （e.g., sexual dimorphism）, we expect that most bovid species they will share a common morphological pattern in their postcranial structure, indicative of their locomotor performance.

The algorithms proposed here include only a few variables whose contribution to the discrimination among habitat groups is especially relevant. In doing so, our approach differs from the one used in Mendoza et al. （2002）, which was oriented to the obtaining of complex algorithms that allow us to infer the ecological adaptations of ancient species. The main advantage of the new algorithms is that they identify robust morphological patterns which enable us to understand the relationship between the postcranial structure of bovids and their adaptations to live in different

habitat types. Minimizing the number of variables incorporated in the algorithms, we also minimize the probability of obtaining a good discrimination merely by chance, because this probability increases with the number of variables included in the discriminant functions （see discussion in Mendoza et al., 2002, 2005）. Although the resulting algorithms may misclassify some species, they are more accurate than those based on many measurements, because they include only those morphological traits more clearly related with the adaptive patterns. A third advantage of our approach is that these simple morphological patterns can often be depicted in bivariate scatter-plots, which are a useful tool for determining the habitat adaptations of extinct bovids.

It is worth noting that if the discriminant functions are applied to an extinct bovid that shows a postcranial morphology identical to any of the 39 modern species with no clear habitat preferences, this species will be classified in one of the three habitat groups compared （open/forested/mountain）, as the discriminant functions are designed for doing so. This does not mean that the extinct species only lived within the predicted habitat; rather, what this means is that such habitat is the one for which the postcranial anatomy of the ancient species was better adapted.

Another important aspect of the new methodological approach is that the species analyzed are weighted according to the diversity of their taxonomic groupings, which helps to avoid the obtaining of phylogenetically constrained patterns （see below and Mendoza and Palmqvist in this volume）. Overweighing the species of those groups under-represented in the database forces the analysis to take into account the information contributed by these few species at the same level than that provided by the species from other groups more abundantly represented. In this way, the taxonomic evenness of the database is maximized and the morphological pattern captured by the resulting algorithms is more general. However, phylogeny is not the only factor that may disrupt ecological inferences, because bovids may move into new habitats or have alternative modes of locomotion not expressed morphologically in the same way as in other bovids （e.g., see the peculiar adaptations of the postcranial skeleton in *Myotragus balearicus*, an endemic fossil goat from the Pleistocene of the Balearic Islands in the Mediterranean Sea; Köhler and Moyà-Solà, 2001, 2004）.

Two types of algorithms were obtained: 1） those involving measurements from a combination of all major limb bones; and 2） algorithms obtained from sets of morphological variables estimated in a single limb bone. In the second case, the variables were size-ad-

justed.

Although algorithms developed for single limb bones will have a lower discrimination power than those based on measurements from several bones, the former can be useful to apply to skeletal remains from different individuals or to disarticulated and fractured specimens (see reviews in Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001).

The algorithms can be used to characterize the ecological adaptations of bovid species not included in the original data set. In order to identify more complex combinations of algorithms, a machine learning program, called decision trees (Quinlan, 1985), was used. Decision trees represent a type of machine learning, whereby computer systems acquire knowledge inductively from the input of a large number of samples (e.g., bovid species and postcranial measurements in our case). The product of this learning is a piece of procedural knowledge that can assign an object (e.g., an extinct bovid whose feeding preferences are unknown) to one of a specified number of disjoint classes (e.g., habitat categories) based on the iterative division of the multidimensional space defined by the input variables. The result is a bifurcating tree pattern or dichotomous key with decisions at each branching point that combines the information provided by the postcranial measurements in a logical way, making the characterization of any extinct bovid easier.

1.2　Body size

The values of the morphological variables in a given species not only depend on its body size, but also on its phylogenetic legacy and ecological adaptations (Köhler, 1993; Köhler and Moyà-Solà, 2004). Therefore, the predictions of mass derived from single measurements are not always precise and accurate (e.g., Palmqvist et al., 1999, 2002). Our hypothesis establishes that this bias can be compensated for by the use of several measurements combined in a multiple regression equation. The predictions are that these combinations of morphological variables will allow a better characterization of body mass, and that the resultant algorithms will show a higher predictive power when applied to new species (see Mendoza et al., 2006).

Bovids are one of the most sexually dimorphic groups of hoofed mammals, with the males of several species weighing twice as much as the females. However, in most species the dimorphism ratio (i.e., mass of males: mass of females) fluctuates between 1.05 and 1.25 (e.g., see data in Mysterud, 2000) and in some groups such as the dwarf antelopes (neotragines) these values may be even reversed. In addition, most bovids show variations in individual mass related to geographic and seasonal changes (e.g.,

rainfall and primary productivity) as well as to habitat types (e.g., the average mass of the African buffalo *Syncerus caffer* is 620 kg in the populations that live in plains and 300 kg in those from forest areas; Brashares et al., 2000). In this study, we use the mean body mass of bovid species instead of separate mass estimates for each sex or body mass ranges. Although the use of mean masses may entail some problems, especially in the highly dimorphic species, this procedure is the one most employed for dealing with extinct taxa (e.g., Scott, 1985, 1990; Janis, 1990b; Gagnon and Chew, 2000; Mendoza et al., 2002, 2006).

Average body mass values of 97 out of 110 bovid species (wild catch individuals) were obtained from different sources and calculated as the arithmetic mean of both sexes (Janis, 1990a, 1990b; Kingdon, 1982; Nowak, 1999; Huffman, 2005; Myers et al., 2005). Their logarithmically transformed body masses were used as the dependent variable, and the 43 postcranial morphological measurements, also log-transformed, as independent or predictor variables (Table 1, Fig.1). Given that the postcranial measurements and the mass averages used for the species come from different individuals, this represents an additional source of error in the regression adjustments (Turner and O'Regan, 2002).

Table 1　Algorithms that characterize the postcranial anatomy of bovids adapted to dwell in mountainous terrains (all the variables are size-adjusted by the variable included between brackets)

Alg	Discriminant function
1.1(Rd_2)	$13.923Mc_5 - 39.673Hm_4 - 1.222Hm_2 + 21.975Fm_4 + 25.311$
1.2(Rd_2)*	See legend for Fig.3
1.3(Hm_4)	$15.573Hm_6 + 41.709Hm_7 - 29.361$
1.4(Rd_2)	$10.071Rd_4 - 23.910R_5 + 13.673Rd_6 + 17.870R_7 - 3.288$
1.5(Mc_2)	$9.05Mc_4 + 20.98Mc_5 - 15.276Mc_6 + 8.657Mc_7 - 15.867$
1.6(Fm_5)	$1.255Fm_1 + 28.443Fm_4 + 10.829Fm_7 - 13.375$
1.7(Tb_2)	$1.031Tb_1 + 45.064Tb_4 - 63.498Tb_5 - 25.728T_6 + 6.984$
1.8(Mt_4)	$23.358Mt_2 - 15.769Mt_6 - 11.723$

* Algorithm 1.2 was not selected (see text and legend for Fig.3).

According to Mendoza et al. (2006), the functions with highest predictive power are those that incorporate only very significant variables and explain a relatively high value of the variance of body mass. In addition, according to these authors but contrary to our expectations, the taxonomic restriction of the multiple regression analysis to bovid species does not improve the predictive abilities of the resultant algorithms as it did for all ungulates; in fact, the ability
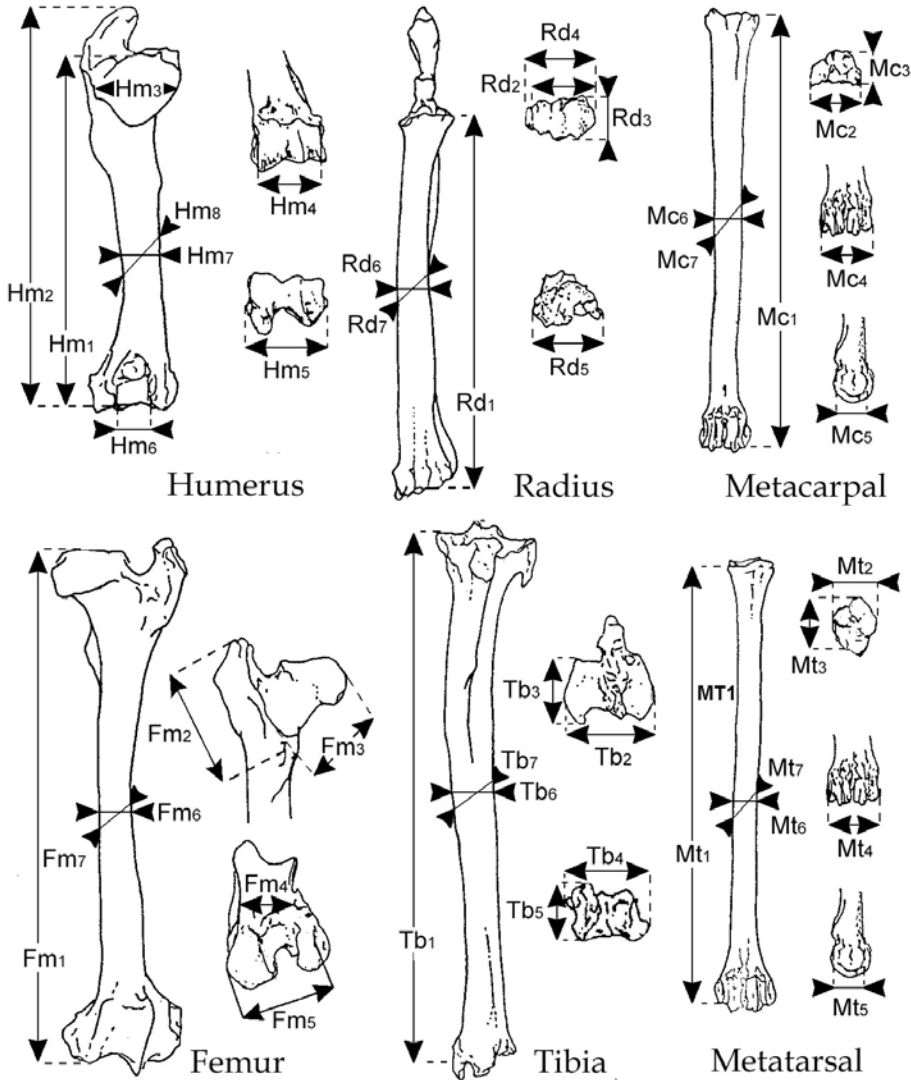
Fig.1   Postcranial measurements used in this study（adapted from Scott，1985）

of these algorithms even decreases（see Fig.3 in Mendoza et al.，2006）. However，because the algorithms proposed in Mendoza et al.（2006）were obtained for the craniodental structure，new algorithms can be obtained from the postcranial structure of the bovids.

In order to determine the predictive power of the regression functions，ten test-species were excluded from a preliminary set of analyses，ranging more or less homogeneously from 3 kg（*Neotragus batesi*）to 800 kg（*Bos sauveli*）. The algorithms finally proposed for estimating the body mass of extinct bovids，however，were derived from the complete database，according to the results obtained in the preliminary analyses.

2   Results

2.1   Habitat adaptations

2.1.1   Postcranial adaptations to life in mountainous terrain

Algorithm 1.1（Table 1）was adjusted to dis-

criminate between bovid species living in open plains from those living in mountainous terrain and hilly areas. This algorithm involves four morphological variables and correctly discriminates all the species from both groups（Fig.2a）. It also clusters together bovids from forested habitats（these species were not used in the generation of the algorithm）and open plains（Fig.2a），thus allowing the identification of the traits characterizing the postcranial morphology of species adapted to mountainous terrains.

The stepwise process of adjustment of the discriminant function reveals that the morphological pattern that characterizes the postcranial skeleton of bovids adapted to mountainous terrain is described by the combined morphological information of Mc_5 and Hm_4，Hm_4 and Fm_4，and Fm_4 and Hm_2，rather than each individual variable acting alone or in other combinations（see Figs.2b－e）.

Thus，bovid species adapted to mountainous terrain are mainly characterized by two features：1）a
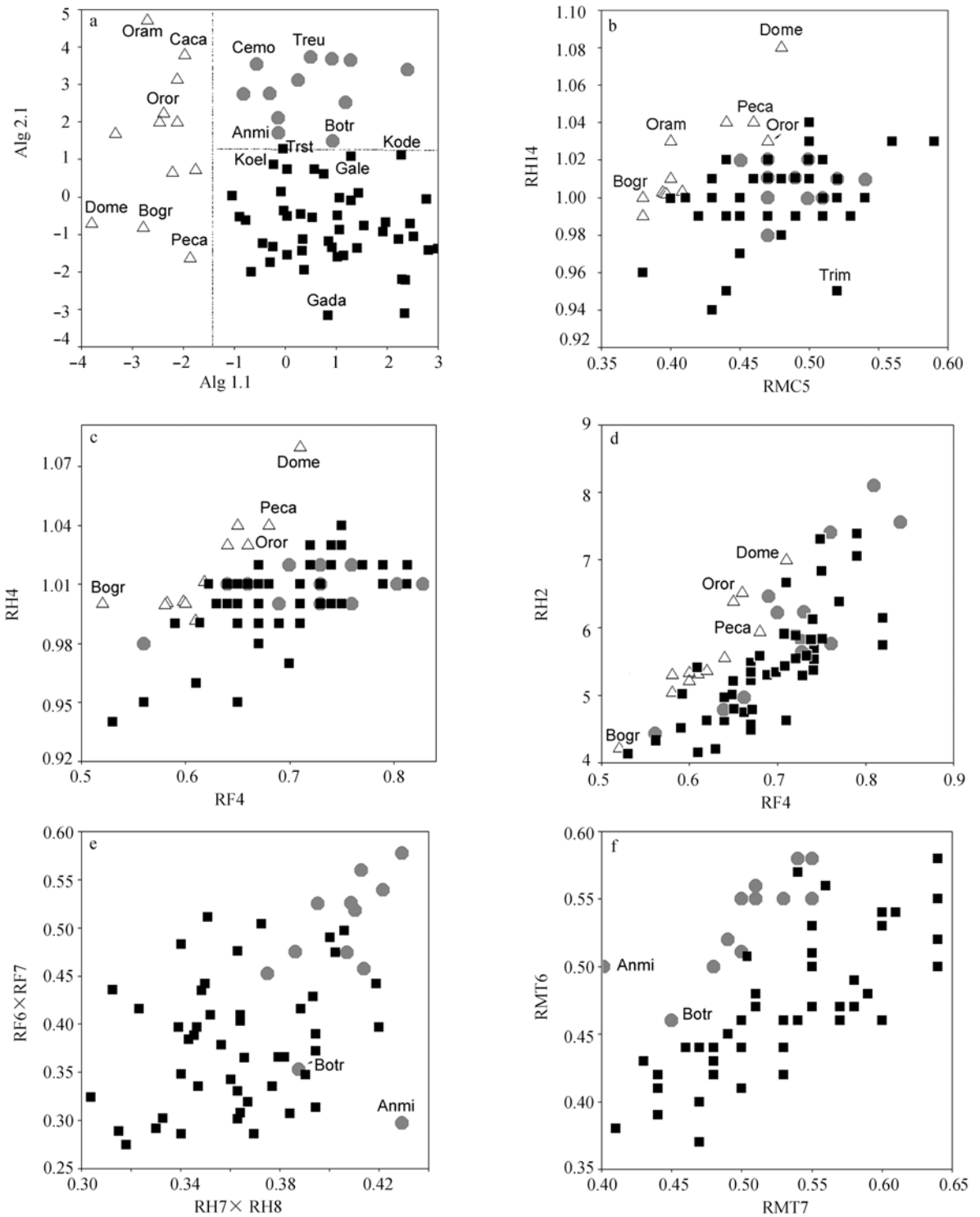
Fig. 2　Scatter-plot of projections of bovid species on algorithms 1.1 *vs*. 2.1（a）; partial representations of the morphological pattern captured by algorithm 1.1（b－d）; partial representations of the pattern depicted by algorithm 2.1（e－f）

Black squares: species from open plains; Gray circles: forest species; Open triangles: species from rugged mountainous areas and ridges.

wide distal articular surface of the humerus（Hm_4）relative to the antero-posterior width of the distal metacarpus（Mc_5, Fig.2b）and to the patellar groove width（Fm_4, Fig.2c）; and 2）a comparatively long

humerus（including the dimensions of the greater tuberosity, Hm_2）relative to the patellar groove width（Fm_4, Fig.2d）. Although all of these features seem to be morphological adaptations to mountainous ter-

rain，none of them considered alone are diagnostic of such a habitat（see Figs.2b – d）. Algorithm 1.1 combines them and captures the real morphological pattern that allows dwelling in mountainous areas (Fig.2a).

Eight out of twelve species classified as adapted to mountainous terrain and hilly areas are members of the tribe Caprini，which is not represented in the two other habitat categories（Appendix Ⅰ）. The four non-Caprini species are *Pelea capreolus*，*Boselaphus tragocamelus*，*Dorcatragus melanotis*，and *Oreotragus oreotragus*. Of these species，only the latter is well adapted to life in mountains，the other three live in hilly landscapes. This opens up the possibility that the morphological pattern may be reflective of the phylogenetic signal of the tribe Caprini，rather than resulting from a convergent ecological adaptation of bovids to mountainous terrains. In order to avoid such bias，new analyses were performed overweighting the four non-Caprini species（for details on this procedure，see Mendoza et al.，2006）.

Other analyses were performed with non-weighted species for discriminating between bovids adapted to open plains and those living in mountainous areas. Algorithm 1.2（see legend for Fig.3）is based on the elongation of the major limb bones rather than on their joint dimensions，as is the case for algorithm 1.1，and includes as variables the greatest lengths of one major bone of the forelimb and two of the hind limb，metacarpus（Mc_1），femur（Fm_1）and tibia（Tm_1）（Figs.3a – c）. Algorithm 1.2 correctly reclassifies 94% of bovids（i.e.，63 out of 67 species），but misclassifies also the four non-Caprini species of the mountainous group. While three of these species are not as clearly adapted to mountainous terrains as the caprines，*O.oreotragus* is a typical mountain species and is placed by algorithm 1.2 in the non-mountainous group（Fig.3a）. According to Scott (1985)，bovids living in open country are more cursorially adapted and have proportionally longer distal limb elements（especially metapodials）than those living in mountainous terrains，which are specialized for climbing（Figs.3b – c）. In fact，this is the morphological pattern captured by algorithm 1.2，although it seems to reveal a phylogenetic pattern exclusive of the tribe Caprini（Fig.3a）. This precludes considering the species analyzed as independent samples.

In spite of this methodological consideration，the pattern identified could have an ecomorphological base characteristic of the tribe Caprini. However，according to the information available，it is not possible to determine the extent to which the correlation between morphology and adaptation is a functional response of these species，or merely reflects the common phylogenetic legacy of the tribe. The four non-Caprini species

of the mountainous group do share the morphological pattern identified by algorithm 1.1 along with the rest of species adapted to mountainous terrain（see Figs.2a – d），which suggests that the features identified in algorithm 1.1，mainly based on limb joint dimensions，are related to the morphological adaptations for mountain life.

2.1.2 Postcranial adaptations to life in forested environments

Algorithm 2.1 was developed to discriminate between bovids living in open plains and those living in forests. It involves only three variables and discriminates 100% of the species from both groups (Fig.3a). In addition，those bovids with intermediate scores in this discriminant function are less adapted to the two general types of habitat compared.

In the derivation of algorithm 2.1，before the inclusion of any variable，Hm_8，Hm_7，Fm_7 and Fm_6 （medio-lateral and antero-posterior width of the humerus and femur，respectively）proved to be very significant. This indicates that bovids adapted to forests have more stoutly built humeri and femora. After the inclusion of Hm_8 in the discriminant function，the significance of the other four variables decreased although Fm_7 is still the most significant variable and thus the second one to be included within the discriminant function. This is because those species adapted to forested habitats，which possess a wide humerus，also possess a wide femur. Therefore，contrary to what occurred in the generation of algorithm 1.1，the humerus and the femur contribute similarly to the discrimination process and in an independent manner，because the capacity of discrimination of both variables does not depend on each other. The third variable included is Mt_7. Its inclusion increases the significance of M_6，so the contribution of both variables is linked together. Accordingly，bovid species living in forests are shown to also possess an antero-posteriorly flattened metatarsus，as reflected by their low values of Mt_7 compared to Mt_6.

Most bovids adapted to open plains and forests belong to the subfamily Antilopinae. Only two species included in the forest group belong to the subfamily Bovinae，*Anoa mindorensis*（Anmi）and *Boselaphus tragocamelus*（Botr）. Their femur is not as robust as in the antilopines. *A.mindorensis* clearly shares the morphological pattern captured by algorithm 2.1，because it compensates a slender femur with both a more robust humerus and a flatter metatarsus. *B.tragocamelus* is located in an intermediate area (Fig.3a)，but its habitat ranges from grassy，steppe woodlands，to hillsides with moderate cover of thin forest，avoiding densely wooded areas.

2.1.3 Postcranial adaptations to life in open plains
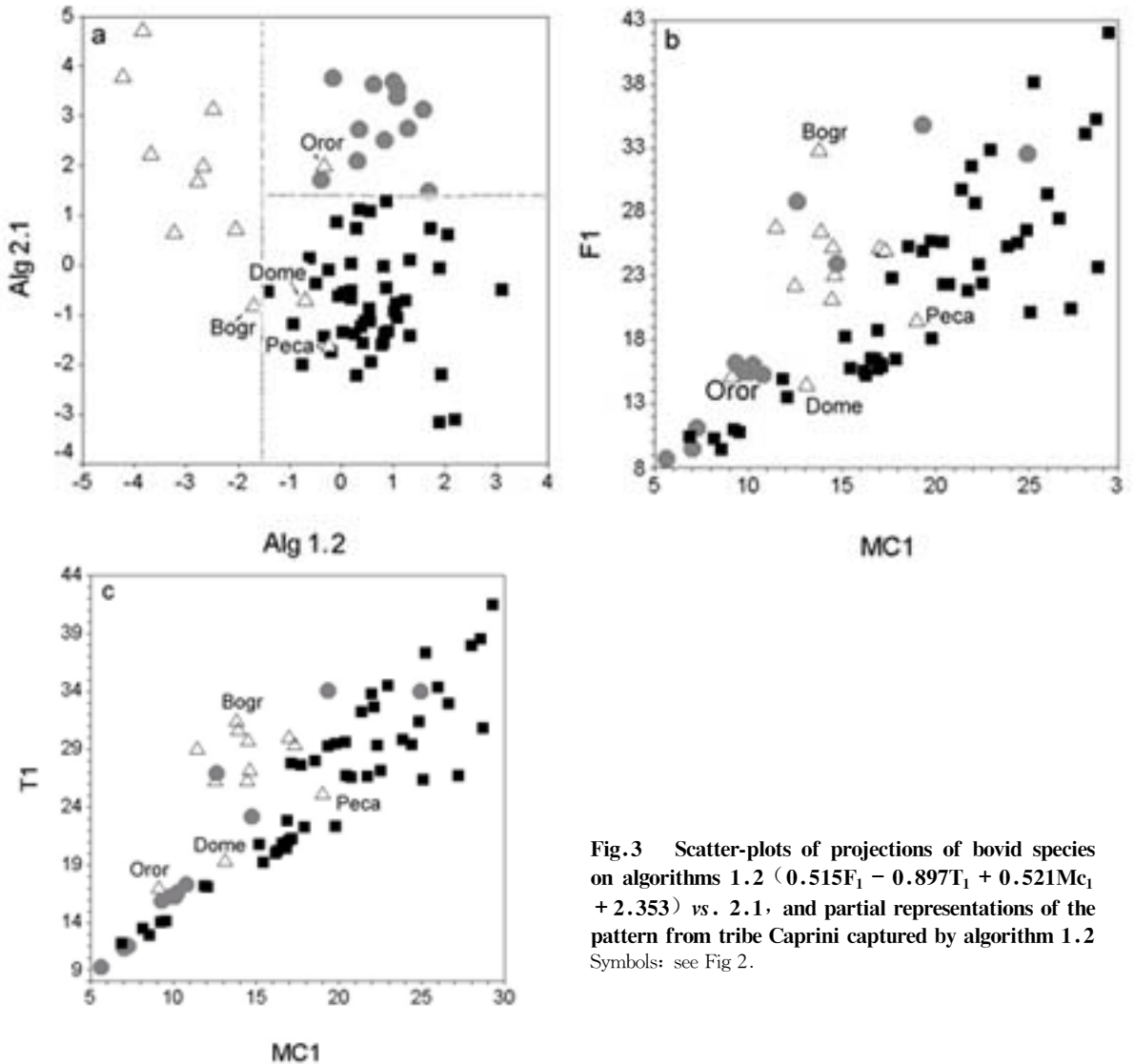
Mountain species were characterized in compari-

Fig.3 Scatter-plots of projections of bovid species on algorithms 1.2（$0.515F_1 - 0.897T_1 + 0.521Mc_1 + 2.353$）vs. 2.1，and partial representations of the pattern from tribe Caprini captured by algorithm 1.2
Symbols: see Fig 2.

son to all other bovids，and forest species were compared to open plain species. Given that the morphological adaptations of bovids from open habitats can be defined as the opposite of those of the other two groups，no additional analysis was required.

2.1.4 Morphological adaptations of each major limb bone to different types of habitat

Each major limb bone was analyzed independently. Thus，any trait involved in a given morphological pattern is always defined in comparison with other variables measured in the same limb bone.

Fig.4 shows the scatter-plots of bovid species projections on those algorithms obtained with measurements from each major limb bone. These algorithms were adjusted for characterizing the morphological adaptations of mountain species（Table 1，algorithms 1.3 to 1.8）and forest species（Table 2，algorithms 2.2 to 2.7）.

None of the combinations of these algorithms allows a good characterization of the habitat adaptations of bovids. However，given that they were obtained using measurements from single limb bones，they can

Table 2 Algorithms that characterize the postcranial skeleton of bovids adapted to forested environments

Alg	Discriminant function
2.1（Rd_2）	$20.885Hm_8 + 22.388Fm_7 - 20.014Mt_7 - 17.823$
2.2（Hm_4）	$0.625Hm_2 - 7.343Hm_3 + 35.463Hm_7 + 18.872Hm_8 - 28.126$
2.3（Rd_2）	$0.854Rd_1 + 16.116Rd_4 - 42.074Rd_7 - 5.703$
2.4（Mc_2）	$0.504Mc_1 - 26.777Mc_3 - 12.717Mc_5 + 34.178Mc_7 + 4.251$
2.5（Fm_5）	$14.495Fm_3 - 16.890Fm_4 + 15.280Fm_7 - 13.093$
2.6（Tb_2）	$-1.393Tb_1 + 29.781Tb_3 + 40.210Tb_4 - 70.060Tb_6 - 8.174$
2.7（Mt_4）	$-24.829Mt_3 + 18.479Mt_5 + 21.432Mt_6 - 1.673$

All the variables are size-adjusted by the variable included between brackets.

be used in the ecomorphological characterization of the skeletal remains from different individuals，which is not the case of those algorithms that combine measurements from several limb bones. Thus，the information provided by a given bone can be complemented
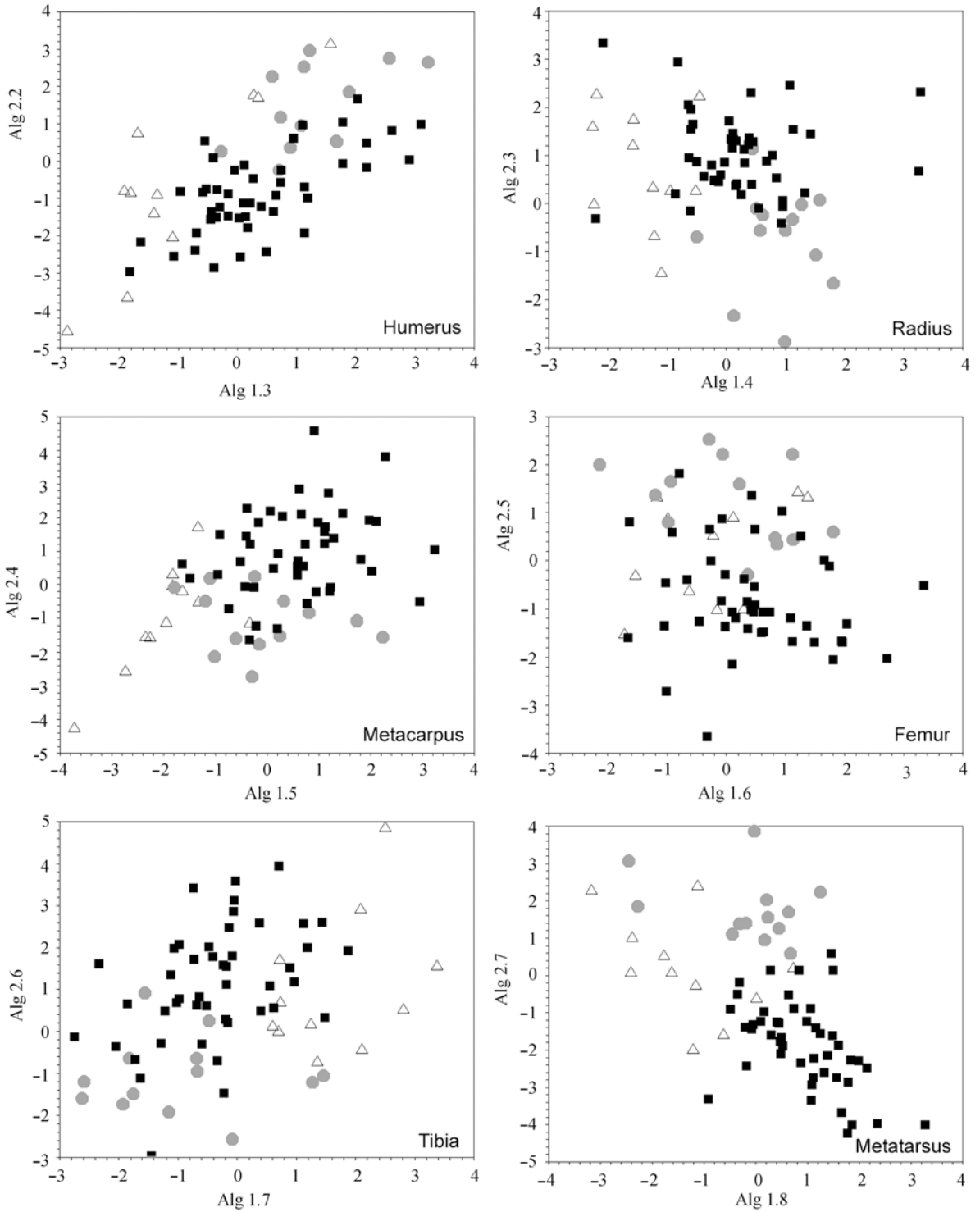
Fig. 4　Scatter-plots of projections of bovid species on those algorithms obtained from each major fore and hind limb bone
Symbols： see Fig. 2.

with that derived from other limb elements. In many cases the position of a given species in the morphospace defined by one limb bone rules out the possibility that this bovid is adapted to one of the three habitat categories compared. If another bone allows excluding a second category，then the species can be then classified with an elevated degree of certainty within the third habitat category.

Several decision trees combining the information provided by these algorithms were developed （Fig. 5）. Given that only a single measurement is used at each branching point，the trees can be used as a dichotomous key. This allows an easier characterization of the morphological adaptations involved in the
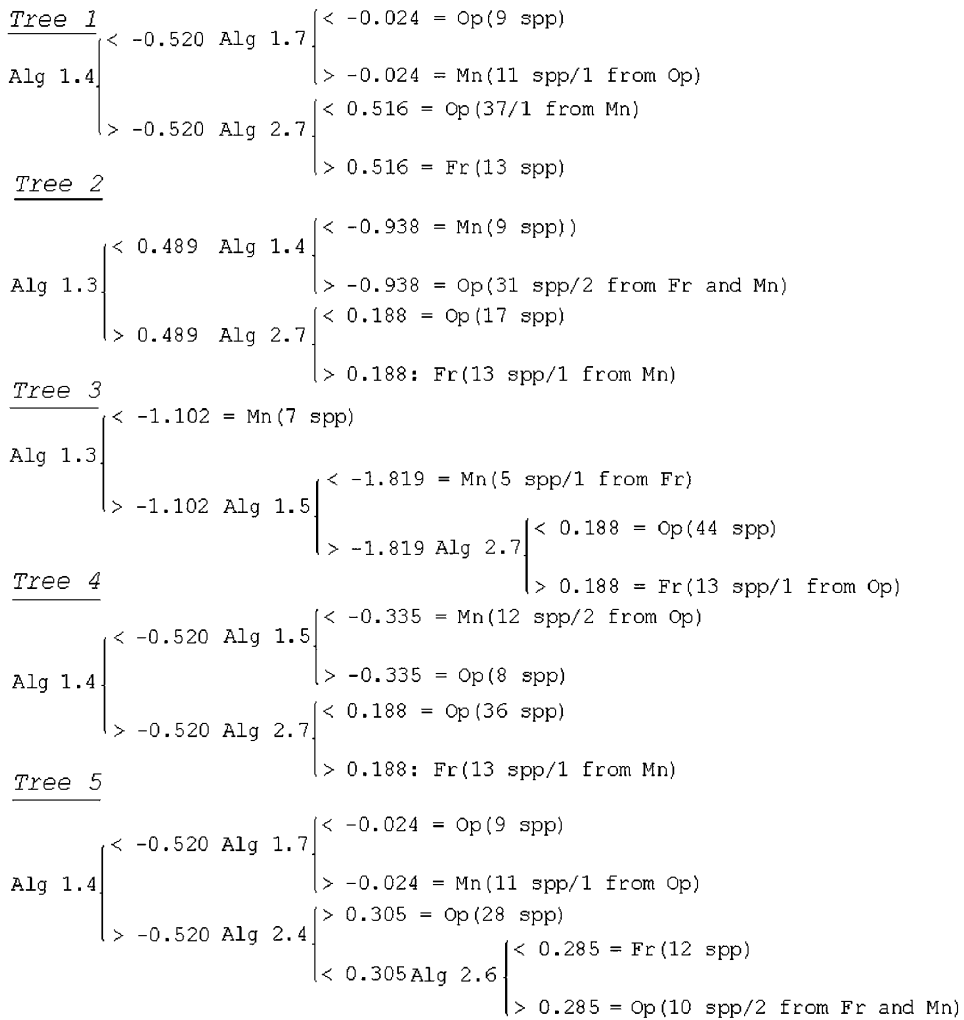
Tree 1

Alg 1.4 $\Big\lbrace$ < -0.520 Alg 1.7 $\Big\lbrace$ < -0.024 = Op(9 spp)

> -0.024 = Mn(11 spp/1 from Op)

> -0.520 Alg 2.7 $\Big\lbrace$ < 0.516 = Op(37/1 from Mn)

> 0.516 = Fr(13 spp)

Tree 2

Alg 1.3 $\Big\lbrace$ < 0.489 Alg 1.4 $\Big\lbrace$ < -0.938 = Mn(9 spp))

> -0.938 = Op(31 spp/2 from Fr and Mn)

> 0.489 Alg 2.7 $\Big\lbrace$ < 0.188 = Op(17 spp)

> 0.188: Fr(13 spp/1 from Mn)

Tree 3

Alg 1.3 $\Big\lbrace$ < -1.102 = Mn(7 spp)

> -1.102 Alg 1.5 $\Big\lbrace$ < -1.819 = Mn(5 spp/1 from Fr)

> -1.819 Alg 2.7 $\Big\lbrace$ < 0.188 = Op(44 spp)

> 0.188 = Fr(13 spp/1 from Op)

Tree 4

Alg 1.4 $\Big\lbrace$ < -0.520 Alg 1.5 $\Big\lbrace$ < -0.335 = Mn(12 spp/2 from Op)

> -0.335 = Op(8 spp)

> -0.520 Alg 2.7 $\Big\lbrace$ < 0.188 = Op(36 spp)

> 0.188: Fr(13 spp/1 from Mn)

Tree 5

Alg 1.4 $\Big\lbrace$ < -0.520 Alg 1.7 $\Big\lbrace$ < -0.024 = Op(9 spp)

> -0.024 = Mn(11 spp/1 from Op)

> -0.520 Alg 2.4 $\Big\lbrace$ > 0.305 = Op(28 spp)

< 0.305 Alg 2.6 $\Big\lbrace$ < 0.285 = Fr(12 spp)

> 0.285 = Op(10 spp/2 from Fr and Mn)

Fig. 5 Decision trees that allow the characterization of the postcranial morphology of bovids living in open plains and savannas（Op），forested environments（Fr）and mountainous areas（Mn）

These trees can be used as a tool for determining the habitat adaptations of extinct bovids，even in those cases for which only disarticulated and fragmented skeletal remains are available. The values obtained for a given algorithm，based on a single limb element，are used as a dichotomous key at each branching point.

three types of habitat compared to the algorithms derived from discriminant analysis. In addition，they are a more useful tool for determining the habitat adaptations of extinct bovids in those cases in which only disarticulated and/or fragmented skeletal remains are available. Figure 6 shows some combinations of algorithms identified using decision trees（Figs. 6a – c）and the scatter plot representation of the three first trees（Figs. 6d – f）.

As in discriminant analysis，the tree branches associated with errors can be used in a probabilistic way，according to the proportion of misclassifications for each type of habitat. However，some of these potential errors can be avoided using a combination of trees: for example，the single mountainous species misclassified by the third branch of Tree 1（Fig. 5）is correctly placed in the region of the morphospace occupied by mountainous bovids，as depicted in Fig. 6d.

2.2 Body size predictors

Table 3 shows the predictions of body mass obtained for the ten test-species using the preliminary functions adjusted following the procedure for multiple regression described in Mendoza et al. （2006）. These results reveal that those functions that only incorporate very significant variables and explain a relatively high percentage of variance show the highest predictive power when applied to the test-species. The addition of new variables to the ones already included in these functions does not entail a substantial increase of the variance explained（estimated by the coefficient of determination，r^2）but the exclusion of any of these variables results in a decrease of r^2. The functions with highest predictive power derived from the craniodental structure of ungulates include between six and ten variables（Mendoza et al.，2006）. However，most of the best functions derived from the
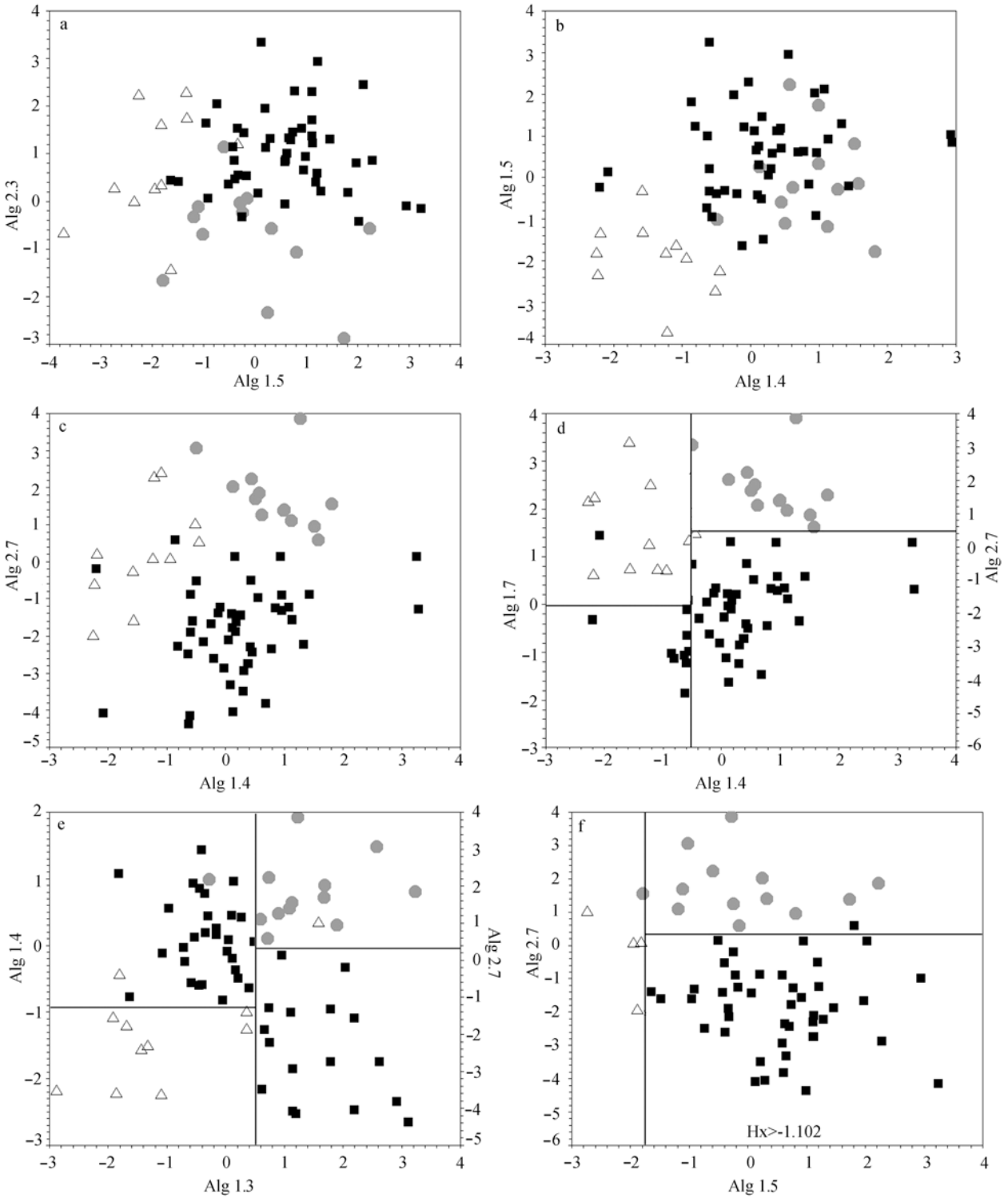
Fig. 6　Scatter-plots of projections of bovid species on selected combinations of algorithms obtained from single limb bones（a－c）. Representation of between-group limits depicted by decision trees 1－3（d－f）
Symbols: see Fig. 2.

postcranial structure of bovids include only one or two variables. The ten test-algorithms were generated using the forward method for stepwise inclusion of variables within the regression function. This procedure selects the independent variable best correlated with body mass and，after incorporating it within the re-

gression function，searches among the others for the variable that accounts for most variance of the independent variable not explained by others previously included in the function. However，many of the algorithms were obtained using the backward method，which begins by incorporating all the variables in the

regression function and then excludes at each step the one which explains less variance of the independent variable (see details in Mendoza et al., 2006). Algorithms 1 and 2 were obtained starting from the full set of variables. Algorithms 3 and 4 were adjusted excluding Rd_2. The other algorithms were obtained excluding each time, in addition to Rd_2, the first variable included in the former algorithm. This procedure provided a wide spectrum of regression functions with similar predictive power and incorporating different sets of morphological variables, which may be used with fossil specimens depending on the measurements available. It is worth mentioning that only algorithms 4 and 8 include more than two variables, but they show less predictive power than the others. Thus, multiple regression techniques do not represent a clear improvement over single regression methods in the derivation of algorithms that allow the estimation of body mass from postcranial remains in bovids (Table 3). Taking into account these results, only the best algorithms obtained by simple regression analysis, derived from morphological variables measured in each single major limb bone, were selected (Table 4).

Table 3　Results of the application of the test-algorithms to ten test-species after transformation to non-logarithmic data

Alg (NV) (PVE)	Maki (5)	Cema (8)	Sygr (13)	Ceca (20)	Aeme (50)	Cesy (65)	Sili (181)	Anmi (224)	Hini (241)	Tade (580)	MPE
1 (1) (97.7%)	5.8	7.8	13	20	55	61	192	222	218	517	6.6%
2 (2) (98.1%)	6.1	9.0	13	20	49	62	192	228	207	511	7.7%
3 (1) (97.4%)	5.6	8.1	13	21	53	61	199	224	219	487	6.9%
4 (5) (98.3%)	5.0	11.7	12	23	47	67	201	224	234	474	10.9%
5 (1) (97.3%)	5.6	7.4	13	19	53	64	184	214	221	471	6.4%
6 (2) (97.6%)	5.7	8.4	13	19	47	66	181	216	213	450	6.9%
7 (1) (97.2%)	5.6	8.5	15	21	53	69	174	241	232	571	6.5%
8 (3) (97.8%)	5.6	9.9	16	23	51	72	192	292	255	577	13.0%
9 (1) (97.9%)	5.4	7.7	13	20	52	61	186	220	228	598	4.0%
10 (1) (96.9%)	5.6	8.1	14	17	53	59	208	231	215	515	9.3%

Algorithms 1 and 2 were obtained using the full set of postcranial variables. Algorithms 3 and 4 were adjusted excluding Rd_2. Algorithms 5 – 10 were obtained excluding each time, apart from Rd_2, the first variable selected in the previous analysis. Species keys (see Appendix Ⅰ) with the body mass below, Alg: test-algorithm number, NV: number of variables involved by the algorithm, PVE: percentage of variance explained, MPE: mean percent prediction error of body mass [(predicted mass − observed mass)/observed mass •100].

The width of the proximal articular surface of the radius (Rd_2) is the single morphological variable best correlated with body mass (Alg. 3.3, Table 4), which confirms the results obtained by Scott (1990). However, in this study Rd_2 explains 98% of the variance of body mass instead of 96% in Scott (1990), probably as a consequence of an improvement during the last 15 years in the knowledge of the body masses of the species analyzed. The maximum width of the proximal epiphysis of the radius (Rd_4), the width of the distal articular surface (Hm_4) and the maximum width of the distal epiphysis (Hm_5) of the humerus also explain almost 98% of the variance of body mass (Table 4).

Table 4　Selected functions derived from single major limb bones for estimating body mass in bovids

Bone limb	Alg	Function	r^2 Aj
Humerus	3.1	$2.535Hm_4 + 0.991$	0.977
Humerus	3.2	$2.617Hm_5 + 0.676$	0.976
Radius	3.3	$2.495Rd_2 + 1.046$	0.980
Radius	3.4	$2.448Rd_4 + 0.893$	0.978
Metacarpus	3.5	$2.634Mc_2 + 1.436$	0.973
Tibia	3.6	$2.879Tb_2 - 0.578$	0.967
Femur	3.7	$2.894F_5 - 0.116$	0.964
Metatarsus	3.8	$2.708Mt_4 + 1.361$	0.957

Equations are of the form: log (mass, in kg) = b_1 (log X) + c, where X represents the morphological variable, measured in cm.

The percentage of variance of body mass explained by the most accurate function derived from each of the other limb bones ranges from 95.7% to 97.3% (Table 4). The predictive power of these functions was not tested with the ten test-species. The reason is that the mean error percentage of the prediction for those functions obtained through simple regression analysis does not add any information to the percentage of variance of body mass explained (R^2). Rather, it is affected by the arbitrary selection of the test-species. However, according to the results obtained for the multiple regression functions with the test-species, the relative error percentages of these functions may be tentatively estimated in between 4% and 10%, probably around 6% in most cases.

3 Discussion

3.1 Methodology

A multivariate approach to analyze the postcranial morphology of bovids allows characterization of their ecological adaptations to specific habitats. Given the phylogenetic relationship between species, to consider them as independent samples may lead to erroneous conclusions about the significance and interpretation of the results obtained. The weighting of some species is a suitable procedure in order to avoid the bias derived from phylogenetic constraints. The representation of the species analyzed according to their phylogenetic affinities allows the evaluation of the effects of phylogeny in the patterns identified. Decision trees are a machine learning approach suitable for combining in a logic way the partial information provided by different algorithms. A multivariate approach does not represent an improvement over single regression methods in the derivation of algorithms that allow the estimation of body mass in bovids based on postcranial structures.

3.2 Habitat adaptations

Bovid species adapted to mountainous areas show: 1) a wide distal articular surface of the humerus relative to the width of the patellar groove and the antero-posterior dimension of the distal metacarpus; and 2) a long humerus in relation to the width of the patellar groove. Scott (1985) proposed that the bovids dwelling in mountainous areas have short metacarpals and metatarsals in relation to the size of the proximal limb elements, which shows evidence of an adaptation to minimize lateral bending during climbing. However, this feature is more likely to be a phylogenetic attribute exclusive of the tribe Caprini, which is over-represented in this habitat category by eight out of twelve species, as other bovids adapted to climbing in mountainous areas do not show relatively shorter distal limb bones. This opens up the possibility that the morphological pattern captured by

the algorithms may arise from the evolutionary legacy of the tribe Caprine, rather than reflecting an adaptive convergence of bovids to mountainous terrains. Obviously, this would limit its use in paleoautecology (see Felsenstein, 1985; Harvey and Pagel, 1991; Mendoza and Palmqvist, 2006). Such bias, however, could be avoided overweighting the four non-Caprini species in the analyses, which led to the obtaining of "taxon-free" discriminant functions that may be confidently used for deriving paleoautecological inferences on extinct taxa. Bovid species living in forested areas have a more robust humerus and femur, as well as a more antero-posteriorly flattened metatarsus, than those adapted to open plains. It is worth noting that Kappelman et al. (1997) have studied in depth the linkage between the femoral anatomy of bovids and their locomotor patterns and habitat preferences. Bovids living in closed canopy settings encounter a three-dimensional substrate that limits high-speed cursorial locomotion. These species have a nearly spherical femoral head shape reflecting a more mobile hip joint, providing a high degree of maneuverability. In contrast, those bovids from open habitat only encounter ground-level obstacles occasionally, and have a femoral head that is more cylindrical in shape, which limits movements to the parasagittal plane. They also have a distal femur with a larger moment arm for the extensor muscles, which facilitates more rapid cursorial locomotion across an essentially two-dimensional substrate. Finally, those bovids from open habitat are characterized by the absence of those morphological adaptations of mountain and forest species.

Algorithms obtained from each single limb bone do not provide a full characterization of the habitat adaptations of bovids. However, this approach is useful in the autecological reconstruction of extinct species, because it can be applied to disarticulated skeletal remains. The combined contribution of the information provided independently by different limb bones permits a good ecomorphological characterization.

The algorithms that incorporate measurements from different limb elements reclassify correctly 100% of bovid species according to their habitat of preference (mountainous areas, open plains, and forests; Fig.2a). Those others adjusted with measurements from single limb elements provide between 95% and 97% of correct reclassifications when they are combined in decision trees (Fig.5). Compared with the results obtained in previous studies on the postcranial anatomy of bovids, our results represent a clear improvement. For example, Kappelmann et al. (1997) analyzed the relationship between eight femoral variables measured in 188 African bovids and

the amount of vegetative cover in their habitat (forest, heavy cover, light cover, and open country). Their discriminant functions provided correct habitat reclassifications for 85% of the specimens. Other limb elements also reveal interesting clues for habitat preference in bovids. For example, DeGusta and Vrba (2003) used the habitat categories defined by Kappelman et al. (1997) and found that the functional morphology of the astragalus correctly predicted the habitat preference for 67% of 218 African bovids. Similarly, DeGusta and Vrba (2005a) used measurements of the bovid phalanges and obtained 71% accuracy for the reclassification among habitat types. Later, DeGusta and Vrba (2005b) used non-metric characters of the phalanges proposed by Gentry (1970) and Köhler (1993) as habitat indicators in bovids, and their previous results were improved to 88% - 97% accuracy.

3.3 Body size prediction

The width of the articular surface of the proximal radius is the single morphological variable best correlated with body mass, which confirms the results obtained by Scott (1990). The maximum width of the proximal radius, as well as the width of the articular surface and the maximum width of the distal humerus, are also very well correlated with body mass. All these variables account for nearly 98% of the variance of body mass. The best functions derived from each of the other major limb bones explain between 95.7% and 97.3% of the variance in body mass. The expected percentages of relative error of the best function derived from each major limb bone of the postcranial skeleton of bovids range between 4% and 10%, and are in most cases around 6%.

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Appendix Ⅰ Postcranial variables used in this study

Humerus
Hm_1: length from head at base of bicipital groove to deepest point of trochlear groove
Hm_2: length from greatest extent of greater tuberosity to deepest point of trochlear groove
Hm_3: width of head
Hm_4: width of distal articular surface in anterior view
Hm_5: maximum width of distal epiphysis
Hm_6: width of olecranon fossa
Hm_7: medio-lateral width at midshaft
Hm_8: antero-posterior dimension at midshaft
Radius
Rd_1: length from deepest point of sagittal groove of proximal articular surface to medial facet of distal articular surface
Rd_2: width of proximal articular surface
Rd_3: antero-posterior dimension of proximal articular surface
Rd_4: maximum width of proximal epiphysis
Rd_5: maximum width of distal epiphysis
Rd_6: medio-lateral width at midshaft
Rd_7: antero-posterior dimension at midshaft
Metacarpus
Mc_1: length from articular surface for fourth carpal to lateral distal condyle
Mc_2: width of proximal articular surface
Mc_3: antero-posterior dimension of proximal articular surface
Mc_4: maximum width of proximal epiphysis
Mc_5: antero-posterior dimension of distal epiphysis
Mc_6: medio-lateral width at midshaft
Mc_7: antero-posterior dimension at midshaft
Femur
Fm_1: length from head to medial condyle
Fm_2: length from tip of greater trochanter to base of lesser trochanter
Fm_3: length from lesser trochanter to fovea capitis
Fm_4: width of patellar groove
Fm_5: distance between distal condyles
Fm_6: medio-lateral width at midshaft
Fm_7: antero-posterior dimension at midshaft
Tibia
Tb_1: length from proximal medial condyle to groove lateral to distal medial malleolus
Tb_2: width of proximal articular surface
Tb_3: antero-posterior dimension of lateral proximal articular surface
Tb_4: maximum width of proximal epiphysis
Tb_5: antero-posterior dimension of distal epiphysis
Tb_6: medio-lateral width at midshaft
Tb_7: antero-posterior dimension at midshaft
Metatarsus
Mt_1: length from lateral facet of proximal surface to lateral distal condyle
Mt_2: width of proximal articular surface
Mt_3: antero-posterior dimension of proximal articular surface
Mt_4: maximum width of proximal epiphysis
Mt_5: maximum antero-posterior dimension of distal epiphysis
Mt_6: medio-lateral width at midshaft
Mt_7: antero-posterior dimension at midshaft

Appendix Ⅱ   Bovid species used in this study

Species	Code	TH	BM	Species	Code	TH	BM
Addax nasomaculatus	Adna	Op	111	*Hippotragus equinus*	Hieq	Op	262
Aepyceros melampus	Aeme	Op	50	*Hippotragus niger*	Hini	Op	241
Ammodorcas clarkei	Amcl	Op	29	*Kobus defassa*	Kode	Op	–
Anoa depressicornis	Ande	Fr	150	*Kobus ellipsyprimnus*	Koel	Op	161
Anoa mindorensis	Anmi	Fr	224	*Kobus kob*	Kokk	Op	58
Antidorcas marsupialis	Anma	Op	35	*Kobus lechwe*	Kole	Op	87
Antilope cervicapra	Ance	–	37	*Kobus megaceros*	Kome	Op	87
Bison bison	Bibi	–	611	*Kobus vardoni*	Kova	Op	76
Bos banteng（*javanicus*）	Boba	–	500	*Litocranius walleri*	Liwa	Op	40
Bos gaurus	Boga	–	755	*Madoqua guentheri*	Magu	Op	4
Bos grunniens（*mutus*）	Bogr	Mn	562	*Madoqua kirki*	Maki	Op	5
Bos sauveli	Bosa	–	800	*Madoqua phillipsi*	Maph	Op	–
Boselaphus tragocamelus	Botr	Fr	210	*Madoqua saltiana*	Masa	Op	5
Bubalus bubalis	Bubu	–	725	*Nemorhedus goral*	Nego	–	39
Budorcas taxicolor	Buta	–	250	*Neotragus batesi*	Neba	Fr	3
Capra aegarus	Caae	–	38	*Neotragus moschatus*	Nemo	Op	5
Capra caucasica	Caca	Mn	83	*Neotragus pygmaeus*	Nepy	Fr	4
Capra falconeri	Cafa	–	71	*Oreamnos americanus*	Oram	Mn	97
Capra ibex	Caib	Mn	87	*Oryx gazella*	Orga	–	200
Capra pyrenaica	Capy	Mn	58	*Oryx leucoryx*	Orle	–	155
Capricornis sumatraensis	Casu	–	102	*Oryx tao*（*dama*）	Orta	–	178
Cephalophus callipygus	Ceca	Fr	20	*Oreotragus oreotragus*	Oror	Mn	14
Cephalophus dorsalis	Cedo	Fr	21	*Ourebia ourebi*	Ouou	Op	17
Cephalophus leucogaster	Cele	Fr	17	*Ovibos moschatus*	Ovmo	–	290
Cephalophus maxwelli	Cema	–	8	*Ovis canadiensis*	Ovca	Mn	90
Cephalophus monticola	Cemo	Fr	5	*Ovis dalli*	Ovda	–	80
Cephalophus natalensis	Cena	Fr	16	*Ovis musimon*	Ovmu	Mn	40
Cephalophus nigrifons	Ceng	Fr	14	*Pantholops hodgsoni*	Paho	–	40
Cephalophus niger	Ceni	–	20	*Pelea capreolus*	Peca	Mn	25
Cephalophus sylvicultor	Cesy	Fr	65	*Procapra guttorosa*	Prgu	–	30
Cephalophus zebra	Ceza	–	17	*Pseudois nayaur*	Psna	Mn	59
Connochaetes gnou	Cogn	Op	150	*Raphicerus campestris*	Raca	Op	11
Connochaetes taurinus	Cota	Op	216	*Redunca arundinum*	Rear	Op	62
Damaliscus dorcas	Dado	Op	69	*Redunca fulvorufula*	Refu	–	31
Damaliscus hunteri	Dahu	Op	110	*Redunca redunca*	Rere	Op	46
Damaliscus korrigum	Dako	Op	–	*Rupicapra rupicapra*	Ruru	Mn	36
Damaliscus lunatus	Dalu	Op	142	*Saiga tatarica*	Sata	Op	41
Dorcatragus megalotis	Dome	Mn	11	*Sigmoceros lichtenstein*	Sili	Op	181
Gazella cuvieri	Gacu	Op	30	*Sylvicapra grimmia*	Sygr	Op	13
Gazella dama	Gada	Op	63	*Syncerus caffer*	Syca	–	650
Gazella dorcas	Gado	Op	19	*Taurotragus derbianus*	Tade	Op	580
Gazella gazella	Gaga	Op	23	*Taurotragus oryx*	Taor	Op	490
Gazella granti	Gagr	Op	50	*Tetracerus quadricornis*	Tequ	–	20
Gazella leptoceros	Gale	Op	21	*Tragelaphus angasi*	Tran	–	93
Gazella pelzeni	Gape	Op	18	*Tragelaphus buxtoni*	Trbu	–	183
Gazella soemmeringii	Gaso	–	42	*Tragelaphus euryceros*	Treu	Fr	205
Gazella spekei	Gasp	Op	20	*Tragelaphus imberbis*	Trim	Op	82
Gazella subguttorosa	Gasu	Op	26	*Tragelaphus scriptus*	Trsc	–	48
Gazella thomsonii	Gath	Op	23	*Tragelaphus spekei*	Trsp	–	88
Gazella tilonura	Gati	Op	–	*Tragelaphus strepsiceros*	Trst	Op	218
Hemitragus jegmlagicus	Heje	–	80				

TH：type of habitat（*Op*：open plains，*Fr*：forests，*Mn*：Mountainous terrain）. *BM*：body mass（in kg）.