ELSEVIER

Journal of Archaeological Science 32 (2005) 1115–1123

Journal of Archaeological SCIENCE

http://www.elsevier.com/locate/jas

# Methods for inferring paleohabitats from discrete traits of the bovid postcranial skeleton

David DeGusta [a,*], Elisabeth Vrba [b]

[a] *Department of Anthropological Sciences, Building 360, 450 Serra Mall, Stanford University, Stanford, CA 94305-2117, USA*
[b] *Department of Geology and Geophysics, Yale University, New Haven, CT 06511, USA*

Received 7 April 2003; received in revised form 22 February 2005

**Abstract**

Various "ecomorphological" methods exist for using the functional morphology of bovid postcranial remains to reconstruct paleohabitats. Most such methods use measurements, but both Gentry [The Bovidae (Mammalia) of the Fort Ternan fossil fauna, in: L.S.B. Leakey, R.J.G. Savage (Eds.), Fossil Vertebrates of Africa, vol. 2, Academic Press, London, 1970, pp. 243–323] and Köhler [Skeleton and Habitat of Recent and Fossil Ruminants, Münchner Geowissenschaftliche Abdhandlungen 25 (1993) 1–88] have identified numerous discrete (non-metric) traits of the bovid postcranial skeleton that are said to be indicative of habitat preference. However, these traits have not been systematically tested on a modern bovid sample. We report here such a test. Eighty-six non-metric characters were evaluated using a sample of modern African bovids ($n = 197$). Of the 86 characters, 48 were either insufficiently defined or exhibited too much intra-individual variation to be potentially indicative of habitat. Two characters were invariant in the sample. Of the remaining 36 characters, 11 were sufficiently correlated with habitat preference (Cramer's $V > 0.5$) to be of some potential use in reconstructing paleohabitats. These characters are primarily concentrated on the phalanges, and provide a means by which fragmentary phalanges can be used for habitat reconstruction, albeit at a broad level of resolution (open or closed habitat). The estimated accuracy of these methods is greater than 80%. Their use on fragmentary remains may lessen the bias introduced by basing habitat reconstructions on more complete fossils.


*Keywords:* Bovidae; Ecological morphology; Locomotor behavior; Non-metric traits; Paleoecology; Paleoenvironment

## 1. Introduction

The functional morphology of mammalian postcranial remains can be used to infer locomotor adaptations and, by association, habitat preferences [1–5,7–13]. Such methods are commonly considered "ecomorphological" approaches. These techniques typically use continuous variables; namely, measurements of skeletal elements. However, Gentry [5] and Köhler [11] proposed numerous discrete variables (non-metric traits) of bovid postcranial elements which they suggested were indicative of habitat preference. Such traits are potentially useful for reconstructing paleohabitats since, unlike measurements, they can often be evaluated in fragmentary fossils. They may also provide an additional line of evidence to supplement metric-based estimations of habitat preference.

However, no systematic test of the Gentry [5] and Köhler [11] characters has been reported. Thus the

* Corresponding author. Fax: +1 650 725 9996.
*E-mail address:* degusta@stanford.edu (D. DeGusta).

0305-4403/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jas.2005.02.011

linkage between the non-metric traits they describe and habitat preference has not been empirically tested. We carried out such a test of the Gentry [5] and Köhler [11] non-metric characters, as well as some additional characters that we developed, using a sample of modern African bovids.

## 2. Materials and methods

Our test used a sample of modern African bovids from the American Museum of Natural History (Table 1). The sample is limited to adult individuals (as determined by complete fusion of postcranial epiphyses) that lack postcranial pathological processes and are documented as wild-caught (non-captive). The specimens were sampled without regard to sex, since this parameter cannot currently be determined for isolated postcranial fossils. For a given specimen, all preserved elements (e.g., left and right elements, forelimb and hindlimb phalanges) were examined, and traits that varied within an individual were excluded, as described below.

The descriptions of Gentry [5] and Köhler [11] were used to define characters and their various states, with each character state corresponding to a different habitat preference as determined by the authors. Thirty-seven characters were defined based on Gentry [5] alone,

Table 1
Taxonomic composition and habitat assignments of the modern African bovid sample, using taxonomy of Gentry [6]

| Subfamily | Tribe | Species | Number of individuals[a] | Habitat group |
|---|---|---|---|---|
| Alcelaphinae | Aepycerotini | *Aepyceros melampus* | 1 | Light Cover |
| | Alcelaphini | *Alcelaphus buselaphus* | 15 | Open |
| | | *Connochaetes gnou* | 1 | Open |
| | | *Connochaetes taurinus* | 15 | Open |
| | | *Damaliscus dorcas* | 7 | Open |
| | | *Damaliscus hunteri* | 2 | Open |
| | | *Damaliscus lunatus* | 5 | Open |
| Antilopinae | Antilopini | *Antidorcas marsupialis* | 8 | Open |
| | | *Gazella thomsoni* | 5 | Open |
| | Neotragini | *Madoqua kirki* | 3 | Forest |
| | | *Neotragus batesi* | 4 | Forest |
| | | *Ourebia ourebia* | 10 | Light Cover |
| | | *Raphicerus campestris* | 3 | Light Cover |
| Bovinae | Cephalophini | *Cephalophus monticola* | 3 | Forest |
| | | *Cephalophus natalensis* | 2 | Forest |
| | | *Cephalophus niger* | 1 | Forest |
| | | *Cephalophus nigrifrons* | 3 | Forest |
| | | *Cephalophus sylvicultor* | 2 | Forest |
| | | *Cephalophus weynsi* | 1 | Forest |
| | Tragelaphini | *Taurotragus oryx* | 4 | Open |
| | | *Tragelaphus buxtoni* | 7 | Heavy Cover |
| | | *Tragelaphus euryceros* | 9 | Heavy Cover |
| | | *Tragelaphus imberbis* | 4 | Heavy Cover |
| | | *Tragelaphus scriptus* | 13 | Forest |
| | | *Tragelaphus spekei* | 6 | Heavy Cover |
| | | *Tragelaphus strepiceros* | 9 | Heavy Cover |
| Hippotraginae | Hippotragini | *Addax nasamaculatus* | 4 | Open |
| | | *Hippotragus equinus* | 1 | Open |
| | | *Hippotragus niger* | 4 | Open |
| | | *Oryx dammah* | 3 | Open |
| | | *Oryx gazella* | 6 | Open |
| | Reduncini | *Kobus ellipsiprymnus* | 7 | Heavy Cover |
| | | *Kobus kob* | 6 | Light Cover |
| | | *Kobus megaceros* | 6 | Heavy Cover |
| | | *Redunca arundinum* | 5 | Light Cover |
| | | *Redunca fulvorufula* | 8 | Light Cover |
| | | *Redunca redunca* | 4 | Light Cover |

[a] Each specimen had different numbers of elements that could be scored, so the exact sample size for each character varies, up to the maximum listed.

another 37 on Köhler [11] alone, and two characters were drawn from both sources. We developed a further 10 characters based on our own examination of bovid skeletal remains, for a total of 86 characters. The characters and their definitions are provided in Appendix A.

The characters were scored in our modern African bovid sample. This was done by one person (DD), with frequent reference to Gentry [5] and Köhler [11]. As such, the scoring should be internally consistent. Even so, we emphasize that the definition and scoring of non-metric characters is inherently somewhat subjective. Thus the lack of a correlation between some of the characters and habitat may be due to our definition and scoring.

All "ecomorphological" methods of this sort must use a habitat grouping scheme, in which the range of possible habitats is partitioned into a set of discrete categories. We used the four category scheme of Kappelman et al. [10] but performed our own assignment of bovid taxa to habitat categories [2] (Table 1). The "Forest" taxa are, naturally, forest-dwelling taxa. "Heavy Cover" taxa are those which frequent bush, woodland, swamp, and near-water habitats [10]. "Light Cover" taxa are those which frequent light bush, tall grass, and hilly areas [10]. "Open" taxa (the "plains" category in [10]) are those which frequent edge or ecotone, open country, and arid country [10]. These categories are a significant simplification of the range of bovid habitats and, since many bovid taxa range over several habitat types, the assignment of a taxon to a particular category is a "best fit" designation.

The association between each of the characters (as scored in the modern bovid sample) and habitat preference was evaluated using the correspondence coefficient, Cramer's $V$ (a chi-square based measure of nominal association, essentially the categorical version of Pearson's correlation coefficient for more than $2 \times 2$ cases). In addition, we examined the actual distribution of character states across habitat groups.

## 3. Results

Of the 86 characters, 48 proved either insufficiently defined or too variable in our sample to be potentially indicative of habitat. For characters which were insufficiently defined, the problem was generally that the range of variation observed was too continuous to be objectively divided into the defined discrete states. For example, Gentry [5] states that the central anterior hollow of the astragalus (character #59) is "deep" in plains taxa. However, we observed a generally continuous range of hollow depth, with no clear demarcation between "deep" and "shallow". Even so, it is certainly possible that, with further work, at least some of the characters that we found to be insufficiently defined could be modified so as to be applicable and potentially informative.

For characters which were too variable, the problem was generally one of intra-individual variation. For

Table 2
Correlation of character states with habitat group

| Character #[a] | Element | Correspondence | Cramer's $V$ |
|---|---|---|---|
| 1 | Proximal phalanx | 0.444 | 0.496 |
| 2 | Proximal phalanx | 0.413 | 0.453 |
| 3 | Proximal phalanx | 0.195 | 0.199 |
| 4* | Proximal phalanx | 0.596 | 0.742 |
| 5 | Proximal phalanx | 0.23 | 0.236 |
| 6* | Proximal phalanx | 0.451 | 0.505 |
| 7 | Proximal phalanx | 0.337 | 0.358 |
| 8 | Proximal phalanx | 0.417 | 0.324 |
| 9 | Proximal phalanx | 0.386 | 0.419 |
| 10 | Intermediate phalanx | 0.432 | 0.479 |
| 11* | Intermediate phalanx | 0.542 | 0.645 |
| 12 | Intermediate phalanx | 0.422 | 0.466 |
| 13* | Intermediate phalanx | 0.499 | 0.576 |
| 14* | Intermediate phalanx | 0.454 | 0.51 |
| 15 | Intermediate phalanx | invariant | invariant |
| 16* | Intermediate phalanx | 0.529 | 0.623 |
| 17 | Intermediate phalanx | 0.14 | 0.141 |
| 18 | Intermediate phalanx | 0.311 | 0.327 |
| 19 | Terminal phalanx | 0.525 | 0.436 |
| 20* | Terminal phalanx | 0.616 | 0.783 |
| 21* | Terminal phalanx | 0.651 | 0.858 |
| 22 | Terminal phalanx | 0.207 | 0.211 |
| 23* | Terminal phalanx | 0.496 | 0.572 |
| 24 | Terminal phalanx | 0.479 | 0.315 |
| 25 | Terminal phalanx | 0.411 | 0.451 |
| 38* | Femur | 0.637 | 0.584 |
| 41 | Femur | 0.42 | 0.463 |
| 44 | Femur | 0.363 | 0.39 |
| 45 | Tibia | 0.319 | 0.336 |
| 46 | Tibia | 0.153 | 0.155 |
| 47 | Tibia | 0.263 | 0.273 |
| 48 | Tibia | 0.153 | 0.155 |
| 49 | Tibia | 0.242 | 0.249 |
| 50 | Tibia | invariant | invariant |
| 51 | Tibia | 0.098 | 0.099 |
| 52 | Tibia | 0.115 | 0.115 |
| 68 | Radius | 0.41 | 0.45 |
| 69 | Radius | 0.149 | 0.15 |
| 70 | Radius | 0.125 | 0.126 |
| 71 | Radius | 0.342 | 0.363 |
| 72 | Radius | 0.142 | 0.102 |
| 73 | Radius | 0.116 | 0.117 |
| 77 | Astragalus | 0.535 | 0.448 |
| 78 | Astragalus | 0.435 | 0.342 |
| 79 | Astragalus | 0.372 | 0.401 |
| 80 | Astragalus | 0.273 | 0.283 |
| 81 | Tibia | 0.541 | 0.455 |
| 82 | Tibia | 0.524 | 0.435 |
| 83 | Tibia | 0.524 | 0.355 |
| 84 | Tibia | 0.421 | 0.464 |
| 85* | Humerus | 0.492 | 0.566 |
| 86 | Humerus | 0.348 | 0.371 |

[a] Characters sufficiently correlated with habitat to be useful indicators are flagged with an asterisk. Characters not listed were insufficiently defined or too variable (see text). All characters are defined in Appendix A.

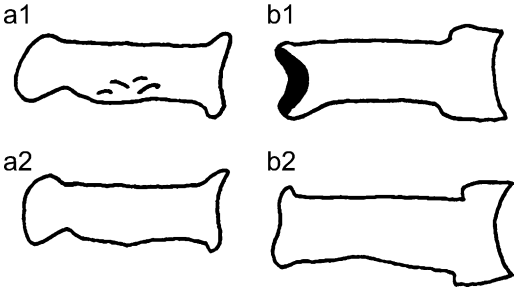


Fig. 1. Proximal phalanx characters shown to be correlated with habitat group. Surface of interdigital side (character #4) is either very rough (a1, Forest or Heavy Cover habitat) or smooth (a2, Light Cover or Open habitat). Facet for distal articulation in dorsal view (character #6) is either very visible (b1, not informative of habitat) or not visible (b2, Light Cover or Open habitat). Redrawn after Köhler [11], which contains more illustrations and descriptions of these features.

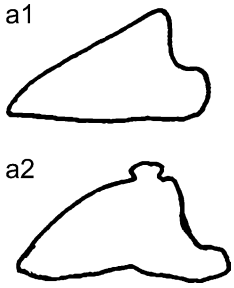


Fig. 3. Distal phalanx characters shown to be correlated with habitat group. Proximo-superior process (character #20) is either absent (a1, Forest or Heavy Cover habitat) or present (a2, Light Cover or Open habitat). Amount of bone inferior to articular process (character #21) is either substantial (a1, Forest or Heavy Cover habitat) or limited (a2, Light Cover or Open habitat). Interdigital border of plantar surface (character #23) is either flat (a1, not informative of habitat) or angled (a2, Light Cover or Open habitat). Redrawn after Köhler [11], which contains more illustrations and descriptions of these features.

example, some of the characters of the metapodials identified by Köhler [11] appeared to vary within individuals, either between metacarpals and metatarsals, or even bilaterally. Again, with further investigation, it may well be possible to modify the definition of these characters so as to be useful for habitat discrimination. It is also possible that our reading of the underlying sources [5,11] differs from that intended by the authors. Therefore, we conclude only that we were unable to implement these 48 characters.

Two characters were invariant in the sample (Table 2). Of the remaining 36 characters, 11 were sufficiently correlated with habitat preference (Cramer's $V > 0.5$) to be of some potential use in reconstructing paleohabitats (Table 2). Of these 11 characters, two are of the proximal phalanx (Fig. 1), four of the intermediate phalanx (Fig. 2), three of the terminal phalanx (Fig. 3), one of the femur, and one of the humerus. However, the correlation between these characters and habitat preference is not precise (Table 3), so that no single character, in isolation, can be used for reliable habitat prediction. As such, the lone humerus character (#85) and the sole femur character (#38) are not dealt with further here, though the latter (shape of proximal articular surface) provides non-metric confirmation of the metric techniques used to estimate habitat from bovid femora [8–10].

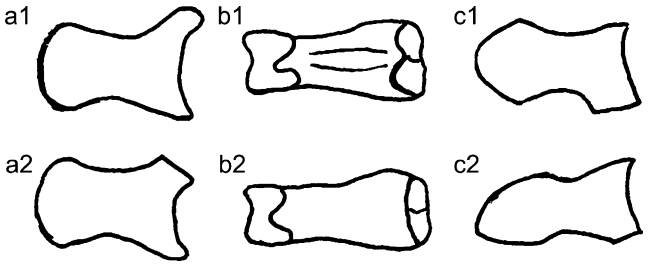


Fig. 2. Intermediate phalanx characters shown to be correlated with habitat group. Proximo-inferior plateau (character #11) is either proximately elongated (a1, not Light Cover habitat) or short (a2, Light Cover or Open habitat). Proximal volar end (character # 13) either has strong marks (b1, not informative of habitat) or weak marks (b2, Light Cover or Open habitat). A broad palmar sagittal groove (character # 16) is either present (b1, Forest or Heavy Cover habitat) or absent (b2, not informative of habitat). Outline of distal articular surface in internal view (character # 14) is either triangular with apex directed distally (c1, Forest or Heavy Cover habitat) or oval with apex directed palmarly (c2, Light Cover or Open habitat). Redrawn after Köhler [11], which contains more illustrations and descriptions of these features.

Since multiple informative non-metric characters are available for the phalanges, it is possible to derive habitat predictions for these elements. This can be done by scoring an "unknown" phalanx for the relevant non-metric characters, and then comparing the distribution of character states with that given for the various habitat groups, as summarized in the classification keys in Table 3. The habitat predictions generated by this will generally be of limited precision, typically either "Forest or Heavy Cover" or "Light Cover or Open" (essentially a closed habitat/open habitat dichotomy). The overlap noted in metric proportions of the phalanges between Forest and Light cover specimens, as well as Heavy Cover and Open specimens [3], does not seem to hold for non-metric traits (Table 3).

The accuracy of the above procedure was tested by using it to estimate the habitat preferences of the modern bovid sample. The accuracy of the resulting classifications was 88% for the proximal phalanx, 85% for the intermediate phalanx, and 97% for the distal phalanx (Table 4). This indicates that habitat preferences can be estimated, at a broad level, from non-metric characters of the phalanges with reasonable accuracy. Even so, it is important to realize that these estimates of accuracy are likely maxima, since the

Table 3
Distribution of informative characters relative to habitat groups

| Character # | Element | State #1[a] | State #2[a] | State #3[a] | Classification key[b] |
|---|---|---|---|---|---|
| 4 | Proximal phalanx | 14/37/3/7 | 5/5/27/64 | na | 1 = F or H, 2 = L or O |
| 6 | Proximal phalanx | 19/42/14/60 | 0/0/16/11 | na | 2 = L or O |
| 11 | Intermediate phalanx | 10/36/5/16 | 5/1/21/43 | na | 1 = not L, 2 = L or O |
| 13 | Intermediate phalanx | 10/37/11/19 | 5/0/16/40 | na | 2 = L or O |
| 14 | Intermediate phalanx | 11/28/5/15 | 4/9/22/44 | na | 1 = F or H, 2 = L or O |
| 16 | Intermediate phalanx | 5/26/3/3 | 10/11/24/56 | na | 1 = F or H |
| 20 | Terminal phalanx | 9/25/0/2 | 1/9/22/43 | na | 1 = F or H, 2 = L or O |
| 21 | Terminal phalanx | 7/34/4/2 | 3/0/18/46 | na | 1 = F or H, 2 = L or O |
| 23 | Terminal phalanx | 8/34/7/21 | 2/0/15/27 | na | 2 = L or O |
| 38 | Femur | 23/31/2/0 | 2/15/34/78 | 4/2/0/0 | 1&3 = F or H, 2 = not F |
| 85 | Humerus | 12/21/10/73 | 17/26/25/5 | na | 2 = not O |

[a] The occurrence of a given character state is reported by habitat groups as follows: # of Forest (F) specimens/# of Heavy Cover (H) specimens/# of Light Cover (L) specimens/# of Open (O) specimens.
[b] *F* = Forest, *H* = Heavy Cover, *L* = Light Cover, *O* = Open.

specimens evaluated with the non-metric classification keys were also those used to generate the keys.

## 4. Conclusion

The non-metric traits of the bovid postcranial skeleton proposed as habitat indicators by Gentry [5] and Köhler [11] were tested on a sample of modern African bovids. We found that most of these characters are either not scorable or not correlated with habitat preference in African bovids. However, multiple characters that are correlated with habitat were identified for the proximal, intermediate, and distal phalanges. These allow broad habitat preferences to be predicted with reasonable (>80%) accuracy, even if the remains are not sufficiently complete for measurement. As such, they represent a useful extension of existing metric methods for inferring paleohabitats from the functional morphology of bovid remains [2,10,12]. These non-metric characters can be used to include a greater proportion of specimens in such habitat reconstructions, thus lessening potential biases introduced by using only fossils complete enough for measurement.

Table 4
Accuracy of habitat prediction using classification key

| Element | Accuracy (%) | Sample size | Right | Wrong | Indeterminate[a] |
|---|---|---|---|---|---|
| Prox phx | 88 | 162 | 143 | 19 | 1 |
| Int phx | 85 | 111 | 94 | 17 | 28 |
| Dist phx | 97 | 99 | 96 | 3 | 15 |

[a] In the cases where the habitat prediction key (Table 3) led to contradictory results (i.e. different characters gave contradictory habitat predictions) the specimen was considered indeterminate (no prediction could be generated) and was not included in the sample size or accuracy calculations.

## Acknowledgements

We thank Bob Randall, Chris Norris, Rob MacPhee, and Eric Delson of the American Museum of Natural History (AMNH) for access to modern bovid material and F. Clark Howell and Tim White of the Laboratory for Human Evolutionary Studies (UC Berkeley), two anonymous reviewers, and Richard Klein (Stanford) for helpful comments. We thank Meike Köhler and Alan Gentry for describing and publishing most of the characters we tested. We especially thank all the collectors of the skeletal material used in this study for their efforts. This study was funded by the Laboratory for Human Evolutionary Studies (UC Berkeley), the Albert Preston Hendrickson Fund of the Museum of Vertebrate Zoology (UC Berkeley), and a Collection Study Grant from the AMNH.

## Appendix A. Character definitions

Characters 1–38 are from Köhler [11], characters 2 and 38–76 are from Gentry [5], and characters 77–86 were developed for this study. The characters are divided according to whether their association with habitat preference was "verified" by our analysis, or whether they remain "unverified". Within those divisions, characters are listed by element, and then by character number. For verified characters, the correspondence between character states and habitat groups is given in square brackets (see also Table 3). For additional descriptions and illustrations of these characters and character states, see Köhler [11] and Gentry [5].

*Verified*

Proximal phalanx (Fig. 1)

4. Surface of Interdigital Side
   1 = very rough [Forest or Heavy Cover]
   2 = smooth, even [Light Cover or Open]
6. Facet for Distal Articulation in Dorsal View
   1 = very visible
   2 = not visible [Light Cover or Open]

Intermediate phalanx (Fig. 2)

11. Proximo-inferior (Postarticulaire) Plateau
   1 = proximately elongated [not Light Cover]
   2 = short [Light Cover or Open]
13. Proximal Volar End
   1 = strong marks
   2 = weak marks [Light Cover or Open]
14. Outline of Distal Articular Surface in Internal View
   1 = triangular, with angle directed distally [Forest or Heavy Cover]
   2 = oval, with apex directed more palmarly [Light Cover or Open]
16. Broad Palmar Sagittal Groove
   1 = present [Forest or Heavy Cover]
   2 = absent

Terminal phalanx (Fig. 3)

20. Proximo-Superior Process
   1 = absent [Forest or Heavy Cover]
   2 = present [Light Cover or Open]
21. Amount of Bone Inferior to Articular Process
   1 = substantial [Forest or Heavy Cover]
   2 = limited [Light Cover or Open]
23. Interdigital Border of Plantar Surface
   1 = flat
   2 = angled [Light Cover or Open]

Femur

38. Overall Shape of Proximal Articular Surface
   1 = long, narrow lateral extension [Forest or Heavy Cover]
   2 = long, broad lateral extension [not Forest]
   3 = short, narrow lateral extension [Forest or Heavy Cover]

Humerus

85. Attachment Surface on Medial Portion of Medial Epicondyle
   1 = Extends posteriorly past main shaft midline
   2 = Does not extend posteriorly [not Open]

*Unverified*

Proximal phalanx

1. Overall Form
   1 = robust
   2 = slender
2. Incision for Metapodial Verticillus
   1 = weak
   2 = strong
3. Interosseous Muscle Tendon Sulcus
   1 = present
   2 = absent
5. Outline of Dorsal Surface
   1 = convex
   2 = concave
7. Lateral View of Distal End
   1 = well-rounded
   2 = flattened on volar side
8. Lateral View of Volar Shaft Curvature
   1 = starts midshaft
   2 = flat
   3 = starts at proximal end
9. External Side in Dorsal View
   1 = weak to no curvature
   2 = strongly concave

Intermediate phalanx

10. Proximal Articular Surface in Lateral View
   1 = weakly concave
   2 = strongly concave
12. Proximo-superior (Dorsal Extensor) Process
   1 = does not extend as proximally as volar edge
   2 = extends almost as proximally as volar edge
15. Dorsal-Palmar Extent of Distal Articular Surface
   1 = limited
   2 = extensive
17. Outline in Dorsal View
   1 = sides roughly parallel
   2 = some pinching in
18. Interdigital Portion of Distal Articular Surface in Dorsal View
   1 = extends only as far distally as external portion
   2 = extends much farther distally than external portion

Terminal phalanx

19. Dorsal Ridge in Lateral View
   1 = straight
   2 = almost straight, but slight angle in middle
   3 = curved
22. Proximo-Inferior Articular Surface
   1 = does not form a flat wedge
   2 = forms a flat wedge

24. Dorsal Ridge in Dorsal View
    1 = long, inclined to interdigital side
    2 = short, runs to external side
    3 = short, runs down midline
25. Proximal-Inferior-most Bone Viewed in Dorsal View
    1 = articular
    2 = non-articular

Distal metapodial

26. Outline in Anterior View
    1 = triangular
    2 = inflated/bulging
    3 = straight, very little change in medial-lateral dimension
    4 = abruptly increased medial-lateral dimension
27. Proximal Extension of Articular Surfaces
    1 = limited
    2 = extend proximally
28. Separation of Articular Surfaces
    1 = slight
    2 = moderate
29. Verticilli (Ridges) on Articular Surfaces
    1 = weak
    2 = jigh and sharp
    3 = high and very sharp, clearly separating surfaces into two different-shaped (triangular and trapezoidal) segments
30. Sagittal Groove Between Articulations
    1 = present
    2 = absent
31. Lateral View of Articulations
    1 = flattened distal-dorsally
    2 = well-rounded
    3 = flattened distal-palmarly
32. Anterior Shaft Sulcus
    1 = long and narrow
    2 = long and broad
    3 = present only distally, broad and flat
    4 = absent or obscured
33. Lateral View of Shaft Proximal to Articulations
    1 = palmarly concave, dorsally convex
    2 = parallel
34. Intertrochlear Incision
    1 = u-shaped
    2 = narrow v-shaped
    3 = broadly v-shaped
35. Notches Proximal to Anterior Articular Surface
    1 = absent
    2 = present
36. Distal-Lateral Protuberance for Interosseous
    1 = absent
    2 = present

Proximal metapod

37. Tendon Furrow
    1 = long
    2 = short or absent

Femur

39. Greater Trochanter Shape
    1 = large great trochanter, deep hollow between trochanter and articular head in anterior view, a horizontal top edge of articular head
    2 = not like 1
40. Greater Trochanter Angulation
    1 = back edge of greater trochanter set obliquely
    2 = back edge of greater trochanter set uprightly
41. Accessory Fossa
    1 = a deep roughened fossa low on lateral side of posterior surface
    2 = no such fossa
42. Patellar Fossa
    1 = wide
    2 = not wide
43. Medial Side of Patellar Fossa
    1 = projects strongly anteriorly
    2 = does not project strongly anteriorly
44. Lateral Side of Distal Condyles
    1 = deep hollows
    2 = shallow hollows

Proximal tibia

45. Proximal Articular Surface Flanges
    1 = high flanges
    2 = no high flanges
46. Proximal Articular Surface Morphology
    1 = pronounced, but localized, central swelling with medial depression
    2 = no such swelling
47. Patellar Groove at Top of Cnemial Crest
    1 = present
    2 = absent
48. Lateral Surface of Cnemial Crest
    1 = well-hollowed
    2 = not well-hollowed

Distal tibia

49. Depth of Articular Facets
    1 = deep
    2 = not deep
50. Posterior Edge of Articular Facets
    1 = indented in ventral view
    2 = not indented in ventral view
51. Anterior Edge of Articular Facets
    1 = narrow central anterior flange
    2 = non-narrow central anterior flange

52. Anterior Surface
    1 = prominent ridges just proximal to distal end
    2 = no prominent ridges just proximal to distal end
81. Groove on Medial Shaft Near Distal End
    1 = Shallow, anterior border terminates anteriorly on distal edge
    2 = Deep, anterior border terminates posteriorly on distal edge
82. Incision on Medial Edge of Distal Anterior Surface in Anterior View
    1 = Deep and v-shaped
    2 = Shallow and u-shaped
83. Shape of Rugosity on Lateral Portion of Distal Anterior Shaft
    1 = No rugosity, or discrete small bump position near midline
    2 = More diffuse rugosity extending proximo-distally
    3 = Discrete rugosity positioned near distal edge of shaft surface
84. Shape of Antero-Lateral Facet of Distal Tibia in Distal View
    1 = Oval, joined with postero-lateral facet
    2 = More circular and distinct from postero-lateral facet

Proximal metatarsal

53. Proximal Articular Facets
    1 = markedly upwardly curved in medial view
    2 = not markedly upwardly curved in medial view
54. Shape of Proximal End in Dorsal View
    1 = posterior part medial-laterally narrower than central part
    2 = posterior part not medial-laterally narrower than central part
55. Foramen on Proximo-Posterior Surface
    1 = present and deep
    2 = not present or not deep

Distal metatarsal

56. Outer Edges of Distal Condyles
    1 = parallel
    2 = not parallel
57. Hollows Antero-Superior to Distal Condyles
    1 = deep
    2 = not deep
58. Anterior Surface of Distal Condyles
    1 = strong paired flanges
    2 = no strong paired flanges

Astragalus

59. Central Anterior Hollow
    1 = deep
    2 = not deep
60. Medial Side
    1 = deep grooves and ridges
    2 = no deep grooves and ridges
77. Impingement of Posterior Articular Surface on Medial Surface in Medial View
    1 = none
    2 = partial
    3 = full
78. Indentation Distal to Posterior Articular Surface
    1 = slight to none
    2 = moderate
    3 = deept
79. Proximal-Lateral Ridge on Anterior Surface
    1 = Veers medially as it joins distal articular surface
    2 = Veers laterally as it joins distal articular surface
80. Projection of Posterior Proximal Corner in Medial View
    1 = In line with rest of posterior edge
    2 = Projects more posteriorly than rest of posterior edge

Scapula

61. Teres Minor Insertion
    1 = deep
    2 = not deep
62. Tuber
    1 = near lateral edge of glenoid facet in ventral view
    2 = not near lateral edge of glenoid facet in ventral view

Humerus

63. Bicipital Groove
    1 = wide
    2 = not wide
64. Hollow for Distal Lateral Ligament
    1 = deep
    2 = not deep
65. Medial Groove of Distal Articular Surface
    1 = well marked
    2 = not well marked
66. Distal Condyles
    1 = oriented uprightly
    2 = not oriented uprightly
67. Medial Distal Condyle
    1 = high
    2 = not high
86. Anterior Outline of Distal Lateral Articular Surface in Distal View
    1 = Lacks a sharp lateral rim
    2 = Has a sharp lateral rim

Radius

68. Proximal Lateral Tubercle
    1 = large
    2 = not large
69. Proximal Medial Facet
    1 = no rim on medial side
    2 = rim on medial side
70. Proximal Lateral Facet
    1 = antero-posteriorly shorter
    2 = not antero-posteriorly shorter
71. Distal End in Side View
    1 = swollen
    2 = not swollen
72. Distal Anterior Surface
    1 = prominent flanges set close together in ventral view
    2 = lacks prominent flanges set close together in ventral view
73. Distal Facets
    1 = deep
    2 = not deep

Proximal metacarpal

74. Magnum-Trapezoid Facet Size
    1 = antero-posteriorly short
    2 = not antero-posteriorly short
75. Magnum-Trapezoid Facet Angulation
    1 = angled
    2 = not angled
76. Area of Unciform Facet
    1 = small relative to that of magnum-trapezoid facet
    2 = not small relative to that of magnum-trapezoid facet

## References

[1] L.C. Bishop, Pigs and the Ancestors: Hominids, Suids, and Environments during the Plio–Pleistocene of East Africa, PhD dissertation, Yale University, 1994.
[2] D. DeGusta, E.S. Vrba, A method for inferring paleohabitats from the functional morphology of bovid astragali, Journal of Archaeological Science 30 (2003) 1009–1022.
[3] D. DeGusta, E.S. Vrba, Methods for inferring paleohabitats from the functional morphology of bovid phalanges, Journal of Archaeological Science, in press, doi:10.1016/j.jas.2005.02.010.
[4] S. Elton, Locomotor and habitat classifications of cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2, South Africa, Palaeontologica Africana 37 (2001) 115–126.
[5] A.W. Gentry, The Bovidae (Mammalia) of the Fort Ternan fossil fauna, in: L.S.B. Leakey, R.J.G. Savage (Eds.), Fossil Vertebrates of Africa, vol. 2, Academic Press, London, 1970, pp. 243–323.
[6] A.W. Gentry, The subfamilies and tribes of the family Bovidae, Mammal Review 22 (1992) 1–32.
[7] J. Kappelman, The Paleoecology and Chronology of the Middle Miocene Hominoids from the Chinji Formation of Pakistan, PhD dissertation, Harvard University, 1987.
[8] J. Kappelman, Morphology and locomotor adaptations of the bovid femur in relation to habitat, Journal of Morphology 198 (1988) 119–130.
[9] J. Kappelman, The paleoenvironment of *Kenyapithecus* at Fort Ternan, Journal of Human Evolution 20 (1991) 95–129.
[10] J. Kappelman, T. Plummer, L. Bishop, A. Duncan, S. Appleton, Bovids as indicators of Plio–Pleistocene paleoenvironments in East Africa, Journal of Human Evolution 32 (1997) 229–256.
[11] M. Köhler, Skeleton and habitat of recent and fossil Ruminants, Münchner Geowissenschaftliche Abdhandlungen 25 (1993) 1–88.
[12] T.W. Plummer, L.C. Bishop, Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains, Journal of Human Evolution 27 (1994) 147–175.
[13] R.S. Scott, J. Kappelman, J. Kelley, The paleoenvironment of *Sivapithecus parvada*, Journal of Human Evolution 36 (1999) 245–274.