16. Evolutionary Morphology of the Guenon Postcranium and Its Taxonomic Implications

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16.1 Introduction

Guenons (Primates, Cercopithecini) are relatively small-bodied (Table 16.1) Old World monkeys endemic to Africa. They exhibit a variety of substrate preferences, spanning from arboreal to semiterrestrial to terrestrial (Table 16.2). The ancestral guenon was likely arboreal; indeed, the postcranial morphology of semiterrestrial guenons, including the basal *Allenopithecus* (Tosi et al., 2004, 2005), resembles that of their arboreal relatives (Gebo and Sargis, 1994). Morphological modifications attributable to terrestriality are only found in three guenon taxa (Gebo and Sargis, 1994): patas monkeys (*Erythrocebus patas*), the lhoesti group (*Cercopithecus lhoesti, C. preussi*, and *C. solatus*), and vervet monkeys (*Cercopithecus aethiops*; Manaster, 1979; Anapol and Gray, 2003; Anapol et al., 2005).

16.1.1 Functional Morphology

Gebo and Sargis (1994) conducted both qualitative and univariate analyses on the postcranium of guenons. They found that *Erythrocebus patas, Cercopithecus lhoesti*, and *C. preussi* exhibit numerous, but variable, terrestrial adaptations, whereas *C. aethiops* is characterized by far fewer modifications for terrestriality (Table 16.3). They combined Lernould's (1988) classification of guenons with the consensus tree from Ruvolo's (1988) electrophoretic analysis of 14 proteins, and mapped terrestriality onto this cladogram. From this, Gebo and Sargis (1994) hypothesized that terrestriality and the postcranial adaptations for this substrate preference evolved independently three times among guenons. In this paper, we re-evaluate this proposal in light of new molecular

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TABLE 16.1. Number of specimens per taxon, taxon abbreviations used for all plots, and mean body weight (in g) of each taxon.

Taxon	Abbreviation	*n*	Body weight*
Allenopithecus nigroviridis	AN	2	4678
Cercopithecus aethiops	CAe	11	4656
Cercopithecus ascanius	CAs	10	3426
Cercopithecus cephus	CC	4	3355
Cercopithecus diana	CD	6	4643
Cercopithecus hamlyni	CH	1	4638
Cercopithecus lhoesti	CL	1	4663
Cercopithecus mitis	CM	14	5656
Cercopithecus neglectus	CN	6	5701
Cercopithecus pogonias	CPo	1	3187
Cercopithecus preussi	CPr	2	?
Erythrocebus patas	EP	6	7661
Miopithecus talapoin	MT	5	1795

*Mean body weights from Delson et al. (2000) appendix 2; see their appendix 1 for sources of raw body weights.

TABLE 16.2. Guenon substrate preferences.

Taxon	Substrate preferences	Sources
Allenopithecus nigroviridis	Semiterrestrial	Gautier-Hion, 1988
Cercopithecus aethiops	**Semiterrestrial***	Rose, 1979
Cercopithecus ascanius	Arboreal	Gebo and Chapman, 1995
Cercopithecus campbelli	Semiterrestrial	McGraw, 1998, 2000
Cercopithecus cephus	Arboreal	Gautier-Hion, 1988
Cercopithecus diana	Arboreal	McGraw, 1998, 2000
Cercopithecus hamlyni	Semiterrestrial	Gebo and Sargis, 1994
Cercopithecus lhoesti	**Terrestrial**	Kaplin and Moermond, 2000
Cercopithecus mitis	Arboreal	Gebo and Chapman, 1995
Cercopithecus neglectus	Semiterrestrial	Gautier-Hion, 1988
Cercopithecus nictitans	Arboreal	Gautier-Hion, 1988
Cercopithecus petaurista	Arboreal	McGraw, 2000
Cercopithecus pogonias	Arboreal	Gautier-Hion, 1988
Cercopithecus preussi	**Terrestrial**	Gautier-Hion, 1988
Cercopithecus solatus	**Terrestrial**	Gautier-Hion, 1988
Erythrocebus patas	**Terrestrial**	Isbell et al., 1998
Miopithecus talapoin	Arboreal	Gautier-Hion, 1988

* *C. aethiops* may be terrestrial; this species exhibits some postcranial modifications like those of the terrestrial species. (From Gebo and Sargis, 1994.)

evidence on the phylogeny of guenons and we perform a re-analysis of the morphological data.

Although vervet monkeys do not exhibit as many terrestrial adaptations as l'Hoest's or patas monkeys, they can still be distinguished from arboreal guenons in studies of postcranial morphology (Gebo and Sargis, 1994). For example, in his qualitative analysis of the humerus and femur, Nakatsukasa (1994) was able to differentiate *C. aethiops* from the arboreal *C. mitis* and *C. mona*. In addition to osteological differences, the fiber architecture of forelimb and hind limb muscles differs between the more terrestrial *C. aethiops* and the arboreal *C. ascanius* (Anapol and Barry, 1996; Anapol and Gray, 2003). Specifically, the muscle fiber architecture in *C. aethiops* allows higher velocity/excursion for terrestrial running, whereas that of *C. ascanius* is better suited for storage of passive elastic strain energy for use in the compliant canopy (Anapol and Barry, 1996; Anapol and Gray, 2003). Furthermore, Anapol and Gray (2003) showed that the distribution of force potential in the shoulder and arm muscles of *C. aethiops* is better for transitioning between the ground and canopy and for braking during terrestrial running, while that of *C. ascanius* is better suited for stabilization during quadrupedal descent and propulsion during arboreal running. These myological differences led them to propose that "semiterrestrial" is a discrete locomotor category, intermediate between arboreal and terrestrial (Anapol and Gray, 2003; Anapol et al., 2005).

16.1.2 Scaling

Martin and MacLarnon (1988) conducted several logarithmic bivariate regression (major axis) analyses to examine the scaling of various craniodental variables to body size. They explored scaling of 18 cranial variables relative to prosthion-inion (skull) length. Of these, five cranial variables scale isometrically, nine are negatively allometric, and four are positively allometric. Martin and MacLarnon (1988) also examined the scaling trends of seven dental variables relative to body weight, all of which scaled isometrically. Although it is possible that there is a real difference in scaling between cranial and dental measures in guenons, it is perhaps more likely that the variable patterns of scaling seen in the two data sets are a result of Martin and MacLarnon's (1988) use of different body size surrogates for the cranial and dental analyses (Shea, 1992). In this paper, we will explore scaling patterns in the postcrania of guenons.

Shea (1992) also studied scaling in guenons, specifically ontogenetic scaling of *M. talapoin* and *C. cephus*. He analyzed 11 cranial and 6 postcranial measurements; the latter are of particular interest for our study. In his bivariate regression (least-squares and reduced major axis) analyses, he found that the scaling of humerus and tibia length relative to femur length is negatively allometric (Shea, 1992); the same is true when regressing individual limb elements to pelvic height. Here, we examine adult interspecific data, which, unlike the ontogenetic data examined by Shea (1992), do not allow us to examine process. However, scaling patterns are important to explore in our effort to elucidate both the functional and evolutionary patterns of association among guenons.

16.1.3 Multivariate Analyses

Further evidence for the distinction of *C. aethiops* from arboreal guenons comes from Manaster's (1979) multivariate analysis of 67 postcranial variables in 7 guenon species. She conducted a canonical analysis, which separated three groups: (1) *C. aethiops*; (2) *C. mitis* and *C. neglectus*; and (3) *C. mona, C. cephus, C. nictitans*, and *C. diana*. In this analysis, canonical axis 1 separated the terrestrial *C. aethiops* from the six arboreal and semiterrestrial taxa (Manaster, 1979).

TABLE 16.3. Postcranial adaptations present in terrestrial taxa (from Gebo and Sargis, 1994).

Character	Taxa
1. Elongated fore- and hind limbs (Hurov, 1987)	*patas*
2. High intermembral index	*patas*
3. High brachial index	*patas*
4. Long, narrow scapula (short vertebral border)	*patas*
5. Short infraspinous fossa	*patas*
6. Square glenoid fossa	*patas*
7. Strongly retroflexed humerus	*patas*
8. Narrow posterior humeral trochlea with high medial edge	*patas*
9. Straight ulna and radius	*patas*
10. Strongly retroflexed femur	*patas*
11. Deep (a-p) knee with high lateral patellar rim	*patas*
12. Digitigrade feet	*patas*
13. Short supraspinous fossa	*patas, lhoesti*
14. Oblique angle of humeral head	*patas, lhoesti, preussi*
15. Medially curved humeral shaft	*patas, lhoesti, preussi*
16. Deep radial and ulnar fossae on humerus	*patas, lhoesti, preussi*
17. Small radial facet on ulna	*patas, lhoesti, preussi*
18. Distal radial facets flat (not concave)	*patas, lhoesti, preussi*
19. Small femoral head articular surface	*patas, lhoesti, preussi*
20. Small/reduced anterior calcaneal facet (distal part)	*patas, lhoesti, preussi*
21. Shallow calcaneocuboid pivot (on calcaneus)	*patas, lhoesti, preussi*
22. Narrow and smooth (no lateral ridge) humeral trochlea	*lhoesti, preussi*[a]
23. Medially twisted distal ulnar shaft	*lhoesti, preussi*
24. Femoral head/neck perpendicular to shaft (not oblique)	*lhoesti, preussi*
25. Short tibial crest	*lhoesti, preussi*
26. Small peroneal tubercle (on calcaneus)	*lhoesti, preussi*
27. Narrow and tall talar head	*lhoesti, preussi, aethiops*
28. Acromion process/spine not angled cranially	*lhoesti*
29. Small infraspinatus flange	*lhoesti*
30. Narrow humeral head	*lhoesti*
31. Greater/lesser tuberosities extend above humeral head	*lhoesti*
32. Short deltopectoral crest	*lhoesti*
33. Vertical medial trochlear rim (posterior humerus)	*lhoesti*
34. Small radial head and articular surface	*lhoesti*
35. Greater trochanter extends above femoral head	*lhoesti*
36. Posterior position of lesser trochanter	*lhoesti*
37. Narrow patellar groove (with sharp medial rim)	*lhoesti*
38. Deep (a-p) distal tibial facet with small medial part	*lhoesti*
39. Deep, pronounced tibial cup (medial talar facet for tibia)	*lhoesti*
40. Less medially angled (straighter) calcaneal tuber	*lhoesti*
41. Reduced attachment areas on calcaneus for ligaments	*lhoesti*
42. Low humeral mid-shaft cortical areas	*lhoesti*[b]
43. Long cuboid	*lhoesti, aethiops*
44. Narrow humeral facet on ulna	*aethiops*
45. Long navicular	*aethiops*
46. Short third metatarsal	*aethiops*
47. Long calcaneus (Kingdon, 1988)	*aethiops, patas*[c]
48. Short manual and pedal digits (Kingdon, 1988)	*aethiops, patas*[c]

[a] *C. preussi* has a small lateral trochlear ridge.

[b] *C. lhoesti* was the only terrestrial taxon to be scanned.

[c] More extreme in *E. patas* than *C. aethiops* (Kingdon, 1988).

Martin and MacLarnon (1988) also performed multivariate analyses on 12 guenon species, although their study focused on craniodental morphology. They conducted cluster and multidimensional scaling analyses on 18 cranial and 7 dental variables, as well as analyses on a combined data set that included the 7 dental variables and 11 of the 18 cranial variables. In their cranial analysis, *C. lhoesti* was united to *Miopithecus talapoin* and *E. patas* clustered with these two taxa, while *Allenopithecus nigroviridis* and *C. neglectus* were distant. The dental analysis united *E. patas* with *M. talapoin* and *C. lhoesti* clustered with these two genera. Again, *Allenopithecus* was distant, but it formed a cluster with *C. aethiops* in this analysis. The combined craniodental analysis produced results similar to the cranial analysis in some ways and to the dental analysis in other ways. Specifically, *C. lhoesti* joined *M. talapoin* and *E. patas* joined these two species, as in the cranial analysis. Furthermore, *Allenopithecus* was, once again, distant, and, as in the dental analysis, it clustered with *C. aethiops*. In summary, *C. lhoesti, M. talapoin*, and *E. patas* are phenetically similar craniodentally, whereas *Allenopithecus* is dissimilar. Although *C. aethiops* was united to *Allenopithecus* in the dental analysis, it clustered with arboreal *Cercopithecus* species in the cranial analysis. Based on these results, Martin and MacLarnon (1988) stated that the topologies from their cluster analyses were similar to those from the karyotype analyses of Dutrillaux et al. (1988), which supported a terrestrial group including *C. lhoesti, E. patas*, and *C. aethiops*. However, this group was not precisely supported in Martin and MacLarnon's (1988) multivariate analyses, as *M. talapoin* replaced *C. aethiops* in a cluster with *C. lhoesti* and *E. patas*. An additional similarity between the craniodental and chromosomal studies is the distant position of *Allenopithecus*. Based on these similarities, Martin and MacLarnon (1988) proposed that their phenetic analysis was more indicative of phylogeny than function even though this was not expected at the outset of their study. They also proposed that taxonomically restricted analyses, such as their examination of guenons, might better elucidate phylogenetic patterns, while more inclusive analyses may emphasize functional convergences (Martin and MacLarnon, 1988). Here, we compare our results from a cluster analysis of guenon postcrania to those from Martin and MacLarnon's (1988) craniodental analyses.

16.1.4 Molecular Phylogenetics

Both the karyotype analysis of Dutrillaux et al. (1988) and the Y-chromosome sequence data of Tosi et al. (2002, 2003, 2004) support a terrestrial clade that includes *E. patas, C. aethiops*, and *C. lhoesti*. Additional sequence data from an X-chromosome intergenic region also support this terrestrial clade, as well as the basal divergence of *Allenopithecus* (Tosi et al., 2004, 2005). Within the terrestrial clade, the X-chromosome evidence supports a *C. aethiops*-*E. patas* sister taxon relationship (Tosi et al., 2004, 2005), which is also supported by three cranial synapomorphies (Groves, 2000). Based on these phylogenetic results, Tosi et al. (2002, 2003, 2004) proposed that terrestriality is derived and evolved only once among guenons. This contradicts Gebo and Sargis' (1994) proposal that terrestriality evolved three times among guenons, which was based on a phylogeny from Ruvolo (1988) where *E. patas, C. aethiops*, and *C. lhoesti* were not closely related. We re-evaluate this proposal in light of recent molecular evidence (see Tosi et al., 2002, 2003, 2004, 2005).

16.1.5 Taxonomy

The inclusion of *C. aethiops* and *C. lhoesti* in a clade with *E. patas* to the exclusion of other *Cercopithecus* species makes the genus *Cercopithecus* paraphyletic (Tosi et al., 2002, 2003, 2004). Four different solutions to this taxonomic problem have been proposed (Tosi et al., 2002, 2003, 2004): (1) patas monkeys could be sunk into *Cercopithecus*; (2) patas monkeys could be left in *Erythrocebus* (Trouessart, 1897), vervet monkeys could be restored to *Chlorocebus* (Gray, 1870), and l'Hoest's monkeys could be reinstated to *Allochrocebus* (Elliot, 1913); (3) vervet, patas, and l'Hoest's monkeys could be placed in *Chlorocebus*, which has priority over *Erythrocebus*, to formally recognize the close relationship between these taxa in the terrestrial clade; (4) l'Hoest's monkeys could be restored to *Allochrocebus* and vervet and patas monkeys could be placed in *Chlorocebus*, which would formally recognize the sister taxon relationship between these two species (Tosi et al., 2004). Proposal #3 is the favored classification of Tosi et al. (2002, 2003, 2004). Here, we use the postcranial evidence to assess each of these four proposals.

16.2 Materials and Methods

16.2.1 Sample

The number of guenon specimens of each taxon included in this study is summarized in Table 16.1. Gebo and Sargis (1994) reported 37 measurements (their table 3) and 26 indices (their table 4), which we used in our multivariate and scaling analyses.

16.2.2 Scaling Analyses

Scaling patterns were assessed using reduced major axis (RMA) regression of natural logarithm transformed species mean data. RMA (Bohonak, 2002) was used to estimate regression parameters. All 13 taxa were included in analyses focusing on the scaling of long bone lengths with other long bone lengths. We also develop scaling equations for all long bones on species mean body weight (see Table 16.1). No weight data are available for *Cercopithecus preussi* (Delson et al., 2000), so only 12 taxa are included in this portion of the scaling analysis.

16.2.3 Multivariate Analyses

A cluster analysis (unweighted pair-group average [UPGA]) was performed on the raw species means of the 26 indices reported by Gebo and Sargis (1994, table 4). The tree is presented with Euclidean distances (see Table 16.1 for abbreviations).

A principal components analysis (PCA) was performed on a correlation matrix computed from the natural logarithm transformed species means of the 37 measurements reported by Gebo and Sargis (1994, table 3). No additional rotations (e.g., Varimax) were performed (see Neff and Marcus, 1980, p. 104). The first two factors of the PCA, which were the only factors with eigenvalues greater than one, were compared in a bivariate plot (see Table 16.1 for abbreviations), and this is included with the eigenvalues, percent of total variance, factor scores, and factor loadings below. Statistica (StatSoft Inc., Tulsa, OK) was used to perform these multivariate analyses.

16.3 Results

16.3.1 Cluster Analysis

The cluster analysis of 26 postcranial indices shows that three terrestrial taxa, *Cercopithecus preussi, C. lhoesti*, and *Erythrocebus patas*, are linked to the semiterrestrial *Allenopithecus* (Figure 16.1). The other terrestrial taxon, *C. aethiops*, is linked to four arboreal taxa in a separate cluster. A third cluster is formed by an arboreal taxon and two semiterrestrial species. The arboreal *C. pogonias*, a relatively small-bodied species (see Table 16.1), is quite distant from all other guenons. It is worth noting that *E. patas* is linked to much smaller taxa and *Miopithecus talapoin* is linked to much larger species, thereby indicating that the clusters are not simply related to body size.

16.3.2 Principal Components Analysis

Figure 16.2 shows a bivariate plot of the first two factors from the principal components analysis (see Tables 16.4–16.6 for eigenvalues, factor scores, and factor loadings, respectively). Factor 1, which accounts for 88.3% of the total variance (Table 16.4), is likely a size vector because it separates large- (*Erythrocebus patas*), medium- (*Cercopithecus, Allenopithecus*), and small- (*Miopithecus*) bodied guenons (see Figure 16.2; Table 16.1). Factor 2, however, separates *C. lhoesti* from all other guenons, including *C. preussi* (Figure 16.2).

Some of the measurements with the highest loadings for factor 2 (Table 16.6) reflect the qualitative (and univariate) differences between the terrestrial *C. lhoesti* and the arboreal *C. mitis* outlined by Gebo and Sargis (1994). For instance, *C. lhoesti* has a relatively narrow humeral head (Figure 16.3a) and short supraspinous fossa (Figure 16.3b) compared to those of *C. mitis* (Gebo and Sargis, 1994), and humeral head width (measurement #1) and supraspinous fossa height (measurement #4) have relatively high loadings for factor 2 (Table 16.6). Similarly, *C. lhoesti* has a very small ulnar radial facet (Figure 16.3c) relative to that of *C. mitis* (Gebo and Sargis, 1994), and ulnar radial facet width (measurement #8) has the highest loading for factor 2 (Table 16.6). Finally, *C. lhoesti* has a relatively short olecranon process and a very narrow patellar groove (Figure 16.3d) relative to those of *C. mitis* (Gebo and Sargis, 1994), and ulnar olecranon process length (measurement #9) and femoral patellar groove width (measurement #19) have relatively high loadings for factor 2 (Table 16.6).

16.3.3 Scaling

Table 16.7 presents the reduced major axis equations for the entire sample. Correlations are uniformly high, indicating that the relationship uncovered is unlikely to be much affected by model selection. Each talapoin-to-patas monkey equation is characterized by an isometric slope. This indicates no change in gross shape of the fore- and hind limbs with size change among guenons.

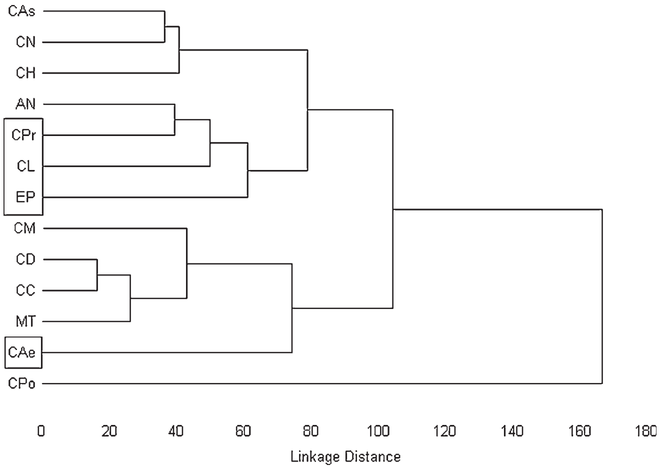

FIGURE 16.1. Cluster analysis of 26 postcranial indices. See Table 16.1 for abbreviations. Note that three terrestrial taxa (CPr, CL, EP) are linked to the semiterrestrial *Allenopithecus* (AN) rather than the terrestrial *Cercopithecus aethiops* (CAe).

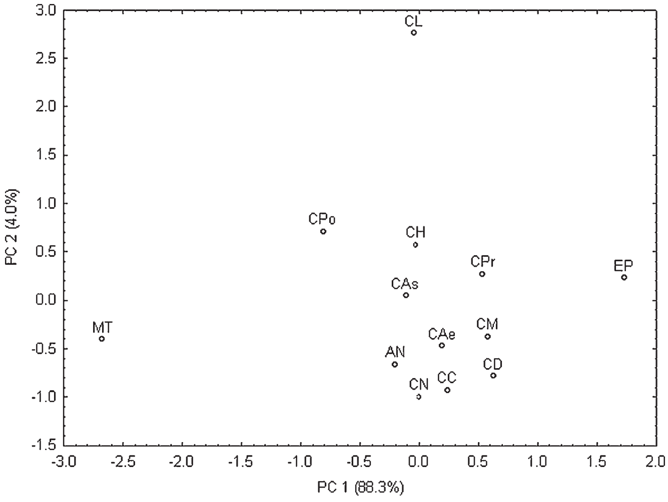

FIGURE 16.2. Bivariate plot of Factors 1 and 2 from the principal components analysis. Note that Factor 1 is likely a size vector and Factor 2 separates *Cercopithecus lhoesti* (CL) from all other guenons. See Table 16.1 for abbreviations.

TABLE 16.4. Eigenvalues from principal components analysis.

Factors	Eigenvalues	% of Total variance	Cumulative eigenvalues	Cumulative % of total variance
1	32.7	88.3	32.7	88.3
2	1.5	4.0	34.2	92.3

TABLE 16.5. Factor scores from principal components analysis.

Taxon	Factor 1	Factor 2
Allenopithecus nigroviridis	–0.2032	–0.6587
Cercopithecus aethiops	0.1893	–0.4726
Cercopithecus ascanius	–0.1166	0.0512
Cercopithecus cephus	0.2395	–0.9238
Cercopithecus diana	0.6260	–0.7833
Cercopithecus hamlyni	–0.0303	0.5737
Cercopithecus lhoesti	–0.0518	2.7605
Cercopithecus mitis	0.5778	–0.3736
Cercopithecus neglectus	–0.0009	–0.9922
Cercopithecus pogonias	–0.8159	0.7125
Cercopithecus preussi	0.5332	0.2742
Erythrocebus patas	1.7315	0.2346
Miopithecus talapoin	–2.6786	–0.4023

Table 16.8 presents the reduced major axis scaling equations of long bone length on mean body weight. The femur and tibia scale isometrically with body weight. The forelimb (humerus, radius, and ulna) is characterized by slight positive allometry. However, the correlation between any two variables does not exceed 0.80. Although all are significant, it is difficult to have much confidence in these slope (or y-intercept) point estimates. As such, we regard the scaling patterns identified here as tentative.

TABLE 16.6. Factor loadings from principal components analysis*.

Measurement	Factor 1	Factor 2
1. Humeral head width	–0.931	**0.263**
2. Humeral head height	–0.979	0.041
3. Humerus length	–0.986	–0.086
4. Supraspinous fossa height	–0.963	**0.193**
5. Supraspinous fossa length	–0.950	–0.016
6. Ulnar sigmoid notch length	–0.944	0.153
7. Ulnar humeral facet width	–0.885	0.170
8. Ulnar radial facet width	–0.416	**0.865**
9. Ulnar olecranon process length	–0.934	**0.298**
10. Ulna length	–0.962	–0.061
11. Radius length	–0.962	–0.087
12. Pisiform length	–0.974	0.133
13. Innominate length	–0.990	–0.093
14. Ischium length	–0.974	0.094
15. Pubis length	–0.874	–0.146
16. Ilium length	–0.977	–0.149
17. Femur length	–0.982	–0.052
18. Femoral greater trochanter height	–0.948	0.055
19. Femoral patellar groove width	–0.910	**0.292**
20. Femoral epicondylar width	–0.990	0.011
21. Femoral condylar height	–0.982	–0.084
22. Femoral medial condyle width	–0.985	0.081
23. Femoral lateral condyle width	–0.937	–0.108
24. Tibia length	–0.973	–0.085
25. Tibial patellar crest length	–0.787	0.093
26. Calcaneus length	–0.982	–0.078
27. Distal calcaneal length	–0.947	–0.250
28. Posterior calcaneal facet length	–0.956	–0.225
29. Calcaneal heel width	–0.982	0.072
30. Talar trochlea width	–0.992	–0.092
31. Talar head width	–0.947	–0.235
32. Talar head height	–0.960	–0.109
33. Talus length	–0.974	–0.092
34. Talar neck length	–0.945	–0.133
35. Navicular length	–0.790	0.061
36. Cuboid length	–0.953	–0.057
37. Third metatarsal length	–0.961	–0.084

*Values in bold are discussed in the text.

16.4 Discussion

16.4.1 Scaling

We focused on the scaling of long bone lengths because they have been examined previously by Shea (1992). Our data differ from those examined by Shea in several important ways. He examined two taxa and his data were ontogenetic. Our sample is restricted to adults, although we included the entire range of body size within Cercopithecini. From these analyses, we can suggest that limb bone lengths are geometrically similar across all guenons.

However, some interesting patterns are evident when species mean body weights are used (Table 16.8). Hind limb long bones (femur and tibia) are isometric with body weight among guenons. On the other hand, all of the forelimb long bones scale with slight positive allometry. This pattern reflects the relatively elongated forelimb (Figure 16.4), high intermembral index, and high brachial index (Figure 16.5) of *E. patas* (Table 16.3).

16.4.2 Locomotor Evolution

By mapping substrate preference onto the consensus tree from Ruvolo's (1988) electrophoretic analysis of proteins, Gebo and Sargis (1994) proposed that terrestriality evolved three times among guenons. Alternatively, when this character is mapped onto the maximum likelihood (ML) tree from the analysis of X-chromosome sequence data in Tosi et al. (2005), terrestriality appears to have evolved only once in this group (Figure 16.6; Tosi et al., 2002, 2003, 2004). Their ML topology is congruent with their maximum parsimony tree (Tosi et al., 2005), and the terrestrial clade is also supported by their Y-chromosome data (Tosi et al., 2002, 2003, 2004), as well as the karyotype data of Dutrillaux et al. (1988). Based on the congruence of these data sets, their topology appears to represent a robust phylogenetic hypothesis (i.e., species tree) of guenon relationships (Tosi et al., 2004). We (DLG and EJS) therefore retract our previous proposal that

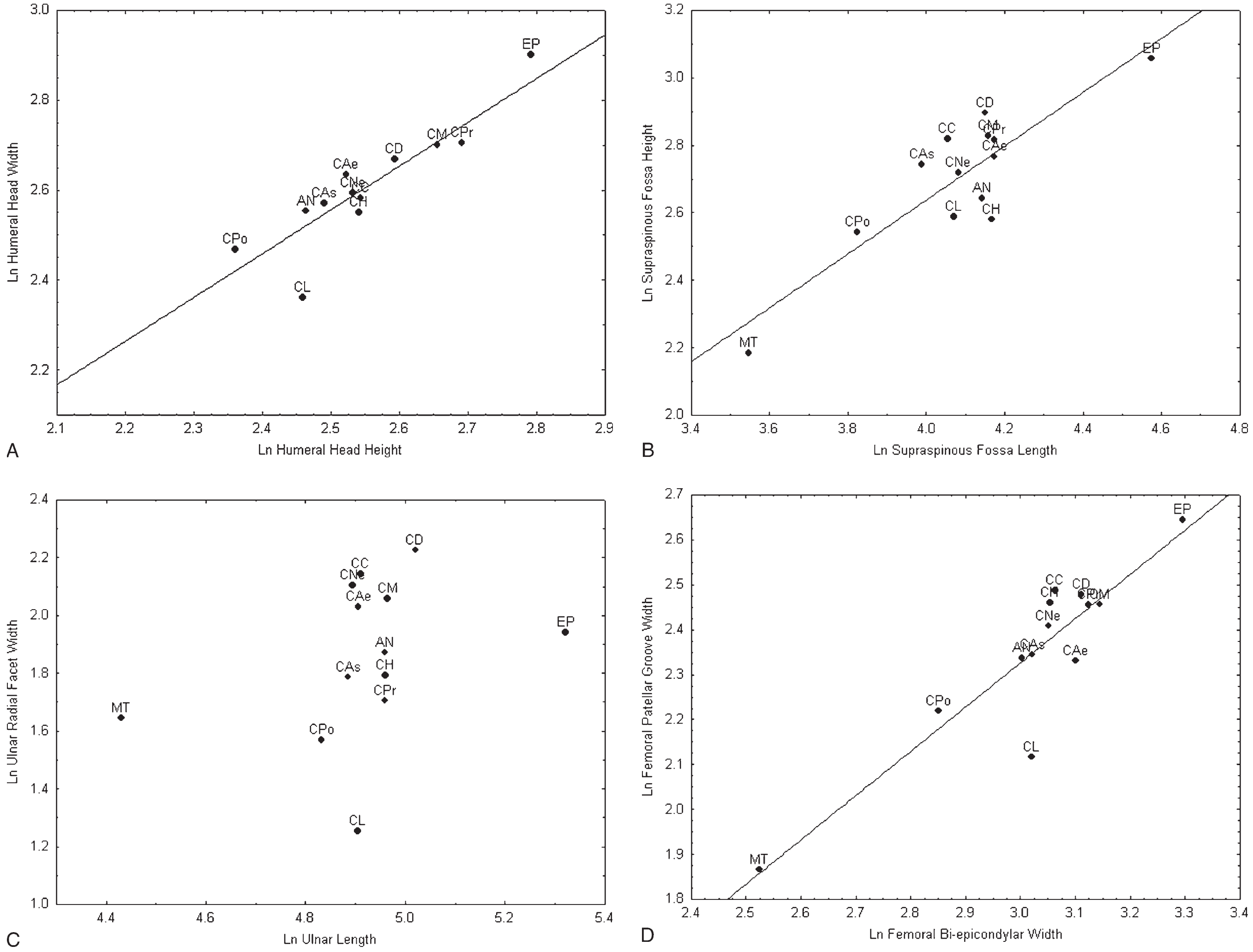

FIGURE 16.3. Bivariate plots of variables with high loadings for Factor 2 from the principal components analysis (see Table 16.6). A, Note the relatively narrow humeral head of *Cercopithecus lhoesti* (CL). B, Note the relatively short supraspinous fossa of *C. lhoesti* (CL). C, Note the relatively small ulnar radial facet of *C. lhoesti* (CL). A best fit line is not depicted because linear regression is not significant. D, Note the relatively narrow patellar groove of *C. lhoesti* (CL).

TABLE 16.7. Reduced Major Axis regression parameters and scaling patterns for long bone length regressed on long bone or innominate length.

	Slope	95% CI, Slope	y-Intercept	R^2	*n*[a]	Scaling
Humerus * Radius	0.96	0.82–1.1	0.23	0.95	13	Isometric
Humerus * Ulna	0.95	0.78–1.1	0.13	0.92	13	Isometric
Humerus * Femur	0.99	0.84–1.2	–0.20	0.94	13	Isometric
Femur * Tibia	1.05	0.93–1.2	–0.25	0.97	13	Isometric
Tibia * Radius	0.91	0.72–1.1	0.64	0.91	13	Isometric
Tibia * Ulna	0.91	0.69–1.1	0.54	0.88	13	Isometric
Humerus * Innominate	1.08	0.95–1.2	–0.33	0.97	13	Isometric
Radius * Innominate	1.13	0.90–1.4	–0.59	0.91	13	Isometric
Ulna * Innominate	1.14	0.92–1.4	–0.48	0.92	13	Isometric
Femur * Innominate	1.08	0.93–1.2	–0.14	0.96	13	Isometric
Tibia * Innominate	1.03	0.86–1.2	0.11	0.95	13	Isometric
Forelimb * Hind limb	1.05	0.86–1.2	–0.21	0.93	13	Isometric

[a] *n* = Number of taxa.

TABLE 16.8. Reduced Major Axis regression parameters and scaling patterns for long bone length regressed on body weight*.

	Slope	95% CI, Slope	y-Intercept	R^2	n^a	Scaling
Humerus * Weight	0.50	0.34–0.66	0.61	0.74	12	Positive
Radius * Weight	0.54	0.35–0.72	0.33	0.76	12	Positive
Ulna * Weight	0.57	0.37–0.70	0.44	0.80	12	Positive
Femur * Weight	0.50	0.32–0.69	0.79	0.74	12	Isometric
Tibia * Weight	0.48	0.30–0.67	0.95	0.71	12	Isometric

*Mean body weights from Table 16.1.
[a] n = Number of taxa.

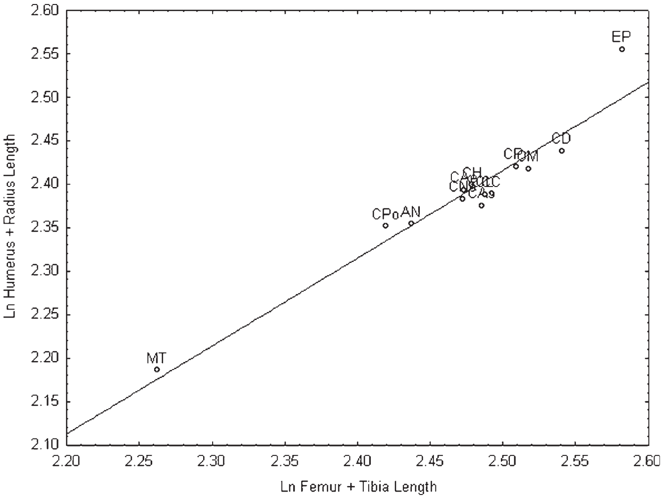

FIGURE 16.4. Bivariate plot of forelimb and hind limb length. Note the relatively long forelimb of *Erythrocebus patas* (EP). This illustrates the high intermembral index of *E. patas* (Table 16.3).

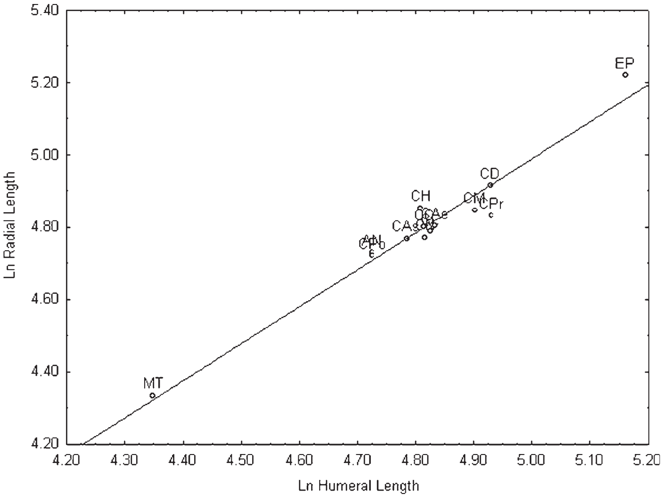

FIGURE 16.5. Bivariate plot of radial and humeral length. Note the relatively long radius of *E. patas* (EP). This illustrates the high brachial index of *E. patas* (Table 16.3).

terrestriality evolved three times in Cercopithecini (Gebo and Sargis, 1994) since Ruvolo's (1988) phylogenetic hypothesis has subsequently been rejected in analyses of a larger and more diverse data set (see Tosi et al., 2004). However, if terrestrial locomotion evolved only once among extant guenons, does this mean that a single suite of terrestrial adaptations also evolved once in the ancestor of this terrestrial clade?

16.4.3 Character Evolution

Surprisingly, the terrestrial species do not form a group in our cluster analysis (Figure 16.1). Although *Cercopithecus preussi, C. lhoesti*, and *Erythrocebus patas* cluster together, they do so with *Allenopithecus* rather than with *C. aethiops*; the latter appears to be quite different from the other terrestrial taxa given this phenetic assessment of postcranial morphology. This is particularly surprising because one would have predicted that the terrestrial taxa would cluster together because of postcranial adaptations for terrestriality, whereas one would not necessarily have predicted that they would form a clade in a molecular phylogenetic analysis. Alternatively, it is not surprising that *C. aethiops* is distant from the terrestrial taxa in the cluster analysis given Gebo and Sargis' (1994) earlier assessment that it lacks many of the qualitative terrestrial features present in the other terrestrial taxa (see Table 16.3). Furthermore, Martin and MacLarnon's (1988) cluster analyses also recovered a group that included *C. lhoesti* and *E. patas*, although with *Miopithecus* rather than *Allenopithecus*, to the exclusion of *C. aethiops*.

In contrast to the cluster analysis, *C. lhoesti* and *E. patas* are distinct in the principal components analysis (Figure 16.2). *E. patas* is separated on Factor 1, whereas *C. lhoesti* is separated on Factor 2. The separation of *E. patas* on Factor 1 is likely due to its large body size, just as the separation of *M. talapoin* is likely due to its small body size (see Table 16.1). Alternatively, the separation of *C. lhoesti* on Factor 2 is not related to body size. In fact, many of the highest loadings for Factor 2 (see Table 16.6) correspond to qualitative traits that differentiate *C. lhoesti* from other guenons (see above; Gebo and Sargis,

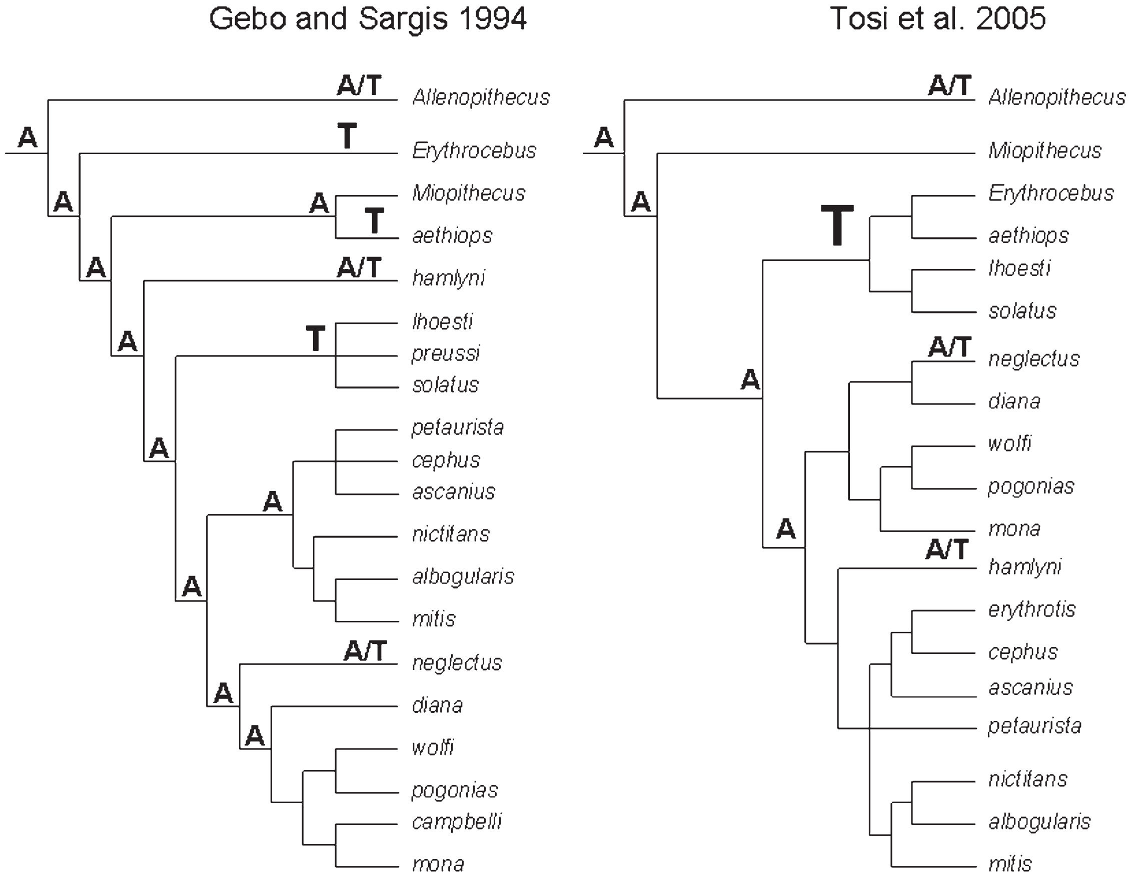

FIGURE 16.6. Cladogram used by Gebo and Sargis (1994) with substrate preference mapped on (left). Cladogram from Tosi et al. (2005) with substrate preference mapped on (right). A: arboreal; T: terrestrial; A/T: semiterrestrial. Note that terrestriality is derived in both cases, but either evolved three times (left) or only once (right); see text for discussion. Also note that semiterrestrial guenons are postcranially similar to arboreal guenons (Gebo and Sargis, 1994).

1994). In summary, the cluster analysis differentiates *C. aethiops* from the other terrestrial taxa, whereas the principal components analysis differentiates *C. lhoesti* and *E. patas*.

The results of these multivariate analyses show that terrestrial guenons are quite different from one another in their postcranial morphology (Figures 16.1–16.2), a conclusion also reported by Gebo and Sargis (1994). In fact, there do not appear to be any terrestrial adaptations that are shared by all three terrestrial groups (*E. patas, C. aethiops*, and *C. lhoesti/preussi*; see Table 16.3; Gebo and Sargis, 1994). Although there are terrestrial features that are shared by two of the three taxa, many appear to be unique to *E. patas* or *C. lhoesti* (see Table 16.3, nos. 1–12 and 28–42, respectively). This leads us to conclude that although terrestrial locomotion may have evolved only once among guenons (Tosi et al., 2002, 2003, 2004), the postcranial morphology of the three terrestrial taxa must have diverged significantly from the condition found in the common ancestor of the terrestrial clade. This is particularly true of *E. patas* and *C. lhoesti*, whose numerous postcranial differences indicate independent acquisition of many terrestrial adaptations. This view was stated previously by Gebo and Sargis (1994) when they proposed that terrestriality evolved three times among guenons, and it remains probable even if terrestrial locomotion evolved only once. The contrast is simply continued postcranial divergence of *E. patas* and *C. lhoesti* from a terrestrial ancestor (i.e., within the terrestrial clade) rather than independent evolution of terrestriality in these taxa.

Despite their numerous postcranial differences, *E. patas* and *C. lhoesti/preussi* share many more terrestrial features (Table 16.3, nos. 13–21) than *C. lhoesti/preussi* shares with *C. aethiops* (Table 16.3, nos. 27 and 43) or *E. patas* shares with *C. aethiops* (Table 16.3, nos. 47–48). This is surprising considering that the X-chromosome data support a *C. aethiops-E. patas* sister taxon relationship within the terrestrial clade (Tosi et al., 2004, 2005). This relationship was predicted by cranial morphology (three synapomorphies; Groves, 2000), but not by postcranial morphology. Table 16.3 lists eight characters shared by *E. patas* and *C. lhoesti/preussi* (nos. 14–21), but only two are shared by *E. patas* and *C. aethiops* (nos. 47–48) and both are more extreme in *E. patas* (Kingdon, 1988). In addition to differences in limb morphology, Hurov (1987) outlined a number of differences in axial skeleton morphology and sagittal back motion between *E. patas* and *C. aethiops*. For example, *C. aethiops* exhibits an increased range of sagittal back motion when galloping speed increases, but *E. patas* does not. Sagittal back mobility is increased in *C. aethiops* by the presence of thicker intervertebral disks and reduced dorsoventral diameter of the thoracic cage relative to the conditions found in *E. patas*. Hurov (1987) summarized these differences between vervet and patas monkeys by concluding that *C. aethiops* increases stride length by increasing its range of sagittal back motion, whereas *E. patas* increases stride length via its elongated fore- and hind limbs.

Reconstructing the ancestral condition for the terrestrial clade is difficult because no terrestrial features are ubiquitous among the terrestrial taxa (Table 16.3). The terrestrial clade is subdivided into the *Lhoesti*-group (*C. lhoesti, C. preussi*, and *C. solatus*) and the *C. aethiops-E. patas* sister group (Figure 16.6; Tosi et al., 2004, 2005). It is therefore tempting to use postcranial features shared by members of these two groups to characterize the last common ancestor of the terrestrial clade (e.g., Table 16.3, nos. 13–21, 27, and 43). For example, it is possible that the ancestor of the terrestrial clade exhibited more terrestrial adaptations than *C. aethiops*, possibly some of those shared by *E. patas* and *C. lhoesti*, and that *C. aethiops* subsequently lost some of these features. We do not consider this to be a likely scenario. It is also possible that this ancestor was most similar to *C. aethiops*, which is considered the least specialized of the terrestrial taxa because it exhibits the fewest terrestrial adaptations (Table 16.3; Gebo and Sargis, 1994). We consider the latter possibility more likely. Consequently, we propose that the ancestral condition of the terrestrial clade was postcranially similar to *C. aethiops* and that *E. patas* and *C. lhoesti* became increasingly specialized through the independent acquisition of their numerous terrestrial adaptations.

16.4.4 Taxonomy

As noted above, the genus *Cercopithecus* is paraphyletic because *C. aethiops* and *C. lhoesti* are more closely related to *E. patas* than they are to other species of *Cercopithecus* (Tosi et al., 2002, 2003, 2004). Tosi et al. (2004) outlined four solutions to this taxonomic problem, all of which were summarized above. Here, we evaluate each of these four proposals in light of the postcranial evidence discussed above.

We reject the proposal (#1) to sink patas monkeys into *Cercopithecus* because it fails to formally recognize the terrestrial clade, thereby ignoring the various terrestrial adaptations found among *E. patas, C. aethiops*, and *C. lhoesti* (Tosi et al., 2002, 2004). Alternatively, each of the terrestrial taxa exhibit a different suite of terrestrial adaptations, and none of these characters are present in every terrestrial taxon (Table 16.3; see above). We also reject the proposal (#4) to reinstate l'Hoest's monkeys to *Allochrocebus* and place vervet and patas monkeys in *Chlorocebus*, thereby formally recognizing their sister taxon relationship. This view overemphasizes the derived nature of l'Hoest's monkeys' postcrania, while simultaneously undervaluing the autapomorphous postcranial morphology of patas monkeys (Tosi et al., 2004). Although our principal components analysis separates l'Hoest's monkeys (Figure 16.2), patas monkeys are certainly as derived based on qualitative data (Table 16.3; Gebo and Sargis, 1994). Concerning proposal #3, we agree with Tosi et al. (2002, 2003, 2004) that vervet, patas, and l'Hoest's monkeys should be placed in *Chlorocebus* to formally recognize the terrestrial clade. *Chlorocebus* (Gray, 1870) has priority over *Erythrocebus* (Trouessart, 1897), and *Cercopithecus* cannot be used for the terrestrial clade because *Cercopithecus diana*, an arboreal guenon that is not included in this clade, is the type species of the genus (International Commission on Zoological Nomenclature, 1954). We also see some value in proposal #2, which places patas monkeys in *Erythrocebus*, vervet monkeys in *Chlorocebus*, and l'Hoest's monkeys in *Allochrocebus* (Tosi et al., 2002, 2003, 2004). Ultimately, we reject this option because it does not formally recognize the terrestrial clade (Tosi et al., 2002, 2003, 2004), but we appreciate that it acknowledges the numerous differences found in the postcrania of vervet, patas, and l'Hoest's monkeys (Table 16.3; Figures 16.1–16.2; Gebo and Sargis, 1994). In the end, we propose a compromise classification of the terrestrial taxa (Table 16.9) that both formally recognizes the terrestrial clade by placing all of these taxa in *Chlorocebus*, but also acknowledges the postcranial diversity within this clade by placing them in separate subgenera. This arrangement further acknowledges the relatively long Y-chromosome lineages of the three terrestrial cercopithecin taxa, which are as long or longer than those of papionin genera (Tosi et al., 2003, 2004).

TABLE 16.9. Classification of terrestrially adapted guenons advocated here (see text)

Taxonomic names	Species group	Common names
Chlorocebus (Chlorocebus) aethiops	*Aethiops*-Group	Vervet, Grivet, Green monkeys
Chlorocebus (Erythrocebus) patas		Patas monkeys
Chlorocebus (Allochrocebus) lhoesti	*Lhoesti*-Group	l'Hoest's monkeys
Chlorocebus (Allochrocebus) preussi	*Lhoesti*-Group	Preuss's monkeys
Chlorocebus (Allochrocebus) solatus	*Lhoesti*-Group	Sun-tailed monkeys

Our proposal to use subgenera to distinguish vervet, patas, and l'Hoest's monkeys is similar to one of Groves' (2000) three taxonomic proposals regarding vervet and patas monkeys. He suggested using the subgenera *Chlorocebus* and *Erythrocebus* for vervet and patas monkeys, respectively, although he proposed these as subgenera of *Cercopithecus* rather than *Chlorocebus* and he favored his alternative proposal of recognizing them as distinct genera. Groves' (2000) third proposal would place both vervet and patas monkeys in *Chlorocebus*. He considered this option to be confusing because patas and vervet monkeys are so different morphologically, citing six distinctive features in patas monkeys and five in vervets. We consider this additional evidence for distinguishing these taxa at the level of subgenus, in an attempt to acknowledge the many differences among the terrestrial taxa. Furthermore, we disagree with Groves' (2000) favored proposal of separating patas and vervet monkeys as distinct genera because this arrangement fails to formally recognize the terrestrial clade.

In summary, we agree with Tosi et al. (2002, 2003, 2004) that terrestriality evolved only once among guenons. However, vervet, patas, and l'Hoest's monkeys exhibit many postcranial differences indicating that they have diverged significantly from the common ancestor of the terrestrial clade. We have recognized this terrestrial clade taxonomically by placing all three taxa in the genus *Chlorocebus* (see Tosi et al., 2002, 2003, 2004). We have also acknowledged their numerous postcranial differences by placing them in separate subgenera (Table 16.9).

Although terrestrial locomotion evolved only once among guenons, the "terrestrial" taxa, particularly patas and l'Hoest's monkeys, all exhibit different terrestrial adaptations (Table 16.3). This conclusion is significant for the proposal made by Tosi et al. (2003) to use substrate preference as a character. They consider this to be additional evidence in support of the terrestrial clade because a single transition to terrestriality would be more parsimonious than three independent transitions. However, we would caution against the use of such a character because vervet, patas, and l'Hoest's monkeys may engage in terrestrial locomotion in different ways (see Hurov, 1987). They have certainly acquired distinct postcranial adaptations for this substrate preference.

In conclusion, our study has demonstrated significant postcranial variation within the terrestrial clade of guenons. Although our sample permitted an examination of variation among patas, vervet, and l'Hoest's monkeys, we were unable to assess variation within the *Lhoesti*-group. Any future analysis that focuses on this group should increase the sample size of *Chlorocebus (Allochrocebus) lhoesti* and *Chlorocebus (Allochrocebus) preussi*, as well as incorporate samples of *Chlorocebus (Allochrocebus) solatus*. Such a study has the potential to reveal yet more evolutionarily significant variation within the terrestrial clade. This would further demonstrate that the evolution of terrestriality among guenons was not simply a single transition, but included continued divergence in multiple lineages.

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