# LOCOMOTOR AND HABITAT CLASSIFICATIONS OF CERCOPITHECOID POSTCRANIAL MATERIAL FROM STERKFONTEIN MEMBER 4, BOLT'S FARM AND SWARTKRANS MEMBERS 1 AND 2, SOUTH AFRICA

by

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## ABSTRACT

Much southern African cercopithecoid postcranial material is not associated with craniodental remains. Consequently, this postcranial material cannot be confidently assigned to a particular taxon, with the result that little is known about the locomotor strategies and habitat preferences of specific Plio-Pleistocene cercopithecoids from southern Africa. However, cercopithecoid postcrania can provide important information about habitats that were present at fossil sites, even when the material is not attributed to taxa. In this paper, ecomorphic analysis is used to assign cercopithecoid postcranial material from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2 to one of three habitat/locomotor categories: forest-living arboreal quadrupeds ('forest arboreal'), open habitat terrestrial quadrupeds ('open terrestrial') and open habitat cercopithecoids using a mix of arboreal and terrestrial quadrupedalism ('open mixed'). Cercopithecoids representing all three habitat categories were found in the samples from Sterkfontein Member 4 and Bolt's Farm, suggesting that monkeys using a range of habitats and locomotor strategies were present at these sites. However, no 'forest arboreal' cercopithecoids were found in the samples from Swartkrans Members 1 and 2, indicating that cercopithecoids at these localities probably depended largely on open habitats. The habitat and locomotor strategy data were also used in combination with locality-based listings of fossil cercopithecoid craniodental remains to suggest possible locomotor strategies for several southern African Plio-Pleistocene cercopithecoid taxa, including *Parapapio broomi* (possibly 'forest arboreal'), *Parapapio jonesi* ('open terrestrial'), *Papio robinsoni* ('open terrestrial') and *Cercopithecoides williamsi* ('open mixed').

KEYWORDS: Cercopithecoidea, postcranial, Plio-Pleistocene, ecomorphology

## INTRODUCTION

The Pliocene and early Pleistocene deposits of Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2 (Gauteng Province, South Africa) have yielded a wide variety and relatively large number of fossils from the Cercopithecoidea (Primates, Mammalia). However, much of the postcranial material is not associated with craniodental material, with the result that it cannot be confidently taxonomically assigned (Szalay & Delson 1979). The lack of association between the craniodental and postcranial remains has also resulted in uncertainty over the locomotor repertoires of many Pliocene and Pleistocene fossil cercopithecoids from southern Africa, including members of the genera *Parapapio* and *Papio* (Szalay & Delson 1979).

To date, there has been very little work on these fossil cercopithecoid postcranial specimens. The most comprehensive study of taxonomically unassigned postcrania from southern African cercopithecoids was that of Ciochon (1993), who used multivariate analysis to assign various fossil specimens to the most likely genus and/or species of Plio-Pleistocene monkey.

In this paper, the approach is somewhat different. Taxon-free multivariate analysis is used to assign the postcranial specimens to the most likely locomotor strategies and habitat preferences. This gives important and useful information about the range of habitats that were present in or around Sterkfontein, Bolt's Farm and Swartkrans, which in turn helps to reconstruct the environment inhabited by early hominins. Furthermore, while no attempt is made to taxonomically assign the cercopithecoid postcrania, the results of the habitat and locomotor analysis are used here to reconstruct the most likely locomotor strategies of southern African cercopithecoids from the Plio-Pleistocene.

Cercopithecoids have been used in several reconstructions of the palaeohabitats of southern African Plio-Pleistocene sites (Butzer 1974; McKee 1991; Reed 1997; Kuman *et al.* 1997; Clarke *et al.* 1998; Kuman & Clarke 2000). However, given that craniodental material is more easily identified, and often more prevalent than postcranial remains, the reconstructions of the probable habitats of these cercopithecoids often rely on assumptions based on the ecology of the most closely-related extant Old World monkey species, and there has been very little investigation of habitat preferences as suggested by postcranial morphology. This has created contradictions in the way individual cercopithecoid taxa have been used in habitat reconstruction: colobines, for example, have been used to indicate woodland or forest

(e.g. Kuman *et al.* 1997; Kuman & Clarke 2000), despite other research in which it is suggested that at least one Plio-Pleistocene colobine species, *Cercopithecoides williamsi*, found at Sterkfontein Member 4, Swartkrans Member 2 and Bolt's Farm, was 'hyper-terrestrial' (Birchette 1982, but see below for further discussion of this). In light of the importance of cercopithecoids in the reconstruction of palaeohabitat, it is therefore necessary and useful to review the postcranial evidence for habitat use and locomotor strategies in cercopithecoids from southern African Plio-Pleistocene sites, attributing habitat and locomotor preferences to individual species wherever possible.

## MATERIALS AND METHODS

The analytical method used in this study was an ecomorphic one, in which morphological features, such as bone shape and muscle lever arms, are used to distinguish between cercopithecoid groups of different habitat preferences and locomotor types. Assigning postcranial material to habitat-type and locomotor strategy in this way makes it possible to reconstruct the habitat of fossil species without having to rely on assumptions based on the ecology of the most closely related extant species (Plummer & Bishop 1994). Additionally, as specimens used in this type of analysis need not be taxonomically assigned (Plummer & Bishop 1994), this technique is especially useful in assigning the taxon-less southern African Plio-Pleistocene cercopithecoid postcranial specimens to the relevant habitat and locomotor categories.

The proximal and distal humerus, proximal ulna, and distal femur from nine extant African cercopithecoid species, representing three habitat and locomotor categories (described below) were included in the comparative sample (Table 1). All but 10 of the 194 specimens used in this sample were from wild-shot adult individuals without obvious skeletal pathology. Ten of the *Theropithecus gelada* sample were captive animals but were judged sufficiently similar to wild-shot individuals in univariate analysis to include in the multivariate study. Maturity was judged by the epiphyseal fusion of all

postcranial elements, and only adults with complete or near-complete fusion were measured. The sample was not separated by sex because none of the fossil specimens used in this study could be assigned to male or female.

The modern comparative sample was divided into three habitat types: forest-living arboreal quadrupeds ('forest arboreal'), open habitat terrestrial quadrupeds ('open terrestrial') and open habitat cercopithecoids using a mix of arboreal and terrestrial quadrupedalism ('open mixed'). These classifications are based on data on wild-living primates, taken from the literature (Napier & Napier 1967; Gebo & Chapman 1995; McGraw 1998a, 1998b) and have been designed to reflect the spectrum of habitat use and locomotion seen in the African cercopithecoids.

The fossil sample comprised 40 cercopithecoids from Plio-Pleistocene deposits at Sterkfontein, Bolt's Farm and Swartkrans, held in the collections at the Bernard Price Institute and Department of Anatomical Sciences, University of the Witwatersrand, and the Transvaal Museum, Pretoria (Appendix 1). The specimens included in the sample were all well preserved. They represented only a fraction of the total amount of cercopithecoid postcranial material found at the sites under discussion, much of which was too badly damaged to be used in the analyses described below.

Linear measurements (Appendix 2), adapted from Ciochon (1993) and Bishop (1994), were taken with digital calipers on both the modern and fossil specimens, and entered directly into a laptop computer using a caliper interface. Very few complete bones are found in the southern African fossil cercopithecoid postcranial sample, so in this study, morphological features from only the proximal and distal ends were quantified. Measurements were transformed into simple ratios (Appendix 3), to reflect both shape and functional lengths over which muscles act, and also to reduce the effects of differential size between individuals. To ensure that it was morphology rather than body mass that was determining habitat classification, each ratio was regressed against the relevant species and sex mean body mass, taken from Smith & Jungers (1997). If the

**TABLE 1.**
**Monkeys in Extant Comparative Sample, Body Mass and Habitat/Locomotor Classification**

| Species | N | Male body mass (kg) | Female body mass (kg) | Habitat and locomotor category |
|---|---|---|---|---|
| *Cercopithecus neglectus* | 16 | 7.35 | 4.13 | Forest arboreal |
| *Lophocebus albigena* | 16 | 8.25 | 6.02 | Forest arboreal |
| *Colobus guereza* | 30 | 13.5 | 9.2 | Forest arboreal |
| *Cercopithecus aethiops* | 28 | 4.26 | 2.98 | Open mixed |
| *Papio cynocephalus* | 28 | 21.8 | 12.3 | Open mixed |
| *Papio anubis* | 27 | 25.1 | 13.3 | Open mixed |
| *Papio ursinus* | 20 | 29.8 | 14.8 | Open mixed |
| *Papio hamadryas* | 12 | 21.0 | 11.4 | Open terrestrial |
| *Theropithecus gelada* | 17 | 19 | 11.7 | Open terrestrial |

Body mass data from Smith & Jungers (1997)
Habitat and locomotor data from sources cited in text

adjusted-$r^2$ value for the regression of body mass and the ratio exceeded 0.3, that ratio was excluded from further analysis.

A multivariate statistical technique, discriminant function analysis (DFA), was used to examine whether the morphology of each bony element could be used to distinguish between cercopithecoids of different habitat and locomotor preferences. The FORWARD STEPDISC routine from SAS 6.12 (SAS Institute Inc, 1996) was used to determine the most useful classificatory variables and to reduce intercorrelation between ratios. Once the best discriminatory variables had been selected, the quadratic DISCRIM procedure from SAS 6.12 was used to calculate the discriminant function for membership in each habitat group, which was then used to reassign each individual modern specimen to the most probable of the three habitat categories. The misclassification rates were estimated using the standard resubstitution procedure. These estimates form the basis for assessing the correctness and utility of the DFA for each dataset. The discriminant functions calculated using the modern cercopithecoid sample were then applied to the fossil sample, to assign each fossil specimen to the most likely habitat category. Only fossils with the complete suite of variables for each bony element were included in the analysis, as the computer program automatically excluded incomplete specimens.

## RESULTS AND DISCUSSION
### Discriminant function analysis: modern sample

Table 2 details the resubstitution results (indicating the utility of each bone in distinguishing between cercopithecoids of different habitat and locomotor categories) for the bones in the modern cercopithecoid sample. The four bony elements used in this study (proximal and distal humerus, proximal ulna and distal femur) were selected because of their relatively high resubstitution results, as at least 80% of each sample was re-assigned to the correct habitat and locomotor categories; these resubstitution results are very similar to the resubstitution results reported in ecomorphic studies of bovid postcrania (Plummer & Bishop 1994; Kappelman *et al.* 1997). Further analysis of cercopithecoid postcranial material has demonstrated that two of the other major long bones, the radius and the tibia, along with the distal ulna and proximal femur, do not discriminate between cercopithecoids of different habitat preferences and locomotor strategies as effectively as the bony elements used in this study (Elton 2000). Specimens in the 'open terrestrial' and 'forest arboreal'

categories were both mainly reclassified into 'open mixed', and neither were frequently or extensively reclassified into one another (Tables 3–6), demonstrating that the DFA distinguished effectively between the two locomotor extremes for all the bony elements. The modern cercopithecoid species assigned to the 'open mixed' category share morphological features with species in both the 'forest arboreal' and 'open terrestrial' categories. Thus, specimens in the open habitat mixed locomotion category did not discriminate as well as specimens in the other two habitat categories, and specimens included in 'open mixed' were reassigned to both the 'forest arboreal' and the 'open terrestrial' categories (Tables 3-6). Again, this is similar to the results of ecomorphic studies on bovids, in which 'intermediate' forms were more extensively misclassified than either of the more 'extreme' forms (Plummer & Bishop 1994; Kappelman *et al.* 1997).

Misclassification of the type reported here is an inevitable part of discriminant function analysis (Plummer & Bishop 1994). In the analyses of the cercopithecoid proximal and distal humerus, proximal ulna and distal femur, less than one half of each species group, including those species that originally formed part of the 'open mixed' sample, were incorrectly assigned to habitat and locomotor category (see Elton 2000, for further details). In other ecomorphic studies, it has been suggested that this degree of misclassification is likely to represent normal morphological variation (Plummer & Bishop 1994), a factor for which it is difficult to control. Thus, the results of the DFA for the modern cercopithecoid comparative sample appear to be sufficiently reliable to use the discriminant functions to classify the fossil specimens. However, although the misclassification that occurred in the modern cercopithecoid sample is not unusual for an ecomorphic analysis of this type, the species assigned to the 'open mixed' group were less successfully reclassified than those assigned to the other categories, and it is possible that there is a greater uncertainty over the reliability of the classification of the fossil specimens that are assigned to 'open mixed'. The implications of this for habitat reconstruction are discussed below.

### Discriminant function analysis: fossil sample

20% of the total fossil sample was assigned to the 'forest arboreal' category, with 30% assigned to 'open terrestrial' and 50% to 'open mixed' (Table 7, Figure 1). Of the 25 specimens from Sterkfontein Member 4, four (16%) were assigned to 'forest arboreal', 15 (60%)

**TABLE 2.**
**Total Percentage of Modern Specimens correctly assigned for each element**

| Element | Total percentage of modern specimens correctly assigned | |
| | Proximal | Distal |
| --- | --- | --- |
| Humerus | 84 | 81 |
| Ulna | 80 | - |
| Femur | - | 81 |

## TABLE 3.
### Proximal humerus resubstitution Summary

| From habitat | Number of observations and percent classified into habitat | | | Total |
|---|---|---|---|---|
| | Forest arboreal | Open mixed | Open terrestrial | |
| Forest arboreal | 51 | 6 | 5 | 62 |
| | 82% | 10% | 8% | 100% |
| Open mixed | 15 | 78 | 10 | 103 |
| | 14% | 76% | 10% | 100% |
| Open terrestrial | 0 | 2 | 27 | 29 |
| | 0% | 7% | 93% | 100% |

## TABLE 4.
### Distal humerus resubstitution Summary

| From habitat | Number of observations and percent classified into habitat | | | Total |
|---|---|---|---|---|
| | Forest arboreal | Open mixed | Open terrestrial | |
| Forest arboreal | 54 | 7 | 1 | 62 |
| | 87% | 11% | 2% | 100% |
| Open mixed | 9 | 67 | 27 | 103 |
| | 9% | 65% | 26% | 100% |
| Open terrestrial | 0 | 3 | 26 | 29 |
| | 0% | 10% | 90% | 100% |

## TABLE 5.
### Proximal ulna resubstitution summary

| From habitat | Number of observations and percent classified into habitat | | | Total |
|---|---|---|---|---|
| | Forest arboreal | Open mixed | Open terrestrial | |
| Forest arboreal | 53 | 5 | 3 | 61 |
| | 87% | 8% | 5% | 100% |
| Open mixed | 15 | 65 | 23 | 103 |
| | 15% | 63% | 22% | 100% |
| Open terrestrial | 0 | 3 | 26 | 29 |
| | 0% | 10% | 90% | 100% |

## TABLE 6.
### Distal femur resubstitution Summary

| From habitat | Number of observations and percent classified into habitat | | | Total |
|---|---|---|---|---|
| | Forest arboreal | Open mixed | Open terrestrial | |
| Forest arboreal | 50 | 10 | 2 | 62 |
| | 81% | 16% | 3% | 100% |
| Open mixed | 14 | 71 | 18 | 103 |
| | 14% | 69% | 17% | 100% |
| Open terrestrial | 0 | 2 | 27 | 29 |
| | 0% | 7% | 93% | 100% |

were assigned to 'open mixed' and six (24%) were assigned to 'open terrestrial'. Nine specimens from Bolt's Farm were analysed. Of these, four (44%) were assigned to the 'forest arboreal' category, four (44%) were assigned to 'open mixed' and one (12%) was assigned to 'open terrestrial'. Five specimens from the Swartkrans Member 1 Hanging Remnant were analysed, none of which were assigned to 'forest arboreal'. Four (80%) of these specimens were assigned to 'open terrestrial', with one assigned to 'open mixed'. Only one specimen from Swartkrans Member 2 was suitable for inclusion in the analysis, and was assigned to 'open terrestrial'.

Only a small proportion of the total fossil sample from Sterkfontein Member 4, Bolt's Farm and Swartkrans was used in analysis, because much of the cercopithecoid postcranial material recovered from these sites was too badly damaged to be included in DFA. Thus, any discussion of the habitat preferences of cercopithecoids present at these sites is based on a small number of fossils, with the possibility that certain cercopithecoid groups may not be represented in the sample. This is especially true for the Swartkrans assemblage, where only six postcranial specimens were suitable for analysis. Interpretation of the results is made more complex by the potential for errors in classification, particularly from and into the 'open mixed' category. Appendix 1 gives the posterior probabilities, indicating the likelihood of membership in each of the three habitat/locomotor categories, for the fossils included in the sample. These probabilities, in combination with the resubstitution results generated from the analysis of modern cercopithecoids (Tables 3–6), indicate that it is unlikely that 'forest arboreal' specimens have been misclassified as 'open terrestrial', and vice versa, but a small number of 'forest arboreal' and 'open terrestrial' fossils may have been misclassified as 'open mixed'. Specimens may also have been misclassified out of 'open mixed' into either 'forest arboreal' or 'open terrestrial'. If misclassification has occurred, the patterns evident at Sterkfontein Member 4 and Bolt's Farm are unlikely to be greatly altered, as all three cercopithecoid habitat categories are represented. At Swartkrans, the small numbers of cercopithecoid fossils have been assigned predominantly to the 'open terrestrial' category. Thus, even with misclassification, the monkeys would still be included in one of the open habitat categories, as misclassification rarely occurs between the 'open terrestrial' and 'forest arboreal' categories. However, it is possible that the specimen assigned to 'open mixed' may have been misclassified from 'forest arboreal'. In which case, and given the small sample that represents this site, it cannot be discounted that some monkeys may have been dependent on forest, although it appears that cercopithecoids from Swartkrans exploited predominantly open habitats.

## Habitat preferences of Plio-Pleistocene cercopithecoids

Cercopithecoids belonging to all three habitat categories are found at Sterkfontein Member 4. From this evidence, it appears that the cercopithecoids in and around Sterkfontein in Member 4 times inhabited forest, as well as open woodland/bushland habitats and grassland. The presence of fossilized lianas (*Dichapetalum mombuttense*), dependent on large trees, supports the view that there were some closed habitats present at Sterkfontein Member 4 (Bamford 1999). Vrba (1974) suggested that the environment at Sterkfontein initially supported bushland and water loving species, later altering to a more open habitat. A similar pattern, with open woodland and bushland in Member 4 and more open habitats in Member 5 has also been reconstructed by Reed (1997). These reconstructions are consistent with the relatively large proportion of 'forest arboreal' and 'open mixed' cercopithecoids found at Sterkfontein Member 4, but 'open terrestrial' species, likely to be dependent on more open, grassland, habitats, are also present in the cercopithecoid sample from Sterkfontein Member 4. Carnivores are likely to have been one of the accumulation agents for the Sterkfontein assemblage (Clarke *et al.* 1998), and it is possible that a proportion of the 'open terrestrial' specimens were carried from a considerable distance. However,

**TABLE 7.**

Habitat categories and locomotor preferences of cercopithecoids from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2.

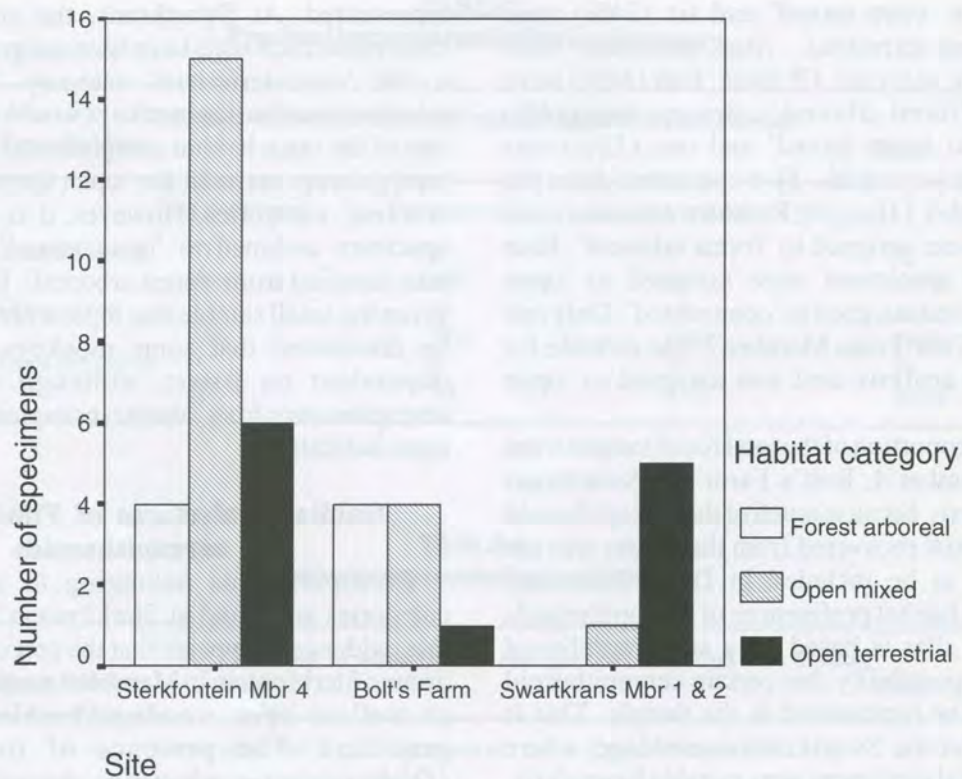| Site<br>From habitat | Number of specimens and percentage classified into each habitat and locmotor category | | | Total |
|---|---|---|---|---|
| | Forest arboreal | Open mixed | Open terrestrial | |
| Sterkfontein Mbr 4 | 4 | 15 | 6 | 25 |
| | 16% | 60% | 24% | 100% |
| Bolt's Farm | 4 | 4 | 1 | 9 |
| | 44% | 44% | 12% | 100% |
| Swartkrans Mbr 1 | 0 | 1 | 4 | 5 |
| | 0% | 20% | 80% | 100% |
| Swartkrans Mbr 2 | 0 | 0 | 1 | 1 |
| | 0% | 0% | 100% | 100% |
| **Total** | 8 | 20 | 12 | 40 |
| | 20% | 50% | 30% | 100% |

Figure 1.  Habitat categories and locomotor preferences of cercopithecoids from Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2.

specimens assigned to 'open terrestrial' comprise very nearly one quarter of the total sample, and it is likely that this material does represent part of the habitat immediately surrounding the Sterkfontein site. Micromammal assemblages at Sterkfontein Members 4 and 5 appear to be variable, with evidence for riverine grassland species in both Members (Avery 2001), a result that corresponds well with the cercopithecoid-based habitat reconstructions.

Bolt's Farm is not a confirmed hominin site, and, to date, there has been very little research on its palaeohabitat. However, the site has yielded craniodental remains from at least three cercopithecoid species (Delson 1984), as well as taxonomically-unassigned cercopithecoid postcranial material, so the inclusion of the Bolt's Farm material gives useful information about the habitat and locomotor preferences of southern African monkeys. Bolt's Farm lies in close proximity to Sterkfontein and Swartkrans, and the cercopithecoid fauna is dated to around 2 Ma (Delson 1984). The inclusion of the Bolt's Farm cercopithecoids in the sample therefore complements the data derived from Sterkfontein Member 4 and Swartkrans Members 1 and 2. Cercopithecoids belonging to all three habitat types are in evidence in the Bolt's Farm sample, as is the case for Sterkfontein Member 4. This indicates that cercopithecoids inhabited grassland, bushland/open woodland, and forest environments at Bolt's Farm.

There were no 'forest arboreal' cercopithecoids in the sample from either Swartkrans Member 1 or Member 2, and as the majority of specimens were assigned to 'open terrestrial', it is probable that many of the Swartkrans cercopithecoids exploited relatively open habitats, such as grassland or open woodland, rather

than forest. Most reconstructions of the Swartkrans palaeohabitat show a predominantly open habitat (Vrba 1975; Watson 1993; Avery 1995; Reed 1997) with varying degrees of woodland or riverine forest surrounding the Blaaubank stream (Watson 1993; Avery 1995).

The Sterkfontein Member 4 and Bolt's Farm cercopithecoid samples contain a relatively large proportion of 'forest arboreal' specimens, which appear to be absent from the Swartkrans Member 1 and Member 2 sample (but see above for discussion of potential error associated with the habitat reconstructions). These results are in accordance with both Vrba (1975), who argued that, based on the representation of Alcelaphini and Antelopini relative to all other bovids, the Sterkfontein Type Site (Member 4) sampled more closed habitats whereas the Swartkrans sites contained more open habitat species, and Reed (1997), who also suggests that there are differences in tree cover and grassland at the two sites. Shipman & Harris (1988) concluded, however, that there is little significant habitat variability among the southern African cave sites. The results from the present study indicate that there were more closed habitat cercopithecoids at Sterkfontein and Bolt's Farm than there were at Swartkrans. However, further investigation into the habitat preferences of the Swartkrans cercopithecoids is necessary before this can be confirmed.

## Probable locomotor behaviours of Plio-Pleistocene cercopithecoids from southern Africa

The primary aim of the research reported here was to assign Plio-Pleistocene cercopithecoid postcranial material to habitat and locomotor categories. However,

it is also possible, based on data from the present study, other data collected by the author (Elton 2000), and from sources that list the craniodental material found at the sites under investigation (Brain 1981; Delson 1984, 1988; Watson 1993; Turner *et al.* 1999), to make some suggestions as to possible locomotor strategies of southern African cercopithecoids. Such an exercise is necessarily tentative, particularly given the potential for sampling and classification errors, but may provide the foundation for more detailed investigation into the locomotor strategies of Plio-Pleistocene monkeys from southern Africa, an aspect of cercopithecoid palaeobiology that has been neglected to date.

Table 8 summarizes the occurrence data for primates found at Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2. Craniodental remains of *Cercopithecoides williamsi* have been identified from Sterkfontein Member 4, Bolt's Farm and Swartkrans Member 2. These sites have all yielded cercopithecoid postcrania assigned to at least one of the two open habitat categories ('open mixed' or 'open terrestrial'). Analysis of East African *C. williamsi* specimens (in particular, the partial skeleton KNM-ER 4420), has indicated that this species should be classified as 'open mixed' (Elton 2000), a result that is consistent with other, recent work on southern African *C. williamsi* locomotor behaviour (Ciochon 1993), although *C. williamsi* has also been described as 'hyper-terrestrial' (Birchette 1982). Thus, it is likely that *C. williamsi*, although a colobine, was not arboreal, and that its postcranial remains may form part of the open habitat sample at Sterkfontein, Bolt's Farm and Swartkrans.

*P. robinsoni* has been identified from craniodental material at all the sites included in this study (Delson 1984), although its presence at Sterkfontein Member 4 has been questioned (McKee 1993). It cannot be discounted that *P. robinsoni* was a forest-dweller, but it is more likely, based on both its high representation in the cercopithecoid craniodental assemblage at Swartkrans (Brain 1981) and the uncertainty over its presence at Sterkfontein Member 4, that it was an open

habitat monkey. Based on this reasoning, *P. ingens*, a very large cercopithecoid found at Swartkrans Member 1, may also have been an open habitat monkey. It is also worth noting that several postcranial specimens (SK 1506, SK 591d, SK unnumbered, and SK 591c) from Swartkrans Members 1 and 2, assigned to 'open terrestrial' in the present study, were classified in another multivariate study as *Papio* cf. *robinsoni* (Ciochon 1993), and may represent one or both of the *Papio* species at Swartkrans.

Based on the analysis of East African material, *T. oswaldi* is classified as 'open mixed' (Elton 2000). This reconstruction differs from traditional interpretations of the locomotor behaviour of this species, which has been argued to have a similar locomotor repertoire to the highly terrestrial *Theropithecus gelada* (Krentz 1993), although it shares postcranial features with both modern *Papio* and *Theropithecus* (Jolly 1972). However, it is possible that there is regional variation in habitat use and locomotion in such a geographically widespread taxon, so southern African forms of *T. oswaldi* may have been as terrestrial as the modern gelada.

The cercopithecoid species *C. williamsi*, *T. oswaldi*, *P. robinsoni* and *P. ingens* were argued above to be open habitat monkeys, using either a mix of arboreal and terrestrial locomotion, or being confined exclusively to terrestriality. However, both the Sterkfontein Member 4 and the Bolt's Farm samples contain postcranial specimens assigned to 'forest arboreal'. Thus, it is possible that some of the *Parapapio* species are forest living arboreal monkeys. One species of *Parapapio*, *P. broomi*, is known from Bolt's Farm, and as the other two species of cercopithecoid, *C. williamsi* and *P. robinsoni*, identified at this site are likely to have been open habitat monkeys, this indicates that *P. broomi*, in the absence of other, as yet undiscovered, cercopithecoid species, was a forest-living arboreal monkey. Three species of *Parapapio*, *P. broomi*, *P. whitei* and *P. jonesi*, have been discovered at Sterkfontein Member 4. *Parapapio* craniodental material, assigned to *P. jonesi*, has also been recovered from Swartkrans Member 1. If the small

**TABLE 8.**
**Primates present at Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2.**

|  | Sterkfontein Mbr 4 | Bolt's Farm | Swartkrans Mbr 1 | Swartkrans Mbr 2 |
|---|:---:|:---:|:---:|:---:|
| *T. oswaldi* |  |  | ✓ | ✓ |
| *Pp. broomi* | ✓ | ✓ |  |  |
| *Pp. jonesi* | ✓ |  | ✓ |  |
| *Pp. whitei* | ✓ |  |  |  |
| *P. izodi* | ✓ |  |  |  |
| *P. robinsoni* | ✓ | ✓ | ✓ | ✓ |
| *C. williamsi* | ✓ | ✓ |  | ✓ |
| *Cercopithecoides* sp. |  |  | ✓ |  |
| *P. ingens* |  |  | ✓ |  |
| *Cercocebus* sp. |  |  | ✓ |  |
| *A. africanus* | ✓ |  |  |  |
| *P. robustus* |  |  | ✓ | ✓ |

Data from Brain 1981; Delson 1984, 1988; Watson 1993; Turner *et al.* 1999

Swartkrans sample presented here is representative, 'forest arboreal' monkeys would be scarce, with the majority of cercopithecoids inhabiting open environments. Thus, it is plausible that *P. jonesi* was an open habitat monkey, possibly 'open terrestrial', inhabiting grassland at Sterkfontein and Swartkrans, and sympatric with arboreal *Parapapio* species at Sterkfontein. A degree of support for this scenario is provided by the results of another multivariate analysis of taxonomically-unassigned forelimb bones from southern African cercopithecoids, in which the specimens STS 377c and SWP 511 from Sterkfontein were attributed to *Parapapio* (Ciochon 1993). Both these specimens were assigned to the 'open terrestrial' category in the present study.

It is possible that different species within the genus *Parapapio* had different habitat preferences and locomotor strategies, with *P. broomi* being arboreal and *P. jonesi* terrestrial. Brain (1981 p.152) commented that it appeared 'remarkable' to find three synchronous species of *Parapapio* at Sterkfontein and other sites in southern Africa. However, there are several sympatric modern cercopithecoid taxa, such as species of *Cercopithecus* in West African forest habitats that forage in mixed-species groups (Fleagle 1988). *Cercopithecus* may provide an arboreal-habitat model for *Parapapio*, but if there was more significant variation in habitat use between *Parapapio* species, an apt ecological model may be *Macaca fascicularis* and *M. nemestrina* in Asia. These modern species are sympatric, with the secondary forest dwelling *M. fascicularis* being more arboreal than *M. nemestrina*, which often travels terrestrially, and inhabits upland and hilly areas (Fleagle 1988).

The taxon-free analysis of cercopithecoid postcranial specimens from Sterkfontein Member 4, Swartkrans Members 1 and 2, and Bolt's Farm indicated that there was variation in cercopithecoid habitat preferences and locomotor strategies within, and possibly between, these sites. In the absence of associated craniodental and postcranial material from southern African Plio-Pleistocene cercopithecoids, it is very difficult to assign postcranial material to a particular taxon, hindering investigation into their probable locomotor strategies. However, using a combination of occurrence data, the results of the ecomorphic analysis undertaken as part of this study, and other work on Plio-Pleistocene monkeys, it has been possible to make tentative suggestions as to the locomotor strategies of cercopithecoids from Sterkfontein Member 4, Swartkrans Members 1 and 2, and Bolt's Farm. Several of the cercopithecines, including *T. oswaldi*, *P. ingens*, *P. robinsoni* and *P. jonesi* may have been open habitat dwellers, with *T. oswaldi* argued to be best described as 'open mixed', and *P. jonesi* 'open terrestrial'. *P. robinsoni* may also have been 'open terrestrial'. Another cercopithecine, *P. broomi*, may have been a forest dwelling arboreal quadruped.

The one colobine represented by craniodental remains at the sites under discussion, *C. williamsi*, is likely to have been an open habitat monkey, described in this study as 'open mixed'. Thus, in the absence of other colobine species at Plio-Pleistocene sites in southern Africa, the presence of colobine craniodental remains does not necessarily indicate forest, although the presence of *P. broomi* specimens may do so.

## CONCLUSIONS

The reconstructions of palaeohabitat from the cercopithecoid data for Sterkfontein Member 4, Bolt's Farm and Swartkrans Members 1 and 2 are generally consistent with other habitat reconstructions for these sites (Vrba 1974, 1975; Watson 1993; Avery 1995; Reed 1997; Bamford 1999; Kuman & Clarke 2000), although the presence of open habitat monkeys at Sterkfontein indicates that there might be more grassland in Member 4 times than is presently supposed. Monkeys assigned to all three habitat categories ('forest arboreal', 'open mixed' and 'open terrestrial') are present at the earlier sites of Sterkfontein Member 4 and Bolt's Farm, but the habitat preferences and locomotor repertoires of cercopithecoids appear to change during the Plio-Pleistocene, with a reduction of 'forest arboreal' monkeys at the more recent site of Swartkrans. This result corresponds well with the pattern of hominin occurrence at these sites: *A. africanus*, found at Sterkfontein Member 4, had an arboreal component to its locomotor behaviour (Wood & Richmond 2000), whereas *P. robustus*, found at the apparently much more open localities of Swartkrans Members 1 and 2, but not at Sterkfontein Member 4, appears to have no morphological features associated with arboreality (Wood & Richmond 2000).

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# APPENDIX 1.
## Southern African Taxonomically-unassigned postcranial speciments used in habitat analysis

| Specimen | Site | Element | DFA posterior probabilities† | | | Habitat category |
|---|---|---|---|---|---|---|
| | | | FA | OM | OT | |
| SWP 1140 | Sterkfontein Mbr 4 | Distal humerus | 0.000 | 0.998 | 0.002 | Open mixed |
| SWP 1156 | Sterkfontein Mbr 4 | Proximal ulna | 0.019 | 0.978 | 0.003 | Open mixed |
| SWP 1176 | Sterkfontein Mbr 4 | Distal humerus | 0.003 | 0.989 | 0.008 | Open mixed |
| SWP 1211 | Sterkfontein Mbr 4 | Distal humerus | 0.000 | 1.000 | 0.000 | Open mixed |
| SWP 1262 | Sterkfontein Mbr 4 | Distal humerus | 0.008 | 0.596 | 0.397 | Open mixed |
| SWP 1271 | Sterkfontein Mbr 4 | Distal humerus | 0.000 | 0.998 | 0.002 | Open mixed |
| SWP 504 | Sterkfontein Mbr 4 | Proximal humerus | 0.276 | 0.551 | 0.173 | Open mixed |
| SWP 506 | Sterkfontein Mbr 4 | Distal humerus | 0.000 | 0.915 | 0.085 | Open mixed |
| SWP 509 | Sterkfontein Mbr 4 | Distal humerus | 0.000 | 0.870 | 0.130 | Open mixed |
| SWP 512 | Sterkfontein Mbr 4 | Distal humerus | 0.000 | 0.676 | 0.324 | Open mixed |
| SWP 525 | Sterkfontein Mbr 4 | Proximal ulna | 0.020 | 0.961 | 0.019 | Open mixed |
| SWP 962 | Sterkfontein Mbr 4 | Proximal humerus | 0.257 | 0.735 | 0.008 | Open mixed |
| STS 377c | Sterkfontein Mbr 4 | Distal humerus | 0.002 | 0.274 | 0.725 | Open terrestrial |
| SWP 1287 | Sterkfontein Mbr 4 | Distal humerus | 0.000 | 0.001 | 0.999 | Open terrestrial |
| SWP 1572 | Sterkfontein Mbr 4 | Proximal ulna | 0.000 | 0.077 | 0.923 | Open terrestrial |
| SWP 510 | Sterkfontein Mbr 4 | Distal humerus | 0.000 | 0.000 | 1.000 | Open terrestrial |
| SWP 511 | Sterkfontein Mbr 4 | Distal humerus | 0.039 | 0.365 | 0.597 | Open terrestrial |
| STS 1905 | Sterkfontein Mbr 4 | Distal femur | 0.968 | 0.018 | 0.014 | Forest arboreal |
| SWP 1175 | Sterkfontein Mbr 4 | Distal femur | 1.000 | 0.000 | 0.000 | Forest arboreal |
| SWP 1535 | Sterkfontein Mbr 4 | Distal femur | 1.000 | 0.000 | 0.000 | Forest arboreal |
| SWP 1710 | Sterkfontein Mbr 4 | Distal femur | 0.987 | 0.013 | 0.000 | Forest arboreal |
| ST #? | Sterkfontein Mbr 4 | Distal femur | 0.157 | 0.842 | 0.002 | Open mixed |
| SWP 1532 | Sterkfontein Mbr 4 | Distal femur | 0.005 | 0.995 | 0.000 | Open mixed |
| SWP 1717 | Sterkfontein Mbr 4 | Distal femur | 0.052 | 0.777 | 0.172 | Open mixed |
| STS 549 | Sterkfontein Mbr 4 | Distal femur | 0.001 | 0.258 | 0.742 | Open terrestrial |
| BF 47 | Bolt's Farm | Distal humerus | 0.079 | 0.921 | 0.000 | Open mixed |
| BF 49 | Bolt's Farm | Distal humerus | 0.000 | 0.974 | 0.026 | Open mixed |
| BF 55 | Bolt's Farm | Proximal humerus | 0.013 | 0.614 | 0.373 | Open mixed |
| BF 56 | Bolt's Farm | Distal humerus | 0.003 | 0.678 | 0.319 | Open mixed |
| BF 48 | Bolt's Farm | Proximal humerus | 0.001 | 0.076 | 0.923 | Open terrestrial |
| BF 26 | Bolt's Farm | Distal femur | 1.000 | 0.000 | 0.000 | Forest arboreal |
| BF 30 | Bolt's Farm | Distal femur | 0.998 | 0.002 | 0.000 | Forest arboreal |
| BF 33 b | Bolt's Farm | Distal femur | 1.000 | 0.000 | 0.000 | Forest arboreal |
| BF 35 a | Bolt's Farm | Distal femur | 0.997 | 0.003 | 0.000 | Forest arboreal |
| SK 1506 | Swartkrans Mbr 1* | Distal humerus | 0.076 | 0.324 | 0.600 | Open terrestrial |
| SK 591 d | Swartkrans Mbr 1* | Proximal ulna | 0.000 | 0.056 | 0.944 | Open terrestrial |
| SK #? | Swartkrans Mbr 1* | Distal humerus | 0.004 | 0.056 | 0.940 | Open terrestrial |
| SK 1500 | Swartkrans Mbr 1* | Distal femur | 0.317 | 0.636 | 0.047 | Open mixed |
| SK 1817 | Swartkrans Mbr 1* | Distal femur | 0.073 | 0.309 | 0.618 | Open terrestrial |
| SK 591 c | Swartkrans Mbr 2 | Distal humerus | 0.000 | 0.012 | 0.988 | Open terrestrial |

* Swartkrans Mbr 1 specimens used in analysis are part of 'Hanging Remnant' assemblage

## APPENDIX 2.1
### Humerus measurements used in the analysis

| Measurement | Description |
| --- | --- |
| Anteroposterior Head Diameter | Maximum diameter of the humeral head in the anteroposterior plane |
| Mediolateral Head Diameter | Maximum diameter of the humeral head in the mediolateral plane |
| Bicipital Groove Width | Minimum width of the bicipital groove at its centre |
| Bicipital Groove Depth | Maximum width of the bicipital groove at its centre |
| Greater Tuberosity Maximum Width | Maximum anteroposterior width of the greater tuberosity |
| Lesser Tuberosity Maximum Width | Maximum anteroposterior width of the lesser tuberosity |
| Biepicondylar Width | Maximum width across the distal humerus between the epicondyles |
| Mediolateral Articular Surface Width | Maximum mediolateral width of the articular surface across the anterior surface of the distal humerus |
| Medial Trochlea Distal Projection | Maximum distal projection of the medial side of the trochlea |
| Olecranon Fossa Depth | Greatest depth of the olecranon fossa |
| Olecranon Fossa Width | Maximum width of the olecranon fossa in the mediolateral plane |
| Posterior Trochlear Articular Surface Width | Greatest mediolateral width of the posterior trochlear articular surface |
| Trochlear Gutter Width | Maximum mediolateral width of the trochlear gutter on the posterior of the distal humerus |

Measurements and descriptions adapted from Ciochon (1993)

## APPENDIX 2.2
### Ulna measurements used in the analysis

| Measurement | Description |
| --- | --- |
| Radial Notch Width | Maximum linear width of the radial notch |
| Radial Notch Height | Maximum height of the radial notch |
| Trochlear Notch Midline Height | Minimum height of the trochlear notch at its midline |
| Trochlear Notch/Olecranon Length | Length of the olecranon process taken from the proximoposterior surface of the trochlear notch |
| Trochlear Notch/Olecranon Width | Maximum width of the olecranon process |
| Proximal Trochlear Notch Width | Maximum width of the proximal part of the trochlear notch articular surface |
| Distal Trochlear Notch Width | Maximum width of the distal part of the trochlear notch articular surface |
| Coronoid Process Projection | Maximum anterior projection of the coronoid process |
| Radial Notch Posterior Width | Minimum width of the shaft posterior to the radial notch |
| Trochlear Notch Posterior Width | Minimum width of the shaft posterior to the trochlear notch |

Measurements and descriptions adapted from Ciochon (1993)

## APPENDIX 2.3.
### Femur measurements used in the analysis

| Measurement | Description |
| --- | --- |
| Intercondylar notch to patellar groove | Minimum distance between the intercondylar notch and the patellar groove, measured anteroposteriorly |
| Patellar groove to posterior medial condyle | Maximum anteroposterior distance between the patellar groove and the posterior aspect of the medial condyle |
| Breadth of medial condyle | Maximum mediolateral breadth of the medial condyle |
| Breadth of lateral condyle | Maximum mediolateral breath of the lateral condyle |
| Length of medial condyle | Maximum posterodistal length of the medial condyle |
| Length of lateral condyle | Maximum posterodistal length of the lateral condyle |
| Intercondylar distance | Maximum distance between the most medial extent of the lateral condyle and the most lateral extent of the medial condyle |

Measurements adapted from Bishop (1994)

## APPENDIX 3.1
### Proximal humerus ratios used in the analysis

| Ratio abbreviation | Composition | Demonstrates |
|---|---|---|
| HS | Anteroposterior head diameter x 100 / mediolateral head diameter | Humeral head shape |
| HP2 | Maximum proximal head projection x 100 / mediolateral head diameter | Humeral head shape |
| BGS | Bicipital groove depth x 100 / bicipital groove width | Bicipital groove depth |
| BGW | Bicipital groove width x 100 / mediolateral head diameter | Bicipital groove width |
| GTUB | Greater tuberosity maximum width x 100 / anteroposterior head diameter | Greater tuberosity size |
| LTUB | Lesser tuberosity maximum width x 100 / anteroposterior head diameter | Lesser tuberosity size |

## APPENDIX 3.2
### Distal humerus ratios used in the analysis

| Ratio abbreviation | Composition | Demonstrates |
|---|---|---|
| TS | Anteroposterior lateral trochlea diameter x 100 / distal trochlea width | Trochlea shape |
| MTP | Trochlea projection x 100 / biepicondylar width | Extent of trochlea projection |
| OFD | Olecranon fossa depth x 100 / olecranon fossa width | Olecranon fossa shape |
| PTA1 | Posterior trochlear articular surface width x 100 / biepicondylar width | Size of the posterior articular surface |
| PTA2 | Posterior trochlear articular surface width x 100 / trochlear gutter width | Size of the posterior anticular surface |
| PTA3 | Posterior trochlear articular surface width x100 / anteroposterior lateral trochlear diameter | Size of the posterior anticular surface |
| TGW | Trochlear gutter width x 100 / biepicondylar width | Size of trochlear gutter |

## APPENDIX 3.3
### Proximal ulna ratios used in the analysis

| Ratio abbreviation | Composition | Demonstrates |
|---|---|---|
| RNS | Radial notch height x 100 / radial notch width | Radial notch shape |
| OH2 | Trochlear notch-olecranon length x 100 / trochlear notch midline height | Olecranon height |
| OS | Trochlear notch-olecranon length x 100 / trochlear notch-olecranon width | Olecranon shape |
| TNS | Distal trochlear notch width x 100 / proximal trochlear notch width | Trochlear notch shape |
| RNW | Radial notch width x 100 / radial notch posterior width | Radial notch width |
| CPP | Coronoid process projection x 100 / trochlear notch posterior width | Coronoid process projection |

## APPENDIX 3.4
### Distal femur ratiors used in the analysis

| Ratio abbreviation | Composition | Demonstrates |
|---|---|---|
| CL | Length lateral condyle x 100 / length medial condyle | Difference in condyle length |
| IFMC | Intercondylar notch to patellar groove distance x 100 / length medial condyle | Medial condyle length |
| SLC1 | Breadth lateral condyle x 100 / length lateral condyle | Lateral condyle shape |
| SMC3 | Length medial condyle x 100 / patellar groove to posterior medial condyle | Medial condyle shape |
| CB | Breadth lateral condyle x 100 / breadth medial condyle | Difference in condyle breadth |
| ICLB | Breadth lateral condyle x 100 / intercondylar distance | Lateral condyle breadth |
| ICD2 | Intercondylar distance x 100 / patellar groove to posterior medial condyle | Intercondylar distance |