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Original article

Cercopithecoid primate postcranial fossils from Cooper's D, South Africa☆

Jeremy M. DeSilva [a,*], Christine M. Steininger [b], Biren A. Patel [c]

[a] Department of Anthropology, Boston University, 232 Bay State Road, Boston, MA 02215, USA
[b] Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, Johannesburg, South Africa
[c] Department of Cell and Neurobiology, Keck School of Medicine, University of Southern California, Los Angeles, CA 90033, USA

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ABSTRACT

Among several highly fossiliferous localities in the Bloubank Valley (Gauteng, South Africa), the Cooper's Cave System has been known since 1938 and has produced a rich fossil assemblage, including some remains of the early hominin *Paranthropus robustus*. In 2001, excavations began at a new locality, Cooper's D, which dates to ~1.4-1.5 Ma. Although hominins are relatively rare in the assemblage, remains of cercopithecoid primates are much more common. Craniodental fossils currently indicate the possible presence of at least three large-bodied cercopithecoid primate genera at Cooper's D: *Gorgopithecus*, *Papio*, and *Theropithecus*. In this study, we identify and describe > 100 cercopithecoid primate postcranial fossils representing all regions of the appendicular skeleton. The specimens come from several age classes and size morphs; more than one third of the fossils described are from sub-adult and juvenile individuals. The adult postcranial fossils vary substantially in size, with body masses estimated between 30 and 60 kg (from 16 of the better preserved specimens). The functional morphology of the postcranial remains indicate that these elements come from animals that likely utilized terrestrial substrates, but they remain difficult to definitively attribute to *Gorgopithecus*, *Theropithecus*, or *Papio* given the absence of associated skeletons. The smaller specimens likely belong to *Papio* while the larger ones can be attributed to the other two genera. Because Cooper's D has also yielded fossils of the early hominin *Paranthropus robustus*, this raises the question of how these four large-bodied, mostly terrestrial primates sympatrically utilized the landscape.

1. Introduction

There are several highly fossiliferous localities in the Bloubank Valley, Gauteng, South Africa (Fig. 1). Cooper's Cave System has been known since 1938 and has produced a rich fossil assemblage, including remains of the hominin *Paranthropus robustus* (Steininger et al., 2008; De Ruiter et al., 2009). In 2001, excavations began at a new locality, Cooper's D, and work has taken place here on a regular basis since its initial discovery (Fig. 1; Berger et al., 2003). Uranium series date the Cooper's D deposits to approximately 1.4–1.5 Ma (De Ruiter et al., 2009). The locality is highly productive, yielding more than 50,000 catalogued fossils. Among the vertebrate fauna are a large number of cercopithecoid primates and some of their craniodental remains have been previously attributed to the genera *Papio* and *Theropithecus* (De Ruiter et al., 2009; Folinsbee, 2009; Folinsbee and Reisz, 2013; Gilbert et al., 2013), and most recently to *Gorgopithecus* (Steininger and Gilbert, ongoing work). In addition to these craniodental fossils, there are numerous unassociated postcranial specimens that can also be confidently attributed to cercopithecoids. Here, we describe for the first time 106 cercopithecoid primate postcranial fossils recovered from Cooper's D (Supplementary material, Table S1).

South African fossil cercopithecoids, including those from Cooper's Cave, have been studied in some detail (Freedman, 1957; Delson, 1988; Folinsbee, 2009; Folinsbee and Reisz, 2013; Gilbert et al., 2013). Most of this research has focused on the craniodental specimens while the postcranial elements have been largely ignored (but see Ciochon, 1993; Elton, 2001, 2007). This contrasts with the descriptive studies of fossil cercopithecoid postcrania from sites in East Africa (Jolly, 1972; Birchette, 1982; Jablonski, 1986; Harrison, 1989; Krentz, 1993; Elton, 2001; Jablonski et al., 2002; Frost and Delson, 2002; Leakey et al., 2003; Frost, 2007; Frost and Alemseged, 2007; Gilbert and Frost, 2008; Jablonski and Leakey, 2008; Gilbert et al., 2011; Harrison, 2011). The fact that most cercopithecoid postcranial fossils lack any meaningful association with craniodental remains is the main reason why they have not been the focus of any comprehensive research. While our description of new Cooper's D cercopithecoid postcrania does not change this fact, these preliminary

☆ Corresponding editor: Gilles Escarguel.
* Corresponding author.
E-mail address: jdesilva@bu.edu (J.M. DeSilva).

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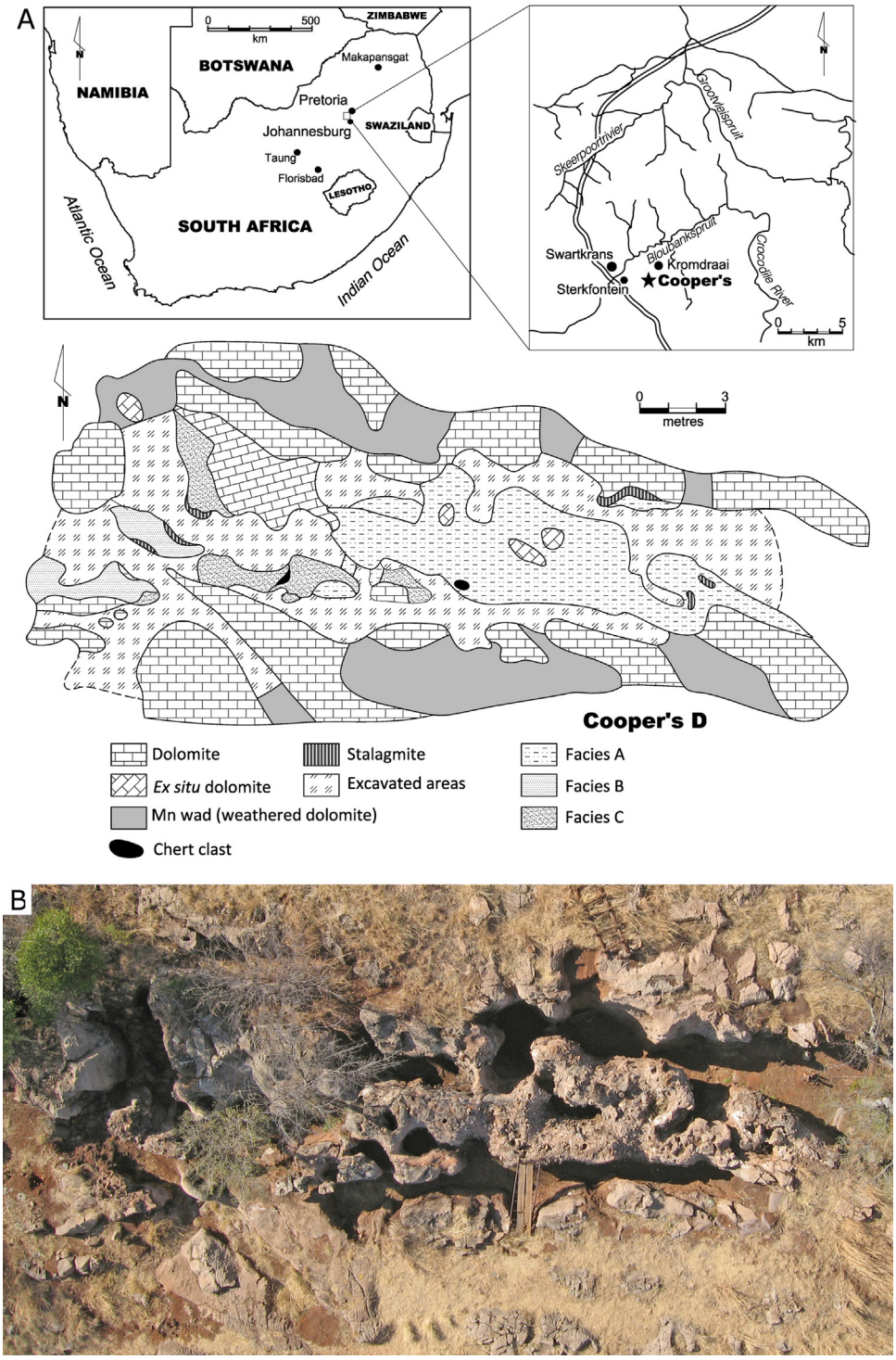

Fig. 1. The Cooper's D locality. **A**. Plane-table geological map illustrating various facies; **B**. Aerial photograph of the site.

descriptions are important in gauging the taxonomic diversity of Cooper's D primates, as well as the locomotor and ecological adaptations of the primates that inhabited the South African landscape during the Pleistocene.

2. Geological context

As with the other hominin sites of the Bloubank Valley, Cooper's Cave occurs within the dolomites of the Monte Christo Formation (Malmani Subgroup, Transvaal Supergroup). The Cooper's Cave System comprises an area of 303 × 198 m in which, at present, three distinct fossiliferous localities have been identified: Cooper's A, B and D. The area of Cooper's D extends along an east-west trend; there are three distinct facies identified based on abundance of fossils, degree of sorting and type of clasts (Fig. 1). Facies A on the east trend comprises of massive, well-calcified reddish-brown sandy sediments containing large dolomite blocks up to 50 cm in diameter, quartz clasts, abundant fossil bone and stone tools. On the west end, facies B is similar to A, but contains finer clasts, more fossils and fewer stone tools. On top of this are finely laminated

sediments with sparse fossil remains that are separated by thin layers of speleothem. In between facies A and B is facies C which has a brownish-red sandy sediment with distinct layering that is rich in microfaunal fossils and contains few clasts. Clasts, fossil bones and teeth are heavily stained with manganese oxides. Both east and west areas have similar faunal assemblages and are considered contemporaneous (De Ruiter et al., 2009).

Recent uranium series dates indicate that the majority of the Cooper's D assemblage likely falls between ~1.5 and 1.4 Ma (De Ruiter et al., 2009). Presently, the U-Pb dates for Cooper's D are the best-constrained dates for a *Paranthropus robustus* assemblage.

3. Material and methods

Because most of the craniodental monkey fossils from Cooper's D have been attributed to extinct taxa of *Theropithecus* and *Papio*, and more recently to *Gorgopithecus*, the cercopithecoid postcranial elements described here were compared with skeletons of extant *Papio hamadryas* ($n = 5$), *Theropithecus gelada* ($n = 3$) and the closely related *Mandrillus sphinx* ($n = 2$) from the American Museum of Natural History, Harvard Museum of Comparative Zoology and the Department of Anatomical Sciences, Stony Brook University. Also, specimens of *Colobus guereza* ($n = 3$) and *Nasalis larvatus* ($n = 3$) were used to assess whether colobine-like morphologies could be found in the fossil assemblage. The present study focuses on anatomical descriptions and are accompanied by linear (in mm) and angular (in degrees) measurements when appropriate. Anteroposterior dimensions are denoted as AP, mediolateral as ML, proximodistal as PD, and superioinferior as SI. Where possible, we hypothesize a taxonomic affiliation for some of this new material (e.g., *Theropithecus*, *Gorgopithecus* or *Papio*). Based on previous estimates of body mass of South African fossil monkeys (Delson et al., 2000), adults of smaller specimens are more likely attributable to *Papio*, whereas the larger specimens could likely belong to either *Theropithecus* or *Gorgopithecus*. It is worth noting that there are no identified *Gorgopithecus* postcrania to which these fossils can be compared, making any taxonomic hypotheses tentative at best; therefore we conservatively did not assign any of the new fossils from Cooper's D to *Gorgopithecus* at this time. Body mass for some of the specimens were estimated from relevant equations in Anapol (1983), Delson et al. (2000), and Ruff (2003) (Table S1). Adult or juvenile status was assessed for each bone, and determined by the presence or absence of epiphyses. If a bone could not be categorized as a juvenile, it was assumed to be from an adult, making the percentage of the assemblage composed of sub-adults a minimum estimate.

4. Descriptions

4.1. Upper limb

4.1.1. Scapula

Parts of three scapulae have been recovered from Cooper's D. Specimen **CD 9265** is a fragmentary left scapula preserving the glenoid fossa and the most lateral aspect of the scapular spine. The spine originates 11.7 mm medially from the glenoid fossa, rooted at a position slightly below the midfossa when viewed laterally. The glenoid is 18.5 mm wide and 27.2 mm tall. It narrows cranially, forming a piriform-shaped facet, though it does not narrow as much as is found in modern *Theropithecus*. The glenoid is relatively deep with the cranial aspect projecting laterally, forming a lip. There is a strong rim along the most inferior margin of the fossa. The infraglenoid tubercle is palpable, and grades into the sharp posterior (or axillary) border for the insertion of the teres minor. Ventrally, an axillary sulcus is present between the sharp crest of the lateral border and a thick, scapular pillar. [Tentative assignment: *Papio*].

Specimen **CD 13477** is a right scapula preserving portions of the glenoid, spine, and superior border. The spine originates 11.6 mm from the glenoid fossa, and is very thick at its origin. The root of the spine emerges slightly inferior to the midfossa. Though the cranial portion of the glenoid is not preserved, the maximum ML dimensions can be estimated to be 21.5 mm. The preserved portion of the superior border (18.9 mm total) is gently sloping, appearing more like the long and narrow scapula of *Papio* and unlike the short and deep scapula of *Mandrillus* and colobines. Thus, the supraspinatous fossa is craniocaudally reduced in area. The infraspinatus fossa is poorly preserved. The preserved ventral aspect of CD 13477 is concave, for the attachment of subscapularis. [Tentative assignment: *Papio*].

Specimen **CD 17811** is another left scapula preserving the glenoid fossa. It is broken cranially and ventrally just as the corocoid is originating from the superior border of the scapula. The spine is not preserved. There is damage along the superior, inferior and ventral aspects of the glenoid border, though general morphology can be assessed and the size measured to 19.2 mm wide and 28.3 mm tall. The glenoid is piriform in shape, similar to *Papio* and not too anteriorly pinched-in, as is the case for *Theropithecus* glenoids. The glenoid is relatively deep and though there is damage, it is clear that the cranial aspect of the fossa is laterally projecting to form a lip. Like CD 9265, there is a strong inferior rim along the glenoid fossa margin. Also like CD 9265, there is a palpable infraglenoid tubercle, and an axillary sulcus present between a scapular pillar, and the lateral border. [Tentative assignment: *Papio*].

4.1.2. Humerus

Seven fragmentary humeri have been recovered from Cooper's D (Fig. 2; Table 1). Specimen **CD 3351** is a robust left humerus preserving the proximal portion except the head, and the shaft to a point just inferior to the deltopectoral crest. Its preserved length is 127 mm. The intertubercular groove at the level of the greater and lesser tubercle measures 8.9 mm wide. The shaft is triangular in cross-section and measures 20.3 mm AP and 16.4 mm ML at a level just distal to the deltoid crest. The deltoid crest is large and measures 18.7 mm at its widest part (in a ML direction). The deltoid crest is a continuation of a well-developed lateral lip of the intertubercular groove, similar to the morphology in *Theropithecus* humeri. Distally, the deltoid lines converge as in *Theropithecus*, whereas in *Papio* these lines remain separated. On the lateral side of the greater tubercle is a large and deep fossa for infraspinatus, similar to our observations in *Theropithecus* but not *Papio*. Although the head is mostly gone, the preserved portion suggests that the greater tubercle would have extended well above the head, as seen in most terrestrial monkeys. [Tentative assignment: *Theropithecus*].

Specimen **CD 5964** is the midshaft of a right humerus. The preserved length is 95.0 mm and begins just distal to the surgical neck. The shaft itself if relatively straight, but without a head and distal end, it is difficult to assess whether it could have had some degree of AP flexion. The cortical bone is exposed on both ends of the midshaft and is thickest posteriorly at each end. The shaft is triangular in cross-section and measured 18.0 mm in AP direction and 15.2 mm ML at a level just distal to the deltoid crest. The deltoid crest itself is large and measures 17.2 mm at its widest part (in a ML direction). The deltoid crest is a continuation of a well-developed lateral lip of the intertubercular groove. On the distal end, there appears to be a moderately developed lateral supracondylar ridge (supinator crest), similar to extant *Papio* and *Theropithecus*, but not like *Mandrillus*. Overall, this specimen is

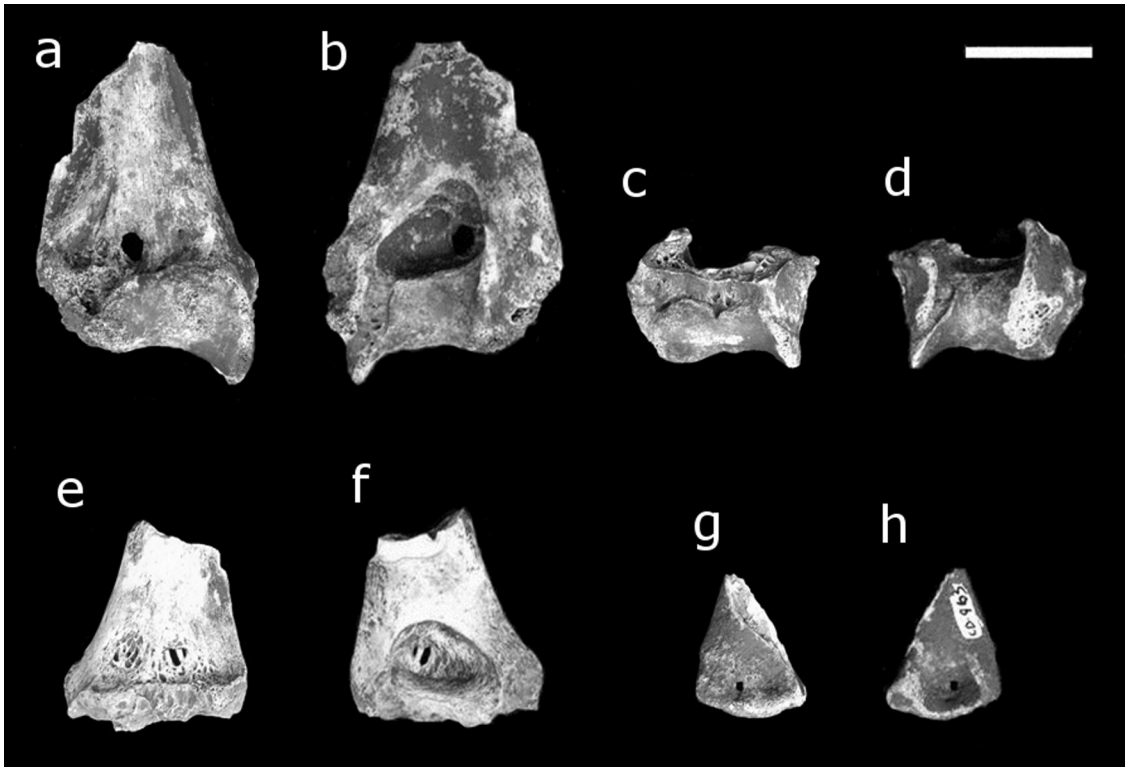

Fig. 2. Distal humeri of cercopithecoids from Cooper's D shown in anterior (left) and posterior (right) views. **a**, **b**: CD 7275, adult; **c**, **d**: CD 9486, adult; **e**, **f**: CD 10502, juvenile; **g**, **h**: CD 963, infant. Both adult fossils are morphologically similar to extant *Theropithecus*. Scale bar: 2 cm.

the size of living male *Theropithecus gelada* and smaller than large male *Papio*.

Specimen **CD 7275** is the distal end of a right humerus (Fig. 2(a, b)). The preserved length is 55 mm. The preserved proximal end is triangular in cross-section with a flattened posterior side. The capitulum is eroded but its ventral surface extends proximally. The lateral epicondyle is damaged, but arising from it is a supinator crest that resembles the condition in CD 5964. The medial epicondyle is broken, but appears to project dorsally as seen in terrestrial primates (Harrison, 1989). The trochlea has a distally-extending medial flange (beyond the level of the capitulum) like other papionin monkeys, and its ML width is 18 mm. There is a foramen in the olecranon fossa that does not appear to be due to damage. Superior to the fossa, the posterior shaft is flat, as in *Theropithecus*. The olecranon fossa is triangular in shape with its apex extending proximally on the lateral side, again as is seen in *Theropithecus*. This contrasts the shape seen in *Papio* that has an olecranon fossa that is more rounded on its proximal side and less triangular in shape. Also, the fossa's lateral wall rolls anteriorly into itself on the proximal aspect, more like *Theropithecus* and not like *Papio*. The dimensions are similar to modern *Papio* (Jolly, 1972), though they do not approach the large size seen in *Theropithecus oswaldi* fossils from East Africa (Jolly, 1972; Jablonski and Leakey, 2008). [Tentative assignment: *Theropithecus*].

Specimen **CD 9486** is the distal end of a right humerus (Fig. 2(c, d)). The preserved length is 23.9 mm. The capitulum is semi-ovoid in shape and its ventral surface extends proximally, but its posterior side is broken and thus its morphology cannot be assessed. The trochlea has a distally-extending medial flange (beyond the level of the capitulum), and its ML width is 20.2 mm. The medial epicondyle is broken, but likely projects dorsally as seen in terrestrial primates (Harrison, 1989). The lateral epicondyle is robust and well-developed. It is similar in size to modern *Theropithecus*. The preserved distal part of the olecranon fossa resembles CD 7275. [Tentative assignment: *Theropithecus*].

Specimen **CD 10502** is the distal end of a left humerus from a juvenile (Fig. 2(e, f)). The distal epiphysis is missing. Its preserved length is 32.5 mm. The medial epicondyle angle projects dorsally,

Table 1
Distal humerus dimensions (in mm) of cercopithecoid remains from Cooper's D locality (Cooper's Cave system, Bloubank Valley, Gauteng, South Africa).

Measurement \ Specimen	CD 963	CD 7275	CD 9486	CD 10502
Biepicondylar breadth	17.5 (min)	35.7 (min)	30.7 (min)	28.8 (min)
ML breadth of distal articulation	–	26.6	22.9	–
AP width of distal articulation	7.9	21.5	17.7 (est)	14.2
AP breadth of trochlea	–	13.1	12.3 (est)	–
PD height of capitulum	–	11.0 (est)	10.1	–
ML breadth of capitulum	–	11.6 (est)	10.3	–
ML breadth from medial trochlear keel to lateral epicondyle	–	34.3 (est)	27.1 (est)	–
Medial trochlear flange length	–	18.7	10.4 (min)	–
Relative flange length	–	70.3	–	–
ML breadth of olecranon fossa	9.2	16.7	–	15.6
PD height of olecranon fossa	6.9	13.6	–	12.4

but its size cannot be assessed. There is a foramen in the olecranon fossa, but this appears to be from damage. The olecranon fossa differs in shape from CD 9486 and is more rounded on its proximal side and less triangular in shape, like *Papio*. Also, the fossa's lateral wall does not roll anteriorly into itself on the proximal aspect as in *Papio*. The lateral epicondyle is not developed, but arising from it is a supinator crest that resembles the condition in CD 5964. [Tentative assignment: *Papio*].

Additional humeral specimens include CD 962 and CD 963. **CD 962** is a fragmentary portion of a right humeral head and the most medial aspect of the neck. Its head is strongly curved craniocaudally, but is only moderately curved dorsoventrally, a feature found in terrestrial quadrupeds like *Papio* and *Theropithecus* (Harrison, 1989). **CD 963** is a very small, right distal humerus and likely comes from an infant (Fig. 2(g, h)). The medial epicondyle appears posteriorly angled even at this early stage of development. There is a small foramen in the olecranon fossa that does not appear to have been caused by damage.

4.1.3. Ulna and radius

Cercopithecoid primate ulnae are represented by three proximal elements and one distal specimen (Fig. 3; Table 2). The proximal ulnae are all similar in size to modern *Papio* and *Theropithecus* and overlap in size with some *Theropithecus oswaldi* fossils from the Upper Burgi member, Koobi Fora, Kenya, including KNM-ER 1572 and KNM-ER 3877 (Jablonski and Leakey, 2008).

Specimen **CD 3349** (Fig. 3(b)) is a large left proximal ulna preserving 43.6 mm from the most proximal portion of the olecranon to a break in the shaft just distal to the coronoid process. The radial notch is only partially preserved. The trochlear notch is anteriorly facing, and there is no midline keel. The coronoid is expanded ML, a common feature in *Papio* (Fleagle and McGraw, 2002). The olecranon is moderately retroflexed as is found in terrestrial cercopithecoids, and extends 13.1 mm superiorly above the trochlear notch, with the highest region medially located. In anterior view, the olecranon slopes proximomedially to distolaterally, like in *Papio*. Anteriorly the groove for the triceps tendon is only weakly palpable as in cercopithecoids (Harrison, 1989). There is a strongly concave region medial to the trochlear notch found in colobines and *Theropithecus* (Krentz, 1993), for the origin of the flexor digitorum profundus, an important muscle for manual dexterity. At the break in the shaft, the bone is 19.4 mm AP, and 14.9 mm ML.

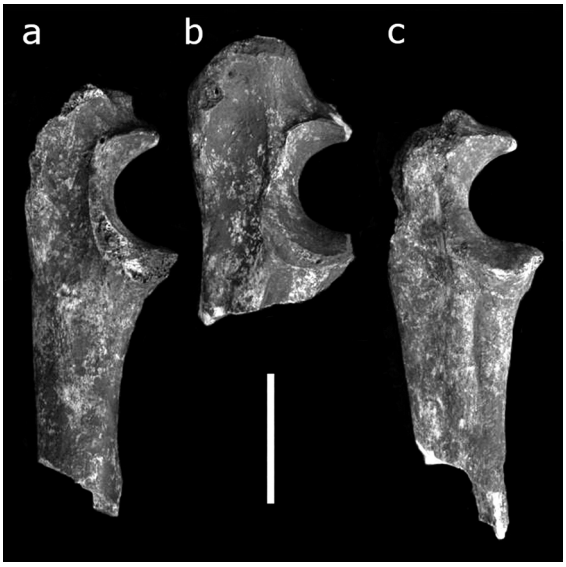

Fig. 3. Left ulnae of cercopithecoids from Cooper's D in medial view. **a**: CD 13315; **b**: CD 3349; **c**: CD 3311. In CD 13315 the trochlear and radial notches are SI tall, and there is a groove for the triceps tendon superior to the trochlear notch that is not found in the other two fossils. These anatomies suggest that CD 13315 may be from a more arboreal cercopithecoid than the other two ulnae. Scale bar: 2 cm.

Table 2
Proximal ulna dimensions (in mm) of cercopithecoid remains from Cooper's D locality (Cooper's Cave system, Bloubank Valley, Gauteng, South Africa).

Measurement \ Specimen	CD 3311	CD 3349	CD 13315
Superoinferior height of trochlear notch	16.5	14.4	16.5
Minimum AP depth of trochlear notch	10.8	8.9	10.7
ML width of trochlear notch	10.5	11.6	–
Superoinferior height of radial notch	6.5 (min)	6.9	9.9
ML width of trochlear notch	8.2	7.9	17.0

Specimen **CD 3311** (Fig. 3(c)) is a left proximal ulna of an adult primate with a damaged olecranon. The relative height of the olecranon and retroflexion cannot be assessed. The bone preserves 65.9 mm from the most proximally preserved portion just superior to the triceps tendon groove to a break in the shaft. The groove for the triceps tendon is only weakly developed. At the break in the shaft, the bone measures 16.2 mm AP and 10.3 mm ML. The trochlear notch is tall and narrow. Like CD 3349, there is a strong pit just inferior and medial to the trochlear notch. Also medial to the trochlear notch is a concave region where there appears to be an impression of a carnivore tooth mark. The inferior aspect of the trochlear notch is only weakly expanded medially. The radial notch faces anteriorly and is ML expanded, as is the case in most terrestrial forms. The lateral aspect of the notch grades into a strong pillar of bone that continues distally, forming two narrow concavities on either side for the insertion of the supinator and muscles of the thumb. Just inferior to the trochlear notch, the shaft measures 19.0 mm AP and 13.5 mm ML (point of break in the CD 3349 specimen).

Specimen **CD 13315** (Fig. 3(a)) is a left proximal ulna of a juvenile primate, and in many ways is quite different from both CD 3349 and CD 3311. While these two specimens appear to have terrestrial adaptations, CD 13315 may be from a more arboreally-adapted monkey. The bone preserves 65.4 mm from the proximal epiphyseal surface to a break in the shaft. At the break, CD 13315 is 13.3 mm AP and 10.2 mm ML. Though there is some erosion around the trochlear notch, it appears to be tall and narrow. Proximally to the notch, there is a groove for the triceps tendon, a morphology best developed in arboreal colobines (Harrison, 1989). The olecranon is not preserved and there is what appears to be a layer of cartilaginous, unorganized bone indicating an epiphyseal surface. Unlike in colobines, the olecranon does not slope anteriorly. Medially, there is a concavity for the origins of deep digital flexors. The radial facet is more SI expanded than in the similarly sized CD 3311, more indicative of an arboreal lifestyle than a terrestrial one (Elton, 2002). The trochlear fossa does not appear to be expanded medially, though erosion precludes an accurate measurement. Just inferior to the trochlear fossa, the shaft is 15.6 mm AP and 13.0 mm ML, and is thus rounder than the homologous location in CD 3349 and CD 3311.

Specimen **CD 7312** is the distal epiphysis of a left ulna of a large cercopithecoid. The styloid is quite large, bulbous, and distally projecting. The carpal surface measures 9.8 mm dorsopalmarly and 7.1 mm ML.

Several fragments of the radius are preserved at Cooper's D. Specimen **CD 1968** is the midshaft region of a right radius. Its preserved length is 57.4 mm. Its ML width is 15.7 mm and AP width is 10.2 mm. A strong interosseous crest is preserved, like in cercopithecine radii, and unlike the radii of colobines. **CD 3217** is

another distal shaft fragment of a right radius, preserving 47.9 mm from the broken shaft to the unfused epiphyseal surface.

Specimen **CD 8309** is a distal epiphysis of a left radius. Its maximum AP diameter is 12.5 mm. Its maximum ML diameter measured from the distal ulnar articular surface to the tip of the styloid process is 19.3 mm, similar in size to an adult modern *Theropithecus* (Jolly, 1972). It has a deep notch on the ventrolateral side that accentuates the size of the styloid process.

Specimen **CD 11445** is the proximal end of a left radius. Its preserved length is 34.7 mm. Its head is 17.3 mm wide in a ML direction, similar in size to modern *Theropithecus* (Jolly, 1972). Its neck length is 14.5 mm from the medial side of the proximal end to the proximal aspect of the radial tuberosity. The neck has a ML width of 11.6 mm and an AP width of 10 mm. The head has a deep articular surface with an eccentrically positioned fovea. The proximal ulnar articular surface has a distinct constriction as it runs from posterior to lateral, like in *Papio* and *Theropithecus*.

Specimen **CD 13317** is the proximal end of a left radius. Its preserved length is 28 mm. Its head is 20.8 mm wide in a ML direction, within the range of *Theropithecus oswaldi* specimens from the Okote formation, Koobi Fora, Kenya (Jablonski and Leakey, 2008). The ML width just distal to the head is 15.4 mm. The head has a deep articular surface with an eccentrically positioned fovea. The anterior side of the head has been sheared off. The proximal ulnar articular surface has a distinct constriction as it runs from posterior to lateral, like in *Papio* and *Theropithecus*.

4.1.4. Metacarpals

Cooper's D preserves several metacarpals and all five digits are represented. Standard linear dimensions, when available, for each metacarpal are presented in Table 3.

Specimens **CD 966** and **CD 7313** are the proximal ends of a first metacarpal. The proximal articular facet is MLly convex and dorsopalmarly concave in both specimens. **CD 3335** is another first metacarpal of a large sub-adult. The entire bone is preserved except for the proximal articular surface, which preserves the unfused epiphyseal surface. **CD 3905** and **CD 5832** are first metacarpals of juvenile primates with unfused (and missing) proximal epiphyses. **CD 667** is the proximal half of a juvenile left second metacarpal. As in most cercopithecoids, the proximal articular surface is dorsally canted and lacks a deep notch on its dorsal aspect. It is similar to both *Papio* and *Theropithecus*.

Specimen **CD 8310** is a right third metacarpal from a juvenile primate. Its head is missing, but the morphology of the metaphysis is intact. **CD 8366** is a left third metacarpal from a medium sized animal. Its head is missing and the palmar portion of the proximal end is broken. It is smaller than living adult male baboons. The distal surface is broken, but there are preserved regions of the unfused epiphyseal surface suggesting this is a juvenile. **CD 7350** is a near complete third metacarpal from a large sub-adult; only its unfused head is missing. The base possesses a pinched-in medial side, more similar to the base morphology of *Theropithecus* than *Papio* third metacarpals. [Tentative assignment: *Theropithecus*].

Specimen **CD 972** preserves the proximal end of a left fourth metacarpal. It is very similar to extant *Theropithecus* and *Papio* in terms of overall size and shape. The proximal articular surface is dorsally canted. The articulation for the fifth metacarpal is rectangular in shape with a shallow concavity. The fifth metacarpal facet is similarly rectangular in extant *Theropithecus*, but is invaginated in *Papio*. On the radial side, the dorsal articular surface is square-shaped, and is separated from the palmar articular surface by a wide furrow. [Tentative assignment: *Theropithecus*].

Specimen **CD 3844** is the proximal half of a right fifth metacarpal from an animal similar in size to extant *Papio*. The proximal articular surface is dorsally canted and there is deep fossa on the medial side of the styloid process. Its morphology is most similar to *Papio*. [Tentative assignment: *Papio*].

Specimen **CD 7316** is a left fifth metacarpal from a gracile primate. Its distal epiphysis is missing. The proximal articular surface is dorsally canted. The dorsal edging of the proximal articular surface makes it appear more like *Theropithecus* or even like colobine monkeys. [Tentative assignment: *Theropithecus*].

4.2. Lower limb

4.2.1. Os coxae

Specimen **CD 3939** is a complete right ischium of a very young primate. The acetabulum preserved is 12.9 mm AP, with the articular surface a maximum 6.0 mm in width. The rim of the obturator groove is fully preserved and is strongly curved with a maximum internal diameter of 13.1 mm. Inferior to the acetabu-

Table 3
Metapodial dimensions (in mm) of cercopithecoid remains from Cooper's D locality (Cooper's Cave system, Bloubank Valley, Gauteng, South Africa).

Specimen	Metapodial (MC or MT)	Side	Length[a]	Distal AP	Distal ML	Proximal AP	Proximal ML	Midshaft AP	Midshaft ML
CD 966	MC1	?	~24.9	–	–	–	7.8	4.2	4.8
CD 3335	MC1	?	~39	10.7	13.4	–	–	6.3	7.7
CD 3905	MC1	?	~24.3	7.0	–	–	–	3.6	4.5
CD 5832	MC1	?	~19.5	4.9	–	–	–	3	3.7
CD 7313	MC1	?	~20.6	–	–	–	9.9	4.6	4.8
CD 667	MC2	Left	~21.8	–	–	9.5	6.4	4.3	4.6
CD 7350	MC3	Left	~39.1	–	–	10.9	9.5	9.3	–
CD 8310	MC3	Right	~28.6	–	–	8	6.5	3.7	4.3
CD 8366	MC3	Left	~33.6	–	–	–	7.3	4.7	5.7
CD 972	MC4	Left	~14.3	–	–	9.6	–	–	–
CD 3844	MC5	Right	~34.7	–	–	–	8.6	6.6	–
CD 7316	MC5	Left	~33	–	–	–	–	–	–
CD 964	MT1	Right	–	–	–	–	–	–	–
CD 1158	MT1	Right	–	–	–	–	–	–	–
CD 1717	MT1	Right	–	–	–	–	–	–	–
CD 3329	MT1	Left	–	–	–	–	–	–	–
CD 5868	MT1	Left	–	–	–	–	–	–	–
CD 3229	MT3	Right	~28.2	–	–	12.5	10.1	7.3	–
CD 8294	MT3	Left	~22.3	–	–	5.9	6.3	–	–
CD 8376	MT3	Right	~23.4	–	–	10.4	10.6	–	–
CD 941	MT4	Left	~22.1	–	–	9.9	6.8	–	–

[a] None of these specimens are complete and these length measurements are their maximum preserved lengths.

lum is a strongly developed pillar of bone, 6.8 mm thick that terminates in the most lateral aspect of the ischial tuberosity. The tuberosity is convex ML, and 6.0 mm in maximum AP width. Medially, the ischium tapers to a point only 2.2 mm SI. The ischiopubic ramus is shallow like that found in *Papio*. The distance from the acetabular rim inferiorly to the start of the ischial tuberosity is 12.5 mm. [Tentative assignment: *Papio*].

Specimen **CD 6682** is a right ischium of a sub-adult primate preserving the most inferior aspect of the acetabulum and much of the ischial tuberosity. It is 72.3 mm from the fractured region of the acetabulum inferiorly to the most distal tip of the ischial tuberosity. The acetabulum is 12.2 mm wide. The inferior aspect of the acetabulum is ML narrow, like that in *Papio*. *Theropithecus* tends to have a ML wider acetabulum inferiorly. Inferior to the acetabulum is a pillar of bone 16.2 mm thick. Medial to this pillar is the rim of the obturator foramen, though there is erosion all around the rim. The most medial preserved region of the ischium is only 15.0 mm SI, making it quite short and stout. The distance from the acetabular rim to the ischial tuberosity is 29.4 mm. The ischial tuberosity itself is 51.6 mm ML and 25.6 mm at its widest AP. It is triangular in shape, with the apex medially and the widest point laterally positioned. It is elongated posteriorly, much like the condition in *Theropithecus*. There is trabecular bone exposed on the surface of the ischial tuberosity and patches of cartilaginous growth plate, suggesting that this bone belonged to a sub-adult. The prominent groove superior to the obturator internus muscle found in CD 13445 (see below) is only moderately palpable in this specimen. The ischiopubic ramus is quite shallow, like that found in *Papio*.

Specimen **CD 13445** is a right os coxa with a complete acetabulum and parts of the ilium and ischium (Fig. 4). It measures 170.6 mm SI from the broken superior iliac crest to the broken base of the ischium. There are several vertical fractures in the ilium, and it is at most only 27.6 mm wide at its most preserved section. Medially, the auricular surface is palpable, and preserved for 52.4 mm of its length SI. Because of damage to the medial aspect of this surface, only 12.5 mm of its width is preserved maximally. The preserved medial surface of the ilium is flat, while the lateral surface is moderately concave ML. The superior part of the ilium does not preserve any borders, with the exception of the partially preserved auricular surface. Inferiorly, a minimum iliac breadth can be estimated: 24.0 mm. The ilium breadth/acetabulum ratio is quite low (82.5), and like that found in *Papio* and *Theropithecus* (Fleagle and McGraw, 2002). The border of the sciatic notch is sharp and the preserved 24.8 mm superior to the acetabulum is quite straight, showing no evidence of curvature. Superior to the acetabulum is a large rugosity for the origin of the rectus femoris. The acetabulum is well preserved and is 31.6 mm SI and 29.1 mm AP, making CD 13445 larger than *T. brumpti*, but smaller than East African *T. oswaldi* (Jablonski and Leakey, 2008; Gilbert et al., 2011). The maximum internal dimension of the acetabulum, not including the rims, is 26.1 mm. The acetabulum is quite deep, 17.4 mm from the deepest point to a tangent connecting the rim of the acetabular surface. The acetabulum is cracked in the most superomedial region, but relative articular widths can be taken. Superiorly, the articular surface is 12.6 mm; laterally, it narrows to 9.8 mm and inferiorly it widens to 13.0 mm. Inferior to the acetabulum is smooth and there is no groove as is found in modern *Theropithecus* os coxae. Inferior and medial to the acetabulum, the rim of the obturator foramen is preserved for 35.2 mm. It is sharp, and there is a small tubercle projecting medially into the foramen just inferior to the level of the acetabulum, like that found in *Theropithecus*, but not *Papio*. Laterally and inferior to the acetabulum is a 17.3 mm thick pillar of bone that flares laterally to begin the ischial tuberosity (not preserved). Medially, there is a palpable groove 13.7 mm wide superior to the attachments for the obturator internus. The distance from the most caudal point of the sacral articular surface to the center of the acetabulum (measurement designated LILILEN in Jablonski and Leakey, 2008) is 77.5 mm [Tentative assignment: *Theropithecus*].

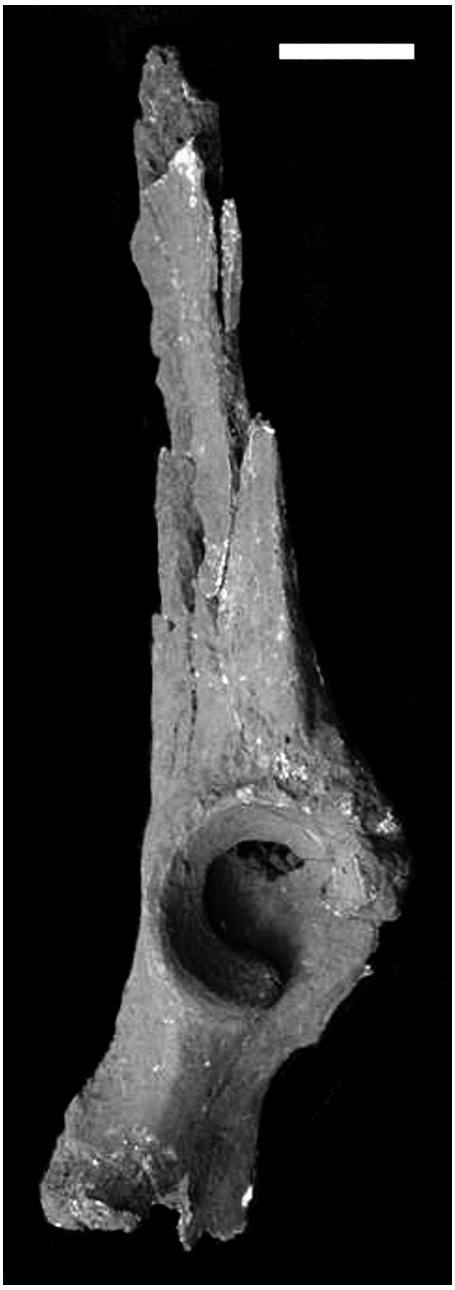

Fig. 4. CD 13445, a well preserved pelvis of cercopithecoid (possibly from a *Theropithecus*) from Cooper's D, in lateral view. Scale bar: 2 cm.

4.2.2. Femur

Femoral fragments are relatively abundant at Cooper's D (Fig. 5; Table 4). Specimen **CD 633** (Fig. 5(e)) is a large right proximal femur preserving the most proximal aspect of the shaft, but not the femoral head, neck or greater trochanter. The lesser trochanter has also been sheared away. The shaft has a small (39.1 mm SI, 18.6 mm ML) piece of bone that has broken away from the main

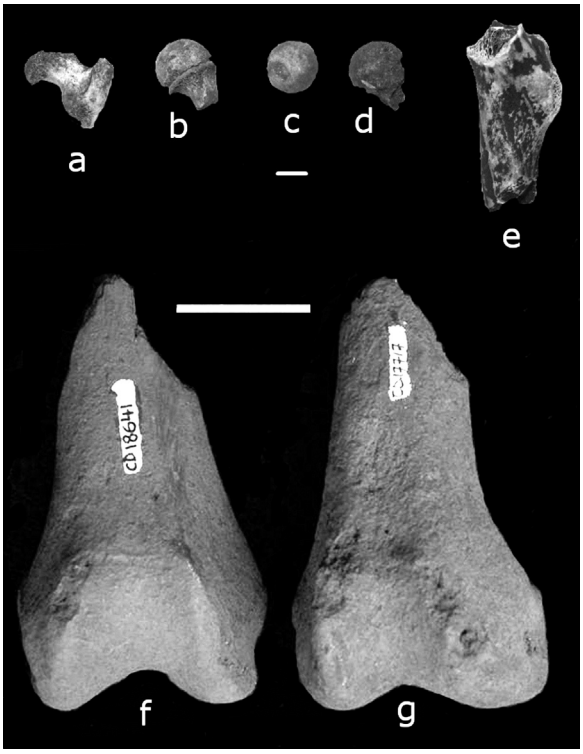

Fig. 5. a-e: Proximal femora of cercopithecoids from Cooper's D in anterior view. a: CD 3319; b: CD 3306; c: CD 3294; d: CD 3926; e: CD 633. **f**, **g**: Distal right femora of cercopithecoids from Cooper's D in anterior view. f: CD 18641; g: CD 17717. Note that CD 18641 has a deeper patellar groove and lacks the indentation superior to the patellar surface found on CD 17717. CD 18641 resembles modern *Papio* whereas CD 17717 is more *Theropithecus*-like. Scale bars: 1 cm (a–e), 2 cm (f, g).

fossil. The fossil is 64.2 mm from the beginning of the femoral neck around the level of the trochanteric fossa to the break in the femoral shaft. The lesser trochanter, though eroded, appears to be quite long and medially oriented. The subtrochanteric region is round, measuring 20.1 mm AP and 20.6 mm ML. At the break in the shaft, the cortical bone is thickest posteriorly. Immediately lateral to the lesser trochanter is a small depression for the insertion of the quadratus femoris. Continuing laterally and slightly inferiorly is a palpable but weakly developed gluteal tuberosity for the gluteus maximus. Inferior and slightly medial to the gluteal tuberosity, just superior to the break in the shaft is a rugose region, presumably for attachment of the adductors. Anteriorly and medially, just inferior to the proximal break, is a groove for the insertion of the gluteus minimus, a morphology typical of *Theropithecus* femora (Krentz, 1993). [Tentative assignment: *Theropithecus*].

Specimen **CD 1379** is a large lateral condyle of a right distal femur. The pit for the popliteus is quite large: 10.8 mm AP, and 7.8 mm SI. Immediately superior to the popliteal origin is a small pit for insertion of the lateral ligaments of the knee. The lateral condylar articular surface is strongly convex. It is 15.4 mm wide posteriorly, and preserves 14.3 mm anteriorly, terminating in a flattening of bone medially, indicating an elevated lateral rim to the patellar groove.

Specimen **CD 3294** (Fig. 5(c)) is the proximal epiphysis of a left femoral head. The head is spherical, with a maximum diameter of 17.7 mm. The fovea capitis is eccentrically positioned, large (6.8 mm AP, 3.9 mm SI) and oval in shape, unlike the elongated fovea found in *Theropithecus oswaldi* (Krentz, 1993). [Tentative assignment: *Papio*].

Specimen **CD 3306** (Fig. 5(b)) is a conjoining set of bones from the right femur of a juvenile primate. It consists of the femoral head epiphysis, and the epiphyseal surface and part of the femoral neck. It is sheared in the transverse plane such that the most superior part of the femoral head and neck are not preserved at all, but reveals trabecular bone in these regions. The femoral head is 19.9 mm in maximum diameter, and contains an oval fovea capitis 7.2 mm AP and 4.2 mm SI. Articulated with the metaphysis, it can be seen that the articular surface of the femoral head is clearly separated from the femoral neck anteriorly and inferiorly, but begins to grade into the neck posteriorly.

Specimen **CD 3319** (Fig. 5(a)) is the right proximal femur of a juvenile primate, sheared in the coronal plane such that the posterior aspect is preserved, but the anterior is not. The inferior rim of the femoral head tilts inferiorly, creating a small lip of bone typical of terrestrial cercopithecoids. The femoral neck is long, 18.0 mm from the edge of the femoral head epiphysis to the trochanteric crest. A relatively elongated femoral neck is a feature found in *Theropithecus* (Elton et al., 2003), though a short femoral neck has also been suggested for this taxa (Krentz, 1993). The neck is 11.6 mm tall SI. The neck shaft angle is approximately 110°, similar to the values found in terrestrial cercopithecoids (Frost and Delson, 2002). The edge of the epiphyseal surface for the greater trochanter is located superiorly, almost level with the superior surface of femoral head epiphysis, suggesting that the greater trochanter may have projected above the surface of the femoral head, as found in terrestrial primates. The epiphysis for the lesser trochanter is quite large, positioned posteriorly, and angled from superomedial to inferolateral. Anteriorly, cortical bone and trabecular struts are visible.

Specimen **CD 3841** is a right distal femoral epiphysis that is associated with the right distal femoral shaft **CD 5294**. The shaft is roughly perpendicular to the femoral condyles, indicating that there is no reverse carrying angle as is found in *Theropithecus*. Articulated, CD 3841/5294 preserves the distal 74.6 mm of the femur. Laterally, just inferior to the break is an oval-shaped large puncture in the shaft measuring 12.7 mm SI and 8.7 mm ML. Posteriorly, supracondylar lines are detectable. Superior to the patellar surface, there is no indentation of bone as is often found in *Theropithecus*. Just superior to this region, the shaft dimensions are 16.1 mm ML and 11.8 mm AP. The epiphyseal surface is strongly undulated with grooves about 3.5 mm rising SI both laterally and medially. Anteriorly and posteriorly, the grooves are wider and shallower (3.0 mm SI) for the corresponding facets on the distal femoral epiphysis. The epiphysis is 28 mm wide ML, and 19.4 mm deep AP. The patellar surface is relatively flat, with only very moderate convexity between lateral and medial lips of bone. The lateral condyle is strongly convex. The medial condyle is only

Table 4
Distal femur dimensions (in mm) of cercopithecoid remains from Cooper's D locality (Cooper's Cave system, Bloubank Valley, Gauteng, South Africa).

Measurement \ Specimen	CD 1379	CD 3841/5294	CD 17717	CD 18641
AP depth of lateral condyle	–	17.0	28.1	26.7
Maximum ML width of lateral condyle	14.1	8.3	10.5	11.7
AP depth of medial condyle	–	17.6	31.3	–
Maximum ML width of medial condyle	–	8.8	13.8	13.3
Intercondylar width	–	11.0	10.8	8.6

slightly larger and also convex. There is a large intercondylar width relative to the size of the bone. Collateral ligament attachments and the groove for the popliteal tendon are not detectable. [Tentative assignment: *Papio*].

Specimen **CD 17717** is a right distal femur (Fig. 5(g)), 62.8 mm from the broken femoral shaft to the end of the femoral condyles. Other than some minor erosion to the lateral condyle, this fossil is well preserved. The lateral and medial patellar rims are equally elevated creating a deep patellar groove. The lateral condyle is strongly convex. The medial condyle is considerably larger, but less convex than the lateral condyle. A medially-dominant knee with a broad intercondylar distance is typical of terrestrial cercopithecoid forms. The lateral surface contains a small pit for insertion of the popliteus. Both laterally and medially, the epicondylar surfaces have small pits for insertion of the stabilizing ligaments of the knee. Anteriorly, the patellar groove rises 18.7 mm superiorly from the most inferior aspect of the femoral condyles. Just superior to the patellar surface is a depression common in modern *Theropithecus* but not often found in *T. oswaldi* (Krentz, 1993). Just superior to this depression, the shaft measures 20.1 mm ML and 16.5 mm AP. The femoral shaft is perpendicularly oriented relative to the femoral condyles, and does not have the reverse carrying angle found in *Theropithecus*. The dimensions of this fossil are similar to *Theropithecus oswaldi* (KNM-ER 3877) from the Upper Burgi member of Koobi Fora, Kenya (Jablonski and Leakey, 2008). [Tentative assignment: *Theropithecus*].

Specimen **CD 18641** is also a right distal femur (Fig. 5(f)). It measures 63.6 mm from the broken femoral shaft to the inferior surface of the femoral condyles. The medial condyle is damaged posteriorly, and much of the shaft is broken, but otherwise preserves important detail. Unlike CD 17717 (see above), the lateral rim of the patellar groove is considerably more elevated than the medial rim. The lateral condyle is strongly convex. The AP dimension of the medial condyle cannot be assessed due to damage posteriorly; however, the width of the condyle can be measured and is considerable larger than the lateral (Table 4). Medial condylar dominance is found in terrestrial forms. Laterally, there is a substantial pit for the popliteus insertion, which may have merged superiorly with insertions for knee ligaments. The lateral epicondyle is located just superiorly and posteriorly to the popliteal groove. The patellar surface extends 20.8 mm superiorly from the condyles, but unlike CD 17717, there is no depression superior to the patellar surface. The femoral shaft measures 22.1 mm ML and 15.7 mm AP. The femoral shaft is perpendicularly oriented relative to the femoral condyles, and does not have the reverse carrying angle found in *Theropithecus*. CD 18641 is smaller than CD 17717 and other fossil *Theropithecus*. [Tentative assignment: *Papio*].

Specimen **CD 3926** (Fig. 5(d)) is a poorly-preserved left femoral head preserving a small part of the femoral neck. It is spherical in shape and measures 19.3 mm in diameter, making it small for the adult primates at Cooper's D and smaller than modern *Theropithecus*. There is a poorly defined fovea capitis, posteriorly located, and not as deeply excavated into the femoral head as is typical in primates. There is also a small groove emanating from the fovea- if this is normal morphology and not erosion, then this is probably a carnivore femur.

There are two fragmentary femoral shafts. Specimen **CD 3925** is a femoral midshaft fragment measuring 73.1 mm in length; **CD 3747** is a femoral midshaft fragment measuring 64.2 mm in length.

4.2.3. Tibia and fibula

Measurements for tibia specimens are found in Table 5. Specimen **CD 960** is a well-preserved left proximal tibial epiphysis, with only minor erosion along the lateral edge of the condyle. The lateral condyle is moderately convex AP and flat ML before rising medially toward the intercondylar eminence. The lateral condyle is 24.7 mm AP and 21.2 mm ML, and resides on a slightly more superior plane than the medial condyle. The medial condyle is flat both AP and ML, and measures 27.5 mm AP and 19.9 mm ML. The intercondylar eminence is 9.1 mm ML and roughly 5.2 mm AP, and angled from anteromedial to posterolateral. Posterolaterally, the fibular facet is 12.2 mm AP and 9.4 mm SI.

Table 5
Distal tibia dimensions (in mm) of cercopithecoid remains from Cooper's D locality (Cooper's Cave system, Bloubank Valley, Gauteng, South Africa).

Measurement \ Specimen	CD 3326	CD 5867	CD 9596	CD 23239
AP metaphysis	18.8	17.7	17.8	23.8
ML metaphysis	20.5	21.5	20.2	27.0
AP talar surface	16.8	13.2	13.9	17.5
ML talar surface	16.6	15.3	13.8	18.5
Superoinferio medial malleolus	10.0	10.4	10.3	10.8
AP medial malleolus	16.3	15.1	12.7	19.4
ML medial malleolus	8.4	7.2	7.5	9.8

Specimen **CD 3318** is a right proximal tibial shaft of a large juvenile primate, missing the proximal epiphysis. It is 55.5 mm from the epiphyseal surface to the break in the tibial shaft. Given the location of discovery, size, and stage of development, it could be from the same individual as CD 960 (see above), though not from the same side. The epiphyseal surface is 35.6 mm ML and 25.9 mm AP, with the medial side occupying more of that area. Anteriorly, the epiphyseal surface grades into the epiphysis for the tibial tuberosity. The region occupied by the elongated tibial tuberosity is roughened with striated bone. At the base of the tibial tuberosity, the shaft is ML compressed: approximately 26.7 mm AP and 17.6 mm ML. Lateral and medial to the tibial tuberosity, there are slight grooves for the attachment of the tibialis anterior and popliteus muscles respectively. Laterally, there is a depression in the bone 13.7 mm SI and 8.4 mm ML that may be a healed wound. Posteriorly, the shaft becomes ML broad, such that the tibia is triangular in the transverse plane.

Specimen **CD 3326** (Fig. 6(d)) is a very-well preserved left distal tibia preserving 89.7 mm from the tip of the medial malleolus to the break in the tibial shaft. It is similar in size to modern *Papio*. The metaphysis is approximately square-shaped. The medial malleolus does not have the strongly bulbous morphology found in modern terrestrial cercopithecoids and is relatively flat instead. Laterally, there is no fibular facet. Posteriorly, there is some erosion, but the malleolar groove can be detected and is quite wide and shallow: 5.6 mm ML, 0.8 mm deep. Anteriorly, there is a very small dorsiflexion facet that spills from the articular surface onto the anteromedial aspect of the bone. The articular surface is roughly square-shaped at the midpoints. A keel divides the medial and lateral surfaces into roughly equal regions, and becomes more pronounced anteriorly. The articular surface is angled relative to the tibial shaft resulting in a valgus set to the ankle joint. Superiorly, the tibial shaft becomes ML compressed, and is 18.0 mm AP and 14.0 mm ML at the point of break, similar to the condition found in terrestrial cercopithecoids.

Specimen **CD 3922** is the right proximal tibial epiphysis of a very young primate. The epiphysis is 25.4 mm ML and 17.9 mm AP. The lateral condyle is convex and approximately 13.3 mm AP and 9.9 mm ML, though these measurements are estimates given that the borders of the condyle are not clearly delineated on such a young individual. The medial condyle is flat and measures 16.2 mm AP and 8.8 mm ML. An intercondylar notch is forming between the two condyles.

Specimen **CD 5867** (Fig. 6(a)) is a well-preserved right distal tibia, 28.2 mm from the tip of the medial malleolus to the break in

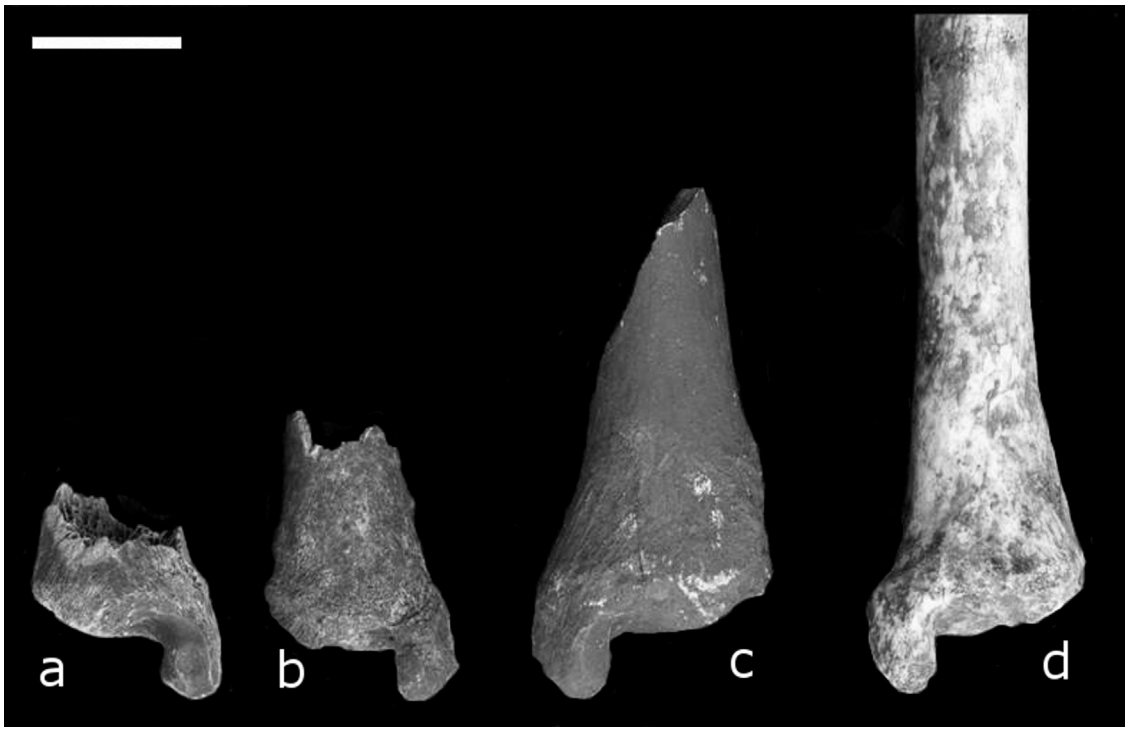

Fig. 6. Well-preserved distal tibiae of cercopithecoids from Cooper's D shown in anterior view. **a**: CD 5867; **b**: CD 9596; **c**: CD 23240; **d**: CD 3326. Scale bar: 2 cm.

the tibial shaft. It is similar in size to modern *Papio*. The metaphysis is cercopithecoid-like in being relatively square-shaped. The malleolus is quite bulbous, a morphology suggested to increase ankle stability in terrestrial cercopithecoids (Harrison, 1989). Laterally, there is no evidence of a fibular facet. The posterior aspect of the bone is dominated by the malleolar groove running superolaterally to inferomedially. It is 3.1 mm wide and 0.4 mm deep. Anteriorly, there is a V-shaped beak at the terminus of the tibial plafond keel, which divides the surface into roughly equal lateral and medial articular surfaces. The articular surface is square-shaped. The articular surface is angled relative to the tibial shaft, producing a valgus set.

Specimen **CD 9596** (Fig. 6(b)) is a right distal tibia preserving 40.1 mm from the tip of the medial malleolus to the break in the tibial shaft. It is similar in size to modern *Papio*. It is quite weathered, with erosion concentrated laterally and posteriorly. The metaphysis is square-shaped. The medial malleolus is SI elongated, robust, and not as bulbous as that found in most terrestrial cercopithecoids. There appears to be a very small fibular facet located just anteriorly to the eroded lateral surface, found occasionally in arboreal quadrupeds (Ford, 1988), though there is erosion in this area. Anteriorly, the rim of the articular surface projects inferiorly in a V-shape formation. There is a very small dorsiflexion facet that is a continuation of the talar articular surface onto the anterior face of the bone. A strong keel dividing the tibial plafond in the sagittal plane becomes more pronounce anteriorly and terminates in a beak. The articular surface is angled relative to the tibial shaft, producing an inverted set to the ankle joint. At the point of break in the tibial shaft, the dimensions are 16.1 mm ML, and 14.8 mm AP, and the cortical bone is thickest anteriorly.

Specimens **CD 23239**, **CD 23240** (Fig. 6(c)), and **CD 23242** are associated fragments of a left distal tibia and tibial shaft from a large primate. The distal dimensions are considerably larger than modern *Papio* or *Theropithecus*, and are similar in size to East African *T. oswaldi* (Jablonski and Leakey, 2008). CD 23239 and CD 23242 join at a clean break to form the middle part of the tibial shaft, though the distal portion of CD 23239 does not form a clean articulation with CD 23240, the distal piece. CD 23240 preserves 62.2 mm from the tip of the broken shaft laterally to the medial malleolus. The metaphysis is roughly square-shaped. Medially, the malleolus is not very bulbous at all and instead is relatively flat for a corresponding cotylar fossa facet on the talus. Laterally, there is no fibular facet. Anteriorly, the rim of the articular surface produces a V-shaped beak that is angled superolaterally. There is a strongly developed dorsiflexion facet that is excavated into the anteromedial aspect of the distal tibia. Posteriorly, the malleolar groove is well developed, 6.4 mm wide and 1.6 mm deep. A strong central keel divides the talar articular surface into roughly equal medial and laterally portions. The articular surface is angled relative to the tibial shaft, producing an inverted set to the ankle joint. The tibial shaft preserved by CD 23239 and CD 23242 is 112.8 mm long, possesses some lateral bowing and is slightly curved AP. The shaft is strongly ML compressed and is 25.1 mm AP and 16.4 mm ML at the location of the nutrient foramen on the posterolateral side of the shaft. Anteriorly, the shaft is dominated by a strong insertion for the tibialis anterior 57.5 mm from the break in the shaft inferiorly. Medially to this insertion are rugosities angled superomedial to inferoposterior for semitendinous, gracilis, and sartorius. Posteriorly and laterally, there are two strong ridges of bone running almost directly along the long axis of the bone demarcating the insertions of the tibialis posterior and the flexor digitorum tibialis.

Specimen **CD 949** is the distal one third of a robust left fibula. It measures 57.7 mm in length. The distal end has an AP width of 15.5 mm and a ML breadth of 12.7 mm. The ML diameter of the preserved proximal end is 5.9 mm and its AP diameter is 8.9 mm. The groove for the tendons of peroneus longus and peroneus brevis is well developed.

Specimen **CD 1145** is approximately the distal one fifth of a gracile left fibula. It measures 27.5 mm in length. The distal end has an AP width of 11.3 mm and a ML breadth of 7.7 mm. The ML diameter of the preserving proximal end is 4.4 mm and its AP

diameter is 5.9 mm. The groove for the tendons of peroneus longus and peroneus brevis is only moderately developed in this specimen.

4.2.4. Tarsals

There are several well-preserved partial tali recovered from Cooper's D, but the majority of them cannot be attributed to any taxon. Specimen **CD 950** is a left talus from a large adult primate. The head and the medial rim of the talar trochlea have some damage and exposed trabecular bone, but otherwise this talus is well preserved. It is quite similar in size and morphology to CD 5733 (see below). The trochlea is grooved, with a high lateral rim. It is 15.3 mm ML at its midpoint. There is a well-developed cotylar fossa, and the fibular facet strongly projects laterally. The groove for flexor hallucis longus is only slightly detectable. The head appears to be similarly shaped to CD 5733, and is 14.9 mm ML, though erosion around the plantar edge makes a height measurement difficult to take. The head and neck are angled medially 27.8° relative to the long axis of the trochlea.

Specimen **CD 5733** is a well-preserved left talus from a large adult primate. It is consistent in size and has a similar patina to the CD 6671 calcaneus (see below). The talar trochlea has a strong groove, and the lateral rim of the trochlea rises significantly above the medial. The trochlea is only mildly wedged. It is 15.6 mm ML at its midpoint, similar in size to modern *Papio*. Laterally, the fibula facet projects weakly. Medially, there is a strongly cupped cotylar fossa to receive a bulbous medial malleolus. The head and neck are angled medially 23.7°relative to the long axis of the trochlea. The head is slightly rotated, and is 15.0 mm along the ML axis and 11.9 mm dorsoplantarly. The distal calcaneal facet extends quite distally and is continuous with the talar head, as is the case in cercopithecine monkeys (Strasser, 1988).

Specimen **CD 7281** is a left talus from a medium-sized adult primate. There is damage to the head, and the anterior part of the talar trochlea. The preserved part of the bone is 27.2 mm PD, and 24.2 mm ML. The lateral rim is elevated above the medial rim. The midpoint of the trochlea is 12.9 mm ML, similar in size to modern *Theropithecus*. The fibular facet only mildly projects laterally. The head and neck are angled medially 33.3° relative to the long axis of the trochlea.

Specimen **CD 8291** is a right talus from a large adult primate. The head is sheared off and there is some damage on the medial aspect of the bone, and along the lateral rim. The trochlea is strongly grooved, and the lateral rim rises well above the medial. The trochlea is 14.9 mm ML at its midpoint, similar in size to modern *Papio*. There is damage in the region of the flexor tibialis groove, making it difficult to characterize that important anatomy (Gilbert et al., 2010).

Several calcanei have been preserved from Cooper's D, representing adults and juveniles of varying size. Specimen **CD 79** is a medium-sized right calcaneus preserving the distal portion from the proximal talar facet to the cuboid articular surface. The preserved bone is 28.8 mm PD, and 16.7 mm dorsoplantarly. The cuboid facet is quite flat, though there is erosion around the perimeter of the facet. It is 13.1 mm dorsoplantarly, and 13.7 mm ML. There is a weakly projecting peroneal trochlea laterally, and medially there is a strong groove for the flexor hallucis longus under the sustentaculum tali. The proximal talar facet is strongly convex, and is 13.1 mm PD and 10.4 mm ML.

Specimen **CD 3350** is a well-preserved right calcaneus of a large adult primate, missing only the calcaneal tuber. The preserved part is 47.7 mm PD. The calcaneal body is relatively shallow compared to the overall length of the bone: 20.2 mm dorsoplantarly. Laterally, there is a distinct but unremarkable peroneal trochlea. Just proximal to that is a deep pit for the calcaneofibular ligament. The proximolateral aspect of the bone is heavily damaged. Medially, a distinct groove for the flexor hallucis longus tendon runs under a weakly projecting sustentaculum tali. The cuboid facet is reniform, strongly concave and 16.7 mm dorsoplantarly and 15.0 mm ML. The proximal talar facet is curved, plantarly inclined, and measures 16.1 mm PD and 10.7 mm ML.

Specimen **CD 5418** is a very small complete left calcaneus, possibly from an infant. It is only 22.5 mm long PD. Laterally, the peroneal trochlea is indistinct perhaps owing to the young age of this individual, though there is a pit for the calcaneofibular ligament. The cuboid facet is flat, and is 7.1 mm high and 8.0 mm wide. The epiphyseal surface of the calcaneal tuber is 9.2 mm high and 6.1 mm wide. The proximal talar facet is 9.3 mm PD and 5.8 mm wide.

Specimen **CD 6671** is a large, well-preserved left calcaneus of a sub-adult primate, missing only the most dorsal part of the calcaneal tuber. It is 53.4 mm PD from the cuboid facet to the most proximal aspect of the tuber, only slightly shorter than a *Theropithecus oswaldi* calcaneus (KNM-ER 569) from the Okote member, Koobi Fora, Kenya (Jablonski and Leakey, 2008). The proximal calcaneal body is 28.2 mm, producing a long lever arm for the triceps surae. The calcaneal body is 24.3 mm dorsoplantarly. The calcaneal apophysis is attached to the body, and the epiphyseal line is still visible. The lateral aspect of the bone is dominated by a large peroneal trochlea, significantly larger than the peroneal trochlea in CD 3350 (see above). Distally, the cuboid facet is reniform in shape, and strongly concave dorsoplantarly. There is some damage medially to the sustentaculum tali, though plantarly a strong groove for flexor hallucis longus can be seen. Proximally on the medial aspect of the bone is a large pit for the calcaneofibular ligament. The proximal talar facet is curved and plantarly inclined. It is 17.0 mm PD and 12.4 mm ML.

Specimen **CD 7852** is a very well preserved, complete left juvenile calcaneus. Proximodistally, this calcaneus is 32.6 mm from the cuboid facet to the epiphyseal surface of the calcaneal tuber. Dorsoplantarly, it is 15.0 mm high. Laterally, there is a strongly projecting peroneal trochlea, and more proximally there is a pit for the calcaneofibular ligament. The cuboid facet is quite flat, perhaps owing to the juvenile nature of the specimen, and is 12.0 mm dorsoplantarly and 12.5 mm ML. Proximally, the calcaneal epiphyseal facet is 14.2 mm high and 9.8 mm wide. The proximal talar facet is 11.7 mm PD and 9.6 mm ML.

Two cuboids have been identified from Cooper's D. They are very similar in anatomy and differ only in size, with specimen **CD 3247** considerably larger than **CD 5738**. The maximum PD length of CD 3247 is 24.1 mm and its maximum ML width is 18.6 mm, whereas the same dimensions in CD 5738 are 16.8 mm and 15.1 mm, respectively. The PD elongation in both specimens is similar to both *Theropithecus* and *Papio*. In dorsal view, the cuboids are asymmetrical in shape with the lateral side of CD 3247 measuring 11.8 mm in length and the medial side measuring 19.5 mm; CD 5738 is 9.7 mm laterally and 13.6 mm medially. The maximum dorsoplantar height of CD 3247 is 16.6 mm; CD 5738 is 11.9 mm. The distal articular surface dorsoplantar height in CD 3247 is 11.7 mm and its ML breadth is 15.3 mm. The distal articular surface is broken on the plantar side in CD 5738 so its height is not measurable, but its ML breadth is 10.9 mm There is a visible keel that demarcates the regions where the fourth and fifth metatarsals would have articulated in both fossils. The proximal articular surfaces are 10.1 mm and 7.3 mm in height in CD 3247 and CD 5738, respectively, at their midpoints; they are lunate-shaped with the plantar-medial side projecting proximally past the lateral side. On the plantar side of this projection region is a deep fossa in both specimens. The lateral cuneiform facets on the medial side of the bones are rectangular, like that found in *Papio*, and unlike the more

teardrop-shaped facet on extant *Theropithecus*. There are well-developed articular surfaces on the lateral side of the peroneal sulcus for an os peroneum on both cuboids.

Specimen **CD 7364** is a right middle cuneiform of a medium-sized gracile primate. Its PD interarticular length is approximately 8.5 mm, and its dorsoplantar height is 12.0 mm. Its overall morphology is similar to both *Theropithecus* and *Papio*.

4.2.5. Metatarsals

The metatarsals of digits I, III and IV are represented in the sample at Cooper's D. Standard linear dimensions, when available, for each metatarsal are presented in Table 3.

Specimens **CD 964**, **CD 1158**, and **CD 1717** are the proximal ends of right first metatarsals. **CD 3329** and **CD 5868** are the proximal ends of left first metatarsals. All five specimens are adult and all have ovoid-shaped proximal articular surfaces with the long axis approximately in the dorsoplantar plane, which is typical of most cercopithecoid primates. All five specimens appear similar to extant *Theropithecus* and *Papio*.

Specimen **CD 3229** is the proximal one third of a right third metatarsal from a large animal. **CD 8294** is a near complete left third metatarsal of a small, and possibly gracile or juvenile primate. The distal epiphysis is missing, but the morphology of the metaphysis is intact. **CD 8376** is the proximal half of a right third metatarsal from a medium-sized primate. There is a deep cleft on the lateral side in the proximal articular surface.

Specimen **CD 941** is the proximal one third of a left fourth metatarsal, about the same size than the fourth metatarsal of extant *Theropithecus*. The specimen appears to come from a more gracile cercopithecoid.

Specimens **CD 1712**, **CD 5871**, **CD 7333**, **CD 7978**, and **CD 8380** are the distal ends of unidentifiable metapodials. The morphology of the proximal articular surface is consistent with that of cercopithecoids. In each specimen, the dorsal surface is ML narrower compared to the palmar/plantar surface (Patel, 2010).

4.3. Phalanges

There are numerous proximal, middle and distal phalanges recovered. Standard linear dimensions, when available, for each element are presented in Table 6.

Specimen **CD 672** is an unfused, short, but robust proximal phalanx. Unfortunately, both ends are missing, so it is not possible to say anything meaningful about this specimen. Specimens **CD 1148** and **CD 6677** are the proximal halves of gracile proximal phalanges. The proximal articular surfaces are dorsally canted. The plantar tubercles are only moderately developed. Specimens **CD 1711**, **CD 3355**, and **CD 8372** are gracile proximal phalanges lacking their proximal articular surfaces. These are most likely from relatively small, gracile adult primates. Specimens **CD 1161**, **CD 1719**, **CD 3354**, **CD 3365**, **CD 7261**, **CD 7264**, and **CD 7273** are juvenile proximal phalanges lacking their proximal articular surfaces. Specimen **CD 1713** is the proximal half of a robust proximal phalanx. Its proximal articular surface is dorsally canted and has plantar tubercles that are well developed.

Specimens **CD 1714** and **CD 6670** are complete proximal phalanges that are from large, robust animals. The size and dimensions are extant *Papio*-like (Jolly, 1972). Again, the proximal articular surfaces are dorsally canted and their plantar tubercles are well developed. Their shafts are not curved and their flexor sheaths ridges are not prominent in size, suggesting that they come from more terrestrial animals. Specimen **CD 8862** is a short, but very robust proximal phalanx. It is highly probable that it is from the pollex, but appears to be too small to be from the hallux. Specimen **CD 3320** is a complete proximal phalanx that is gracile in its build and more *Theropithecus*-like in its size and shape (Jolly, 1972). The proximal articular surface is dorsally canted and its plantar tubercles are only moderately developed. The shaft is not curved in this specimen either.

Specimens **CD 8384** and **CD 9030** are small, gracile middle phalanges missing their proximal ends. Specimens **CD 1151** and **CD 3368** are longer and more robust middle phalanges missing their proximal articular surfaces in both cases. All four specimens appear to be from juvenile individuals. Specimen **CD 9123** is an unfused, small, and gracile proximal phalanx. The proximal end is much wider than its distal end, suggesting that it could be a pollical or hallucal proximal phalanx of a juvenile monkey. Specimens **CD 660**, **CD 3344**, and **CD 8375** are distal phalanges. CD 3344 and CD 8375 are more robust and may represent manual phalanges; they both have well-developed muscle insertion scars for the insertion of digital flexor muscles. Their apical tufts are also larger than CD 660. None of the bones appear to come from the pollex or hallux.

Table 6
Phalanx dimensions (in mm) of cercopithecoid remains from Cooper's D locality (Cooper's Cave system, Bloubank Valley, Gauteng, South Africa).

Specimen	Position	Length	Distal AP	Distal ML	Proximal AP	Proximal ML	Midshaft AP	Midshaft ML
CD 1148	Proximal	–	–	–	6	7.7	–	–
CD 1711	Proximal	–	4.3	6	–	–	–	–
CD 1713	Proximal	–	–	–	7.9	10.5	–	–
CD 1714	Proximal	30.9	5.7	8.2	8.5	11.5	5.2	6.5
CD 1719	Proximal	–	4.3	6.2	–	–	–	–
CD 3320	Proximal	22.9	3.8	5.9	6.2	8.3	3.4	4.7
CD 3354	Proximal	–	3.7	5.6	–	–	–	–
CD 3355	Proximal	–	3.4	4.9	–	–	–	–
CD 3365	Proximal	–	3.4	5.2	–	–	–	–
CD 6670	Proximal	30	5	7.7	8.2	11.5	5.1	6.8
CD 6677	Proximal	–		–	6.5	7.8	–	–
CD 7261	Proximal	–	3.2	4.3	–	–	–	–
CD 7273	Proximal	–	3.4	5	–	–	–	–
CD 8372	Proximal	–	4.5	6	–	–	–	–
CD 8862	Proximal	18.9	5	7.8	6.8	10.6	4.6	6.4
CD 1151	Middle	~14.7	3.9	7.1	~5.5	~6.3	3.5	4.7
CD 3368	Middle	~12.1	3.1	5.6	~4.6	~6.0	3.5	4.1
CD 8384	Middle	~10	2.4	4.2	~4.5	~4.5	2.5	4.4
CD 9030	Middle	8.5	1.9	3.4	2.8	4	1.7	3.1
CD 660	Distal	13.7	2.6	4.5	5.1	7.6	–	–
CD 3344	Distal	16.9	3.3	5.7	5.6	8.7	–	–
CD 8375	Distal	15.4	3.8	6.4	5.5	5.7	–	–

5. Discussion

The majority of the cercopithecoid postcranial fossils from Cooper's D have morphologies that are consistent for animals that are habitually terrestrial rather than arboreal. A humerus (CD 3351) appears to have an elevated greater tubercle, a feature found in terrestrial cercopithecoids (Harrison, 1989). An elevated greater tubercle limits the range of motion at the glenohumeral joint critical for arboreal locomotion while simultaneously increasing the lever arm length for the supraspinatous muscle, which is an important joint stabilizer (Larson and Stern, 1989). The fossil distal humeri (CD 7275 and CD 9486) possess a distally projecting medial flange of the trochlea, an anatomy thought to stabilize the elbow from medially directed ground reaction forces during terrestrial locomotion (Rose, 1988; Schmitt, 2003). There is also a posteriorly projecting medial epicondyle on these specimens, which is often found in terrestrial cercopithecoids and provides an increased lever arm for the digital flexor muscles when the forearm is pronated during quadrupedal locomotion (Harrison, 1989; Elton, 2002; White et al., 2009). The ulnae (CD 3349 and CD 3311) appear to have possessed a retroflexed olecranon, a ML-wide radial notch, and a strongly projecting coronoid process, features also typically found in terrestrial forms (Elton, 2002). A tall and retroflexed olecranon process increases the mechanical advantage of the triceps brachii muscle when the elbow and forearm is relatively extended during terrestrial locomotion. The distal femora (CD 17717 and CD 18614) have elongated and robust medial condyles found in terrestrial monkeys (Elton, 2002). The elongated condyles increase the moment arm for the quadriceps, important for powerful knee extension during terrestrial travel (Harrison, 1989). The distal tibiae lack a fibula facet (with the possible exception of CD 9596), which is characteristic of terrestrial forms (Ford, 1988). This syndesmotic ankle joint of terrestrial cercopithecoids stabilizes the ankle and restricts motion to the parasagittal plane (Ford, 1988; Strasser, 1988). The tarsals, especially the cuboid, are AP elongated (Strasser, 1988), and the metapodials and phalanges are short and robust, as in terrestrial monkeys (Etter, 1973). Short digits can help reduce high bending and joint moments that can result from high substrate reaction forces when walking and running on the ground (Patel and Wunderlich, 2010).

Despite the abundance of elements with clear terrestrial characters, two specimens do show some adaptations that are more consistent with an arboreal habitus: CD 13315 (juvenile proximal ulnae) and CD 9596 (distal tibia). Craniodental remains of colobine monkeys (e.g., *Cercopithecoides williamsi*) have yet to be formally identified at Cooper's D, suggesting that the anatomies found in these two bones may better reflect function than phylogeny. Nevertheless, cercopithecoid postcranial fossils with arboreal adaptations ($n = 2/106$) are quite rare at Cooper's D, suggesting that the region was inhabited by more terrestrially-adapted animals. However, the presence of these two fossils indicates that there may have been some use of arboreal substrates by some of the cercopithecoids in the area. This is not surprising since all living non-human primates are capable of some degree of arboreality (Fleagle, 1999).

Many of the cercopithecoid postcranial specimens at Cooper's D are large, yielding high estimates of body mass (Table S1). The average body mass estimate for the adult specimens ($n = 16$) is 42.5 kg. The smallest primate for which we can estimate body mass come from a distal humerus (CD 9486) which is estimated to be from a 28.7 kg individual. The largest specimen is CD 23239 (associated with CD 23240 and CD 23242), which is a distal tibia estimated to be from a ~60 kg animal. These large body masses are consistent with mass estimates for *Theropithecus oswaldi* at other localities both in South and East Africa, or even *Gorgopithecus* in South Africa (Delson et al., 2000). However, some of these large specimens (CD 13477 [scapula], CD 18641 [distal femur]) possess morphologies more consistent with *Papio*, and not *Theropithecus*. This may suggest the presence of a substantially larger-bodied *Papio* species in South Africa. Delson et al. (2000) estimate that *P. hamadryas robinsoni* males from Swartkrans Member 1 are only 24-30 kg, while females are 16-19 kg. Thus, we are faced with interpreting these data in one of three ways. First, the majority of postcrania recovered at Cooper's D are from *Theropithecus*, specifically *T. oswaldi*, and it possessed many extant *Papio*-like features. Second, *Papio* at Cooper's D was unusually large. Or third, these very large, *Papio*-like postcrania are from *Gorgopithecus*. These alternative explanations can only be assessed when craniodental remains are found in association with cercopithecoid postcrania.

Though we hypothesize that some of these postcrania are from *Papio* and others from *Theropithecus* in this study, we must emphasize that these are very preliminary assessments, and these assessments are complicated by the presence of another large-bodied cercopithecoid, namely *Gorgopithecus* (Steininger and Gilbert, ongoing work). Associated craniodental and postcranial remains from South African Pleistocene cercopithecoids will be necessary templates in determining which of these isolated remains may be from any of these three genera. Using previous studies (Krentz, 1993) and observations on a small sample of extant *Papio* and *Theropithecus*, however, we were able to identify some characters that may distinguish these two taxa. Distinguishing between large-bodied *Papio* and *Theropithecus* should be an avenue of future research that would help reconstruct the relative abundance of, and perhaps the paleoenvironments inhabited by Plio-Pleistocene cercopithecoids and hominins.

Another important pattern we find in the Cooper's D assemblage is the large number of juveniles and sub-adults. Of the 106 fossils described here, at least 40 are from sub-adults, including many from small juveniles and perhaps infants. Thus, more than one third of the monkey bones in this assemblage recovered to date come from sub-adults. This is a minimum since it cannot be known for certain that some bones characterized as "adults" actually are, given the absence of the epiphyseal end of the bone in some cases. Such a high percentage of juveniles, plus the presence of tooth marks on some of the bones, suggests that the Cooper's assemblage may have been accumulated in part by carnivores.

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Appendix A. Supplementary data

Supplementary information (Table S1) associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.geobios.2013.07.001.

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Cercopithecoid primate postcranial fossils from Cooper's D, South Africa

Jeremy M. DeSilva *, Christine Steininger, Biren A. Patel

* Corresponding author; e-mail address: jdesilva@bu.edu

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Supplementary materials

Table S1. List of cercopithecoid primate postcranial fossils from Cooper's D (Bloubank Valley, Gauteng, South Africa).

Table S1. List of cercopithecoid primate postcranial fossils from Cooper's D (Bloubank Valley, Gauteng, South Africa).

Accession number	Element	Tentative taxonomic attribution	Age	Body mass estimate (kg)	Regression reference
CD 79	Calcaneus		Adult		
CD 633	Femur (proximal)	*Theropithecus*	Adult		
CD 660	Phalanx (distal)		Adult		
CD 667	Metacarpal 2		Juvenile		
CD 672	Phalanx (proximal)		Juvenile		
CD 941	Metatarsal 4		Adult		
CD 949	Fibula (distal)		Adult		
CD 950	Talus		Adult		
CD 960	Tibia (proximal epiphysis)		Juvenile	53.5	Ruff, 2003
CD 962	Humerus (head)		Adult		
CD 963	Humerus (distal)		Infant		
CD 964	Metatarsal 1 (proximal)		Adult		
CD 966	Metacarpal 1		Adult		
CD 972	Metacarpal 4	*Theropithecus*	Adult		
CD 1145	Fibula (distal)		Adult		
CD 1148	Phalanx (proximal)		Adult		
CD 1151	Phalanx (middle)		Juvenile		
CD 1158	Metatarsal 1 (proximal)		Adult		
CD 1161	Phalanx (proximal)		Juvenile		
CD 1379	Femur (distal)		Adult		
CD 1711	Phalanx (proximal)		Adult		
CD 1712	Metapodial		Adult		
CD 1713	Phalanx (proximal)		Adult		
CD 1714	Phalanx (proximal)		Adult		
CD 1717	Metatarsal 1 (proximal)		Adult		
CD 1719	Phalanx (proximal)		Juvenile		
CD 1968	Radius (midshaft)		Adult		
CD 3217	Radius (distal shaft)		Juvenile		
CD 3229	Metatarsal 3		Adult		
CD 3247	Cuboid		Adult		
CD 3294	Femur (proximal epiphysis)	*Papio*	Juvenile		
CD 3306	Femur (proximal)		Juvenile		
CD 3311	Ulna (proximal)		Adult		
CD 3318	Tibia (proximal shaft)		Juvenile		
CD 3319	Femur (proximal)		Juvenile		
CD 3320	Phalanx (proximal)		Adult		
CD 3326	Tibia (distal)		Adult	53.4	Ruff, 2003
CD 3329	Metatarsal 1 (proximal)		Adult		

Table S1 (continued).

Accession number	Element	Tentative taxonomic attribution	Age	Body mass estimate (kg)	Regression reference
CD 3335	Metacarpal 1		Juvenile		
CD 3344	Phalanx (distal)		Adult		
CD 3349	Ulna (proximal)		Adult		
CD 3350	Calcaneus		Adult		
CD 3351	Humerus (midshaft)	*Theropithecus*	Adult	50.6-52.0	Delson et al., 2000
CD 3354	Phalanx (proximal)		Juvenile		
CD 3355	Phalanx (proximal)		Adult		
CD 3365	Phalanx (proximal)		Juvenile		
CD 3368	Phalanx (middle)		Juvenile		
CD 3747	Femur (midshaft)		Adult		
CD 3841	Femur (distal epiphysis)		Juvenile		
CD 3844	Metacarpal 5	*Papio*	Adult		
CD 3905	Metacarpal 1		Juvenile		
CD 3922	Tibia (proximal epiphysis)		Juvenile		
CD 3925	Femur (midshaft)		Adult		
CD 3926	Femur (proximal)	Carnivore?	Adult	23.3	Ruff, 2003
CD 3939	Pelvis (ischium)	*Papio*	Infant		
CD 5418	Calcaneus		Infant		
CD 5733	Talus		Adult		
CD 5738	Cuboid		Adult		
CD 5832	Metacarpal 1		Juvenile		
CD 5867	Tibia (distal)		Adult	41.8	Ruff, 2003
CD 5868	Metatarsal 1 (proximal)		Adult		
CD 5871	Metapodial		Adult		
CD 5964	Humerus (midshaft)		Adult	46.5-47.0	Delson et al., 2000
CD 6670	Phalanx (proximal)		Adult		
CD 6671	Calcaneus		Juvenile		
CD 6677	Phalanx (proximal)		Adult		
CD 6682	Pelvis (ischium)	*Papio*	Juvenile		
CD 7261	Phalanx (proximal)		Juvenile		
CD 7264	Phalanx (proximal)		Juvenile		
CD 7273	Phalanx (proximal)		Juvenile		
CD 7275	Humerus (distal)	*Theropithecus*	Adult	31.3	Ruff, 2003
CD 7281	Talus		Adult		
CD 7312	Ulna (distal epiphysis)		Juvenile		
CD 7313	Metacarpal 1		Adult		
CD 7316	Metacarpal 5	*Theropithecus*	Juvenile		
CD 7333	Metapodial		Adult		
CD 7350	Metacarpal 3	*Theropithecus*	Juvenile		

Table S1 (end).

Accession number	Element	Tentative taxonomic attribution	Age	Body mass estimate (kg)	Regression reference
CD 7364	Intermediate cuneiform		Adult		
CD 7852	Calcaneus		Juvenile		
CD 7978	Metapodial		Adult		
CD 8291	Talus		Adult		
CD 8294	Metatarsal 3		Juvenile		
CD 8309	Radius (distal epiphysis)		Juvenile	30.4	Ruff, 2003
CD 8310	Metacarpal 3		Juvenile		
CD 8366	Metacarpal 3		Juvenile		
CD 8372	Phalanx (proximal)		Adult		
CD 8375	Phalanx (distal)		Adult		
CD 8376	Metatarsal 3		Adult		
CD 8380	Metapodial		Adult		
CD 8384	Phalanx (middle)		Juvenile		
CD 8862	Phalanx (proximal)		Adult		
CD 9030	Phalanx (middle)		Juvenile		
CD 9123	Phalanx (proximal)		Juvenile		
CD 9265	Scapula (glenoid)	*Papio*	Adult	35.0	Anapol, 1983
CD 9486	Humerus (distal)	*Theropithecus*	Adult	28.7	Ruff, 2003
CD 9596	Tibia (distal)		Adult	40.0	Ruff, 2003
CD 10502	Humerus (distal)	*Papio*	Juvenile		
CD 11445	Radius (proximal)		Adult	37.8	Ruff, 2003
CD 13315	Ulna (proximal)		Juvenile		
CD 13317	Radius (proximal)		Adult	50.7	Ruff, 2003
CD 13445	Pelvis	*Theropithecus*	Adult		
CD 13477	Scapula (glenoid)	*Papio*	Adult	52.0	Anapol, 1983
CD 17717	Femur (distal)	*Theropithecus*	Adult	44.8	Ruff, 2003
CD 17811	Scapula (glenoid)	*Papio*	Adult	39.0	Anapol, 1983
CD 18641	Femur (distal)	*Papio*	Adult	44.8	Ruff, 2003
CD 23239, 23240, 23240	Tibia (distal and midshaft)		Adult	60.0	Ruff, 2003