Journal of Human Evolution 60 (2011) 83–93

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

New species of *Cercopithecoides* from Haasgat, North West Province, South Africa

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ARTICLE INFO

Article history:
Received 27 August 2008
Accepted 28 August 2010

Keywords:
Cercopithecoides
Haasgat
South Africa
Pleistocene

ABSTRACT

Analyses of new cercopithecid fossil specimens from the South African site of Haasgat point to craniofacial affinities with the genus *Cercopithecoides*. Detailed metric and non-metric comparisons with South African *Cercopithecoides williamsi*, and other East African *Cercopithecoides* species, *Cercopithecoides kimeui*, *Cercopithecoides meaveae*, *Cercopithecoides kerioensis*, and *Cercopithecoides alemyehui* demonstrate that the Haasgat fossils have distinct craniofacial morphology and dental metrics. Specifically, material from Haasgat probably represents one of the smaller *Cercopithecoides*, differing from the others in its particular suite of features that vary within the genus. It is unique in its more vertical ramus, associated with a relatively lengthened mandibular body. Haasgat *Cercopithecoides* has a particularly narrow interorbital region between relatively larger ovoid orbits, with articulation of the maxillary bones at a suture above the triangular nasal bones. Furthermore, the maxillary arcade is more rounded than other *Cercopithecoides*, converging at the M^2 and M^3. The conclusion drawn from this analysis is that the Pleistocene Haasgat fossils are colobines representing a distinct taxon of *Cercopithecoides*, *Cercopithecoides haasgati*, thus adding a second species of the genus to southern Africa.

Introduction

In 1988, excavation of the South African fossil site Haasgat yielded a sample of craniofacial fossils with characteristics of the extinct genus *Cercopithecoides* (Keyser and Martini, 1990; Von Mayer, 1998). These fossils appeared to be different from the representatives of this genus previously found at other South African sites, all of which are currently referred to a single species, *Cercopithecoides williamsi*, and from other members of the genus from East Africa. Here we present background on the context of the fossils and species of *Cercopithecoides*.

Haasgat cave site, geological age, and paleoenvironment

The Haasgat cave is located in the Brits District of the North West Province, at 25°51′31"E and 27°50′9"S. It lies on the steep western slope of the Witwatersrand Spruit Valley (Keyser and Martini, 1990). Haasgat was mined for calcite flowstone in the first quarter of the past century (Keyser and Martini, 1990), with fossiliferous breccia having been dumped down the steep slope below the cave (Plugh and Keyser, 1994). The material used in this study came from these dumps. The breccia is thought to have come from the siltstone beds immediately above the floor flowstone, but has no accurate *in situ* context (Keyser and Martini, 1990).

Keyser and Martini (1990) initially suggested that Haasgat was older than the lower members of Sterkfontein and Makapansgat, because of the high elevation of the cave and the fact that most of its proximal deposits appeared to have been weathered away. Subsequent faunal analyses have suggested a more recent age. Identified mammalian species from Haasgat show an ambiguous mix of mammals (Table 1). Whereas two of the species are known from sites dating to the Pliocene/Pleistocene border, two others only appear in the South African fossil record in the late Pleistocene. Thus the Haasgat assemblage, if it comes from a single temporal horizon, likely dates to the Pleistocene, but further resolution of its age is not possible at this time. Certainly there is the potential that the cercopithecid fossils are coeval with South African *C. williamsi*.

The most abundant species found at Haasgat is *Oreotragus major* (klipspringer [Plugh and Keyser, 1994]). The presence of other browsers such as giraffe and kudu suggests a savannah environment in which trees featured prominently (Plugh and Keyser, 1994). The

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doi:10.1016/j.jhevol.2010.08.002

Table 1
Identified mammalian species from Haasgat.

Family	Species	Temporal frame
Bovidae	*Oreotragus oreotragus major*	Pliocene-Pleistocene
	Kobus leche	Pleistocene-Present
	Kobus ellipsiprymnus	Late Pleistocene-present
	Alcelaphus buselaphus	Late Pleistocene-present
Cercopithecidae	*Papio angusticeps*	Pliocene/Pleistocene border
Procaviidae	*Procavia transvaalensis*	Pliocene/Pleistocene border

Based on: Plugh and Keyser (1994); McKee and Keyser (1994).

presence of waterbuck (*Kobus ellipsiprymus*) suggests that there was water in close proximity and *Kobus leche*, in particular, suggests swampy conditions or shallowly inundated flood plains (Smithers, 1983). Thus the proposed palaeoenvironment surrounding Haasgat at the time of deposition included montane forest, a nearby river, and open woodland or savannah all in close proximity.

Review of the genus Cercopithecoides

Mollett (1947) erected the genus and species *C. williamsi* for the specimen AD 1326-3 from Makapansgat, a male cranium and mandible. He named the genus *Cercopithecoides* because of its resemblance to *Cercopithecus*, and the species *C. williamsi* in honor of the technician, E.W. Williams, who found the skull. *C. williamsi* has now been described from the South African sites of Makapansgat, Sterkfontein (Member 4 and the Graveyard site), Swartkrans, Cooper's A, Bolt's Farm, and Kromdraai B, as well as from Koobi Fora in Kenya (Jablonski et al., 2008), and Leba in Angola (Szalay and Delson, 1979; Delson, 1984). Other species of *Cercopithecoides* have been found at Lothagam (Leakey et al., 2003), Koobi Fora (Jablonski et al., 2008), Hadar (Frost and Delson, 2002), Olduvai Gorge (Leakey, 1982), Rawi (Frost et al., 2003), and Daka (Gilbert and Frost, 2008).

The colobine affinity of the genus *Cercopithecoides* was first proposed by Robinson (1952). Based upon this proposal, Maier (1970) initially assumed that *Cercopithecoides* would therefore have been adapted for an arboreal lifestyle, akin to modern colobines. However, it is now clear from the post-cranial evidence that East African *Cercopithecoides* shows strong morphological adaptations for terrestrial existence (Birchette, 1981; Leakey, 1982; Frost and Delson, 2002; Jablonski et al., 2008). Carbon isotope studies of *C. williamsi* from Sterkfontein and Makapansgat are consistent with at least a degree of terrestrial foraging (Codron et al., 2005; Fourie et al., 2008).

C. williamsi was initially erected as a species and described by various authors as fossils accumulated from Pliocene and Pleistocene sites of South Africa. Fossils representing the species were later found in East African sites, and numerous features from both East and South Africa have been used to define the species (Table 2).

There are morphological variants of the South African fossils, sometimes referred to the species, that warrant further consideration. Freedman (1957) erected the species *C. molletti* based on six specimens from Swartkrans (SK 624, SK 412, SK 551, SK 579, SKII 2813, SKII 29) and one specimen from the Graveyard site at Sterkfontein (GY 1.) All the features described by Freedman (1957) to distinguish *C. molletti* from *C. williamsi* were features of the dentition, as the available parts of the facial skeleton showed no marked differences from *C. williamsi*. The distinguishing features included: buccal surface of upper molars more markedly convex in occlusal view; a definite inward step of the upper tooth row between M^1 and P^4; deep lingual intercusp clefts on the upper molars with a very prominent cingular ridge across the lower margin of the cleft

Table 2
Key published features of *Cercopithecoides williamsi*.

Craniofacial features
Calvarium is well rounded, more so in the female
Calvarium shorter and higher in female, in the male it is slightly more ovoid
Temporal lines form a thickened ridge from the supraorbital torus to the calvarial roof
Temporal lines converge but do not meet, and do not reach the nuchal crest
Post-orbital constriction is marked
Orbits are relatively large and rounded
Supraorbital tori are only moderately developed in males, and lie slightly below bregma
Supraorbital tori are well developed in females and raised above the calvarium roof
Muzzle is short and narrow relative to that of cercopithecines
Muzzle a square outline anteriorly
Maxillary dental arcade maximum width at M^2
Mandibular corpus is shallow and of constant depth
Mandibular fossa absent
Foramen symphyseosum presence variable
Dental features
Teeth are small and show sexual dimorphism only in the C–P_3 complex
Reduced protocone on P^3
$M_1 < M_2 < M_3$ in size and breadth

Based on: Mollett (1947); Freedman (1957); Verheyen (1962); Maier (1970); Eisenhart (1974); Szalay and Delson (1979); Kuykendall and Rae (2008); Jablonski et al. (2008).

which developed into two cuspules on M^3; most notably, all the upper molars had a prominent intercusp cleft on their buccal surface, each with a cingular ridge across its alveolar margin; and larger molars than those of other South African *Cercopithecoides*, particularly in terms of the mesio-distal diameters of M_2 and M^3;

After recovery of new material from Makapansgat, Freedman (1960) argued that this new material bridged the gap between *C. williamsi* and *C. molletti* both in terms of the size differences and the slight morphological differences. Thus, he synonomized the species *C. molletti* with *C. williamsi*. Freedman (1960) also noted a dental size difference between the *C. williamsi* of, in order from smallest to largest, specimens from Sterkfontein, Makapansgat and Swartkrans. These size differences were especially clear for M_2 size. However he concluded that the overall size variation of all these lumped together is still less than that within the *Papio ursinus* species and thus not indicative of separate species status.

Delson (1983) noted that the Kromdraai *C. williamsi* material exceeded the size of specimens from both Makapansgat and Sterkfontein. Delson (1984) debated Freedman's initial claim of size distinctions of the Swartkrans material, and argued that these fossils, along with those from Cooper's A and Kromdraai B, represent a larger variant than the remainder of the South African material.

Eisenhart (1974) proposed a separate taxon of large colobines from the grey breccia at Makapansgat. He acknowledged Eck as the first to identify this taxon but gives no reference. Eisenhart attributed three specimens to this taxon: M 3018 (an isolated M_3), M 3016 (an isolated P^3) and M 2988 (a mandibular symphysis with P_4). Judging by the degree of wear on the teeth, he proposed that it is possible that they all belonged to the same individual. The only features described by Eisenhart (1974) to distinguish the large colobine from *C. williamsi* were dental features. The teeth of the specimens are all typically colobine, only larger than any measured for *C. williamsi* with no overlap in the available molar dimensions. The premolars and molars are narrow relative to *C. williamsi*. There is a tuberculum sextum on the M_3 that is not typical of colobines but may be a size related feature, occurring in very large species such as *Paracolobus* and *Papio*. Eisenhart (1974) did not name this

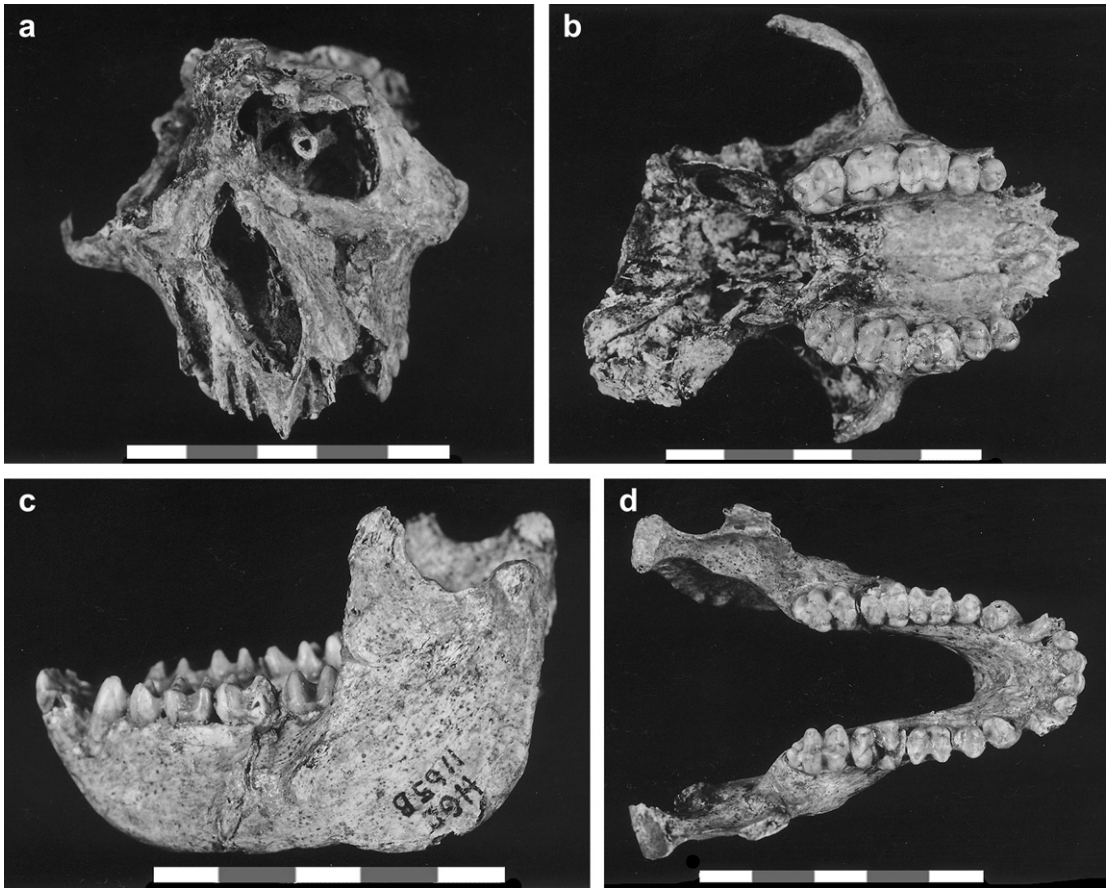

Figure 1. HGD 1165, adult male *Cercopithecoides* from Haasgat; a) frontal view of midface; b) inferior view of palate and basicranium; c) lateral view of mandible; d) superior view of mandible. Scale in centimeters.

taxon, and as yet no further material has been referred to it. However, Eisenhart thought that these specimens most closely resembled *Paracolobus chemeroni*. Leakey (1982) also suggested that this material belongs to either *Paracolobus* or *Rhinocolobus*.

New isotopic data from two specimens of *C. williamsi* from Makapansgat may reopen the notion of multiple species. Fourie et al. (2008) report disparate $\delta^{13}C$ values for these specimens, with one being consistent with a mixed/C_3 oriented diet, in contrast to a mostly C_4 diet implied by the other sample. Likewise, $\delta^{18}O$ values from three Makapansgat *C. williamsi* show high variance that may be attributable to either diet or temporal changes in climate (Chambers et al., 2008). It should be noted, however, that none of these samples tested the larger variant noted by Eisenhart (1974). Interestingly, Codron et al. (2005) report a similar disparity in $\delta^{13}C$ values from a sample of five specimens from Sterkfontein that are attributed to *C. williamsi*. Although the taxonomic significance of these apparent dietary disparities remains untested, it is not what would be expected from a single taxon.

Leakey and Leakey (1973) described a large colobine from Olduvai Gorge that was named by Leakey (1982) as *Cercopithecoides kimeui*. This species, now known from Olduvai Gorge, Koobi Fora, Hadar (Frost and Delson, 2002), and the Rawi Gully System (Frost et al., 2003), is distinct from *C. williamsi* not only in its larger size, but *C. kimeui* also possesses wider upper molars that are flared towards the cervix and with low cusps (Leakey, 1982). In other words the molars are more papionin-like, yet Frost et al. (2003) note the *Cercopithecoides*-like incisors and face. The mandible is more robust than that of *C. williamsi* with a thicker ventral border and a wider buccal groove.

The Hadar Formation of Ethiopia has yielded a distinct species of *Cercopithecoides*, particularly *Cercopithecoides meaveae* (Frost and Delson, 2002), that is smaller than both *C. kimeui* and *C. williamsi*. It is distinctive in its prominent glabellar region and suparorbital torus. Its mandibular symphysis is shallow and straighter, and lacks a thickened mandibular corpus. Unlike *C. kimeui*, the molars are high crowned with prominent lophs. The associated post-cranial bones are consistent with terrestrial locomotion.

Another small East African representative of the genus, *Cercopithecoides kerioensis*, comes from Lothagam. It is further characterized by "relatively thin supraorbital tori, narrow internasal width, well-developed nuchal crests, and presence of a sagittal crest close to inion. The mandibular body is relatively shorter and deeper than that of either of the larger species; anteriorly the inferior margin is inflated and the foramen symphyseosum, absent" (Leakey et al., 2003: 215).

C. alemayehui is yet another small species, represented by a single specimen, coming from the Daka Member of the Bouri Formation in Ethiopia. Its cranium and dentition are comparable in size to *C. meaveae* and *C. kerioensis*. It possesses a distinctively projecting supraorbital torus, and is also distinguished by elongated nasal bones (Gilbert and Frost, 2008)

Materials and methods

The fossils used for this study were retrieved by J.E.J. Martini and A.W. Keyser from breccia that was dumped during lime-mining activity at the Haasgat Cave in the early part of the 20th century (Keyser and Martini, 1990). Those specimens thought to belong to

the genus *Cercopithecoides* were selected from the primate remains found at Haasgat for inclusion in this study. Inclusion of any specimen in the sample was based on the presence of recognizable colobine dentition or facial morphology.

The Haasgat *Cercopithecoides* sample is labeled according to sex and age categories in Figs. 1–3. Sex was determined by the size of the canine, or its alveolar socket, in the upper dentition and by the size of the canine, the size of the canine diastema and the degree of wear on P_3, in the lower dentition. Any individual in whom the third molar had not fully erupted was classified as juvenile. Degree of suture closure was used to determine age category only if no teeth were present on the specimen. Only adult specimens were utilized in the taxonomic analyses.

The Haasgat material was initially compared by Von Mayer (1998) with 78 South African *C. williamsi* specimens described in the literature. Most of this material has been measured by Freedman (1957), Eisenhart (1974), or both (see the specimen list in Table 3). Of the standard linear craniodental measurements, 51 had been measured by Freedman (1957) and Eisenhart (1974) on ten of the *C. williamsi* specimens housed at the Transvaal Museum. These 51 measurements were retaken by Von Mayer (1998). Measurements were compared to those recorded by Freedman (1957) and Eisenhart (1974). This was achieved by determining the percentage error between the current and previously recorded measurements, as per Bland and Altman (1986).

Where the same parameter was measurable on left and right sides of the same specimen, Freedman (1957) performed the measurement on both sides and used the mean of the two values. Eisenhart (1974) does not specify. Von Mayer (1998) recorded the measurements from each side separately, and we used only the side which is more complete (i.e., the side with a greater of measurable parameters) in the statistical analysis. Where the percentage error was greater than 3% between von Mayer's measurements and those of Freedman or Eisenhart, the measurement was repeated (see Kieser et al., 1990), and only included if a consistent reading could be rendered. An additional 40 standard craniodental measurements were taken by Von Mayer (1998) on the Haasgat sample, for a total of 91 measurements (SOM). These measurements were then repeated about a month later and the two sets were compared to determine the percentage error. Again, where the percentage error was greater than 3% the measurement was repeated a 3rd time and the two closest measurements were averaged.

Of the measurements taken, twelve found in both samples had too few data to warrant statistical analysis, but are reported for completeness. There were a further twelve parameters that had been measured on only one adult specimen of the Haasgat sample but had been measured on three or more specimens of *C. williamsi*. In these cases the values for the Haasgat specimens were compared to the ranges for *C. williamsi*.

A remaining set of 48 parameters had at least two values for both Haasgat adults (or juveniles with permanent teeth) and *C. williamsi*. As a result of the small sample sizes, the data cannot be assumed to be normally distributed; thus a non-parametric test was necessary to test for statistically significant differences. The

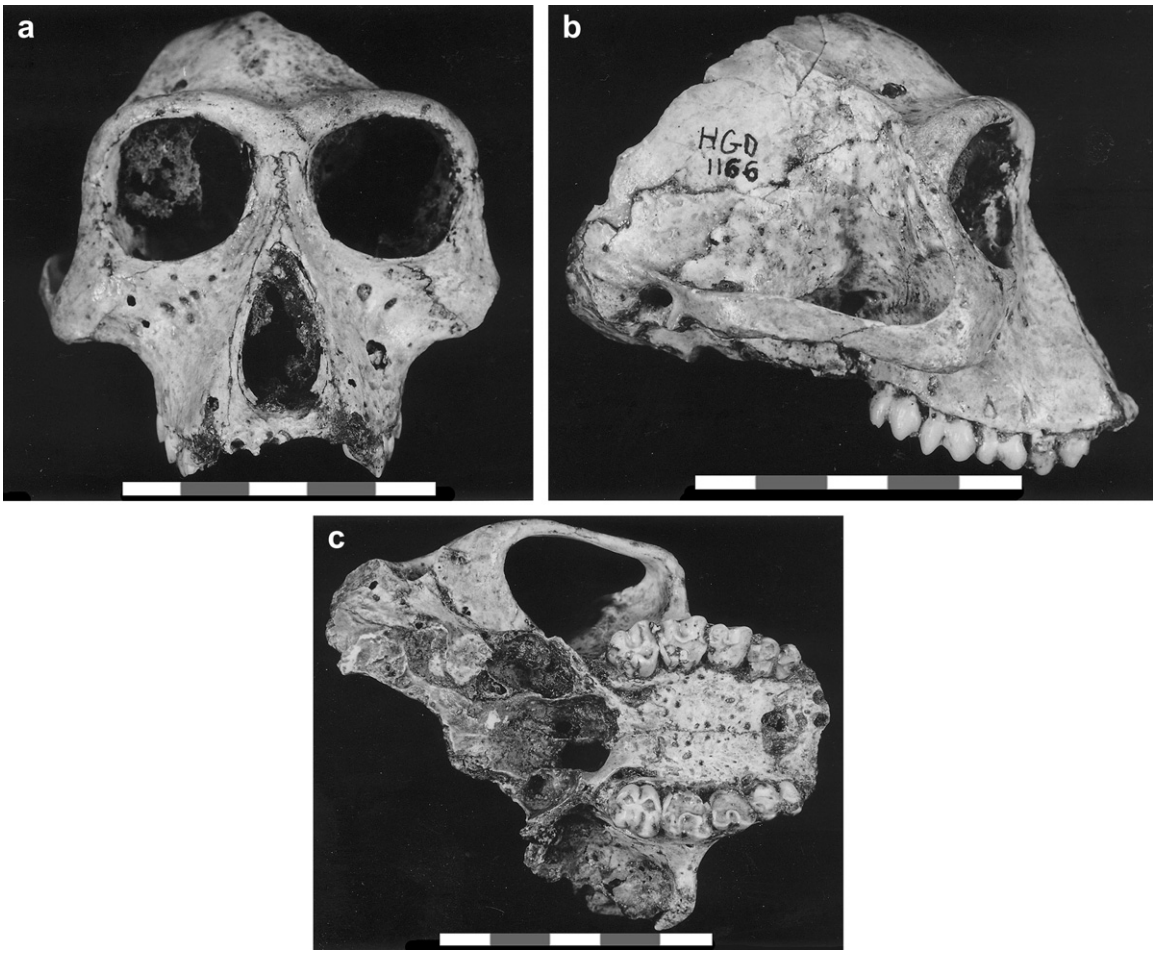

Figure 2. HGD 1166, adult female *Cercopithecoides* from Haasgat: a) frontal view of face; b) lateral view of cranium; c) inferior view of palate, zygomatic arch and basicranium. Scale in centimeters.

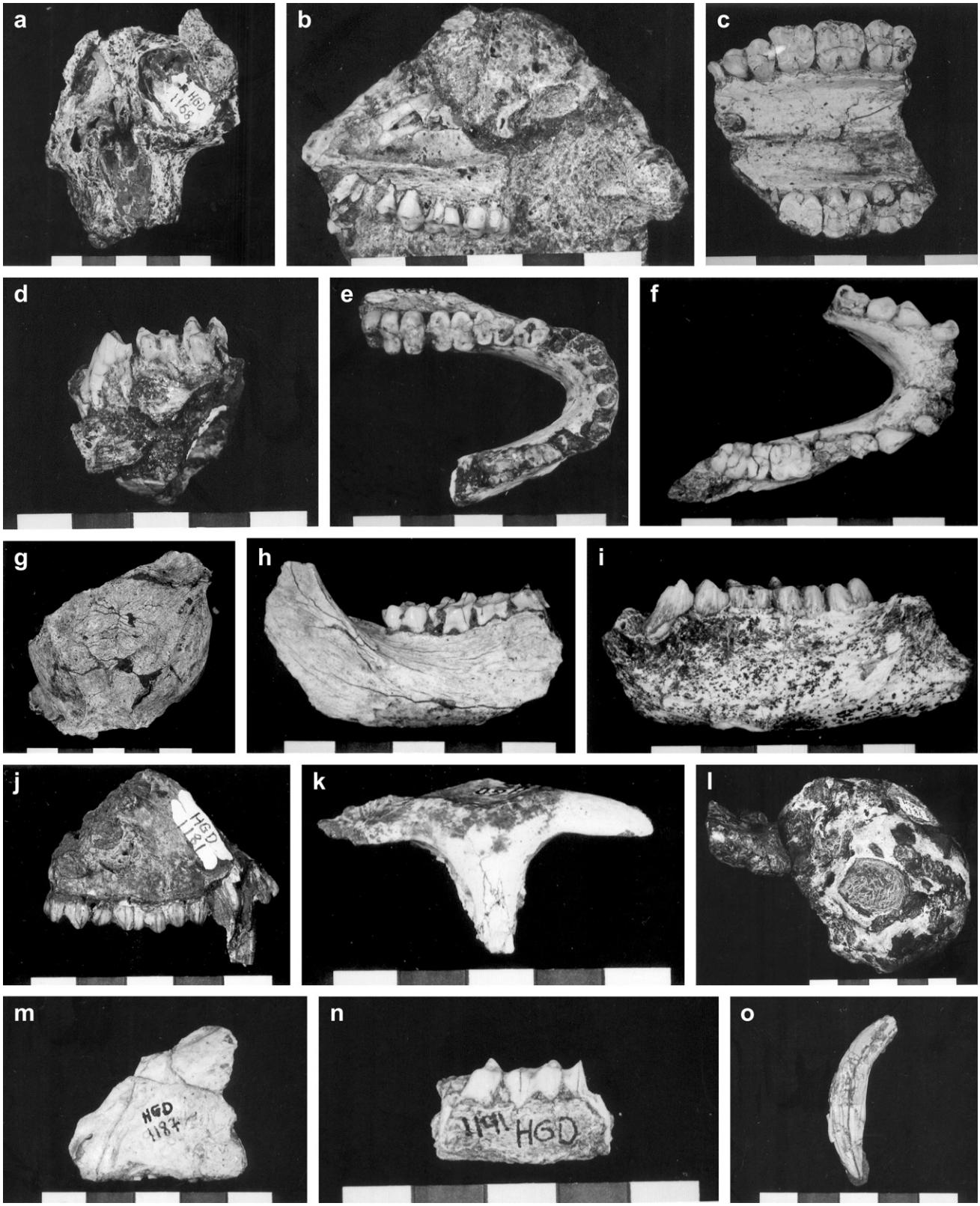

Figure 3. Adult specimens of Haasgat *Cercopithecoides*. Scale in centimeters. a) HGD 1168, female, partial mid-facial skeleton; b) HGD 1169, male, partial right maxilla; c) HGD 1170, female, partial mid-facial skeleton; d) HGD 1173, male, partial mandible; e) HGD 1175, sex unknown, partial mandible; f) HGD 1177, female, partial mandible; g) HGD 1178, sex unknown, partial posterior calvarium; h) HGD 1179, sex unknown, partial mandible; i) HGD 1180, Male, partial mandible; j) HGD 1181, male, partial right maxilla; k) HGD 1185, sex unknown, partial frontal bone; l) HGD 1186, sex unknown, partial cranial vault; m) HGD 1187, male, partial maxilla and premaxilla; n) HGD 1191, sex unknown, fragment of mandibular corpus; o) HGD 1197, male, isolated maxillary canine.

Table 3
South African *C. williamsi* specimens used for metric and non-metric comparisons. Includes Catalogue number (#), Sex (F-female, M-male, U-unknown), Age (A-adult or J-juvenile) and Body Part (C-Cranium, M-Mandible, T-Teeth).

#	Sex	Age	Part	#	Sex	Age	Part	#	Sex	Age	Part
AD 1326	M	A	C	BF 56778	F	A	C,T	BF 56784	F	A	C,T
CO 116	F	A	T	GY 1	M	A	T	KB 122	U	A	C,T
KB 5241	F	A	C,T	M 203	M	A	T	M 235	U	A	T
M 622	F	A	T	M 629	U	J	T	M 631	M	A	T
M 666	M	A	T	M 667	M	A	T	M 710	M	A	T
M676	M	A	M	M 2987	U	A	T	M 2989	M	A	T
M 2990	M	A	T	M 2999	M	A	C,T	M 3000	F	A	C
M 3009	U	A	T	M 3025	U	A	R	M 3026	U	A	T
M 3029	U	A	T	M 3031	U	A	T	M 3055	M	A	C,T
M 3102	U	A	T	M 3103	U	A	T	MP 194	F	A	T
MP 211	U	A	T	MP 69	U	A	T	SK 412	F	A	M
SK 551	M	A	T	SK 552	U	A	T	SK 579	U	A	T
SK 624	F	A	T	SK II28B	U	A	T	SK II29	U	A	T
STS 252	U	A	C,T	STS 279	U	A	T	STS 288	U	A	T
STS 290	U	J	T	STS 295	U	A	T	STS 300	M	J	T
STS 344	U	A	T	STS 347	M	A	T	STS 350	M	A	T
STS 357	U	A	T	STS 361	U	A	T	STS 366	M	A	T
STS 394A	F	A	C,T	STS 394B	F	A	M,T	STS 509	U	A	T
STS 512	U	A	T	STS 516	U	A	T	STS 518	U	A	T
STS 523	U	A	T	STS 532	F	A	T	STS 541	U	A	T
STS 3054	F	A	T	STS 3067	F	A	T	STS 3069	F	A	T
SWP 39	U	A	T	SWP 54	U	A	T	SWP 219	F	A	T
SWP 222	U	A	T	SWP 286	U	A	T	SWP 287	U	A	T
SWP 305	U	A	T	SWP 311	U	A	T				

Mann–Whitney *U* test was chosen for its ability to detect differences in central tendencies of continuous data (Blalock, 1979). The tests were two-tailed, and the null hypothesis of no difference between samples was rejected at the $\alpha = 0.05$ level. We do not correct for multiple comparisons.

Craniofacial and dental indices were calculated to test for morphological differences in the shape of the samples, thus ensuring that metric differences are not merely indicative of a smaller, but otherwise identical, taxon. Non-metric traits were also assessed to determine whether or not there were any morphological differences which may not have been determinable by metric analysis. Dental metrics and non-metric traits of the Haasgat sample were also compared to all other recognized species of *Cercopithecoides*.

Results

Comparisons of the Haasgat fossils with C. williamsi

The comparisons in Table 4 are of individual Haasgat measurements with one or two *C. williamsi* measurements. Of the craniofacial dimensions, *C. williamsi* exceeds the size of the Haasgat *Cercopithecoides* for six out of the seven measurements. Mandibular length (GO-MS) is the only craniofacial dimension for which *C. williamsi* is less than the Haasgat *Cercopithecoides*. *C. williamsi* exceeds the size of the Haasgat *Cercopithecoides* for two of the five dental dimensions measurements listed in Table 4, i.e., I^2 length and lower canine height (UI2L, LCH), but is smaller for the remaining three: I^1 length and breadth and I^2 breadth (UIIL, UI1B, UI2B).

Table 5 presents comparisons of Haasgat measurements with ranges of *C. williamsi*, for which there were insufficient data to warrant tests for statistically significant differences. Of the nine craniofacial dimensions, the values for the Haasgat sample fall outside the range for *C. williamsi* in five measurements, for which the Haasgat values are all smaller than those for *C. williamsi*. Of the three dental dimensions, the values for the Haasgat sample fall within the range of *C. williamsi* for all three: upper canine length and breadth, and lower canine length (UCL, UCB, LCL).

Table 4
Comparison of individual Haasgat dimensions with *C. williamsi* of limited sample size (1 or 2 individuals.) Variable definitions are in SOM.

Measurement	Haasgat values (mm)	*C. williamsi* (mm)	Comparison
N-Rhin	19.17	21.0–24.0	*C. williamsi* > Haasgat
MDBMS	21.98	22.0–27	*C. williamsi* > Haasgat
Tor-Max	10.24	16.22–19.73	*C. williamsi* < Haasgat
UI1L	5.28	4.0	*C. williamsi* < Haasgat
UI1B	5.29	4.6	*C. williamsi* < Haasgat
UI2L	3.36	5.0	*C. williamsi* > Haasgat
UI2B	5.25	4.5	*C. williamsi* < Haasgat
LCH	5.53	6.7–8.5	*C. williamsi* > Haasgat
Go-Cond	35.10	46.0	*C. williamsi* > Haasgat
Go-Cora	45.82	54.0	*C. williamsi* > Haasgat
Go-Ms	52.91	47.0	*C. williamsi* < Haasgat
Ramus-L	26.86	32.0	*C. williamsi* > Haasgat

We analyzed 48 dimensions using the Mann–Whitney *U* test, which tests for statistically significant differences between the two adult samples (Table 6). Of the 18 craniofacial dimensions, seven show statistically significant differences between the two samples. In all seven cases the values for the Haasgat sample range fall completely below the range for *C. williamsi*, diminishing the possibility of a Type I error and showing a distinctively small midfacial morphology. Many of the craniofacial dimensions for which there is no statistically significant difference between the two samples still show values for the Haasgat sample to lie below the range for *C. williamsi*, i.e., mandibular breadth at the canine, M^1, and P^4, mandibular height at the M^1 (MDBCAN, MDBP4M, MBM1M, and MHM1M), showing less robusticity of the mandible. Palatal breadth at the P^3 (PBP3) is also below the *C. williamsi* range.

Of the 30 dental dimensions (Table 6), five show statistically significant differences, including all the dimensions of the M_1. In all five cases, the values for the Haasgat sample overlap with the range for *C. williamsi* but the means for *C. williamsi* are greater, consistent with the greater overall size of the face but possibly subject to a Type I error. All the dental dimensions show overlap between the ranges for the two samples with the exception of M_3 hypoconulid breadth (LM3HYPO) where the values for the Haasgat sample fall above the range for *C. williamsi*, indicating a distinctive morphology for the M_3.

Most craniofacial indices do not have sufficient data for statistical testing, while sufficient data are available for most dental indices (Table 7). The only index that shows a statistically significantly difference between the two samples is UM3DB/UM3MB, measuring the relative breadths of the mesial and distal lophs of the M^3. The index indicates that while the mesial loph is broader than the distal loph in both groups, the distal loph tends to be larger

Table 5
Comparisons of individual Haasgat dimensions with *C. williamsi* ranges. Variable definitions are in SOM.

Measurement	Haasgat (mm)	*C. williamsi* (mm)	Comparison
IDS-NA	47.3	53.0–69.0	Haasgat below range of *C. williamsi*
GL-IDS	50.97	57.56–68.74	Haasgat below range of *C. williamsi*
EXTORB	68.72	79.4–91.0	Haasgat below range of *C. williamsi*
NAPL	21.77	27.0–32.5	Haasgat below range of *C. williamsi*
NAPB	12.88	14.1–20.0	Haasgat below range of *C. williamsi*
FML	19.59	17.3–20.0	Haasgat within range of *C. williamsi*
FMB	17.95	16.2–18.4	Haasgat within range of *C. williamsi*
UCL	9.25	6.58–12.3	Haasgat within range of *C. williamsi*
UCB	6.3	5.8–10.7	Haasgat within range of *C. williamsi*
ORBHT	22.63	20.0–28.47	Haasgat within range of *C. williamsi*
ORBBR	27.01	26.0–29.0	Haasgat within range of *C. williamsi*
LCL	4.21	4.0–4.7	Haasgat within range of *C. williamsi*

Table 6
Results of the Mann–Whitney U-tests comparing Haasgat specimens to *C. williamsi*. Differences are statistically significant when $p \leq 0.05$. Variable definitions are in SOM.

Measurement	*p*-value	*U*-value	Haasgat range (mm)	*C. williamsi* range (mm)
			Range/Mean/n	Range/Mean/n
IDS-PNS	0.04954	0.0	39.10–43.55/41.38/3	51.0–56.0/54/3
INTORB	0.03559	0.0	6.01–7.77/6.88/2	15.0–22.0/17.79/8
MBP3	0.03615	0.0	30.44–31.38/30.91/2	32.0–44.0/37.48/8
MBM1M	0.12135	0.0	35.05–38.59/36.82/2	39.94–42.92/41.43/2
MBM2M	0.24822	1.0	38.06–41.70/39.75/3	41.19–45.21/43.20/2
MBM2D	0.24822	0.0	36.31–40.71/38.83/3	40.22–43.39/41.81/2
MBM3D	0.03559	0.0	33.48–34.27/33.87/2	39.66–46.0/42.46/8
PBP3	0.12135	0.0	18.48–18.57/18.52/2	20.04–22.60/21.32/2
PBM1M	0.04954	0.0	18.66–21.72/20.35/3	22.26–23.0/22.72/3
PBM2M	0.15731	2.0	19.63–22.92/20.93/3	21.65–24.05/22.86/4
PBM2D	0.04954	0.0	19.41–21.32/20.45/3	22.46–24.45/23.58/3
PBM3D	0.04954	0.0	17.54–19.34/18.63/3	19.8–22.19/21.30/3
MENTHT	0.47951	4.0	19.54–28.10/23.80/3	24.0–28.0/25.75/4
MHM1M	0.12135	0.0	23.94–27.58/25.76/2	31.98–48.93/40.45/2
MDHTP4M	0.47951	4.0	17.40–22.96/20.41/4	20.0–24.0/21.67/3
MDHTM3D	0.15731	2.0	19.19–22.28/21.19/3	21.0–30.0/24.50/4
MDBCAN	0.06409	0.0	19.01–19.31/19.16/2	20.0–23.0/21.50 4
MDBP4M	0.05654	0.0	25.31–25.83/25.57/2	29.0–30.0/29.50/4
UCH	1.00000	4.0	20.52–22.31/21.41/2	9.80–32.0/20.43/4
UP3L	0.83067	11.0	4.42–5.13/4.79/4	4.50–5.70/4.90/6
UP3B	0.06128	5.0	5.59–6.40/5.84/4	5.70–7.10/6.40/8
UP3H	0.24822	1.0	6.22–6.45/6.35/4	6.0–6.40/6.20/3
UP4L	0.76260	30.0	4.81–6.02/5.35/6	5.0–6.0/5.36/11
UP4B	0.00917	3.0	6.76–7.34/7.09/5	7.10–9.38/8.01/9
UM1L	0.05755	19.0	7.32–8.37/7.96/6	7.0–9.70/8.40/14
UM1MB	0.05764	12.0	7.72–8.45/8.08/5	7.70–9.61/8.64/12
UM1DB	0.12502	15.5	7.37–8.06/7.72/5	7.40–9.0/8.18/12
UM2L	0.05828	24.0	7.90–9.31/8.64/6	8.20–11.40/9.29/17
UM2MB	0.06539	18.0	8.48–9.93/9.26/6	7.80–11.60/9.72/13
UM2DB	0.42890	30.0	8.32–9.62/8.69/6	7.70–10.30/8.88/13
UM3L	0.40313	41.5	9.38–10.10/9.79/6	8.60–11.0/9.64/18
UM3MB	0.94112	47.0	8.38–9.80/9.40/6	9.0–11.0/9.59/16
UM3DB	0.19511	26.0	7.70–8.74/8.42/5	7.30–9.80/8.06/17
LCB	1.00000	4.0	4.56–8.09/6.32/2	6.40–7.30/6.7/4
LP3B	0.49659	11.0	4.53–5.87/5.35/3	4.0–6.0/5.13/10
LP3H	1.0000	15.0	7.57–12.98/11.07/3	6.20–15.20/10.88/10
LP4L	0.01612	11.0	5.07–6.42/5.96/5	5.60–7.50/6.74/16
LP4B	0.90327	23.0	5.37–6.19/5.70/4	5.10–6.90/5.70/12
LM1L	0.03747	23.0	6.47–8.42/7.54/7	7.40–10.10/8.41/15
LM1MB	0.03776	11.0	5.92–7.38/6.61/5	6.50–8.20/7.25/13
LM1DB	0.02610	10.0	6.25–7.56/7.00/5	7.10–8.30/7.62/13
LM2L	0.45023	55.0	8.25–10.37/9.09/6	8.40–10.70/9.27/23
LM2MB	0.59179	48.0	7.29–8.76/7.95/7	7.50–8.70/8.09/16
LM2DB	0.47239	26.0	7.55–8.37/8.10/4	7.60–9.70/8.34/17
LM3L	0.80742	35.0	9.84–12.73/11.37/4	10.0–12.60/11.70/19
LM3MB	0.73246	32.0	7.58–8.73/8.23/4	7.60–8.90/8.35/18
LM3DB	0.87342	24.0	7.44–8.13/7.89/3	7.0–8.90/7.89/17
LM3HYPO	0.08327	0.0	5.44–7.26/6.16/3	5.0–5.30/5.97/2

(as a proportion of the mesial loph) in the Haasgat specimens. Despite the statistically significant difference, there is considerable overlap in the samples (Haasgat 85.04–93.78, *C. williamsi* 77.55–94.23)

Although the index of the interorbital breadth relative to extraorbital breadth is not tested statistically as a result of the small sample size, it should be noted that the breadth of the interorbital region is considerably smaller, relative to the extraorbital breadth, in the Haasgat sample than in *C. williamsi*. The mean value for the index in *C. williamsi* is 21.52% compared to 10.03% in the Haasgat individual. Likewise, the interorbital region is also far smaller relative to facial length, in Haasgat than in *C. williamsi*. The mean value for the index in *C. williamsi* is 30.31% compared to 14.57% for the Haasgat individual.

The indices showing orbital breadth relative to biorbital breadth (ORBBR/EXTORB), and orbital height relative to facial height (ORBHT/GL-IDS) show higher mean values in the Haasgat sample, indicating that the orbit is larger, relative to the size of the face, in the Haasgat specimens than it is in *C. williamsi*.

Table 7
Comparisons of mean values for indices, including results of the Mann–Whitney *U*-test where possible for Haasgat *C. williamsi*. Variable definitions are in SOM.

Index (× 100)	Mean	*n*	Mean	*n*	*p*-value	*U*-Value
NAPB/MBM3D	41.40	5	38.03	1	–	–
ORBHT/ORBBR	90.21	4	83.78	1	–	–
INTORB/EXTORB	21.52	7	10.03	1	–	–
INTORB/TDS-NA	30.31	5	14.57	1	–	–
IDS-PNS/IDS-NA	91.99	3	87.51	1	–	–
MBM3D/IDS-PNS	78.63	3	81.83	2	0.2482	1.0
ORBBR/EXTORB	33.12	5	39.30	1	–	–
ORBHT/GL-IDS	38.81	3	44.40	1	–	–
UI1L/UI2L	80.00	1	169.05	1	–	–
UM1L/UM1MB	98.95	12	97.71	5	0.8651	26.0
UM2L/UM2MB	98.36	13	98.78	4	0.5271	24.0
UM3L/UM3MB	100.03	16	104.51	6	0.5633	33.0
UM1DB/UM1MB	94.68	11	95.40	5	0.7770	25.0
UM2DB/UM2MB	89.25	12	93.85	6	0.1898	22.0
UM3DB/UM3MB	84.82	15	89.66	6	0.0390	15.0
LM1L/LMIMB	118.05	13	118.08	5	0.6733	26.0
LM2L/LM2MB	116.22	16	113.07	6	0.4495	24.0
LM3L/LM3MB	143.85	14	147.41	3	0.5147	17.0
LM1DB/LM1MB	105.10	12	105.90	5	0.7518	27.0
LM2DB/LM2MB	103.09	16	101.8	4	0.1303	16.0
LM3DB/LM3MB	96.57	16	95.87	3	0.6547	20.0

Whereas the Haasgat fossils share many non-metric traits with *C. williamsi*, as would be expected of a congeneric sample, there are a number of distinctive features. Both the supraorbital torus and ophryonic groove appear to be less-developed in the Haasgat female sample; this may also be associated, in part, with the greater age of the individual. Otherwise there is no obvious craniofacial sexual dimorphism. A metopic suture is not visible.

Several other craniofacial features seem to show distinctions from *C. williamsi*. The external acoustic meatus is flattened and the groove separating it from the postglenoid process and articular fossa is far shallower relative to that of *C. williamsi*. The glenoid fossa is oval rather than rounded and the squamous temporal does not bulge into the infratemporal fossa as it does in *C. williamsi*. The palatal dental arcade in *C. williamsi* is rectangular in males and horseshoe-shaped in females, but in the Haasgat specimens (both male and female) the arcade is markedly rounded due to an increased convergence of the M^2s and M^3s (see Fig. 2c). The nasal bones are more triangular in the Haasgat specimens and more rectangular in *C. williamsi*. The nasal bones in the Haasgat specimens are more narrow and elongate than in *C. williamsi* and meet the surrounding bones differently. In the Haasgat *Cercopithecoides*, the nasal bones project well below rhinion and their inferior margin meets the flattened superior margins of the premaxillae in a nearly horizontal suture. The nasals narrow superiorly and terminate at the inferior end of a short intermaxillary suture which extends to the frontal (see Fig. 4). This trait appears in other colobines (e.g., *Pygathrix nemaeus* (Szalay and Delson, 1979: 324)), but the more common pattern of *C. williamsi* appears consistently in samples of modern colobines (*Procolobus badius*, 51; *Colobus polykomos*, 20; *Pygathrix verus*, 7).

The height of the coronoid process exceeds that of the condyle in Haasgat specimens. Unlike all other *Cercopithecoides*, the ramus is not oblique but vertical (see Fig. 1c). Coupled with a more narrow and vertical mandibular symphysis, this results in a mandibular body that is both relatively and absolutely longer. There is no consistent median mental canal, or foramen symphyseosum, as in *C. meaveae* and *C. kerioensis*.

Dental features also distinguish the Haasgat sample from *C. williamsi*, including a smaller distal lophid on the P_4; the P_4 is also more in line with the tooth row, rather than at an angle to it (as in *C. williamsi*). The M^2 is more rectangular than that of *C. williamsi* which tends to be mesiodistally shortened palatally, giving it

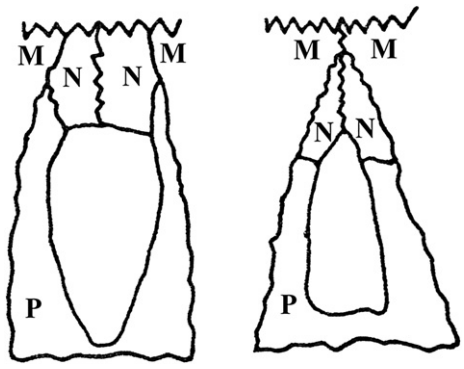

Figure 4. Nasal bone (N), premaxilla (P), and maxilla (M) shape and suture patterns in *Cercopithecoides williamsi* (left), and Haasgat *Cercopithecoides* (right).

a triangular appearance. The diastema which is sometimes found between the canine and I_2 in *C. williamsi* is not present in the Haasgat sample.

Comparisons of Haasgat Cercopithecoides with East African species

East Africa has greater diversity in *Cercopithecoides* species than southern Africa. *C. kimeui* is a considerably larger species than southern African *Cercopithecoides*, with broad upper molars, and a considerably more robust mandible. Dental metrics of *C. kimeui* (Table 8) all exceed the Haasgat means; most are outside the range of the Haasgat sample, excepting the mandibular tooth lengths and M_3 breadth.

The smaller species are at least contenders for referral of the Haasgat material. For example, *C. meaveae* is an East African member of the genus that is similarly small in size. However, it is fundamentally different both facially and dentally. Male specimens from Haasgat have shorter, narrower palates when compared with *C. meaveae* (Frost and Delson, 2002). The upper tooth row curves inward in the Haasgat specimens, resulting in a more rounded dental arcade than in *C. meaveae*. The mandible of the Haasgat specimens is also narrower at the M_1 and M_2, and has a deeper mandibular notch.

The dentition varies between the Haasgat specimens and *C. meaveae* (Table 8). Small sample sizes precluded statistical tests, but the ranges were non-overlapping for P^3 and P^4 breadths, and P_4 length and breadth, with Haasgat sizes smaller. The single male upper canine sample for each set of specimens was also noticeably different, with Haasgat having 77% of the length and 90% of the breadth of *C. meaveae*. The shape differences of the teeth were also striking (Table 9). Excepting the P^3 and P^4, the Haasgat ratios of length to mesial breadth were less than those of *C. meaveae*, resulting in a shorter post-canine tooth row in both the maxilla and mandible. The P_4 ratio had non-overlapping ranges.

C. kerioensis is a smaller *Cercopithecoides* species from Lothagam, compared here on the basis of photos and data published by Leakey et al. (2003) for the holotype specimen KNM-LT 9277. Craniofacially, the Haasgat material is similar in having a relatively narrower interorbital region, relatively thin supraorbital torus, and lack of a median mental foramen, but differs from *C. kerioensis* in having less-developed nuchal crests, lack of sagittal crest, and a longer mandible. *C. kerioensis* also lacks the inward curvature of the Haasgat distal dental arcade.

The dental metrics suggest that the length/breadth ratios are similar between *C. kerioensis* and the Haasgat sample; the former tends to have smaller teeth, excepting P^4 breadth (Tables 8 and 9). *C. kerioensis* was outside the range of the Haasgat sample for P^4 breadth, M^1 length and breadth, P_4 length, and the length and breadth of M_2 and M_3.

The Haasgat material is also distinct from the single specimen of *C. alemayehui* (Gilbert and Frost, 2008), in that its supraorbital torus is not nearly as projecting. The nasal bones are not as long relative to the orbits, and the interorbital distance (INTORB, 6.01–7.77 mm) is narrower than *C. alemayehui* (13 mm). The orbits of Haasgat sample are more ovoid, and the biorbital breadth (EXTORB) is greater (68.7 mm vs. 58 mm.) In general, the maxillary dentition of *C. alemayehui* is smaller than Haasgat (Table 8), overlapping with the Haasgat range in P^4 and M^2 length and breadth and M^3 breadth. There is also overlap in the tooth dimension ratios (Table 9), excepting the P^3 which is relatively and absolutely longer in the Haasgat specimens.

Detailed metric and non-metric assessments suggest that the suite of features presented by the Haasgat fossils is distinctive. Based on these data, we do not see clear justification for referring them to any of the East African species.

Summary

The Haasgat fossil colobines are recognizably *Cercopithecoides*, but there are numerous metric and non-metric differences in detailed comparisons with the only known species of the genus in southern Africa, *C. williamsi*. Moreover, the Haasgat material differs from the four other species of the genus from East Africa. These differences are in size and shape, and particularly, differences in the masticatory complex may have functional significance, particularly given the unique shape of the mandible. Other features, such as the unique mandibular ramus and interorbital suture configuration, at least appear to have taxonomic valence. Therefore, we refer the relevant Haasgat fossils to a new species. Following is the genus diagnosis, revised from Leakey (1982) and Jablonski (2002), and a new species diagnosis.

Genus Cercopithecoides Mollett, 1947

Generic diagnosis

Calvarium is large and rounded, more globular in females. Muzzle relatively narrow and short, face wide and orbits large, frontal process of zygoma narrow. Nasals moderately long, malar region narrow, nasal aperture small and straight in lateral profile, post-orbital constriction slight, supraorbital tori prominent and often raised above the level of the calvaria roof, postglabeller sulcus present, and basioccipital wide. Nuchal crests are small, sagittal crest absent or very small, postglenoid process small. Mandibular body is shallow with marked lateral ridge (prominentia lateralis) and flat anterior surface. Gonial region is small. Ramus is low, superior edge of coronoid process approximately level with or higher than mandibular condyle. Premolars are relatively small and P^3 protocone small or absent. Sexual dimorphism is apparent in the canines and P_3. Molars exhibit high cusps and large central foveae. Post-cranial skeleton shows features typical of more terrestrial cercopithecoids. Differs from *Libypithecus*, *Nasalis*, and *Rhinocolobus* in the short rounded braincase and relatively shorter muzzle. Differs from Asiatic colobines *Paracolobus* and *Rhinocolobus* in the absence or diminution of a P^3 protocone. Differs from all other colobines in a low shallow mandible with a short ramus.

Cercopithecoides haasgati sp. Nov.

Etymology

Haasgat, Afrikaans for “hare hole,” is the cave site from which the defining specimens were excavated.

Table 8
Dental dimensions of Haasgat sample compared to East African *Cercopithecoides*.

	UCL	UCB	UP3L	UP3B	UP4L	UP4B	UM1L	UM1MB	UM2L	UM2MB	UM3L	UM3MB
Haasgat												
Mean	9.25	6.30	4.79	5.84	5.346	7.09	7.96	8.08	8.64	9.26	9.79	9.40
n	1	1	4	4	6	5	6	5	6	6	6	6
Min	9.25	6.30	4.42	5.59	4.81	6.76	7.42	7.72	7.90	8.48	9.38	8.38
Max	9.25	6.30	5.13	6.40	6.02	7.34	8.40	8.45	9.31	9.93	10.10	9.77
C. kimeui												
Mean	.	.	.	.	7.0	.	10.1	9.6	11.28	11.2	11.3	12.0
n	.	.	.	.	2	.	2	2	4	4	1	1
Min	.	.	.	.	6.8	.	9.7	8.6	10.8	10.1	11.3	12.0
Max	.	.	.	.	7.2	.	10.5	10.6	11.7	12.0	11.3	12.0
C. meaveae												
Mean	12.0	7.0	4.9	6.80	5.55	7.60	8.40	7.70	8.90	8.00	9.35	8.10
n	1	1	1	1	2	1	2	2	2	2	2	2
Min	12.0	7.0	4.9	6.80	5.50	7.60	8.00	7.50	8.60	7.40	9.20	7.40
Max	12.0	7.0	4.9	6.80	5.60	7.60	8.80	7.90	9.20	8.60	9.50	8.80
C. kerioensis												
Mean	.	.	.	6.20	5.20	6.60	6.60	7.00	.	.	.	.
n	.	.	.	1	1	1	1	1	.	.	.	.
C. alemayehui												
Mean	8.9	6.8	4.3	5.7	5.1	6.9	7.3	7.7	8.9	8.9	8.9	9.3
n	1	1	1	1	1	1	1	1	1	1	1	1

	LCL	LCB	LP3B	LP4L	LP4B	LM1L	LM1MB	LM2L	LM2MB	LM3L	LM3MB
Haasgat											
Mean	4.21	6.32	5.35	5.96	5.70	7.54	6.61	9.09	7.95	11.37	8.23
n	1	2	3	5	4	7	5	6	7	4	4
Min	4.21	4.56	4.53	5.07	5.37	6.47	5.92	8.25	7.29	9.84	7.58
Max	4.21	8.09	5.87	6.42	6.19	8.42	7.38	10.37	8.76	12.73	8.73
C. kimeui											
Mean	.	.	.	7.4	6.55	9.5	8.6	9.9	9.9	13.25	9.2
n	.	.	.	2	2	1	1	1	1	2	2
Min	.	.	.	5.8	6.5	9.5	8.6	9.9	9.9	11.3	8.5
Max	.	.	.	9.0	6.6	9.5	8.6	9.9	9.9	15.2	9.9
C. meaveae											
Mean	4.80	8.35	4.45	7.30	4.90	8.55	6.55	8.90	7.20	11.35	7.40
n	2	2	2	2	2	2	2	2	2	2	2
Min	4.60	8.20	4.30	6.60	4.90	8.30	6.50	8.60	7.00	10.50	7.00
Max	5.00	8.50	4.60	8.00	4.90	8.80	6.60	9.20	7.40	12.20	7.80
C. kerioensis											
Mean	.	.	.	6.50	4.60	.	.	7.90	6.60	9.60	6.30
n	.	.	.	1	1	.	.	1	1	1	1

Holotype

HGD 1165, a partial midface skeleton and mandible.

Specimens included: HGD 1166, HGD 1167, HGD 1168, HGD 1169, HGD 1170, HGD 1172, HGD 1173, HGD 1174, HGD 1175, HGD 1176, HGD 1177, HGD 1178, HGD 1179, HGD 1180, HGD 1181, HGD 1184, HGD 1185, HGD 1186, HGD 1187, HGD 1191, HGD 1193, HGD 1193, HGD 1197, HGD 1221.

Distribution

Haasgat, North West Province, South Africa.

Table 9
Ratios of length to mesial breadth.

		UP3	UP4	UM1	UM2	UM3	LP4	LM1	LM2	LM3
Haasgat	Mean	0.821	0.763	0.977	0.988	1.045	1.088	1.181	1.131	1.4741
	n	4	5	5	4	6	4	5	6	3
	Minimum	0.78	0.69	0.91	0.94	0.96	1.02	1.09	1.04	1.41
	Maximum	0.86	0.89	1.08	1.05	1.18	1.16	1.36	1.26	1.55
C. meaveae	Mean	0.721	0.737	1.090	1.122	1.165	1.490	1.31	1.238	1.532
	n	1	1	2	2	2	2	2	2	2
	Minimum	0.72	0.74	1.07	1.00	1.05	1.35	1.28	1.16	1.50
	Maximum	0.72	0.74	1.11	1.24	1.28	1.63	1.33	1.31	1.56
C. kerioensis	Mean	.	0.790	0.940	.	.	.	.	1.196	1.52
	n	.	1	1	.	.	.	.	1	1
C. alemayehui	Mean	0.754	0.739	0.948	1.0	0.957				
	n	1	1	1	1	1				

Specific diagnosis

A small *Cercopithecoides* relative to *C. williamsi* and *C. kimeui* for most craniodental features. It differs from *C. williamsi* in that it has a narrower interorbital region, relatively larger orbits, triangular nasal bone configuration and a suture pattern between the maxillae above the nasal bones. The muzzle is narrower and shorter, with a more rounded dental arcade. The mandibular length is greater because of a more vertical mandibular ramus. The external acoustic meatus is flattened and the articular fossa is shallow. The M_1 is smaller than in *C. williamsi*, and the M_3 has a distally greater lophid breadth and larger hypoconulid. The M3 is larger than M2 in length and breadth, rather than the reverse seen in *C. williamsi*. Differs from *C. meaveae* in shorter, narrower, and more rounded palate, narrower mandible, deeper mandibular notch, and smaller premolars and upper canine. Differs from *C. kerioensis* in less-developed nuchal crests, lack of sagittal crest, rounded palate, and longer mandible. Differs from *C. alemayehui* in shorter and narrower nasal bones, less projecting suparorbital torus, and more ovoid orbits. Differs from *C. kimeui* in smaller size, molars less broad, and less robust mandible.

Description

Cercopithecoides haasgati specimens have a short muzzle with shallow maxillary fossa, along with a short and squared premaxilla. The maxillary arcade is rounded, converging at the M^2 and M^3. The shape of the lower border of the nasal aperture is variable, and the lacrimal bone forms only the posterior part of the lacrimal fossa. The interorbital region is narrow, between orbits that are tall and broad. The zygomatic arch originates above the M^2.

The braincase is rounded, the supraorbital torus is thin relative to most other *Cercopithecoides*, and the ophryonic groove is shallower. The metopic suture is absent. The temporal lines are prominent but do not converge. The nuchal crest is weak.

The mandibular body is lengthened, in part due to more vertical mandibular ramus. The depth of the mandibular corpus is constant, and the symphysis is relatively narrow and vertical. There is no consistent foramen symphyseosum.

The dentition is characteristically colobine except the buccolingual diameter of the mesial loph of the M_2 is greater than that of the distal loph rather than smaller. There is a lack of dental sexual dimorphism, aside from the C-P3 complex. The P^3 lacks a protocone. For both length and breadth, the upper and lower molar size sequence is $M1 < M2 < M3$, except for the distal breadth of M_3, which is variable.

There is no discernable consistency in the presence of cuspules on the molars. There is no association between sex and the cuspules. However, it may be noted that with regard to the upper molars, cuspules are more common on M^1 and M^2 than on M^3, and that on M^1 and M^2 they are more frequent on the buccal than on the lingual aspect, while on M^3 they are more frequent on the lingual aspect. With regard to the lower molars, cuspules are more frequent on M_1 and M_3 than on M_2 and that on all three molars, they are more frequent on the buccal aspect.

No post-cranial remains have been definitively associated with the craniodental remains.

Conclusions

Both metric and non-metric comparisons of the Haasgat *Cercopithecoides* sample with other members of the genus indicate substantial differences in craniofacial size and shape between the Haasgat *Cercopithecoides* and other *Cercopithecoides* species, particularly in the masticatory complex and orbits, as well as a few differences in dentition. These trait distinctions are comparable in nature to those used to distinguish the larger *Cercopithecoides*, *C. kimeui*, from *C. williamsi*, yet represent a smaller species than those taxa, with a unique suite of features independent of size. The craniofacial features, notably the palate, mandible, and orbits, also differ from the smaller East African species, *C. kerioensis*, *C. meaveae*, and *C. alemayehui* yet still fall within the key defining characteristics of the genus. Based on these observations, we refer the Haasgat fossils to a new species, *C. haasgati*. *C. haasgati* increases the variability known within the genus *Cercopithecoides*, and is the second confirmed species of the genus in southern Africa. The unique craniofacial features of the Haasgat fossils may be interpretable in the context of dietary adaptation and niche diversification among species.

Acknowledgements

We would like to thank Andre Keyser, formerly of the Geological Survey of Southern Africa, and Heidi Fourie and Francis Thackeray of the Transvaal Museum, for access and help with specimens. W. Scott McGraw kindly provided a sample of modern *Colobus* and *Procolobus* skulls for comparisons. We are grateful to the referees, associate editor Eric Delson, and editor Steve Leigh, for many useful comments and insights.

Appendix. Supplemental online material

Supplementary data related to this article can be found online at doi:10.1016/j.jhevol.2010.08.002.

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