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First *in situ* middle Pliocene cercopithecoid fossils from the Palaeokarst System of Bolt's Farm (South Africa)

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ABSTRACT

Important collections of Plio-Pleistocene cercopithecoid remains has have been discovered in South African karstic sites but few are older than the Late Pliocene. The fossiliferous Palaeokarst System of Bolt's Farm in the Cradle of Humankind World Heritage Site of UNESCO is known to have yielded a few remarkable remains of cercopithecoids, mainly between 1936 and 1948. The excavation done in Brad Pit B (BPB) which was discovered in 2010, led to the *in situ* discovery of some fossils in karst-fill breccia correlated faunally to the Middle Pliocene. The cercopithecoids are represented by *Parapapio broomi* Jones, 1937, and *Cercopithecoïdes* cf. *williamsi* Mollett, 1947. At BPB, we have potentially the oldest known co-occurrence of these two taxa in Southern Africa, the second oldest being at Sterkfontein-Member 2. The currently available evidence suggests dispersal of these two genera from East Africa to Southern Africa, a hypothesis generally accepted by most authors, even though the period of dispersal is now considered to be somewhat earlier than previously thought. Whereas the Early Pliocene environment in the Cradle of Humankind seems to have been drier than that of today, it was probably more humid during the Middle Pliocene which would have allowed the dispersal of these two taxa.

KEY WORDS

Pliocene,
 Primates,
Parapapio,
Cercopithecoïdes,
 Cradle of Humankind,
 Bolt's Farm.

RÉSUMÉ

Premiers fossiles *in situ* de cercopithecoïdes du Pliocène moyen du système paléokarstique de Bolt's Farm (Afrique du Sud).

D'importantes collections de restes de cercopithecoïdes du Plio-Pléistocène ont été découvertes dans des sites karstiques sud-africains, mais peu sont plus anciens que le Pliocène supérieur. Le système paléokarstique fossilifère de Bolt's Farm, dans le Cradle of Humankind World Heritage Site de l'UNESCO, est connu pour avoir livré quelques restes remarquables de ces primates, principalement entre 1936 et 1948. Les fouilles effectuées à Brad Pit B (BPB), découvert en 2010, ont conduit à la découverte *in situ* de quelques fossiles dans une brèche non perturbée datée, biochronologiquement, du Pliocène moyen. Les cercopithecoïdes sont représentés par *Parapapio broomi* Jones, 1937, et *Cercopithecoïdes* cf. *williamsi* Mollett, 1947. A BPB, nous avons potentiellement la plus ancienne cooccurrence connue de ces deux taxons en Afrique australe, la deuxième plus ancienne étant celle de Sterkfontein-Member 2. Cette découverte suggère une dispersion de ces deux genres de l'Afrique de l'Est vers l'Afrique australe, une hypothèse généralement acceptée par la plupart des auteurs, à une période un peu plus ancienne que l'on pensait jusque-là. Alors que l'environnement du Pliocène inférieur dans le Cradle of Humankind semble avoir été plus sec que celui d'aujourd'hui, il était probablement plus humide au Pliocène moyen, ce qui aurait permis la dispersion de ces deux taxons.

MOTS CLÉS

Pliocène,
 Primates,
Parapapio,
Cercopithecoïdes,
 Cradle of Humankind,
 Bolt's Farm.

INTRODUCTION

South African karstic palaeontological sites have yielded an abundant collections of cercopithecoid remains (Jablonski & Frost 2010; Gommery & Bento Da Costa 2016) dated to the terminal Pliocene (corresponding to the final late Piacenzian [Cohen *et al.* 2013]) and the early Pleistocene (including here both the Gelasian and the

Calabrian [Cohen *et al.* 2013]). This is the case for the “historical sites” of Taung (Haughton 1925; Gear 1926; Freedman 1957, 1965; Jablonski & Frost 2010; Gilbert *et al.* 2016) which also yielded the first australopithecine (*Australopithecus africanus* Dart, 1925) and Makapansgat Limeworks (Mollett van der Spuy 1947; Freedman 1957; Maier 1970; Reed 1996; Jablonski & Frost 2010) located in the North of South Africa. The major part of these

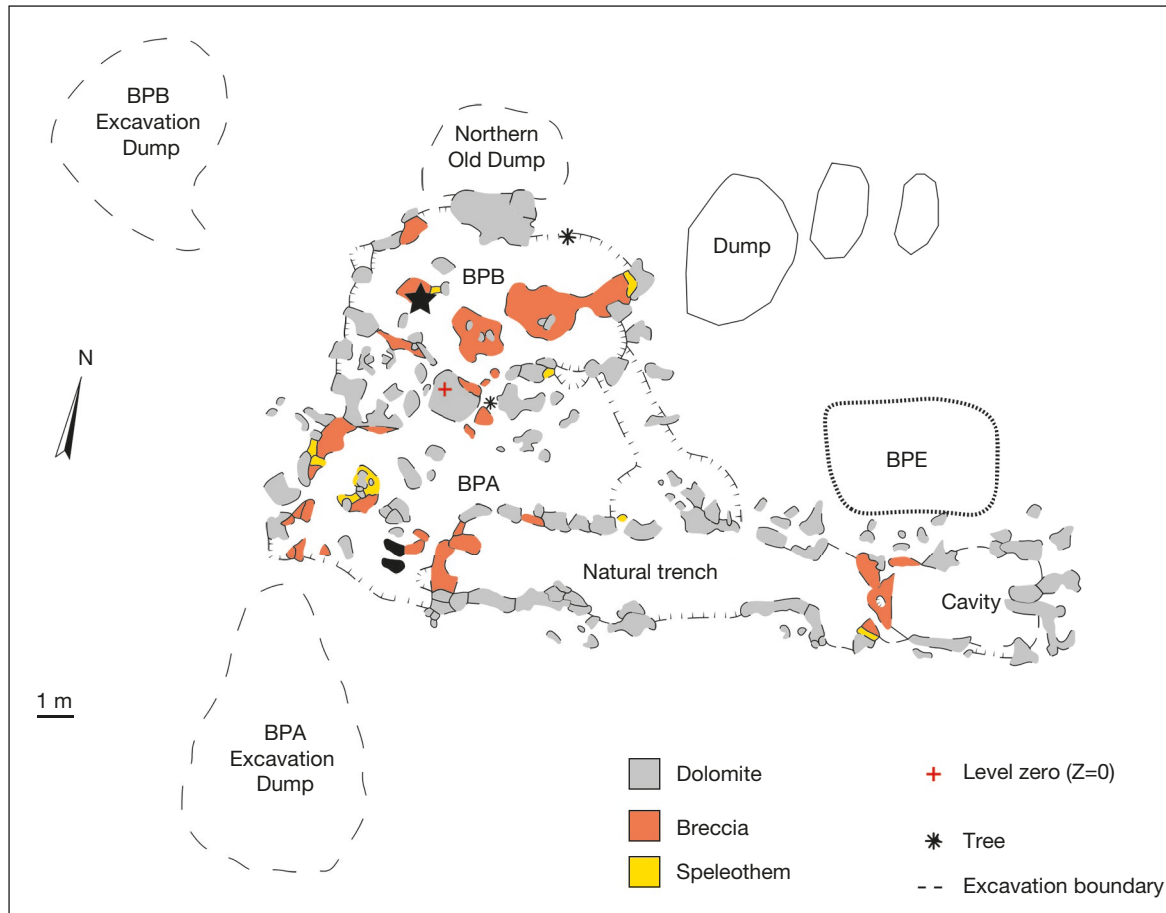


FIG. 1. — Map of the locality of Brad Pit (BP). The different loci: **BPA**, Brad Pit A; **BPB**, Brad Pit B; **BPE**, Brad Pit Extension (newly discovered). “*Parapapio* spot” is indicated by a black star.

collections come from a restricted area in the western part of Gauteng Province and the neighbouring part of the North-West Province. Recognized as the Cradle of Humankind World Heritage Site (COH WHS) in 1999 by the UNESCO and is mainly located around the Sterkfontein Valley. Robert Broom was the first to conduct regular research in this area from 1936 to his death in 1951, in particular on the Palaeokarst System of Bolt’s Farm (called Bolt’s Farm in this article) (Thackeray *et al.* 2008).

Most of the fossiliferous deposits in the Sterkfontein Valley are remnants of karstic systems (Brain 1958, 1981) mined for speleothems by the gold industry in the 19th and the beginning of the 20th century. What the miners regarded as waste, such as blocks of fossiliferous breccia, was discarded onto dumps. The largest fraction of Plio-Pleistocene (classically covering the period 3.1–0.9 Ma in South Africa) fossil material originates from such mine dumps. The second largest fraction originates from decalcified breccia pockets or makondoes (Reynolds & Kibii 2011; Herries *et al.* 2013). A small portion of the fossils are obtained via collecting of specimens from *in situ* breccia, providing a better stratigraphic context than the dump waste and decalcified pockets.

On Bolt’s Farm more than thirty fossil-bearing localities have been identified (Cooke 1991; Sénégas *et al.* 2002; Thackeray *et al.* 2008; Gommery *et al.* 2012, 2016; Monson *et al.* 2015; Pickford & Gommery 2016, 2020; Edwards *et al.* 2019), ranging from the early Pliocene to the end of the early Pleistocene, some of which have yielded cercopithecoid fossils (Freedman 1957, 1961, 1965, 1970, 1976; Szalay & Delson 1979; Delson 1984; El-Zaatari *et al.* 2005; Gilbert 2007a, b; Williams *et al.* 2007; Kuykendall & Rae 2008; Gommery *et al.* 2008a, 2014, 2016; Thackeray *et al.* 2008; Jablonski & Frost 2010; Gilbert *et al.* 2018). The oldest cercopithecoid from Bolt’s Farm, dating to the early Pliocene, came from the locality of Waypoint 160 (Gommery *et al.* 2008b, 2009, 2014, 2019). The locality of Waypoint 160 has been dated biochronologically through the identification of associated rodents, such as *Eurytomys* (Sénégas & Avery 1998; Sénégas & Michaux 2000). Whereas almost all the material of Cercopithecoidea from this locality came from blocks of breccia in the mine dumps, a fragment of a tooth was found *in situ* (Gommery *et al.* 2019). In contrast to East Africa and except for the late Piacenzian, the Pliocene cercopithecoid fossil record in Southern



FIG. 2. — View of the locus BPB with the “*Parapapio* spot” in the white circle.

Africa is not well documented (Jablonski & Frost 2010) being represented only by the material from Waypoint 160 and by one isolated tooth from Langebaanweg in the Western Cape Province (Grine & Hendey 1981) aged approximately 5.1 Ma (Roberts *et al.* 2011).

Brad Pit or BP (with its two loci Brad Pit A or BPA and Brad Pit B or BPB) is a fossiliferous site discovered on the 29th of November 2010 on Klinkert’s portion of Bolt’s Farm (Gommery *et al.* 2012) (Fig. 1). An outcrop of *in situ* breccia at BPB yielded some specimens of a cercopithecoid associated with a rich mammal microfauna. The preliminary study of the rodents suggests a middle Pliocene correlation. BPB probably represents the second oldest fossiliferous deposit in the Cradle of Humankind as well as the oldest co-occurrence of the two genera *Parapapio* Jones, 1937, and *Cercopithecoides* Mollett, 1947, in South Africa (Jones 1937; Mollett Van Der Spuy 1947). Member 2 of Sterkfontein yielded some remains of these two genera and may be of similar age (Pickering *et al.* 2004; Granger *et al.* 2015). This article describes the first craniodental and postcranial remains of the cercopithecoids from BPB, retrieved from *in situ* breccia. This study increases our knowledge about the Cercopithecoidea of the middle Pliocene in South Africa, which are rare, and will contribute to a better understanding of their evolutionary history.

GEOLOGICAL AND PALAEOONTOLOGICAL CONTEXTS

Until recently, the two loci BPA and BPB were considered to represent different karst infills (Fig. 1). The excavations done since 2013 have exposed more geological details since the discovery of the locality. A preliminary geological study done in 2019 suggests that the two loci represent in fact a single infill. BP consists of an un-roofed section of palaeokarst infill hosted in Palaeoproterozoic dolomites of the Malmani Subgroup (Chuniespoort Group, Transvaal Supergroup). The effects of the past mining activity at BPB, as well the western part of BPA, were less intense than at some other loci at Bolt’s Farm. The primate material described herein comes from the north-western corner of BPB and was retrieved from the top section of the exposed breccia, informally referred to as the “*Parapapio* spot” (Fig. 2). At the time of the discovery of BPB on the 29th of November 2010, a tooth and some fragments of bones were noticed at the top of this spot (Fig. 3) which, after acid preparation are in fact parts of a skull of *Parapapio* Jones, 1937.

The excavation activities have confirmed the *in situ* context of “*Parapapio* spot” as well as two other important outcrops of breccia at BPB. It was important to confirm the *in situ* context of the “*Parapapio* spot” because the geology of the palaeokarstic sites in the Sterkfontein Valley is complex and



FIG. 3. — Specimen BPB 1 (*Parapapio broomi* Jones, 1937) still embedded in the *in situ* breccia before extraction: muzzle extremity (A); skull vault (B); skull back (C); right M3/(D).

often disrupted by past mining activities. The preliminary geological study (Fig. 4A) recognized three main sedimentary units, ranging between 3.25 and 3.75 m thick. The “*Parapapio* spot” belongs to Unit 2 (0.85 m thick) (Fig. 4B) which has a finer matrix, when compared to Unit 1, comprised of medium sands with conglomeratic debris. The whole deposit consists of a fining-upward sequence with conglomeratic levels at the base changing to sand/silt at the top (Fig. 4A). Unit 2, like Unit 1, shows numerous fluid escape figures and locally fossiliferous accumulations. They correspond to the sedimentary filling of the karst cavity.

Some breccia samples taken from the top of the “*Parapapio* spot” were prepared by chemical means (see material and method). Associated with the primate fossils, there are other macrofaunal remains which include a few post-cranial bones of a large felid and of a medium-sized bovid, which are currently under study. A well-preserved cranial fragment of a bald ibis, *Geronticus thackerayi* Pavia, 2019, was also extracted (Pavia 2019; Pavia *et al.* 2017). In contrast, the microfaunal component is rich and is dominated by a new taxon of rodent. This taxon would represent the last species of *Euryotomys* Pocock, 1976, in the fossil record prior to the occurrence of *Otomys* F. Cuvier, 1824, which appears in younger Late Pliocene and Early Pleistocene sites. The oldest occurrence of *Otomys* is known at Makapansgat Lime-works (Pocock 1987), more specifically at Rodent Corner probably dated to 3.5–3.3 Ma (Hopley *et al.* 2006, 2007) and in Member 3 dated to 3.03–2.61 Ma (Reed *et al.* 2022, modified from Herries *et al.* 2013). So far no *Euryotomys*

remains have been found in Members 2 and 4 of Sterkfontein but some *Otomys* (Pocock 1987; Avery 2001; Reynolds & Kibii 2011) have been recovered. The Member 2 is dated to approximately 3.67 Ma (Granger *et al.* 2015; Van Couvering & Delson 2020). The Member 4 was previously dated between 2.8 and 2 Ma by different methods (Pickering & Kramers 2010; Herries & Shaw 2011; Reynolds & Kibii 2011; Van Couvering & Delson 2020) and current dating techniques date the deposit at 3.4 Ma (Granger *et al.* 2022). The new species of *Euryotomys*, more derived than *E. bolti* Sénégal & Avery, 1998, from Waypoint 160, would place the site biochronologically between Waypoint 160 and the oldest deposits at Makapansgat suggesting a middle Pliocene age for BPB. This new species of *Euryotomys* is also present at BPA. Some teeth of a Suidae belonging to *Gerontochoerus koobiforaensis* Pickford, 2013, confirm the Pliocene age of the infill, probably middle Pliocene (Pickford *et al.* 2019).

MATERIAL AND METHODS

The BPB specimens are housed in the Plio-Pleistocene Palaeontology section at the Ditsong: National Museum of Natural History (DNMNH) in Pretoria, South Africa. With these fossil specimens being very fragile and fragmentary, it was decided that the most controlled method of preparation of the surrounding breccia matrix, was chemical preparation (6% solution of acetic acid and protected with Paraloid B-72 consolidant) (Kgasi *et al.* 2021).

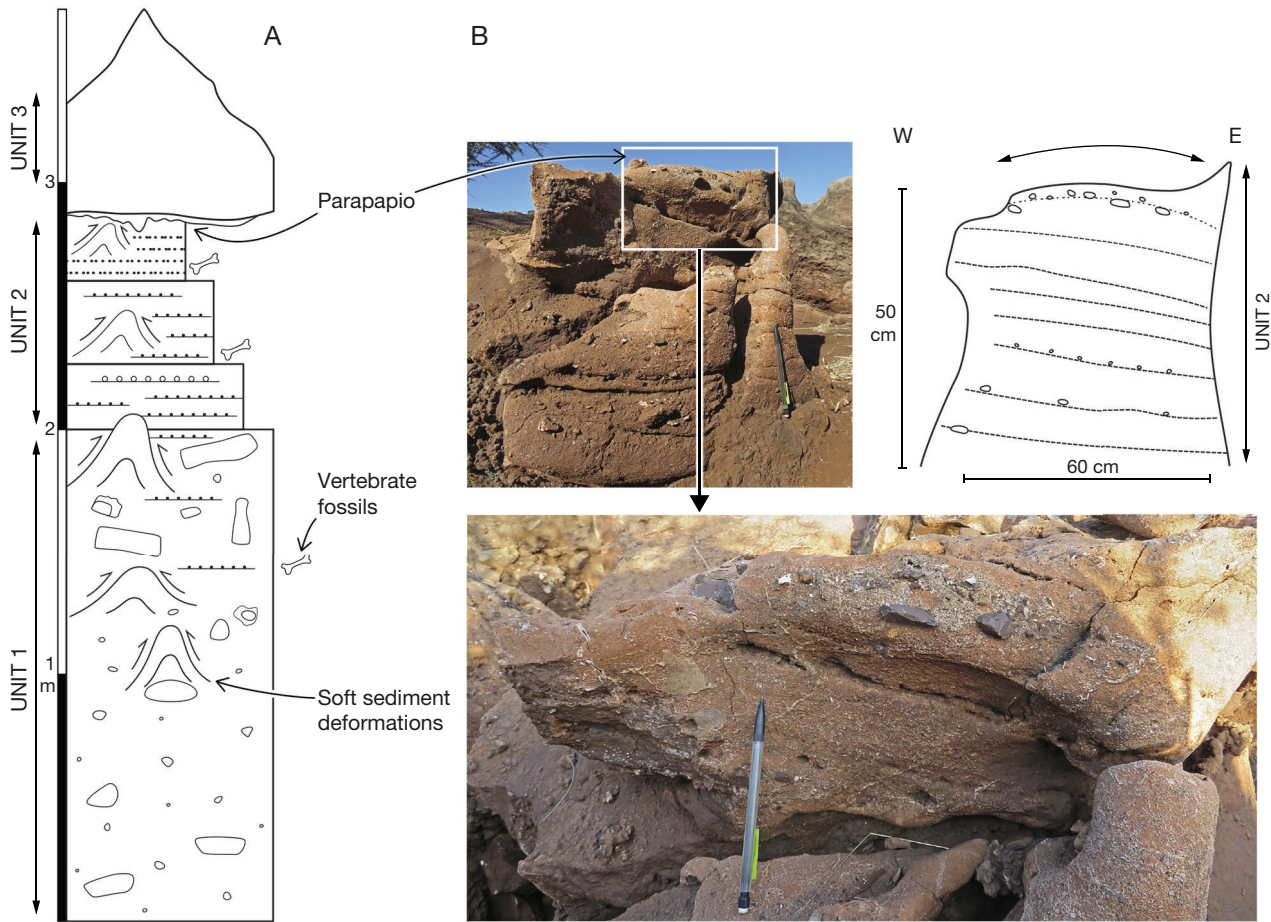


FIG. 4. — Preliminary observations concerning the breccia infilling of the “Parapapio spot” at the locus BPB: **A**, synthetic log of the locus BPB showing the stratigraphic position of *Parapapio* fossils within Unit 2; **B**, geological details of the “Parapapio spot” evidencing that the original bedding has been partly deformed by soft sediment deformation features at its topmost part.

Upper case letters are used for upper teeth and lower case for lower teeth, followed by the meristic position (see abbreviations). To prevent confusion due to the diversity of dental nomenclatures employed in the literature, a “/” is placed after the letter and the meristic position for upper teeth (e.g. M1/, upper first molar) and the “/” is placed between the letter and meristic position for lower teeth (e.g. p/3 lower third premolar) the forward slash representing the occlusal plane. The deciduous stage of the tooth is indicated by a “d” placed before the tooth. The dental anatomical nomenclature is based on and adapted from Delson (1975), Swindler (2002) and Szalay & Delson (1979). Dimensions of the teeth are given in millimetres and follow the method of Freedman (1957), in particular for the mesial (Mb) and distal (Dd) widths of the molars.

The present study corresponds to anatomical descriptions with some linear measurements in mm taken with a manual plastic calliper with an accuracy of 0.1 mm. The BPB fossils have been compared with some *Parapapio* and *Cercopithecoides* specimens and as well other Papionina in the collections from Sterkfontein (from Member 4) and Taung (from Pit 5, fossils collected by the Southern Section of the University of California African Expedition (UCAE) led by Charles L. Camp between 1947-1948) curated in the Ditsong National Museum of Natural History (DNMNH)

at Pretoria and from Makapansgat Limeworks (Members 3 & 4) and Pit 23 of Bolt’s Farm Cave System (as well fossils collected by the UCAE) in the University of the Witwatersrand (WU) in Johannesburg (Table 1). The systematics of the smallest South African fossils of *Papio* Erxleben, 1777, change regularly, and in this paper we follow the one adopted by Gilbert *et al.* (2018). The specimens from Taung are considered to be *Papio izodi* Gear, 1926, and the others from Kromdraai A and Cooper’s are *Papio angusticeps* (Broom, 1940). For the linear dental measurements concerning the specimens from BPB attributed to *Parapapio broomi* and *Papionina* indet., data from the literature were added to our measurements (Freedman 1957, 1965; Frost 2001; Frost & Delson 2002) to increase the sample (Table 2; Appendices 1-7).

The comparative material of extant primates for the post-cranial specimens are curated at the Zoology Department – Afrika Museum in Tervuren in Belgium and the Department of Large Mammals at the Ditsong: National Museum of Natural History (DNMNH) in Pretoria, South Africa: *Colobus guereza* Rüppell, 1835 = 2, *Colobus angolensis* P. Sclater, 1860 = 1, *Pliocolobus badius* (Kerr, 1792) = 2, *Chlorocebus aethiops pygerythrus* F. Cuvier, 1821 = 6, *Cercocebus agilis* Milne-Edwards, 1886 = 5, *Lophocebus albigena* (Gray, 1850) = 5, *Mandrillus sphinx* (Linnaeus, 1758) = 3, *Papio anubis* Lesson, 1827 = 4, *Papio ursinus* Kerr, 1792 = 4).

TABLE 1. — List of the specimens by taxon, site and anatomical part of the different taxa of original fossil primates from South Africa used for anatomical comparison.

Taxon	Site	Skulls	Mandibles
<i>Parapapio broomi</i> Jones, 1937	Bolt's Farm Sterkfontein	BF 43 Sts 253, Sts 254, Sts 264, Sts 267, Sts 297, Sts 379A, Sts 390, Sts 393, Sts 414B, Sts 534	Sts 255, Sts 335, Sts 337, Sts 338, Sts 363, Sts 379B, Sts 414A, Sts 542, Sts 562
	Makapansgat	MP 2 (M202), M3037	
<i>Parapapio whitei</i> Broom, 1940	Sterkfontein	Sts 259, Sts 266, Sts 389B	Sts 352, Sts 359, Sts 563, Sts 389A, Sts 533
	Makapansgat	M2962	M3062
<i>Parapapio jonesi</i> Broom, 1940	Sterkfontein	Sts 250, Sts 372A, Sts 547, Sts 565	Sts 313, Sts 355, Sts 374A-B, Sts 390A
	Taung	T.14	
<i>Procercocobus antiquus</i> (Haughton, 1925)	Taung	T.17, T.20, T.25	
<i>Papio izodi</i> Gear, 1926	Taung	T.10, T.13, T.16	T.18, T.21
<i>Papio angusticeps</i> (Broom, 1940)	Kromdraai A	KA 194	KA 165, KA 166A-B, KA 168, KA 179
<i>Cercopithecoides williamsi</i> Mollet, 1947	Bolt's Farm	BF 42A	BF 42B
	Sterkfontein Makapansgat	Sts 394A MP3 (AD. 1326/3), MP62 (M668), MP113 (M2999), M676 (MP72), M3055	Sts 394B MP45 (M622), MP104 (M2990)

TABLE 2. — List of the specimens by taxon and site of fossil Papionines from South Africa with some from East Africa used in the metric analyses of lower and upper teeth (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study).

Taxon\Specimen	Upper dentition	Lower dentition
<i>Pp. broomi</i> BF	BF 43, BF 56786	BF 56787, BF 56796
<i>Pp. broomi</i> Sts	Sts 251, Sts 253, Sts 260, Sts 261, Sts 264, Sts 267, Sts 274, Sts 297, Sts 301, Sts 325, Sts 354, Sts 368A, Sts 377, Sts 378 A-D, Sts 379A, Sts 380B, Sts 383B, Sts 385, Sts 388, Sts 390, Sts 393, Sts 397, Sts 398A, Sts 410A, Sts 414B, Sts 424, Sts 534, Sts 535, Sts 539, Sts 544	Sts 255, Sts 256, Sts 261, Sts 268, Sts 270, Sts 271, Sts 280, Sts 299, Sts 309, Sts 323, Sts 335, Sts 337, Sts 338, Sts 353, Sts 360, Sts 363, Sts 369A-B, Sts 371, Sts 374, Sts 379B, Sts 400, Sts 414A, Sts 426, Sts 445, Sts 542, Sts 562, 1238/13
<i>Pp. broomi</i> M	MP 2 (M202), MP 224, M202, M205, M635, M2963, M2964, M2966, M2969, M2970, M2975, M2977, M3002, M3015, M3037	M210, M213, M2968, M2978, M2979, M2994, M3024
<i>Pp. whitei</i> Sts	Sts 259, Sts 263, Sts 266, Sts 303, Sts 336, Sts 343, Sts 370A-B, Sts 389B, Sts 462, Sts 503, Sts 548	Sts 232, Sts 342, Sts 352, Sts 359, Sts 370A, Sts 389A, Sts 411A-B, Sts 533, Sts 563
<i>Pp. whitei</i> M	MP 76, MP 151, M2962, M2963, M2973, M3011	M3062
<i>Pp. jonesi</i> Sts	Sts 250, Sts 287, Sts 322, Sts 367, Sts 372A, Sts 547, Sts 565	Sts 258, Sts 269, Sts 270, Sts 280, Sts 307, Sts 313, Sts 317, Sts 329, Sts 331, Sts 348, Sts 355, Sts 374A-B, Sts 381A, Sts 390A, Sts 409, Sts 421, Sts 469, 1238/12
<i>Pp. jonesi</i> T	T.14	
<i>Pp. jonesi</i> M	M.2976, M.3009, M.3013, M.3017	M215, M2984, M2992, M3019, M3021, M3030
<i>Pp. jonesi</i> EA	A.L. 363-1a, A.L. 363-15a	A.L.217-8, A.L.363-1b, A.L.363-15b, A.L.465-1
<i>Pr. antiquus</i> T	TP9, T.17, T.20, T.25, SAM5356	
<i>P. izodi</i> T	T.10, T.13, T.16	T.18, T.21
<i>P. angusticeps</i>	KA 156, KA 157, KA 161, KA 167, KA 174, KA 194, CO 100, CO 101, CO 102, CO 105A-B, CO 117, CO109A, CO127, CO 128, CO 135A	KA 165, KA 166A-B, KA 168, KA 179, CO 103, CO 108A, CO 112, CO 115, CO 135B, CO 136A-C, CO 165

ABBREVIATIONS

Collection references

BF	Bolt's Farm – Collection of UW;
BPA	Brad Pit A – Collection of DNMNH;
BPB	Brad Pit B – Collection of DNMNH;
CO	Cooper's – Collection of DNMNH;
DNMNH	Ditsong: National Museum of Natural History;
EA	East African – Afar Locality in Ethiopia (Frost 2001; Frost & Delson 2002);
KA	Kromdraai A – Collection of DNMNH;
M	Makapansgat Limeworks – Collection of UW;
Sts	Sterkfontein – Collection of DNMNH;
SK	Swartkrans – Collection of DNMNH;
T	Taung – Collections of DNMNH, UW and South African Museum;
UW	University of the Witwatersrand.

Teeth

P3/	Third upper premolar;
p/3	Third lower premolar;
M1/	First upper molar;
m/1	First lower molar;
di/1	Deciduous lower first incisor.

Measurements

MD	Mesio-distal length;
BL	Maximum bucco-lingual breadth;
Mb	Mesial breadth of molar (Freedman 1957);
Db	Distal breadth of molar (Freedman 1957);
Dth	<i>Distoconulus</i> breadth of the upper third molar;
Hb	Hypoconulid breadth of lower third molar (Freedman 1957);
LD	Mesio-distal length of a dental segment.

SYSTEMATIC PALAEOONTOLOGY

- Superfamily CERCOPITHECOIDEA Gray, 1821
- Family CERCOPITHECIDAE Gray, 1821
- Subfamily CERCOPITHECINAE Gray, 1821
- Tribe PAPIONINI Burnett, 1828
- Subtribe of PAPIONINA Burnett, 1828
- Genus *Parapapio* Jones, 1937

Parapapio broomi Jones, 1937

MATERIAL EXAMINED. — **Cranium.** BPB 1, partial skull with right P3/-M3/ (Figs 5, 6; Tables 3, 5). — **Mandibles.** BPB 2 (Fig. 11; Tables 5, 6); BPB 3 (Fig. 14; Tables 5, 6); BPB 4 (Fig. 9); BPB 13 (Fig. 16; Table 6); BPB 30 (Fig. 17; Table 6).

DESCRIPTION

Cranium BPB 1 (Figs 5, 6; Tables 3, 5)

General description and preservation. This fossil is a highly distorted and crushed partial skull (right side of the skull and part of the left side of the face) (Fig. 5A-C). It lacks an important part of its left side probably due to erosion of the “*Parapapio* spot”. At the time of discovery, the skull was partially exposed and the right side of the skull was protected in the breccia (Fig. 4). Due to the fossilisation, the skull is almost flattened, the right part of the calvarium is practically in the same plane as the face, which complicates the anatomical study according to the classical anatomical plans. The fossil

TABLE 3. — Measurements in mm of upper teeth of BPB 1.

BPB1	P4/	M1/	M2/	M3/
MD	6.6	9.3	11.4	12.4
BL	8.9	–	–	–
Mb	–	9.7	11	11.4
Dd	–	8.9	9.8	9.3
Dth	–	–	–	5.1

is 110.4 mm long antero-posteriorly (from the broken anterior part of the muzzle to the preserved posterior part of the skull). The face is 92.8 mm long (from the broken anterior part of the muzzle to the glabella) and the preserved width is approximately 53.6 mm (from the broken lateral edge of the left orbit to the lateral edge of the right orbit). The preserved part of the maxilla is approximately 50 mm long antero-posteriorly (from the fragment of the P3/ to the end of the bone of the dental arch posteriorly to the M3/).

The classical anatomical landmarks are not preserved here for the linear measurements and it is therefore impossible to make a further comparison with data from the literature or on more complete specimens. Much of the back of the skull is not preserved and originally the skull was longer, the muzzle is relatively short if we compare it with skulls of extinct and extant specimens of *Papio*, except for *Papio izodi* (see Gilbert *et al.* 2018). This skull belongs to a medium-sized to large papionine such as *Parapapio*. The skull also presents several other diagnostic features of *Parapapio* (Freedman 1957, 1965; Szalay & Delson 1979, Jablonski & Frost 2010; Harrison 2011; Gilbert 2013) and differs from the smallest taxa of fossil *Papio* such as *P. izodi* and *P. angusticeps* (Gilbert *et al.* 2015, 2018), namely, in lateral view (Fig. 5C), despite some small cracks, the interorbital and nasal regions indicate a slight concavity and lack of an ante-orbital drop. The maxillary ridge is weak in comparison with that of *Papio* and the maxillary fossa seems shallow. In anterior view (Fig. 5B), as well as in superior view (Fig. 5D), despite the lack of some superficial bone, the supraorbital torus is lightly built and not projected anteriorly, and the glabella is not prominent. In superior view, the ophryonic groove is absent. The anterior temporal line is weak. Only the right upper tooththrow (P3/-M3/) is preserved but the P3/ is badly damaged (Figs 5E; 6A, B).

Calvaria. It is represented mainly by the frontal and a part of its right side (sphenoid, anterior parts of temporal and parietal) (Fig. 5C, D). The frontal presents many cracks and is distorted. It lacks some fragments of bone. A hole located postero-laterally has a rounded aspect and perhaps could be related to a predation mark. Despite the distortion, the observations in the anterior and right lateral views suggest that the anterior part of the frontal was moderately rounded. Only the right inferior temporal line is preserved. This line is well defined (weak crest), short (seems to stop abruptly after the postorbital constriction). The frontal doesn't exhibit an ophryonic groove, just a very shallow depression on the right side and probably on the opposite side but this part is badly damaged.

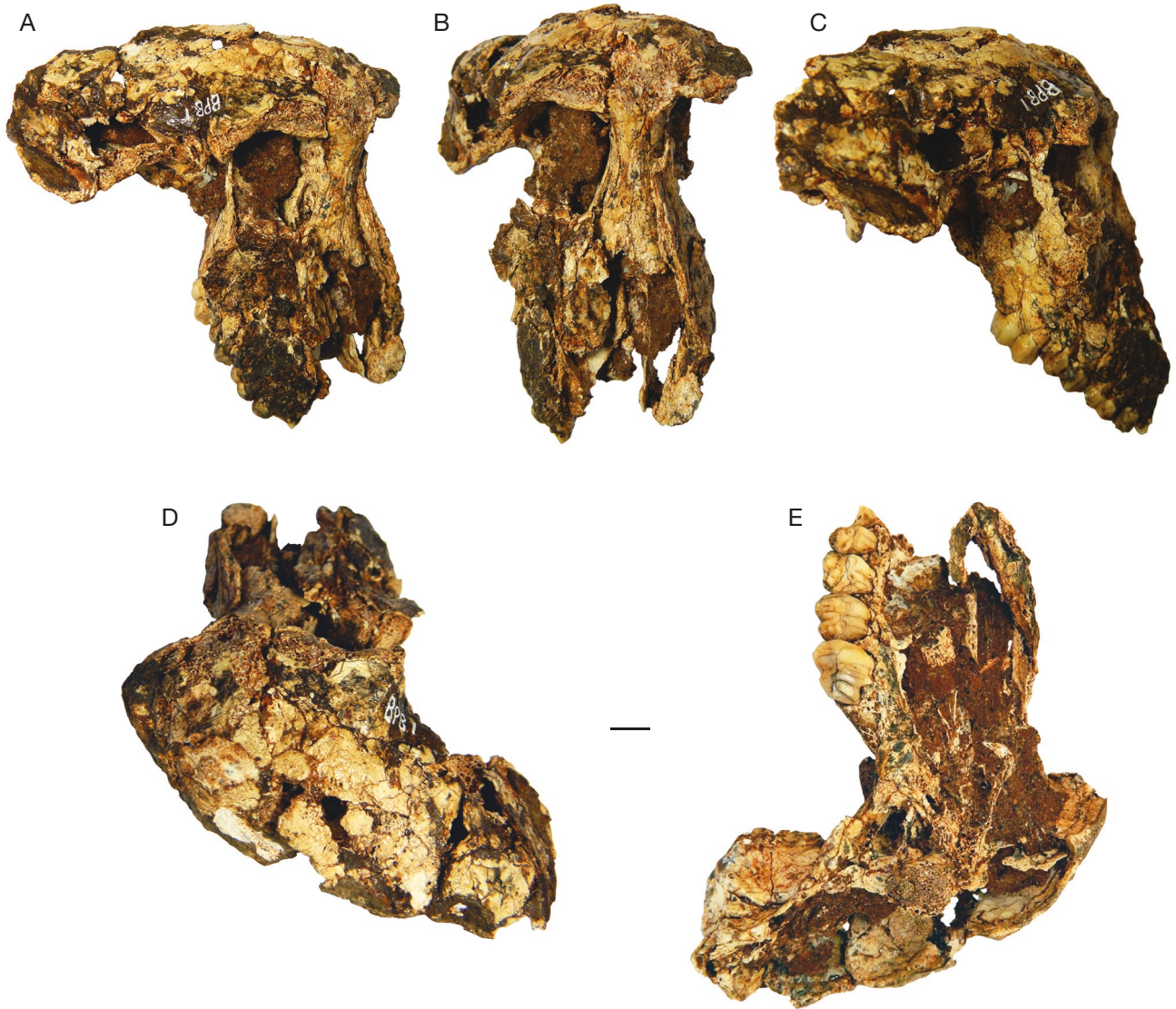


FIG. 5. — Skull of *Parapapio broomi* Jones, 1937, specimen BPB 1: **A**, fronto-right lateral view (as preserved naturally); **B**, frontal view; **C**, right lateral view (of face); **D**, dorsal view; **E**, inferior view. Scale bar: 10 mm.

TABLE 4. — Synthesis of variation in upper tooth measurements in mm (**MD**, mesio-distal length; **BL**, maximum bucco-lingual breadth) in different taxa of fossil Papionines from South Africa with some from East Africa from the literature (Freedman 1957, 1965; Frost 2001; Frost & Delson 2002) and this study (the quantity of specimens is indicated between the brackets).

Taxon	P4/		M1/		M2/		M3/	
	MD	BL	MD	BL	MD	BL	MD	BL
<i>Pp. broomi</i> BF	6.6 (1)	8.9 (1)	9.9 (1)	9.9 (1)	11.2-11.7 (2)	11.7-11.7 (2)	10.9-11.7 (2)	10.5-10.8 (2)
<i>Pp. broomi</i> Sts	5.4-6.9 (17)	7-9.6 (17)	8.4-10.2 (16)	8.7-10.3 (16)	9.5-12.4 (16)	8.8-12.1 (16)	10-11.6 (25)	9.9-12.3 (25)
<i>Pp. broomi</i> M	6.3-6.8 (7)	8.3-9 (7)	9-10.3 (6)	9.3-10.1 (6)	10.2-12.5 (14)	10.5-12.2 (14)	10.2-11.2 (11)	10.2-12.1 (11)
<i>Pp. whitei</i> Sts	6-7.8 (9)	7.8-9.2 (9)	9.7-10.7 (7)	9.5-11 (7)	11.2-13.4 (9)	11.7-12.6 (9)	11.6-12.8 (3)	11.8-12.6 (3)
<i>Pp. whitei</i> M	6-7 (4)	8.7-9.5 (4)	8.7-9.6 (3)	8.8-10.3 (3)	10.8-11.5 (11)	10.5-12.8 (11)	10.2-12.1 (5)	10.4-12.6 (5)
<i>Pp. jonesi</i> Sts	5.2-6.1 (7)	6.1-7.8 (7)	7.6-8.9 (4)	8.7-9 (4)	9.2-10.5 (8)	9.4-10.4 (8)	8.9-10.9 (8)	9.3-10.6 (8)
<i>Pp. jonesi</i> T			8.4 (1)	8.3 (1)				
<i>Pp. jonesi</i> M					9.5 (1)	10.2 (1)	9.5-10 (2)	9.6-9.9 (2)
<i>Pp. jonesi</i> EA	5.4-5.8 (2)	7-9.5 (2)	8-8.2 (2)	8.2-10.2 (2)	10.6 (1)	11.9 (1)	10.5-11.5 (2)	10.4-10.6 (2)
<i>Pr. antiquus</i> T	7.4-7.6 (2)	7.5-8 (2)	10-10.5 (2)	9-10 (2)	11.6-12.8 (6)	10.6-11.8 (6)	10.4-12.1 (4)	10.4-11.4 (4)
<i>P. angusticeps</i>	7.3-8.7 (12)	6-7.6 (12)	8.7-10.8 (10)	9-10.8 (10)	10.4-12.8 (16)	10.7-12.7 (16)	10.3-12.1 (13)	10.4-12.8 (13)
KA & CO								

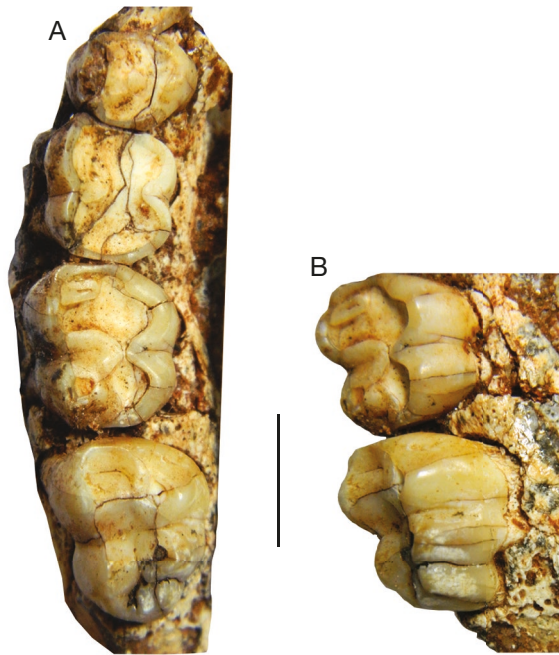


FIG. 6. — Teeth of *Parapapio broomi* Jones, 1937, specimen BPB 1: **A**, occlusal view of the right tooth row P4-/M3/; **B**, oblique-lingual view of M2/ and M3/. Scale bar: 10 mm.

TABLE 5. — Measurements of the mesio-distal length in mm of the dental segments (from Freedman 1957, 1965; this study) (the quantity of specimens is indicated between the brackets).

Taxon	P4-/M3/ LD	M1-/M3/ LD
BPB 1	40.8	34.3
BF 21	–	31.9
<i>Pp. broomi</i> Sts	33.3-37.2 (4)	28-30.8 (4)
<i>Pp. broomi</i> M	–	31.1 (1)
<i>Pp. whitei</i> Sts	37.1-37.6 (2)	31.4-31.8 (2)
<i>Pp. whitei</i> M	41.2-41.8 (2)	30.9-33.7 (3)
<i>Pp. jonesi</i> Sts	32.1-34.1 (3)	26.6-28.6 (3)
<i>Pr. antiquus</i>	35.8-38.7 (3)	31.9 (1)

Taxon	p/4-m/3 LD	m/1-m/3 LD
BPB 2	–	36.7
BPB 3	43.6	35.6
BF 56796	40.1	–
<i>Pp. broomi</i> Sts	40.7-42.3 (2)	33.8-35.7 (3)
<i>Pp. whitei</i> Sts	41.4-44.7 (4)	35.1-37.5 (4)
<i>Pp. whitei</i> M	–	39.7-40.1 (2)
<i>Pp. jonesi</i> Sts	35.7-38.6 (6)	30.1-32.3 (6)
<i>Pr. antiquus</i>	–	35.9 (1)

The morphology of the temporal line and the curved aspect of BPB 1 are similar to BF 43 in which the temporal lines are pinched, as well in other skulls attributed to *Pp. broomi* (Gilbert, 2013). In antero-lateral and lateral views, the sphenoid is covered anteriorly by some breccia and broken posteriorly at the suture with the temporal. The remnant of temporal presents many cracks and is heavily distorted. In its inferior part, a groove marks the beginning of the zygomatic arch.

Basicranium. Only the anterior part of the right side of the basicranium is preserved (Fig. 5E). At the junction with the palate, the lateral pterygoid plate is well preserved, except

for a lack of a central fragment, and as well the deep *fossa pterygoidea*. Laterally, the *fossa mandibularis* is preserved but is slightly distorted and flattened. Posteriorly, there is a well-preserved robust posterior glenoid process which is easier to observe in the lateral view.

Orbital region. The face of BPB 1 is badly damaged and distorted but it is possible to estimate the original morphology (Fig. 5A-C). The face lacks some superficial bone but this doesn't modify greatly the morphology but alters the aspect of the supraorbital torus which seems lightly built and not projected anteriorly. There is no important bulge between the two orbits which means that the glabella is not prominent (Fig. 5C). The inter-orbital pillar (between the superior median corners of each orbit) is slightly broad (11.6 mm) as in BF 43 (11.5 mm) and long. The right orbit is more complete (the median and the superior margins, as well the medio-inferior corner, are preserved) than the left where only the median margin and medio-superior corner remain. The preserved morphology of the right orbit (23.2 mm height) seems to suggest that the orbit is squarish with rounded corners as observed in BF 43. The median part of the orbit is mostly filled with matrix but not near the inter-orbital pillar which allows us to observe inferiorly a developed fossa for a well-preserved lacrimal duct. In the medio-superior corner of the margin of the left orbit, there is a small supra-orbital notch (*Incisura supraorbitalis*). It is impossible to see this anatomical structure in the right orbit because there is a crack in the same area. The right zygomatic process of the maxilla is damaged, but it is possible to observe its origin (or root). The malar height is short as in BF 43 (the malar height is the distance between the inferior orbital margin and the inferior border of the zygomatic process of the maxilla as defined in Gilbert *et al.* (2015)).

Muzzle and palate

The anterior part of the snout is badly damaged (Fig. 5A, B). The premaxilla is not preserved and neither is the nasal aperture. The nasal is preserved only posteriorly and has many cracks. It is slightly distorted but this doesn't affect the morphology. It is convex transversely and slightly concave antero-posteriorly near the level of the inferior edge of the orbits as in BF 43. There is no ante-orbital drop. The root of the right zygomatic process is located above the middle of the M3/ as in BF 43 and suggests that the muzzle is relatively short. The right maxilla is preserved and some fragments of the left maxilla are preserved along the nasal from the orbit to the premaxilla. The right maxilla is distorted but there is no indication of a strong maxillary ridge and of a deep maxillary fossa.

Only the right side of the palate is preserved (Fig. 5E). The postcanine tooth row is slightly curved and the lingual wall of the dental arch is moderately tall which suggest that the palate was moderately deep. Below and lingually to the M3/, there is an antero-posteriorly oriented depression which corresponds to the groove of the posterior palatine foramen. The bone of the dental arch doesn't end immediately posteriorly

P4/

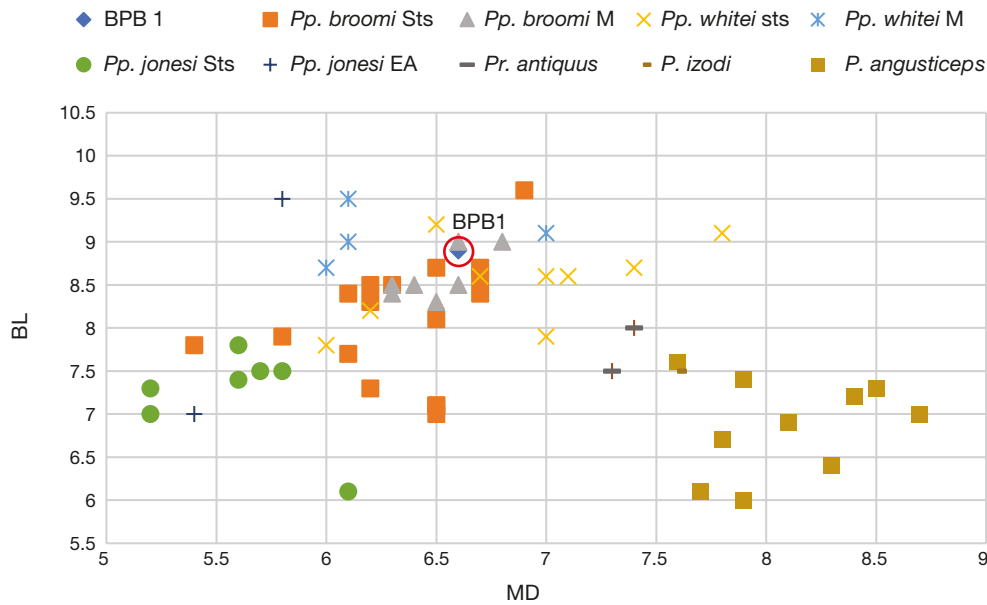


FIG. 7. — Bivariate plots MD × BL (mesio-distal length × maximum bucco-lingual breadth in mm) of upper fourth premolars (P4/) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) (Appendix 1).

to the M3/ but presents the same aspect observed in BF 43, forming a robust bony bulge. This suggests that the hard palate ends behind the M/3.

Dentition. The post-canine teeth are well preserved except for the P3/ which is just represented by a lingual fragment and the P4/ which has lost a fragment on the buccal edge of occlusal surface (Fig. 6 A; Tables 3-5). The P4/ and M1/ are worn. The M2/ is less worn (more lingually than buccally). The M3/ is slightly worn at the apex of the protocone and the hypocone. The degree of wear of the preserved post-canine teeth is typical of a mature, but not very old, adult. Despite an important MPI (maxillary premolar index (Fleagle & McGraw 1999, 2002) of 65.11 which correspond to the upper variation of *Pp. broomi* and perhaps the lower variation of *Pr. antiquus* (Haughton, 1925) (Gilbert 2007a), the size of this premolar enters into the variation of *Pp. broomi* and *Pp. whitei* Broom, 1940, from Sterkfontein and Makapansgat Limeworks (Tables 3, 4; Fig. 7). The molars increase in size from the M1/ to the M3/ (Tables 3; 4). The range of variation in molar size overlaps with different taxa of fossil South African papionines (Figs 8; 9) but differs from that of *Papio jonesi*. The size of the two molars of BPB1 plots within the range of variation of *Pp. broomi*, especially true for the M2/. The M3/s have a reduced distal loph as in BF 43. Heaton (2006) found this feature in *Pp. broomi*. The shape outline of the base of the crown is more trapezoidal than for the M2/. The well-preserved aspect of the occlusal surface of the M3/ permits observation of the intercuspid distance which is small and the molar reversed W-shaped in outline as described by McKee (1993). The M3/ presents an additional cusp linguo-distally (Fig. 6A, B), a developed *distoconulus* (Saheki 1966) as in an isolated M3/ from BPA (BPA 230 under study) and

TABLE 6. — Measurements in mm of lower teeth of BPB2, BPB 3, BPB 13, BPB 14, BPB 15 and BPB 30. *, incomplete measurement for broken tooth.

	BPB2	BPB3	BPB 13	BPB 14	BPB 15	BPB 30
p/3 MD	–	13.3	–	–	–	–
p/3BL	–	5.7	–	–	–	–
p/4L	7.5	7.8	–	–	8.0	–
p/4BL	7.9*	7.1*	–	–	6.6	–
m/1MD	8.8	8.5	–	–	–	–
m/1Mb	8*	7.3*	–	–	–	–
m/1Db	7.9	7.7	–	–	–	–
m/2MD	11.4	11.3	–	10.6	–	–
m/2Mb	9.9	9.3	–	8.9	–	–
m/2 Db	8.9*	9.1	–	8.5	–	–
m/3MD	15.2	14.2	14.3	–	–	13.6
m/3Mb	10.1	9.9	9.0	–	–	9.1
m/3 Db	9	8.3	8.6	–	–	8.4
m/3Hd	7.8	7	6.5	–	–	6.4

Sts 378A but less robust in this tooth than specimen BPB 1 (Freedman 1957). This strongly increases the mesio-distal length of the M3/ of BPB 1 (Fig. 10). In the oblique-lingual view (Fig. 6B), there is an additional strong root beneath the *distoconulus* for BPB 1 and the same applies to BPA 230. This *distoconulus* increases the length of the dental row P4/-M3/ or M1/-M3/ (Table 3). It seems that no *distoconulus* is observed in extant *Papio* (Swindler 2002).

Mandible BPB 2 (Fig. 11; Tables 5-7)

General description and preservation. BPB 2 is a partial right mandible broken mesially to the p/3 and the symphysis is absent (maximum length: 100.4 mm; breadth: 25.4 mm; height: 34.7 mm). The anterior part is badly damaged, and the two premolars are fragmentary. The *corpus mandibularis* is poorly preserved with some more or

M1/

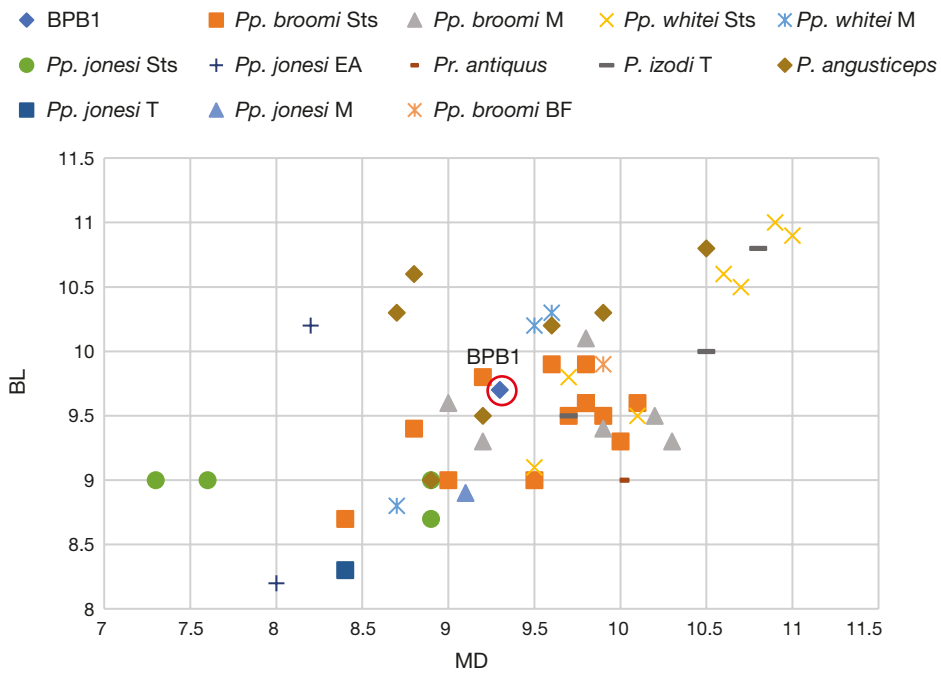


FIG. 8. — Bivariate plots MD × BL (mesio-distal length × maximum bucco-lingual breadth in mm) of upper first molars (M1/) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) (Appendix 2).

M2/

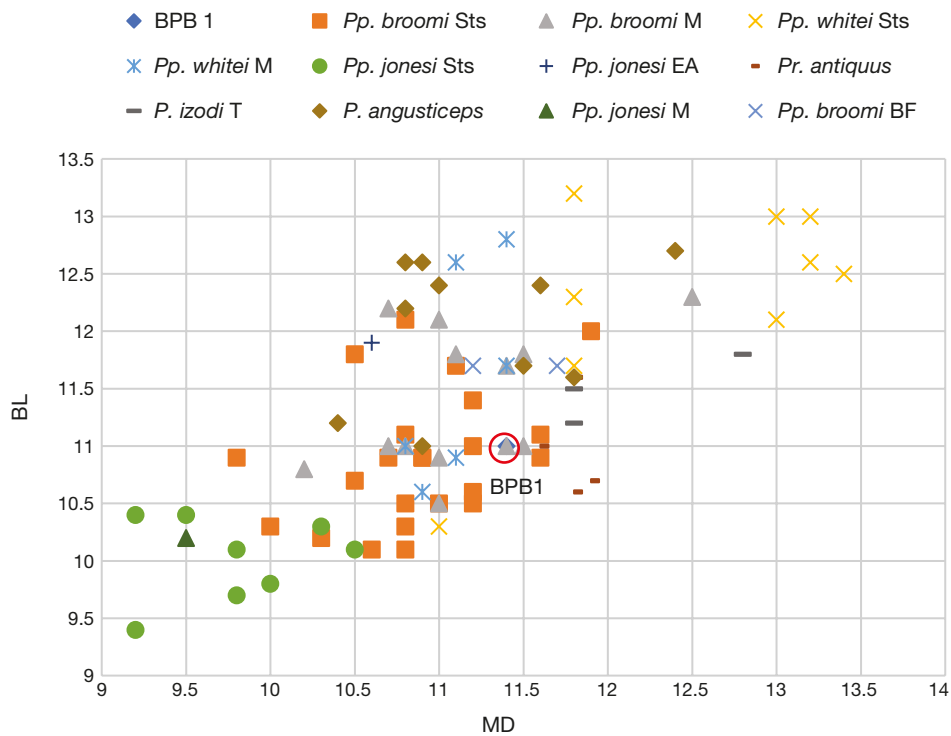


FIG. 9. — Bivariate plots MD × BL (mesio-distal length × maximum bucco-lingual breadth in mm) of upper second molars (M2/) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) (Appendix 3).

less important cracks and fragments of bone missing but it is better preserved on its posterior part but broken along the inferior edge. The ascending ramus is well preserved

as is the mandibular condyle but the coronoid process is absent. The post-canine teeth are present but in various states of preservation.

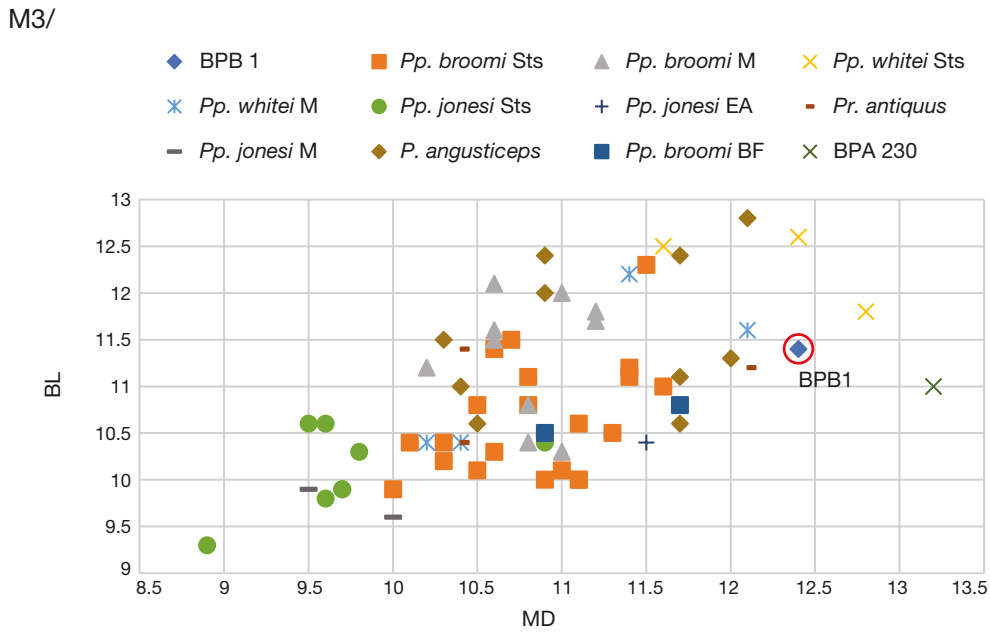


FIG. 10. — Bivariate plots MD × BL (mesio-distal length × maximum bucco-lingual breadth in mm) of upper third molars (M3) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) (Appendix 4).

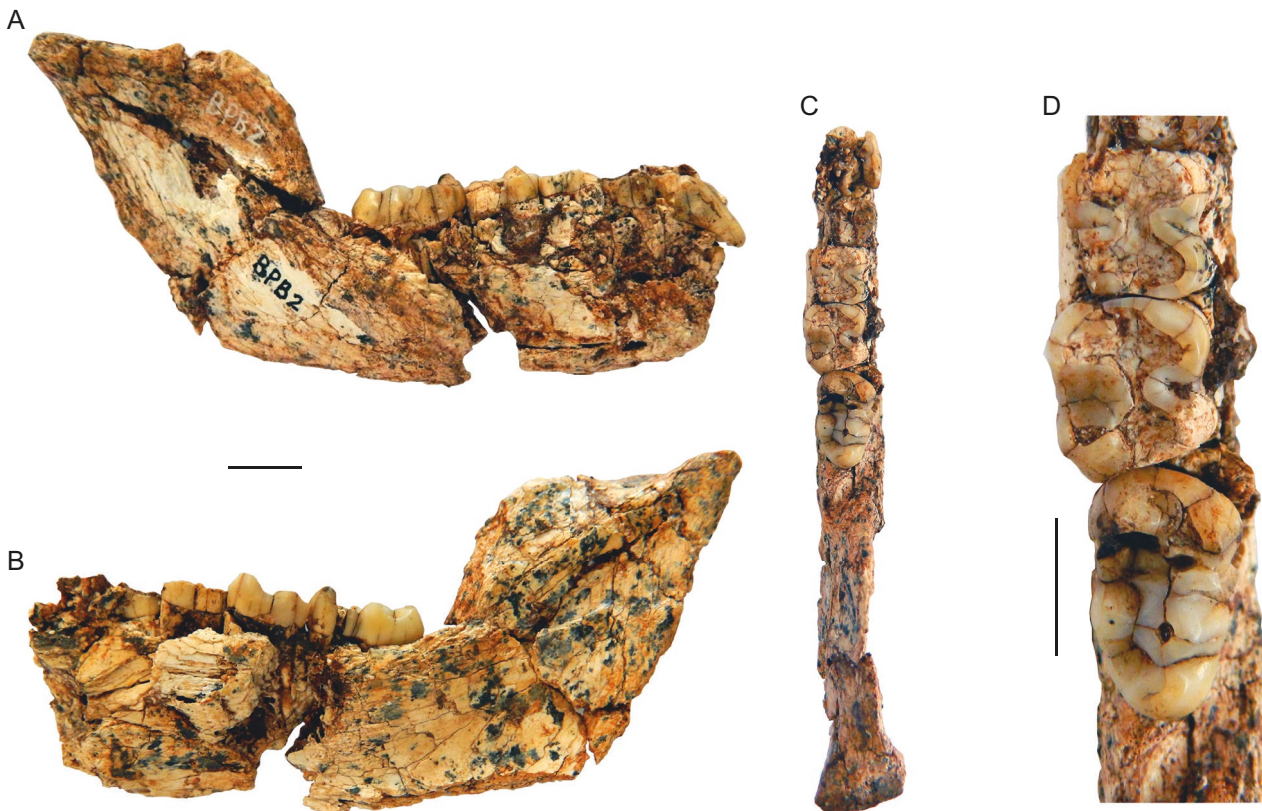


FIG. 11. — Right mandible of *Parapapio broomi* Jones, 1937, specimen BPB 2: **A**, buccal view; **B**, lingual view; **C**, superior view; **D**, occlusal view of m/1-m/3. Scale bar: 10 mm.

Mandibular corpus and ramus. It is poorly preserved on the anterior portion which presents cracking, and some fragments of bone are missing. The mandibular corpus and the gonial region are broken along the inferior edge. Despite this damage, the mandibular corpus is moderately

deep (preserved height between m/1-m/2 is 25.4 mm and between the m/2-m/3 is 24.9 mm). Buccally, there is no *prominentia lateralis* under the m/3 (Fig. 11A) unlike *C. williamsi* which presents a well-developed one. The buccal surface of the posterior part of the mandibular corpus

TABLE 7. — Synthesis of variation in lower tooth measurements in mm (**MD**, mesio-distal length; **BL**, maximum bucco-lingual breadth) in different taxa of fossil Papionines from South Africa with some from East Africa from the literature (from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002) and this study (the quantity of specimens is indicated between the brackets).

Taxon	p/4		m/1		m/2		m/3	
	MD	BL	MD	BL	MD	BL	MD	BL
<i>Pp. broomi</i> BF	6.6 (1)	6.9 (1)	9.1 (1)	7.9 (1)	11 (1)	9.5 (1)	13.5-14.2 (2)	9.3-9.9 (2)
<i>Pp. broomi</i> Sts	5.7-8.3 (16)	5.9-7.7 (16)	7.4-10.3 (14)	7.1-8.6 (14)	9.5-12.4 (16)	8.8-10.8 (16)	11.5-15.6 (16)	8.7-10.7 (16)
<i>Pp. broomi</i> M	6.4-7.4 (3)	6.6-7.9 (3)	8.6-9.6 (5)	7.8-8.6 (5)	10.5-11.8 (5)	9.6-10.4 (5)	14-15.3 (3)	10.3-10.5 (3)
<i>Pp. whitei</i> Sts	6.9-8.1 (7)	6.3-7.7 (7)	9.1-10.2 (7)	7.4-9.1 (7)	11.5-13.1 (6)	9-10.9 (6)	15.9-16.5 (5)	10.6-11.6 (5)
<i>Pp. whitei</i> M	7-7.2 (2)	7.4-8.1 (2)	10.9 (1)	8.4 (1)	—	—	16.5 (1)	11.6 (1)
<i>Pp. jonesi</i> Sts	6-7.5 (18)	5.9-7.5 (18)	7.8-9.7 (11)	6.8-7.8 (11)	9.6-11.4 (14)	8.6-10.1 (14)	12.2-13.7 (10)	8.5-10 (10)
<i>Pp. jonesi</i> M	—	—	8.3-9 (3)	6.7-7.3 (3)	9.5-10.8 (2)	7.6-9 (2)	11.1-13.2 (4)	7.9-9.3 (4)
<i>Pp. jonesi</i> EA	6.3-6.4 (2)	6-6.5 (2)	7.9-10 (2)	7.2-7.6 (2)	10-10.4 (2)	9.2 (2)	13.6-14.1 (4)	8.2-9.7 (4)
<i>Pr. antiquus</i> T	7.5 (1)	7.1 (1)	9.8-10.3 (2)	7.8-8.3 (2)	12.1 (1)	9.6 (1)	14.6 (1)	10 (1)
<i>P. angusticeps</i> KA	7.7-8.3 (4)	6.4-7.4 (4)	7.8-8.7 (4)	9.4-10.4 (4)	11.6-12.6 (5)	9.3-10.1 (5)	14.2 (7)	9.9-10.7 (7)

is flat and vertical as in *Parapapio*. Inferiorly the lingual surface (Fig. 11B) presents an important submandibular fossa. The ascending ramus is almost in the alignment of the molar tooth row. In contrast, in BF 42B (*C. williamsi*), the ascending ramus is not so laterally located. The extramolar sulcus is narrow medio-laterally as well as mesio-distally. The ramus is low and 31.3 mm long antero-posteriorly. The distal edge of the ascending ramus tilts disto-superiorly. On the lingual surface, the mandibular foramen is low, located at the same level as the alveolar margin, and the groove of this foramen is deep and pronounced. The ascending ramus has lost the coronoid process. The mandibular condyle is well preserved and is more developed medially (maximum length: 8.5 mm; breadth: 13.7 mm).

Dentition. The two premolars are very poorly preserved (Fig. 11C). The mesio-buccal flange on the p/3 (Fig. 11A) is the only well-preserved part and is short as in female individuals of *Parapapio*. The flange is fairly well developed and not honed by the upper canine which suggests that this specimen represents a female. The three molars have lost some fragments of enamel. The molars increase in size from m/1 to m/3 as is usual in papionines (Tables 5-7). The m/1 is the least well preserved and the most deeply worn of the three molars (the preservation doesn't permit inclusion in the bivariate plots MD x BL). The molars possess relatively thick enamel and the less worn cusps are low (Fig. 11D). On the m/3, the prominent and salient hypoconulid is located buccally. This continues buccally by a developed distal marginal ridge and the distal fovea is deep, spacious and short mesio-distally as in many specimens of *Pp. broomi* (such as Sts 414A and Sts 565) and also but sometimes less pronounced in *Pp. whitei* (such as Sts 563). The dimensions of the two molars enter into the range of variation in molar size of different species of *Parapapio* but the m/2 doesn't enter in the range of variation of *Pp. jonesi* (Figs 12-13).

Mandible BPB 3 (Fig. 14; Tables 5-7)

General description and preservation. BPB 3 represents a left mandible in two pieces, broken between the p/3 and

p/4. The smaller fragment (21.9 mm long antero-posteriorly, 19.6 mm broad and 19.3 mm tall under the p/3) corresponds to the left part of the symphysis. The second fragment from the mesial side of the p/4 to the posterior of the ramus is 82.4 mm long antero-posteriorly and 40.1 mm high. The two fragments fit together well. The upper part of the ramus is absent and the gonial region is damaged. The bone presents some superficial cracking.

Symphysis. Only the left part of the symphysis is preserved. The inferior edge is broken. In buccal view (Fig. 14A), the symphysis extends at least as far posteriorly as the m/1 (a fragment is preserved at the inferior edge of the mandibular corpus below the contact p/4-m/1). In lingual view, the *planum alveolare* seems long and slopes moderately disto-inferiorly (Fig. 14B). This is moderately developed transversely and is moderately deep. The superior transverse torus is smooth. The digastric fossa seems small and shallow. The anterior surface is eroded.

Mandibular corpus. The mandibular corpus is better preserved than that of BPB2. It presents some superficial cracking, especially below the m/3. The inferior edge of the mandibular corpus is well preserved. It is moderately deep (height between m/1-m/2 is 25 mm and m/2-m/3 is 24.7 mm) and robust (mid-height width between m/1-m/2 is 11.5 mm and m/2-m/3 is 13 mm). The buccal surface (Fig. 14A) is slightly convex and vertical. Buccally, there is a mental foramen under the p/3 and no *prominentia lateralis* under the m/3. Distally the lingual surface (Fig. 14B) presents a shallow depression (submandibular fossa). The preserved part of the ascending ramus suggests that it is almost in the alignment of the molar tooth row. The extramolar sulcus is narrow medio-laterally as well as mesio-distally.

Dentition. The canine and incisors are absent (Fig. 14C). The premolars and molars are better preserved than in BPB 2 despite presenting some cracking (especially in p/4, m/1 and m/2) (Fig. 14D). The molars increase in size from m/1 to m/3 as for BPB 2 (Tables 5-7). The two premolars and

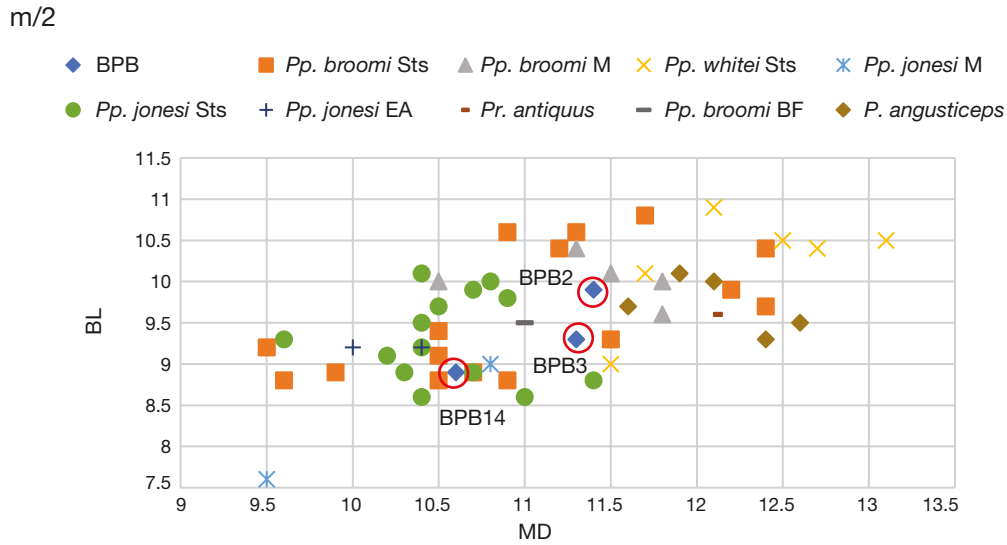


FIG. 12. — Bivariate plots MD × BL (mesio-distal length × maximum bucco-lingual breadth in mm) of lower second molars (m/2) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) (Appendix 5).

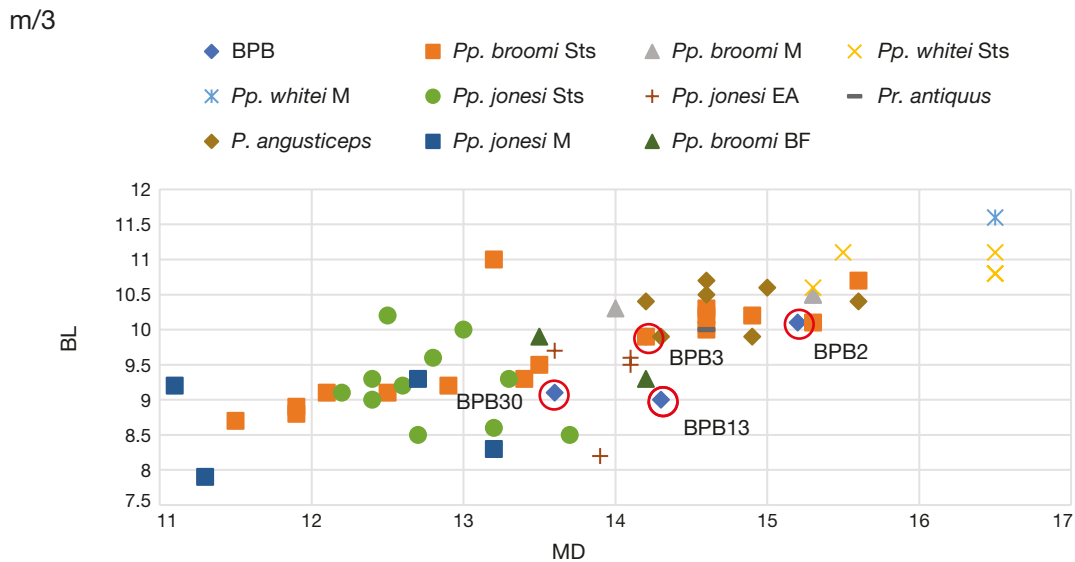


FIG. 13. — Bivariate plots MD × BL (mesio-distal length × maximum bucco-lingual breadth in mm) of lower third molars (m/3) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) (Appendix 6).

the m/1 are deeply worn, m/2 is moderately worn and the m/3 has the two mesial cuspids worn (protoconid and paraconid) which suggest a mature adult individual. The degree of wear of the three molars corresponds to that observed in BPB 2. Probably, BPB 2 and BPB 3 specimens belong to the same individual. The mesio-buccal flange on the p/3 is fairly developed as is typical of females. The hypoconulid is well developed and located buccally as in BPB 2. The aspect of the distal fovea is very similar to that of BPB 2 as well. Concerning the dimensions of the m/2 and the m/3, they are the same as for BPB 2 (Figs 12-13).

Mandible BPB 4 (Fig. 15)

General description and preservation. BPB 4 is the distal part of the right mandible (maximum length: 75.4 mm;

height: 49.3 mm). The coronoid process is broken as is the mesial edge of the ascending ramus. The fossil presents some cracking, the most important are on the distal part of the ascending ramus. The mandibular condyle is well preserved but the coronoid process is absent. No tooth is preserved, only the sockets for the roots of the m/3.

Mandibular corpus and ramus. Only the portion below the m/3 is present and suggests that the mandibular corpus is vertical, high and moderately large (below the alveolar margin at m/3, height: 28.2 mm; breadth: 12.7 mm). The buccal surface (Fig. 15A) is slightly convex and there is no *prominentia lateralis* under the m/3. The extramolar sulcus is only preserved buccally. Inferiorly the lingual surface (Fig. 15B) presents a depression which corresponds to the submandibular fossa.

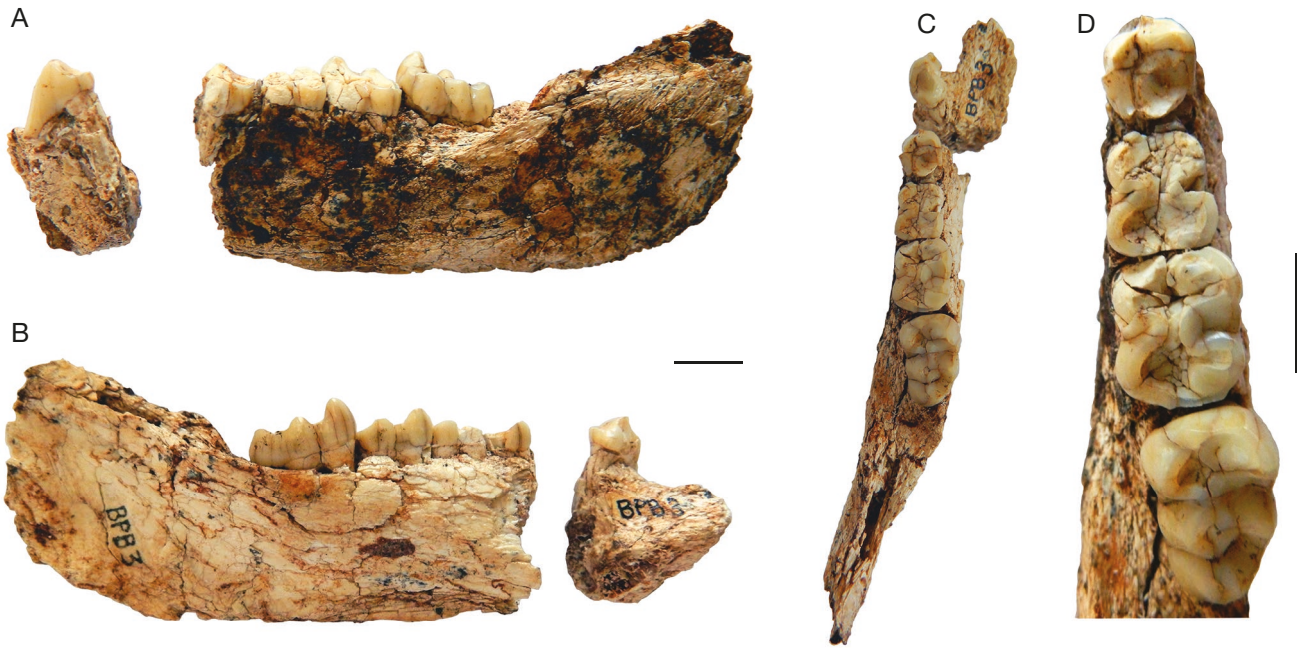


FIG. 14. — Left mandible of *Parapapio broomi* Jones, 1937, specimen BPB 3: **A**, buccal view; **B**, lingual view; **C**, superior view; **D**, occlusal view of p/4-m/3. Scale bar: 10 mm.

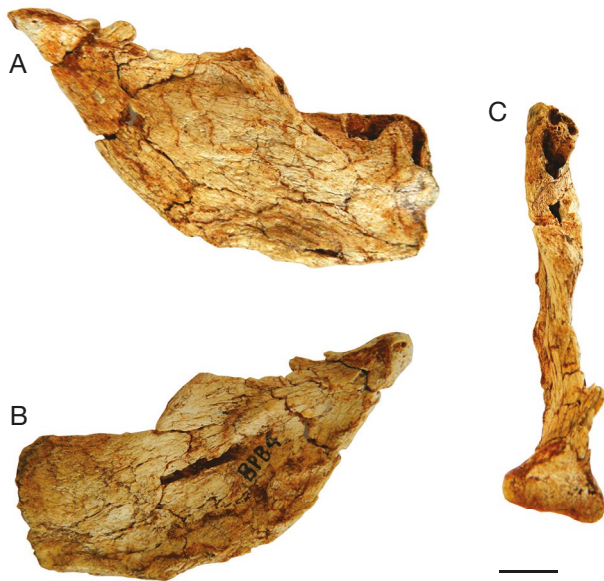


FIG. 15. — Distal part of the right mandible of *Parapapio broomi* Jones, 1937, specimen BPB 4: **A**, buccal view; **B**, lingual view; **C**, superior view. Scale bar: 10 mm.

The gonial region is well preserved and only a small fragment of the inferior edge is broken. This region doesn't expand distally or inferiorly but presents an open convex outline. In the lingual surface, at the junction of the gonial region with the distal edge of the ascending ramus, there are three smooth bulges which correspond to medial pterygoid tubercles. The ascending ramus is low and 36 mm long antero-posteriorly. The distal edge of the ascending ramus tilts disto-superiorly. On the buccal surface (Fig. 15A), the mandibular foramen is present

and the surface bone covering the canal of this foramen is lacking, probably due to damage during fossilization. The mandibular condyle is well developed medially (maximum length: 7.1 mm; preserved breadth: 17.4 mm). The general morphology of the ascending ramus of BPB 4 is very similar to that of BPB 2.

Dentition. This fragment is edentulous, but the sockets for the roots of the m/3 are present, well preserved for the distal root and partially preserved for the mesial root (Fig. 15A, C).

Mandible BPB 13 (Fig. 16; Tables 6, 7)

General description and preservation. BPB 13 is the distal part of a left mandible with the m/3 (maximum length: 43.9 mm; height: 42.6 mm). The fossil presents some cracking. The coronoid process is broken and the mandibular condyle is damaged. The gonial region is preserved as is most of the posterior part of the ascending ramus. The tooth row is only represented by the well-preserved m/3.

Mandibular corpus. Just a part of the mandibular corpus is preserved below the m/3. The buccal surface (Fig. 16A) is almost flat and there is no *prominentia lateralis* under the m/3. The extramolar sulcus is short mesio-distally and narrow bucco-lingually as in BPB 3 (Fig. 16C).

The gonial region is well preserved, except for a few fragments of missing bone. The dorso-inferior outline of this region is convex. The lingual surface of the gonial region (Fig. 16B) is slightly concave. The mandibular foramen is well preserved and the mylohyoid notch is also well preserved. The ascending ramus is better preserved in its posterior part and the posterior edge of the ascending ramus tilts slightly



FIG. 16. — Distal part of the left mandible of *Parapapio broomi* Jones, 1937, specimen BPB 13: **A**, buccal view; **B**, lingual view; **C**, superior view; **D**, occlusal view of m/3. Scale bar: 10 mm.

dorsally. The anterior edge of this ramus is broken but the ramus is clearly low and long. The mandibular condyle is broken lingually and abraded (maximum preserved length: 5.9 mm and breadth: 9.9 mm).

Dentition. The m/3 is well preserved and just the apex of the two mesial cusps (protoconid and metaconid) are slightly worn (Fig. 16D). This fossil corresponds probably to a younger adult than BPB 2 and BPB 3. The cusps are more centrally positioned than in *Papio robinsoni* (laterally positioned). This molar presents different extra-cusp and cusplet. A small *Tuberculum intermedium* is present between the metaconid and the entoconid. A low accessory cusp, near the base of the crown is also present between the protoconid and the hypoconid. The distal part of the molar is developed with a *Tuberculum sextum*. The hypoconulid is important and is located disto-lingually. Buccally, there is a clear distal marginal ridge and the distal fovea is deep. The size of the molar plots within the range of variation of *Pp. broomi* (Tables 4-5; Fig. 13).

Mandible BPB 30 (Fig. 17; Tables 6, 7)

General description and preservation. BPB 30 is part of a left mandible with fragmentary m/2 and worn m/3 (maximum length: 44.9 mm; breadth: between m/2-m/3: 10.9 mm; height: 29.3 mm).

Mandibular corpus. The mandibular corpus is only preserved below the m/2 and the m/3 and is not preserved over the entire height. It seems narrow inferiorly. On the lingual surface (Fig. 17B), a deep concave depression slopes from mesio-inferiorly to disto-superiorly and corresponds to the submandibular fossa. On the buccal surface (Fig. 17A), there is a smooth concavity probably due to fossilization and it seems that the *prominentia lateralis* doesn't exist. The mandibular corpus presents a slender aspect unlike *Cercopithecoidea*. A short portion of the extramolar sulcus is preserved. This is reduced and located disto-buccally to the m/3 and not buccally as in *Cercopithecoidea*.

The crown of the m/2 is represented only by a fragment of dentine (Fig. 17C). The m/3 is very worn suggesting that it represents an old adult and lingually it lacks some fragments of enamel at the metaconid and entoconid. The enamel is thick and the median buccal and lingual clefts are narrow as usual in Papionina. The hypoconulid is developed and located buccally. As for BPB 13, the size of the m/3 of BPB 30 enters into the range of variation of *Pp. broomi* (Tables 6-7; Fig. 13).

REMARKS

In the literature, there is more information concerning the skulls than the mandibles to distinguish the different taxa of Papionini. So here, despite the preservation of BPB 1,

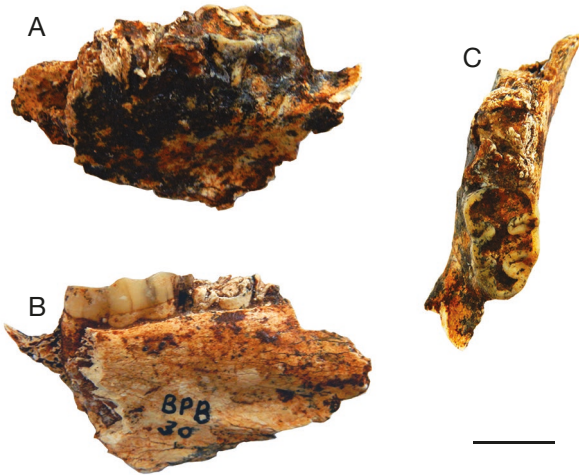


FIG. 17. — Part of the left mandible of *Parapapio broomi* Jones, 1937, specimen BPB 30: **A**, buccal view; **B**, lingual view; **C**, occlusal view of m/3. Scale bar: 10 mm.

this skull is most useful for the discussion. We must consider the biochronological age of the specimen and it is necessary to discuss older taxa (from East Africa) but also the Plio-Pleistocene Papionini. BPB 1 cannot belong to another Pliocene papionin taxon such as *Pliopapio* Frost, 2001 (5.2-4.2 Ma; Ethiopia) (Frost 2001; Jablonski & Frost 2010) which has a clear ante-orbital drop and an ophryonic groove. It cannot be attributed to *Procercocobus antiquus* either (Gilbert 2007a) which occurs at Taung (South Africa), and is characterized by an extremely straight nasal profile, widely divergent anterior temporal lines, relatively larger premolars, more prominent maxillary ridges and relatively more extensive maxillary/suborbital fossae than *Parapapio*. As indicated in the general description of BPB 1, the morphology of the interorbital and nasal regions indicates a slight concavity and lack of an ante-orbital drop which exclude the possibility that this specimen represents an individual of the smaller taxa of fossil *Papio* such as *P. izodi* and *P. angusticeps* (Gilbert *et al.* 2015, 2018).

Three species of *Parapapio* are recognized in South Africa (Jablonski & Frost 2010; Harrison 2011; Gilbert 2013) during the Plio-Pleistocene: *Pp. jonesi*, *Pp. broomi* and *Pp. whitei*. Older fossils exist in the Early Pliocene at Langebaanweg (Grine & Hendery 1981) and Waypoint 160 (Gommery *et al.* 2008b, 2009, 2014) but they are too fragmentary or limited to assign to a specific taxon. In BPB 1, the maxillary ridge is more developed and the maxillary fossa is deeper than in *Pp. jonesi*. The premaxilla is not preserved in BPB 1 but it would not have extended much further anteriorly, as suggested by the anterior morphology of the maxilla, and as such the muzzle appears short and broad and its dorsum is flattened. All these features are typical of *Pp. broomi*. In *Pp. whitei*, the muzzle is long and narrow. The nasal bone and muzzle, especially in males, have a peaked aspect (Gilbert 2013). The morphology of BPB 1 is similar to *Pp. broomi* specimens such as BF 43 from Pit 23 at Bolt's Farm or M 202 from Makapansgat, so it can confidently be assigned to this species.

Pp. ado (Hopwood, 1936), a smaller species, is known from Kenya (Jablonski *et al.* 2008a) and Tanzania (Harrison 2011) (4.1-3.49 Ma). Its frontal and maxilla have similar morphologies (Harrison 2011) to *Pp. broomi*. These two species differ by the nasals which form a midline keel in *Pp. broomi* which is absent in *Pp. ado*. Despite the distortion of the nasals, the preserved transversal convexity in BPB 1 suggests that a midline keel was present. An older species exists, *Pp. lothagamensis* Leakey *et al.*, 2003 (Leakey *et al.* 2003; Jablonski & Frost 2010; Gilbert 2013) (7.4-c. 5 Ma; Kenya), but it is considered to be more primitive than the younger species (Gilbert 2013).

The mandibles BPB 2 and BPB 3 probably belong to the same individual, which must have been a female. The teeth of these mandibles show a stage of wear corresponding to that of BPB 1. These two mandibles were found in a reduced sample of breccia taken from the “*Parapapio* spot”. It is very likely that these three fossils belong to the same individual.

Tribe PAPIONINI Burnett, 1828
Subtribe PAPIONINA Burnett, 1828

Papionina indet.

MATERIAL EXAMINED. — **Isolated teeth.** BPB 14 (Fig. 18A-C; Tables 6, 7); BPB 15 (Fig. 18D-F; Tables 6, 7); BPB 27 (Fig. 18G-H). — **Postcranial bones.** BPB 5 (Fig. 20A, B); BPB 6 (Fig. 20C, D).

DESCRIPTION

Isolated teeth

BPB 14 (Fig. 18A-C; Tables 6,7). This isolated lower molar is probably a left m/2. The mesial contact surface is bigger and located more buccally than the distal one which is located more centrally. The enamel is thick and the buccal cusps are more worn than the lingual cusps. The protoconid and the hypoconid are low. The protoconid is the largest and the most deeply worn cusp. The metaconid is located slightly more mesially than the protoconid. The median clefts are narrow. The beginning of the mesial and distal roots is preserved. The anatomical features of this tooth correspond to the molars of papionines. BPB 14 is smaller than the m/2 of BPB 2 and BPB 3 but enters into the range variation of the m/2 of *Pp. broomi* (Tables 6, 7; Fig. 12).

BPB 15 (Fig. 18D-F; Tables 6, 7). The crown of this right p/4 is well preserved and is unworn. The roots are fragmentary. The protoconid and metaconid are close and clearly separated by a V-shaped transverse crest. These two cusps are moderate salient from the crown and their apex is very slightly worn. The protoconid is slightly lower and is the most prominent cuspid. In buccal view (Fig. 18F), there is a slight mesio-buccal flange but also a deep distal and a mesial buccal cleft. The mesial fovea is small and moderately deep. The talonid is developed and high with a deep distal basin edged by a well-developed distal cingulum. The hypoconid is developed but narrower than the mesial part

of the tooth. There is a small entoconid. The prehypocristid and the pre-entoconid are very short. There is a split on the lingual edge of the crown between the prehypocristid and the postprotocristid and between the pre-entoconid and the post-entoconid. The morphology of BPB 15 corresponds to a p/4 of papionines. The size of this premolar enters more into the range of variation of *Pp. whitei* than that of *Pp. jonesi* (Tables 6, 7; Fig. 19).

BPB 27 (Fig. 18G, H). This small tooth should be a left di/1 and the apex of the root is broken (maximum height: 10.6 mm). The crown is very worn and presents an isosceles triangular outline (MD: 3 mm, BL: 3.9). The enamel is only preserved on the buccal surface (preserved height: 3.5 mm). The root is well preserved except for the apex (preserved height: 7.3 mm). The root is slightly curved. The buccal surface of the root is concave mesio-distally and the lingual one is slightly convex. The morphology of this incisor looks like some juvenile specimens of Plio-Pleistocene papionines.

Post-cranial bones.

BPB 5 (Fig. 20A, B). This left patella is well preserved except for the disto-inferior part and the median side which have lost some superficial bone (maximum length: 18.2 mm; breadth: 12.9 mm; thickness: 8.3 mm). This patella presents a general morphology similar to WP 3 (a right patella from Waypoint 160, Bolt's Farm [Gommery *et al.* 2008b]), less elongated than in *Papio ursinus*. In anterior view (Fig. 20A), the medial part is more convex and shorter medio-laterally than the lateral part. In posterior view (Fig. 20B), the medial part of the articular facet is longer proximo-distally and shorter medio-laterally than the lateral part, and as well more concave proximo-distally. The distal apex is low, broad and has a rounded aspect with a groove posteriorly as in WP 3 (corresponding to the insertion of the lateral and medial *Vasti* and the *M. rectus femoris*). Despite the damage posteriorly, the proximal part of the patella is more elongated proximo-distally than the distal part. The morphology of this patella seems to suggest a mixed locomotor behaviour (terrestrial and arboreal).

BPB 6 (Fig. 20C, D). This fossil is a fragment of a right talus (length: 24.4 mm, breadth: 11 mm). Only a part of plantar surface is preserved with the head (*Caput tali*) and the neck (*Collum tali*), as well as the distal part of the body of the talus (*Corpus tali*) (Fig. 20C). The neck is broad relatively to its length (length 14.7 mm; breadth: 10.8 mm). On the head, the plantar part of the articular surface for the navicular is preserved and presents a slightly convex outline. The anterior and medial calcaneal articular surfaces are well preserved. These form a large proximo-distally elongated rectangle and occupy a large part of the surface along the medial edge of the talar neck. This morphology is typical of cercopithecines and differs from those of extant colobines where the two surfaces are distinct (Olivier & Fontaine 1957; Strasser 1988; Gilbert *et al.* 2010) but

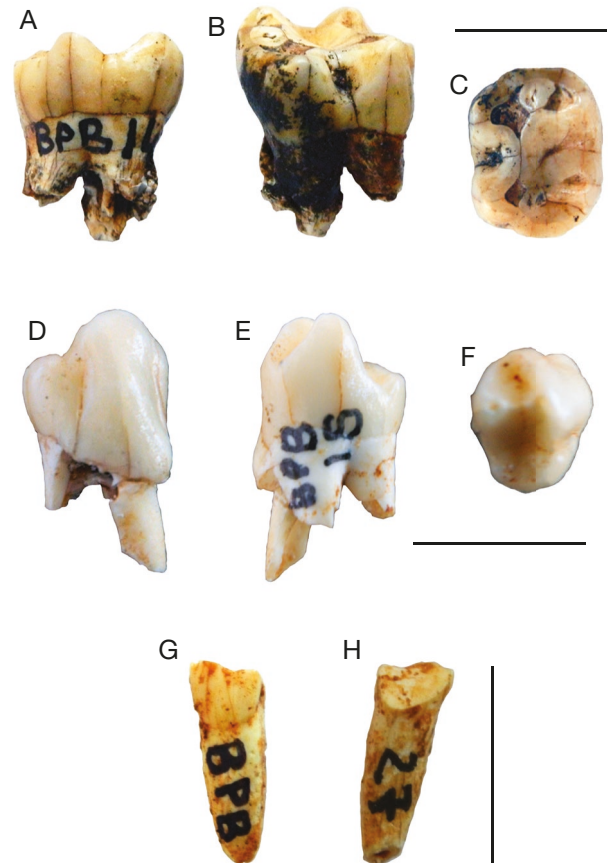


FIG. 18. — **A-C**, Left lower molar of *Papionina* indet., specimen BPB 14: **A**, buccal view; **B**, lingual view; **C**, occlusal view; **D-F**, right lower fourth premolar (p/4) of *Papionina* indet., specimen BPB 15: **D**, buccal view; **E**, lingual view; **F**, occlusal view; **G, H**, lower left deciduous first incisor (di/1) of *Papionina* indet., specimen BPB 27: **G**, labial view; **H**, lingual view. Scale bar: 10 mm.

not in *Paracolobus mutiwa* (Anderson 2021). Pina *et al.* (2011) have observed that the anterior calcaneal surface is more laterally developed in some cercopithecines such as *Lophocebus* and *Miopithecus* but not in *Papio* and many species of *Macaca*. In BPB 6, this surface is not developed laterally and is more similar to *Papio*. This morphology of the anterior and the medial articular surfaces is more related to weak rotation of the head of the talus as is usual in cercopithecines and different from the stronger rotation observed in colobines (Strasser 1988). Laterally, the fovea of the anterior astragalo-calcaneal ligament is moderately deep. The talar sulcus (*Sulcus tali*) is narrow and shallow laterally but broader and deeper medially below the groove for *flexor hallucis longus*.

The posterior calcaneal facet is preserved in its distal part. This facet seems deeply concave latero-distally to medio-proximally as in *Papio*. The junction with the groove for *flexor hallucis longus* is very salient. This groove has lost some superficial bone and is narrow. There is no swelling distally to the groove for the *flexor hallucis longus* as in *Papio*, *Cercocebus* and *Cercopithecus* (Strasser 1988; Gilbert *et al.* 2010).

BPB 6 is very damaged in dorsal view (Fig. 20D). Medially, a small fragment of the tibial malleolar facet is

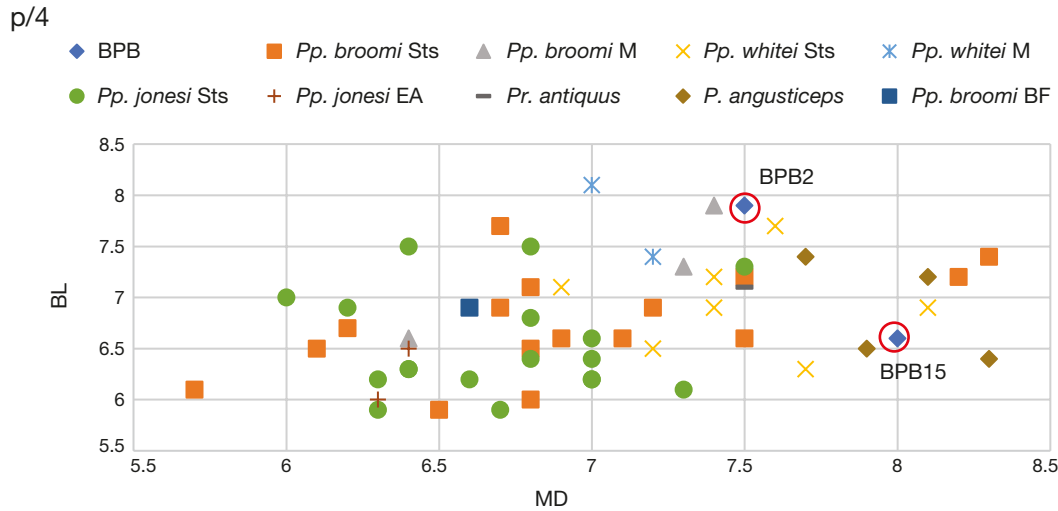


FIG. 19. — Bivariate plots MD × BL (mesio-distal length × maximum bucco-lingual breadth in mm) of lower fourth premolars (p/4) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) (Appendix 7).

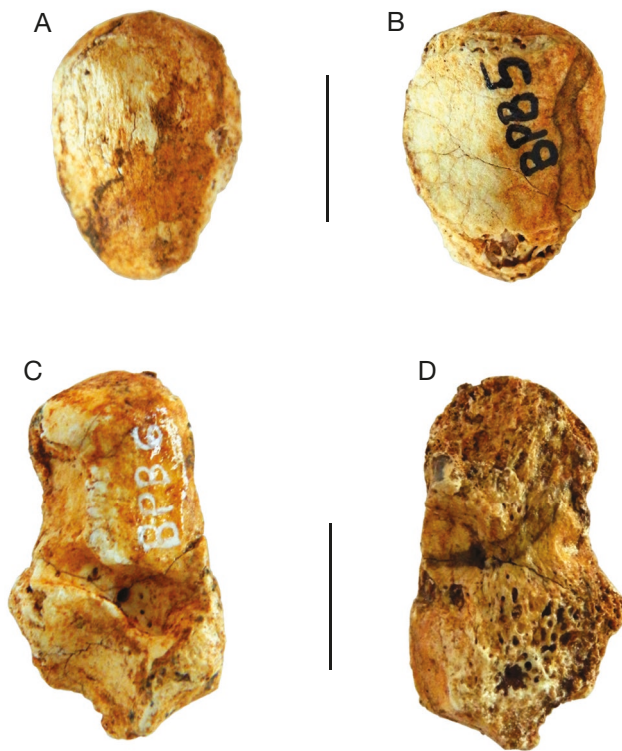


FIG. 20. — **A, B**, Left patella of Papionina indet., specimen BPB 5: **A**, anterior view; **B**, posterior view; **C, D**, fragment of a right talus of Papionina indet., specimen BPB 6: **C**, inferior view; **D**, superior view. Scale bar: 10 mm.

preserved distally and shows the contact with the medial calcaneal articular surface as in *Cercocebus* (Strasser 1988) and in *Papio* but not in extant colobines. A fragment of the medial tubercle is preserved proximally. No groove for the *flexor tibialis* can be observed on this bone as is generally the case in cercopithecines but present in colobines (Olivier & Fontaine 1957; Strasser & Delson 1987; Gilbert *et al.* 2010).

Subfamily COLOBINAE Jerdon, 1867
Genus *Cercopithecoides* Mollett, 1947

Cercopithecoides cf. *williamsi* Mollett, 1947

MATERIAL EXAMINED. — **Cranium**. BPB 7, frontal bone (Fig. 21).

DESCRIPTION

Cranium BPB 7 (Fig. 21)

General description and preservation. This specimen is the anterior part of the calvaria (maximum length: 54.9 mm; breadth: 83.5 mm) (Fig. 21A-C) comprised of two isolated pieces (Fig. 21D). It is less distorted than BPB 1. The left anterior part (corresponding to the upper part of the left orbit) is the most affected by distortion. Many cracks are present mainly in the posterior part. In anterior view, the upper part of the orbits, the glabella and the interorbital pillar are preserved. The latter is well preserved and broad (15.9 mm), typical of colobine monkeys, especially *Cercopithecoides* (Freedman 1957, 1965, Szalay & Delson 1979; Frost & Delson 2002; Jablonski *et al.* 2008b; Jablonski & Frost 2010). This genus is common in South African Plio-Pleistocene sites. In superior view (Fig. 21A), there is an important ophryonic groove as is usual in *Cercopithecoides*. There are a few bits of bone missing from the frontal but one of them, the biggest, presents an oval outline and probably corresponds to a predation mark.

Calvaria. In superior view (Fig. 21A), the ophryonic groove is deep and broad antero-posteriorly. Posterior to the ophryonic groove, the frontal has a rounded aspect. The temporal lines are well developed anteriorly with a strongly salient aspect as in BF 42A. Despite the damage, the postorbital constriction seems weak.

Orbital region. The superior orbital margins and parts of the lateral orbital margins are preserved and thick (thickness of the superior: 7.9 mm at left and 7.4 mm at right) (Fig. 21C). The supraorbital torus is well developed and thick. The preserved

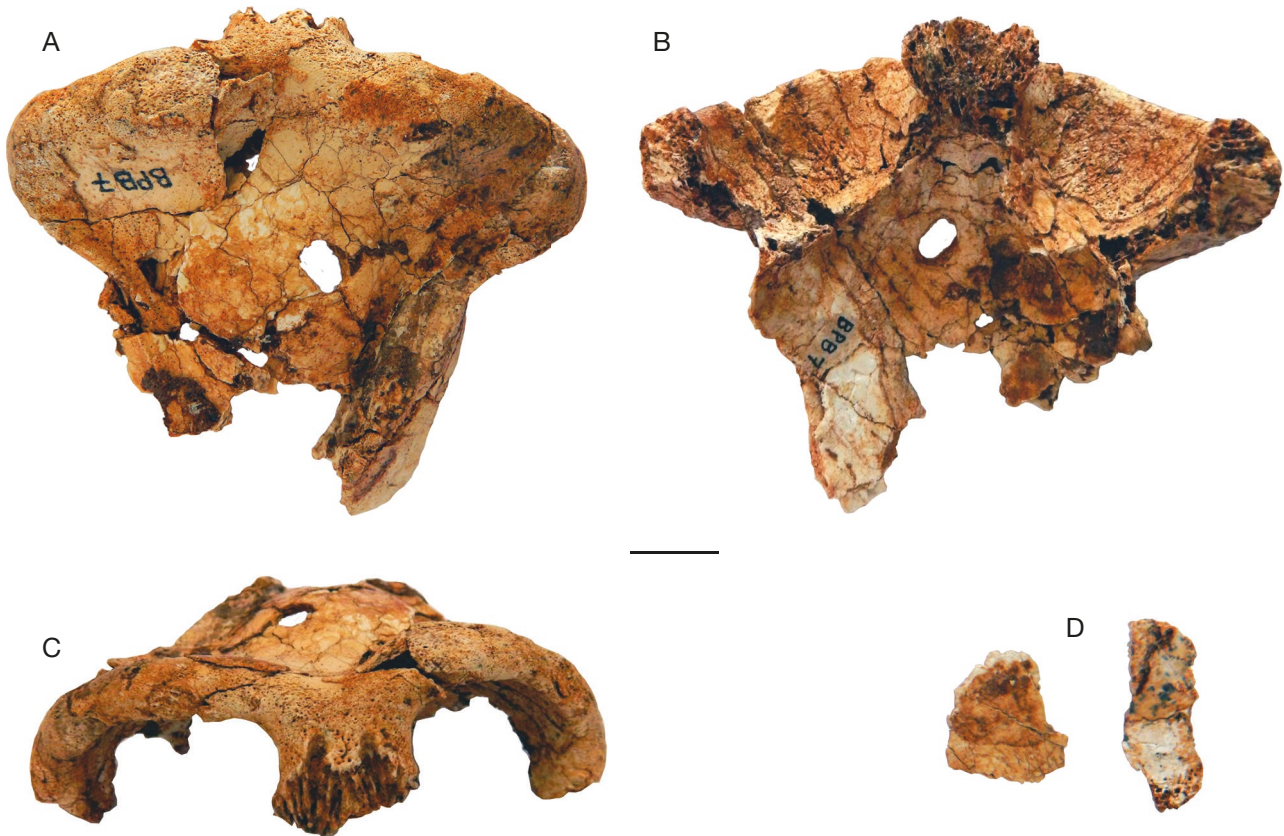


FIG. 21. — Anterior part of calvaria of *Cercopithecoides cf. williamsi* Mollett, 1947, specimen BPB 7: **A**, superior view; **B**, inferior view; **C**, frontal view; **D**, two isolated fragments of the calvaria. Scale bar: 10 mm.

part suggests that the orbits were large. The lower aspect of the interorbital pillar suggests that the nasal and maxilla sutures are not fused; this frontal bone probably belongs to a sub-adult. The interorbital pillar is large. The glabellar region is moderately inflated anteriorly but this part is abraded.

Remarks. The morphology and the size of the specimen are comparable to the homologous frontal areas of different specimens of the very large colobine *Cercopithecoides williamsi* such as BF 42A (Pit 23, BFCS) or AD 1326-6/M 236 (type specimen), M 2999/MP 113 and M 3055 (from Makapansgat Limeworks). In the absence of a complete muzzle and dentition (Frost & Delson 2002; Jablonski & Frost 2010), we provisionally assign the fossil BPB 7 to *C. cf. williamsi*. It differs from the older species, *C. keriensis* Leakey *et al.*, 2003 (Leakey *et al.* 2003; Jablonski & Frost 2010) (*c.* 5-4.2 Ma; Kenya), by its greater dimensions and thicker supraorbital torus despite the fact that this last feature seems variable in *Cercopithecoides* (Anderson *et al.* 2013; Frost *et al.* 2014). Some colobine remains from Woranso-Mille (Ethiopia) dated between 3.8 and 3.6 Ma were attributed to *Cercopithecoides cf. meaveae* Frost & Delson, 2002 (Frost *et al.* 2014). This species was known previously only at Leadu and Hadar (Ethiopia) between 3.4 to 3.28 Ma (Frost & Delson 2002; Jablonski & Frost 2010). The remains from Woranso-Mille are larger than the youngest remains from Leadu and Hadar but are still smaller than those of *C. williamsi*. Another

large colobine, similar in size to the genus *Paracolobus* Leakey, 1969, is presumed to occur at Makapansgat (Jablonski & Frost 2010) but it is represented by isolated teeth. *Paracolobus* differs from *Cercopithecoides* by a marked postorbital constriction, not present on BPB 7.

Family CERCOPITHECIDAE Gray, 1821

Cercopithecidae indet.

MATERIAL EXAMINED. — **Mandible.** BPB 8 (Fig. 22A, B); BPB 26 (Fig. 22C, D). — **Postcranial bone.** BPB 19 (Fig. 22E, F).

DESCRIPTION

Mandible

BPB 8 (Fig. 22A, B). This fossil (maximum length: 20.8 mm; height: 20 mm) is the distal part of the ascending ramus and the mandibular condyle of a right mandible. The median part of the condyle is damaged and the lateral part is very salient (length: 9.3 mm; breadth: 16.6 mm).

BPB 26 (Fig. 22C, D). The preserved part (maximum length: 26.1 mm; height: 24.7 mm) comprises the ascending ramus and the mandibular condyle (maximum length: 7.8 mm; preserved breadth: 6.4 mm) of a right mandible.

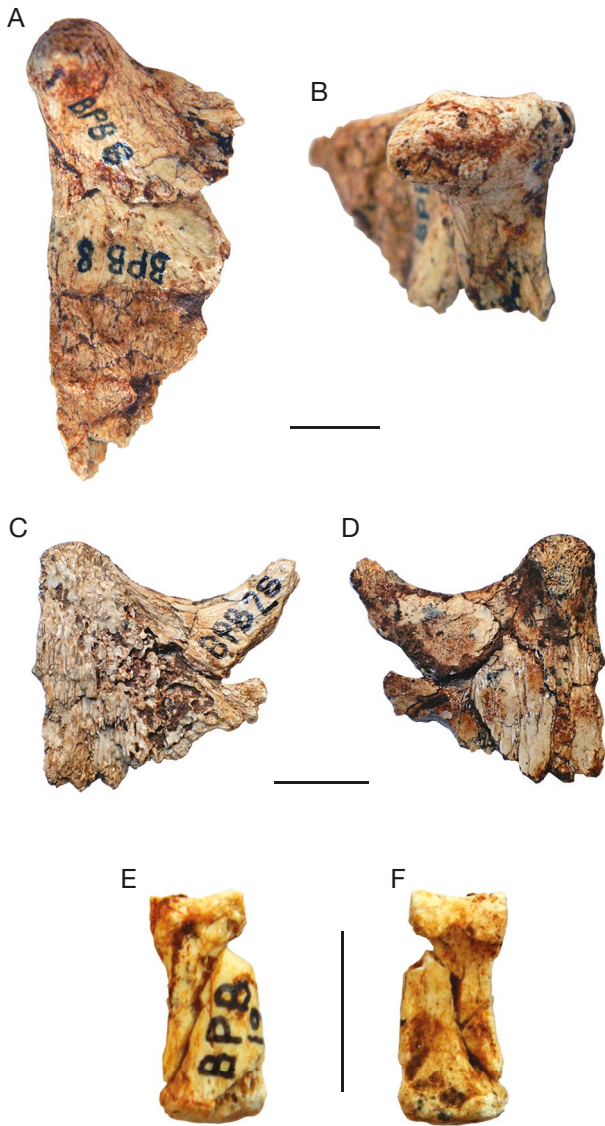


FIG. 22. — **A, B**, Distal part of the ascending ramus of a right mandible of *Cercopithecidae* indet., specimen BPB 8: **A**, lateral view; **B**, distal view; **C, D**, distal part of the ascending ramus of a right mandible of *Cercopithecidae* indet., specimen BPB 26: **C**, lateral view; **D**, medial view; **E, F**, right intermediate manual phalanx of *Cercopithecidae* indet., specimen BPB 19: **E**, dorsal view; **F**, volar view. Scale bar: 10 mm.

Post-cranial bone

BPB 19 (Fig. 22E, F). This right intermediate manual phalanx presents a big crack latero-distally to medio-proximally and it has lost a fragment latero-distally and a dorsal flake of bone latero-proximally which has damaged the proximal articular facet. The phalanx is short and presents a flat aspect (length: 15 mm; mid-shaft thickness: 3.2 mm). The intermediate phalanges of the hand and foot of colobines and *Papio* present nearly the same size and almost the same aspect except that they are slightly flatter in the hand (Begun *et al.* 1994). The proximal extremity is slightly larger (preserved breadth: 6.9 mm, height: 5.4 mm) than the distal extremity (breadth: 6.1 mm, height: 4.1 mm). The proximal articular facet presents a double concavity as is usual in a median phalanx. In dorsal view (Fig. 22E), a small hole is present

in the distal extremity and corresponds probably to a predator mark. In volar view (Fig. 22F), along all the shaft, there are extensions underlined by deep depressions which correspond to the insertion of collateral ligaments of the manual interphalangeal joint. The central part of the shaft is convex medio-laterally and forms a pillar. The proximal extremity presents a smooth bulge on each side. There is a small oval cavity which possibly corresponds to a mark of predation. The distal extremity presents a trochlear aspect. In plantar view, the medial condyle of this trochlea is the narrower and the more convex of the two condyles. It is not possible to say more about this phalanx.

DISCUSSION AND CONCLUSION

It is not uncommon to find *Cercopithecoides* and *Parapapio* associated in South African Plio-Pleistocene sites. At BPB, we have potentially the oldest known co-occurrence of these two taxa, the second oldest could be at Sterkfontein-Member 2 (Pickering *et al.* 2004; Reynolds & Kibii 2011). The BPB *Pp. broomi* specimen indicates that this species constitutes an old South African taxon. It is almost contemporary with the oldest known remains of *Pp. jonesi* surely known in the Lower Kada Hadar member of the Hadar Formation in Ethiopia (3.18-2.92 Ma) and perhaps at Ahmado (3.22-3.18 Ma) also in Ethiopia (Frost & Delson 2002; Jablonski & Frost 2010) which represents the earliest papionin with a nearly Pan-African distribution but which cannot represent the base of *Parapapio* in South Africa. At Koobi Fora in Kenya, except for an isolated m/3 dated at around 3.5 Ma, most of the material of *C. williamsi* was considered to be younger (2.5-1.5 Ma) (Jablonski *et al.* 2008b). This species is known at Sterkfontein (Pickering *et al.* 2004; Reynolds & Kibii 2011) from Member 2 dating approximately 3.67 Ma (Granger *et al.* 2015; Van Couvering & Delson 2020) and Member 4 dated recently around 3.4 Ma (Granger *et al.* 2022). This species is also present at Makapansgat Limeworks in Member 3 (Freedman 1957, 1961, 1976; Maier 1970) dating between 3.03 and 2.61 Ma (Reed *et al.* 2022). There has been a debate since the 1950s about the potential existence of a second species of *Cercopithecoides* in early Pleistocene sites in South Africa (Swartkrans, Cooper's and Kromdraai) (Freedman 1957, 1961; Delson 1984). More recently, McKee *et al.* (2011) published a new species, *Cercopithecoides haasgati*, at Haasgat dated *c.* 1.95 Ma (Leece *et al.* 2016) and revived the debate concerning a younger species of *Cercopithecoides* in South Africa. The BPB *Cercopithecoides* specimen thus represents one of the oldest known remains with the classical morphology of this genus (Frost & Delson 2002; Jablonski & Frost 2010). The new material of *C. cf. meaveae* from Woranso-Mille (3.8-3.6 Ma) (Frost *et al.* 2014) is probably contemporary with the *C. cf. williamsi* remains from BPB. Until now, it was considered that the inferred dispersal from East Africa to South Africa of *Parapapio* and *Cercopithecoides* took place during the Late Pliocene. This new discovery at BPB demonstrates that these two Plio-Pleistocene genera were already well established in

South Africa during the mid-Pliocene. We conclude that primate migrations between East and Southern Africa occurred earlier than previously thought. Southern Africa could also have been an important centre of primate diversification during the Pliocene and the beginning of the Quaternary. Although the remains of Early Pliocene Cercopithecoidea from Southern Africa are scarce and fragmentary (Grine & Hendey 1981; Gommery *et al.* 2008b, 2009, 2014, 2019), we cannot rule out the possibility that some Cercopithecoidea evolved first in Southern Africa before dispersing to East Africa.

The Pliocene is recognized as a globally warm period with permanent El Niño conditions and there were wet conditions in East Africa particularly during the Early Pliocene (Jablonski & Frost 2010; Demenocal 2004; Feakins & Demenocal 2010). A progressive cooling starting at around 3.2 Ma (Jablonski & Frost 2010; Demenocal 2004; Feakins & Demenocal 2010) led to a gradual aridification of the environment in East Africa but also in South Africa. The data concerning the climatic and environmental changes in Southern Africa are limited for the Pliocene in comparison with East Africa. The palaeoenvironment at Waypoint 160 in the Early Pliocene seems to have been dry and open as suggested by the rodent fauna and especially the presence of *Petromus* (Sénégal 2004) and *Euryotomys* (Sénégal 2001). BPB is one of the two potential known sites in Southern Africa to be close to the Early/Late Pliocene boundary. The environment at BPB was probably not as open and dry as at Waypoint 160 but it was probably a grassland-woodland mosaic as suggested by the rodents (under study) and the bald ibis (*Geronticus thackerayi*) (Pavia 2019; Pavia *et al.* 2017). The presence of suids as *Gerontochoerus koobiforaensis* (Pickford *et al.* 2019) at BPA seems to confirm that. It is the first known report of this environment for the Pliocene in this part of South Africa (Sterkfontein Valley, Gauteng Province). This environment seems to allow the development of *Parapapio*. It is probably the same for *Cercopithecoides*, even if it presents anatomical characteristics showing that it spent a good part of the time on the ground, like some to modern large-bodied colobines it probably climbed trees to feed and to protect itself from ground-dwelling predators (Jablonski & Frost 2010).

In the Southern Hemisphere, some cooler events related to the Benguela upwelling system (Marlow *et al.* 2000) in the Atlantic are observed during the mid-Pliocene. In the Antarctic (Escutia *et al.* 2009), the cooling transition started earlier, at 3.7–3.6 Ma. These events could have possibly reduced the effect of the permanent El Niño in Southern Africa earlier than in East Africa. At present it is impossible to confirm but something caused a transitional phase which resulted in less dry conditions, necessary for a grassland-woodland mosaic, before the gradual aridification of the environment known since the beginning of the Early Pleistocene in the Sterkfontein Valley. These environmental conditions were probably very favourable to the expansion of certain primate taxa from East Africa to southern Africa and/or a diversification into southern Africa of taxa already present. Further research at both BPB and BPA but also at Waypoint 160 may provide information to answer these questions.

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APPENDICES

APPENDIX 1. — Mesio-distal length (MD) and maximum bucco-lingual breadth (BL) in mm of upper fourth premolars (P4) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) used for the Figure 7.

Locality	MD	BL	Specimen	Locality	MD	BL	Specimen
<i>Parapapio broomi</i> Jones, 1937				<i>Parapapio jonesi</i> Broom, 1940			
Sterkfontein	6.7	8.4	Sts 251	Sterkfontein	5.6	7.8	Sts 372A
	6.7	8.6	Sts 260		5.7	7.5	Sts 372A
	6.2	7.3	Sts 261		5.8	7.5	Sts 547
	6.5	7.1	Sts 264		6.1	6.1	Sts 547
	6.3	8.5	Sts 267		5.2	7.3	Sts 565
	6.5	8.1	Sts 297		5.2	7	Sts 565
	5.8	7.9	Sts 368A		5.6	7.4	Sts 456
	6.5	7.1	Sts 377		East Africa	5.4	7
	6.5	8.7	Sts 383B	5.8		9.5	A.L. 363-15a
	6.2	8.3	Sts 385A	<i>Procercocebus antiquus</i> (Haughton, 1925)			
	6.2	8.5	Sts 390	Taung	7.4	8	TP9
	5.4	7.8	Sts 398A		7.3	7.5	T.17
	6.7	8.7	Sts 414B	<i>Papio izodi</i> Gear, 1926			
	6.9	9.6	Sts 424	Taung	7.6	7.5	T.10
	6.1	8.4	Sts 539	<i>Papio angusticeps</i> (Broom, 1940)			
	6.1	7.7	Sts 544	Kromdaai A	7.9	6	KA 156
	Makapansgat	6.5	8.3		MP2 (M202)	8.5	7.3
6.6		8.5	MP 224		7.9	7.4	KA 174
6.3		8.4	MP 224		7.7	6.1	KA 194
6.6		9	M205A,B		8.7	7	KA 157
6.8		9	M2963		7.8	6.7	KA 167
6.4		8.5	M2964		Cooper's	7.6	7.6
6.3		8.5	M2966	8.3		6.4	CO 135
<i>Parapapio whitei</i> Broom, 1940				8.1		6.9	CO 100
Sterkfontein	6	7.8	Sts 259	8.4		7.2	CO 117
	7.8	9.1	Sts 263				
	7	7.9	Sts 266				
	6.5	9.2	Sts 336				
	7	8.6	Sts 343				
	7.1	8.6	Sts 370A				
	7.4	8.7	Sts 370 B				
	6.7	8.6	Sts 389B				
	6.2	8.2	Sts 548				
	Makapansgat	6	8.7	MP 151			
6.1		9	MP 76				
6.1		9.5	MP 76				
7		9.1	M2973				

APPENDIX 2. — Mesio-distal length (**MD**) and maximum bucco-lingual breadth (**BL**) in mm of upper first molars (M1/) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) used for the Figure 8.

Locality	MD	BL	Specimen
<i>Parapapio broomi</i> Jones, 1937			
Bolt's Farm	9.9	9.9	BF 43
Sterkfontein	9.8	9.6	Sts 251
	9.8	9.9	Sts 253
	9.8	9.6	Sts 260
	8.4	8.7	Sts 264
	9.2	9.8	Sts 267
	9.9	9.5	Sts 274
	9.8	9.6	Sts 297
	9.8	9.6	Sts 301
	10	9.3	Sts 377
	10.1	9.6	Sts 383B
	8.8	9.4	Sts 385
	9.7	9.5	Sts 390
	9	9	Sts 414B
	9.6	9.9	Sts 539
	9.5	9	Sts 544
Makapansgat	9.2	9.3	MP 2 (M202)
	9.9	9.4	MP 2 (M202)
	10.2	9.5	MP 224
	10.3	9.3	MP 224
	9.8	10.1	M2963
	9	9.6	M3037
<i>Parapapio whitei</i> Broom, 1940			
Sterkfontein	9.7	9.8	Sts 259
	10.7	10.5	Sts 263
	9.5	9.1	Sts 266
	10.6	10.6	Sts 336
	11	10.9	Sts 343
	10.9	11	Sts 370A
	10.1	9.5	Sts 548

Locality	MD	BL	Specimen
Makapansgat	9.5	10.2	MP 76
	9.6	10.3	MP 76
	8.7	8.8	MP 151
<i>Parapapio jonesi</i> Broom, 1940			
Sterkfontein	7.3	9	Sts 250
	8.9	9	Sts 287
	8.9	8.7	Sts 372A
	7.6	9	Sts 565
Makapansgat	9.1	8.9	M2976
Taung	8.4	8.3	T.14
East Africa	8	8.2	A.L. 363-1a
	8.2	10.2	A.L. 363-15a
<i>Procercocoebus antiquus</i> (Haughton, 1925)			
Taung	10	9	TP9
<i>Papio izodi</i> Gear, 1926			
Taung	10.5	10	T.10
	9.7	9.5	T.13
	10.8	10.8	T.16
<i>Papio angusticeps</i> (Broom, 1940)			
Kromdaai A	10.5	10.8	KA 161
	9.6	10.2	KA 167
	8.8	10.6	KA 174
	8.9	9	KA 194
Cooper's	8.7	10.3	CO 101
	9.2	9.5	CO 117
	9.9	10.3	CO135

APPENDIX 3. — Mesio-distal length (MD) and maximum bucco-lingual breadth (BL) in mm of upper second molars (M2) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) used for the Figure 9.

Locality	MD	BL	Specimen	Locality	MD	BL	Specimen
<i>Parapapio broomi</i> Jones, 1937				<i>Parapapio jonesi</i> Broom, 1940			
Bolt's Farm	11.2	11.7	BF 56786	Sterkfontein	9.5	10.4	Sts 250
	11.7	11.7	BF 43		10.3	10.3	Sts 287
Sterkfontein	10.8	11.1	Sts 251		10.5	10.1	Sts 322
	11.9	12	Sts 260		9.8	9.7	Sts 372A
	10.3	10.2	Sts 261		9.8	10.1	Sts 372A
	11.2	10.5	Sts 264		10	9.8	Sts 547
	10.5	11.8	Sts 267		9.2	9.4	Sts 547
	10	10.3	Sts 274		9.2	10.4	Sts 565
	11.1	11.7	Sts 297				
	9.8	10.9	Sts 325	Makapansgat	9.5	10.2	M3017
	11.6	10.9	Sts 354	East Africa	10.6	11.9	A.L. 363-15a
	10.8	10.3	Sts 377	<i>Procercocebus antiquus</i> (Haughton, 1925)			
	11	10.5	Sts 378 A-D	Taung	11.8	10.6	TP9
	10.8	12.1	Sts 379A		11.8	11.6	SAM 5356
	10.7	10.9	Sts 380B		11.9	10.7	T.20
	10.9	10.9	Sts 380B		11.6	11	T.25
	10.9	10.9	Sts 383B	<i>Papio izodi</i> Gear, 1926			
	10.8	10.1	Sts 385A	Taung	12.8	11.8	T.10
	11.2	11.4	Sts 388A		11.8	11.2	T.13
11.2	10.6	Sts 397	11.8		11.5	T.16	
10.5	10.7	Sts 398A	<i>Papio angusticeps</i> (Broom, 1940)				
10.6	10.1	Sts 410A	Kromdaai A	11.8	11.6	KA 156	
11.2	11	Sts 414B		11.5	11.7	KA 161	
10.8	10.5	Sts 544		10.4	11.2	KA 194	
				10.8	12.6	KA 157	
Makapansgat	10.2	10.8	MP 2 (M202)	Cooper's	10.8	12.2	CO 100
	11.5	11	MP 2 (M202)		11	12.4	CO 117
	11	10.9	MP 224		12.4	12.7	CO105ab
	10.7	11	MP 224		10.9	12.6	CO101
	11	12.1	M205	11.6	12.4	CO135	
	12.5	12.3	M 635	10.9	11	CO 109A	
	11.4	11.7	M2963				
	11.1	11.8	M2964				
	10.7	12.2	M2966				
	11	10.5	M2969				
	10.8	11	M3011				
	11.5	11.8	M3015				
	11.4	11	M3037				
<i>Parapapio whitei</i> Broom, 1940							
Sterkfontein	11.8	12.3	Sts 259				
	13.2	12.6	Sts 263				
	11	10.3	Sts 266				
	13	12.1	Sts 336				
	13.4	12.5	Sts 370A				
	13.2	13	Sts 370 B				
	13	13	Sts 462				
	11.8	13.2	Sts 503				
	11.8	11.7	Sts 548				
Makapansgat	10.9	10.6	MP 151				
	11.1	10.9	MP 151				
	11.1	12.6	MP 76				
	11.4	12.8	MP 76				
	11.4	11.7	M2963				
	10.8	11	M3011				

APPENDIX 4. — Mesio-distal length (**MD**) and maximum bucco-lingual breadth (**BL**) in mm of upper third molars (M3/) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) used for the Figure 10.

Locality	MD	BL	Specimen	
<i>Parapapio broomi</i> Jones, 1937				
BPA	13.2	11	BPA230	
Bolt's Farm	11.7	10.8	BF 43	
	10.9	10.5	BF 56786	
Sterkfontein	11.4	11.2	Sts 261	
	11.6	11	Sts 261	
	10.8	11.1	Sts 267	
	10.3	10.4	Sts 325	
	11.3	10.5	Sts 378A	
	10.9	10	Sts 380B	
	11.1	10	Sts 383B	
	11.1	10.6	Sts 385	
	10.6	11.4	Sts 388A	
	10.7	11.5	Sts 388B	
	10.1	10.4	Sts 390	
	10.8	10.8	Sts 393	
	11.1	10	Sts 397	
	11	10.1	Sts 397	
	10.5	10.8	Sts 398A	
	10.5	10.1	Sts 410A	
	10.3	10.2	Sts 414B	
	11.5	12.3	Sts 534	
	10	9.9	Sts 535	
	10.6	10.3	Sts 544	
	Makapansgat	10.8	10.4	MP2 (M202)
		11	12	M 205
10.6		12.1	M 635	
11.2		11.7	M2963	
10.6		11.5	M2964	
10.2		11.2	M2970	
11.2		11.8	M2975	
10.6		11.6	M2977	
11		10.3	M3002	
10.8		10.8	M3037	
<i>Parapapio whitei</i> Broom, 1940				
Sterkfontein	12.4	12.6	Sts 259	
	12.8	11.8	Sts 303	
	11.6	12.5	Sts 503	
Makapansgat	10.4	10.4	MP 151	
	10.2	10.4	MP 151	
	11.4	12.2	MP 76	
	12.1	11.6	M2962	

Locality	MD	BL	Specimen
<i>Parapapio jonesi</i> Broom, 1940			
Sterkfontein	10.9	10.4	Sts 250
	9.8	10.3	Sts 322
	9.7	9.9	Sts 322
	9.5	10.6	Sts 367
	9.6	10.6	Sts 367
	9.7	9.9	Sts 372A
	9.6	9.8	Sts 547
	8.9	9.3	Sts 565
Makapansgat	9.5	9.9	M3009
	10	9.6	M3013
East Africa	11.5	10.4	A.L. 363-1a
	10.5	10.6	A.L. 363-15a
<i>Procercocebus antiquus</i> (Haughton, 1925)			
Taung	10.9	10.5	TP9
	12.1	11.2	SAM5356
	10.4	11.4	T.17
	10.4	10.4	T.25
<i>Papio angusticeps</i> (Broom, 1940)			
Kromdaai A	11.7	11.1	KA 156
	10.5	10.6	KA 194
Cooper's	10.9	12.4	CO 100
	10.9	12	CO 101
	11.7	12.4	CO 102
	12.1	12.8	CO 105ab
	11.7	10.6	CO 109A
	10.3	11.5	CO 127
	10.4	11	CO 128
	12	11.3	CO 135

APPENDIX 5. — Mesio-distal length (**MD**) and maximum bucco-lingual breadth (**BL**) in mm of lower second molars (m/2) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) used for the Figure 12.

Locality	MD	BL	Specimen	Locality	MD	BL	Specimen
<i>Parapapio broomi</i> Jones, 1937				<i>Parapapio jonesi</i> Broom, 1940			
Bolt's Farm	11	9.5	BF 56796	Sterkfontein	10.4	10.1	Sts 258
Sterkfontein	10.5	8.8	Sts 256		10.7	8.9	Sts 270
	11.5	9.3	Sts 268		11	8.6	Sts 329
	10.7	8.9	Sts 270		10.5	9.7	Sts 331
	10.9	8.8	Sts 271		10.4	9.2	Sts 355
	10.5	9.4	Sts 299		10.3	8.9	Sts 355
	9.6	8.8	Sts 309		10.2	9.1	Sts 374 A-B
	11.3	10.6	Sts 335		10.8	10	Sts 379 B
	12.4	9.7	Sts 353		11.4	8.8	Sts 381A
	10.9	10.6	Sts 360		10.7	9.9	Sts 390A
	12.4	10.4	Sts 371		10.9	9.8	Sts 390A
	9.9	8.9	Sts 374		9.6	9.3	Sts 409
	9.5	9.2	Sts 400		10.4	8.6	Sts 421
	12.2	9.9	Sts 445		10.4	9.5	Sts 469
	10.5	9.1	Sts 542				
	11.7	10.8	Sts 562	Makapansgat	9.5	7.6	M215
	11.2	10.4	Sts 562		10.8	9	M2992
	Makapansgat	10.5	10	M2968	East Africa	10.4	9.2
11.5		10.1	M2978		10	9.2	A.L. 363-15b
11.3		10.4	M2979	<i>Procercocebus antiquus</i> (Haughton, 1925)			
11.8		9.6	M2994	Taung	12.1	9.6	T.18
11.8		10	M3024	<i>Papio angusticeps</i> (Broom, 1940)			
<i>Parapapio whitei</i> Broom, 1940				Kromdaai A	12.4	9.3	KA 165
Sterkfontein	12.1	10.9	Sts 352	Cooper's	12.4	9.3	KA 165
	12.7	10.4	Sts 359		11.9	10.1	CO 103
	13.1	10.5	Sts 370A		12.6	9.5	CO 112
	11.7	10.1	Sts 414A		12.1	10	CO 115
	11.5	9	Sts 411A-B		11.6	9.7	CO 136 A-C
	12.5	10.5	Sts 563				
Makapansgat	9.5	7.6	M215				
	10.8	9	M2992				

APPENDIX 6. — Mesio-distal length (**MD**) and maximum bucco-lingual breadth (**BL**) in mm of lower third molars (m/3) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) used for the Figure 13.

Locality	MD	BL	Specimen
<i>Parapapio broomi</i> Jones, 1937			
Bolt's Farm	13.5	9.9	BF 56796
	14.2	9.3	BF 56787
Sterkfontein	11.9	8.9	Sts 256
	12.9	9.2	Sts 261
	13.5	9.5	Sts 271
	13.4	9.3	Sts 309
	13.2	11	Sts 335
	14.9	10.2	Sts 369 A-B
	14.2	9.9	Sts 369A
	14.6	10.2	Sts 371
	11.5	8.7	Sts 374
	12.1	9.1	Sts 374
	11.9	8.8	Sts 400
	14.6	10.3	Sts 414A
	14.6	10	Sts 445
	12.5	9.1	Sts 542
	15.6	10.7	Sts 562
	15.3	10.1	1238/13
Makapansgat	15.3	10.5	M 210
	15.3	10.5	M 210
	14	10.3	M213
<i>Parapapio whitei</i> Broom, 1940			
Sterkfontein	16.5	11.1	Sts 342
	15.3	10.6	Sts 352
	16.5	10.8	Sts 352
	15.5	11.1	Sts 533
	16.5	10.8	Sts 359
Makapansgat	16.5	11.6	M3062

Locality	MD	BL	Specimen
<i>Parapapio jonesi</i> Broom, 1940			
Sterkfontein	12.7	8.5	Sts 421
	13	10	Sts 258
	12.5	10.2	Sts 258
	13.7	8.5	Sts 329
	12.8	9.6	Sts 331
	12.4	9.3	Sts 374 A-B
	12.6	9.2	Sts 390A
	12.4	9	Sts 390A
	12.2	9.1	Sts 409
	13.3	9.3	Sts 542
	13.2	8.6	1238/12
	Makapansgat	11.1	9.2
11.3		7.9	M3019
13.2		8.3	M3021
12.7		9.3	M3030
East Africa	13.6	9.7	A.L. 363-15b
	14.1	9.5	A.L. 363-1b
	14.1	9.6	A.L. 217-8
	13.9	8.2	A.L. 465-1
<i>Procercocebus antiquus</i> (Haughton, 1925)			
Taung	14.6	10	T.21
<i>Papio angusticeps</i> (Broom, 1940)			
Kromdaai A	14.3	9.9	KA 165
	14.6	10.7	KA 166 A-B
Cooper's	14.2	10.4	CO 103
	15	10.6	CO 108A
	14.9	9.9	CO 112
	14.6	10.5	CO 115

APPENDIX 7. — Mesio-distal length (MD) and maximum bucco-lingual breadth (BL) in mm of lower fourth premolars (p/4) of different taxa of fossil Papionines from South Africa with some from East Africa (data from Freedman 1957, 1965; Frost 2001; Frost & Delson 2002; this study) used for the Figure 19.

Locality	MD	BL	Specimen	Locality	MD	BL	Specimen	
<i>Parapapio broomi</i> Jones, 1937				<i>Parapapio jonesi</i> Broom, 1940				
Bolt's Farm	6.6	6.9	BF 56796	Sterkfontein	7	6.6	Sts 258	
Sterkfontein	6.1	6.5	Sts 255		6.8	7.5	Sts 269	
	6.8	6	Sts 270		7	6.4	Sts 270	
	6.5	5.9	Sts 280		6.8	6.4	Sts 280	
	8.3	7.4	Sts 323		6.7	5.9	Sts 307	
	8.2	7.2	Sts 323		7	6.2	Sts 313	
	6.2	6.7	Sts 335		6.8	6.8	Sts 317	
	7.5	7.2	Sts 337		6.6	6.2	Sts 329	
	6.7	6.9	Sts 338		6.4	7.5	Sts 331	
	7.5	6.6	Sts 353		6.4	6.3	Sts 348	
	6.8	7.1	Sts 363		6.3	5.9	Sts 355	
	5.7	6.1	Sts 374		6.3	6.2	Sts 355	
	7.2	6.9	Sts 414A		6.4	6.3	Sts 374 A-B	
	6.8	6.5	Sts 426		7.3	6.1	Sts 381A	
	7.1	6.6	Sts 445		6.2	6.9	Sts 390A	
	6.9	6.6	Sts 542		6	7	Sts 390A	
6.7	7.7	Sts 562		7	6.2	Sts 411A		
				7.5	7.3	Sts 542		
Makapansgat	6.4	6.6	M213	East Africa	6.4	6.5	A.L. 363-1b	
	7.4	7.9	M210			6.3	6	A.L. 363-15b
	7.3	7.3	M210	<i>Procercoccebus antiquus</i> (Haughton, 1925)				
<i>Parapapio whitei</i> Broom, 1940				Taung	7.5	7.1	T.18	
Sterkfontein	7.6	7.7	Sts 352	<i>Papio angusticeps</i> (Broom, 1940)				
	7.4	6.9	Sts 359	Kromdaai A	8.3	6.4	KA 166 A-B	
	7.7	6.3	Sts 370A			7.7	7.4	KA 168
	8.1	6.9	Sts 389A	Cooper's	7.9	6.5	CO 135 B	
	7.2	6.5	Sts 411A-B			8.1	7.2	CO 136 A-C
	6.9	7.1	Sts 563					
	7.4	7.2	Sts 563					
Makapansgat	7	8.1	M3062					
	7.2	7.4	M3062					