



REVISION OF *DINOPITHECUS* BROOM, 1937 (PRIMATES, CERCOPITHECIDAE) FROM THE LATE PLIOCENE OR MIDDLE PLEISTOCENE OF SCHURWEBERG, SOUTH AFRICA

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Abstract: *Dinopithecus ingens* is a large, extinct ‘baboon-like’ cercopithecoid defined by Broom in 1937 on the basis of a mandible and crushed partial skull from Schurweberg, Gauteng, South Africa (Plio-Pleistocene). The species remained poorly known for two decades until Freedman added a quantity of fossils from Swartkrans to the hypodigm. For the majority of subsequent researchers, the Swartkrans fossils were accepted as defining the species, despite morphometric differences in the dentitions of the samples from the two sites. Restudy of the type specimens reveals that none of the fossils from Swartkrans resembles the Schurweberg fossils, the Swartkrans assemblage resembling *Papio* and *Gorgopithecus* and differing morphometrically from *Dinopithecus*. Some of the dental features that distinguish *Dinopithecus* from *Papio* and *Gorgopithecus* recall specimens of fossil and extant geladas, as was noted by Arambourg in 1947 when he defined the species *Dinopithecus brumpti* from the Omo region, Ethiopia. The latter species was transferred to the subgenus *Theropithecus* (*Omopithecus*) by Delson in 1993, but it is herein raised to the rank of genus. In 1955, Arambourg recorded *Dinopithecus* from the Humpata Plateau in Angola, from cave breccias now known to have yielded abundant specimens of the extinct gelada lineage, *Omopithecus baringensis*. The Humpata discoveries prompted a close examination of the South African ‘baboon-like’ fossils with which they were previously compared and it is concluded that *Dinopithecus* does not occur in Angola, but its relative *Omopithecus* does. It became apparent during the study that the Humpata breccias are likely to date from the Middle Pliocene (ca. 4 ± 0.5 Ma) whereas the Schurweberg deposits are likely to be aged between 1.4 and 0.4 Ma.

Key words: Cercopithecoidea, mandrills, baboons, geladas, Southern Africa, Plio-Pleistocene, taxonomy, phylogeny, biogeography

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Introduction

When Broom (1937) described the new genus and species of large cercopithecoid, *Dinopithecus ingens*, on the basis of two fossils from Schurweberg, South Africa, he created an enigma that has puzzled researchers ever since (Arambourg 1955, Freedman 1957, Maier 1970a, 1971, 1972, Eisenhart 1974, Brain 1981, Delson and Dean 1993, Jablonski and Frost 2010, Gilbert 2013, Pugh and Gilbert 2018). The holotype of the species, designated in the text, is the mandible, subsequently labelled DNMNH SB 7, and the ‘crushed skull’ of which the M2/ and M3/ were illustrated by Broom (1937) as a ‘type’, is DNMNH SB 3. The features that convinced Broom (1937) that he was in the presence of an undescribed species and genus, were, as concerns the holotype mandible: 1) the great dimensions of the lower teeth within the context of cercopithecoids, 2) the p/3 with a relatively short and broad anterior part, with two deep pits behind the main cusp, and on the inner side of the anterior cusp another deep pit, 3) the p/4

similar to those of baboons with the exception that the fossil has only the faintest indication of a posterior cusp, and 4) the m/2 and m/3 have small subsidiary cusps on the outer side that are usually absent in *Papio* ERXLEBEN, 1777. As concerns the other ‘type’ specimen (the crushed skull) the distinguishing features were: 1) upper molars very large, and 2) they differ in pattern considerably from those of *Papio*, especially the M3/ which has a marked inner cusp between the protocone and hypocone and a well-developed hypoconulid (sic) (hypoconule was meant).

His illustration of the upper molars made comparisons with other large fossil monkeys, *Simopithecus oswaldi* ANDREWS, 1916, *Papio speleus* (sic) BROOM, 1936, and *Papio rhodesiae* (HAAGNER, 1918). He distinguished the Schurweberg species from *Simopithecus oswaldi* (nowadays classified within *Theropithecus* GEOFFROY, 1843) in the following terms: ‘the South African form must be specifically distinct as it is much larger and the teeth are differently shaped. The new species cannot belong to Andrews’ genus as the third upper molar is quite differently shaped in the two species’.

It is notable that Broom (1937) did not make comparisons between the Schurweberg fossils and the teeth and jaws of drills or mandrills (*Mandrillus* RITGEN, 1824) presumably because, at the time of his studies, drills and mandrills were usually classified within *Papio*. It was only during the 1990's that their separation from *Papio* at the genus level was generally accepted by taxonomists (Disotell 1994, Jablonski and Frost 2010), although some authors (Delson and Dean 1993) continued to classify them as a subgenus of *Papio*.

In a subsequent paper, Broom (1940) added a partial cranium (DNMNH SB 2) to the species that Freedman (1957) thought was more likely to belong to *Papio robinsoni* FREEDMAN, 1957.

During the mid-1950's, Freedman (1955, 1957) carried out an exhaustive study of the cercopithecoids from the cave deposits of the Transvaal (now Gauteng). He wrote that the upper molars in SB 3 were crushed and expanded and were thus unreliable indicators of the dimensions of the upper teeth of *Dinopithecus ingens*. He attributed a quantity of specimens from Swartkrans to this species, and for the next 70 years, the upper teeth from Swartkrans became the main reference for comparisons, in particular the palate with left and right cheek tooth rows, SK 604A (Jablonski 2002: fig. 17-12B). However, this palate, and possibly some of the other specimens from Swartkrans do not belong to *Dinopithecus ingens*, but to *Gorgopithecus major* (BROOM, 1940) (see Pugh and Gilbert 2018) or possibly even to *Papio robinsoni* (this paper). Because of this mix-up, many of the systematic and phylogenetic analyses subsequently carried out on the papionines were thrown out of focus, because the content of at least one of the included 'taxa' was a taxonomic chimaera (Text-fig. 1).

Maier (1971) and Eisenhart (1974) opted to classify *Dinopithecus* as a subgenus of *Papio*, along with *Gorgopithecus* BROOM et ROBINSON, 1949, a decision followed by Delson and Dean (1993) and Heaton (2006), but this ranking was eventually abandoned by most palaeo-anthropologists who nowadays treat these forms as distinct genera (Jablonski and Frost 2010, Gilbert 2013, Pugh and Gilbert 2018).

Even though *Dinopithecus* is currently recognised as a valid genus, it remains an enigmatic form in the sense that its phylogenetic placement continues to be unresolved (Heaton 2006: fig. 9-2, Pugh and Gilbert 2018), undoubtedly due to: 1) the relatively limited scope of the Schurweberg fossils attributed to it, and 2) the attribution to the genus of fossils from Swartkrans and Kromdraai (Freedman 1957) most of which do not belong to it (Pugh and Gilbert 2018).

The aim of the present paper is to re-examine the fossils from Schurweberg with a view to throwing light on their taxonomic, systematic and phylogenetic positions. The focus is on the dental remains which have tended to be marginalised by other researchers who focussed their studies more on the osteological features of the fossil and extant baboon-like cercopithecoids and who barely mentioned the teeth from Schurweberg, concentrating their dental comparisons on specimens from Swartkrans, most (if not all) of which do not belong to *Dinopithecus*. The main conclusions of this study are twofold: 1) the holotype mandible (SB 7) of *Dinopithecus ingens* shares a few features of dental morphology with *Mandrillus*, including the presence of a prominent, partly

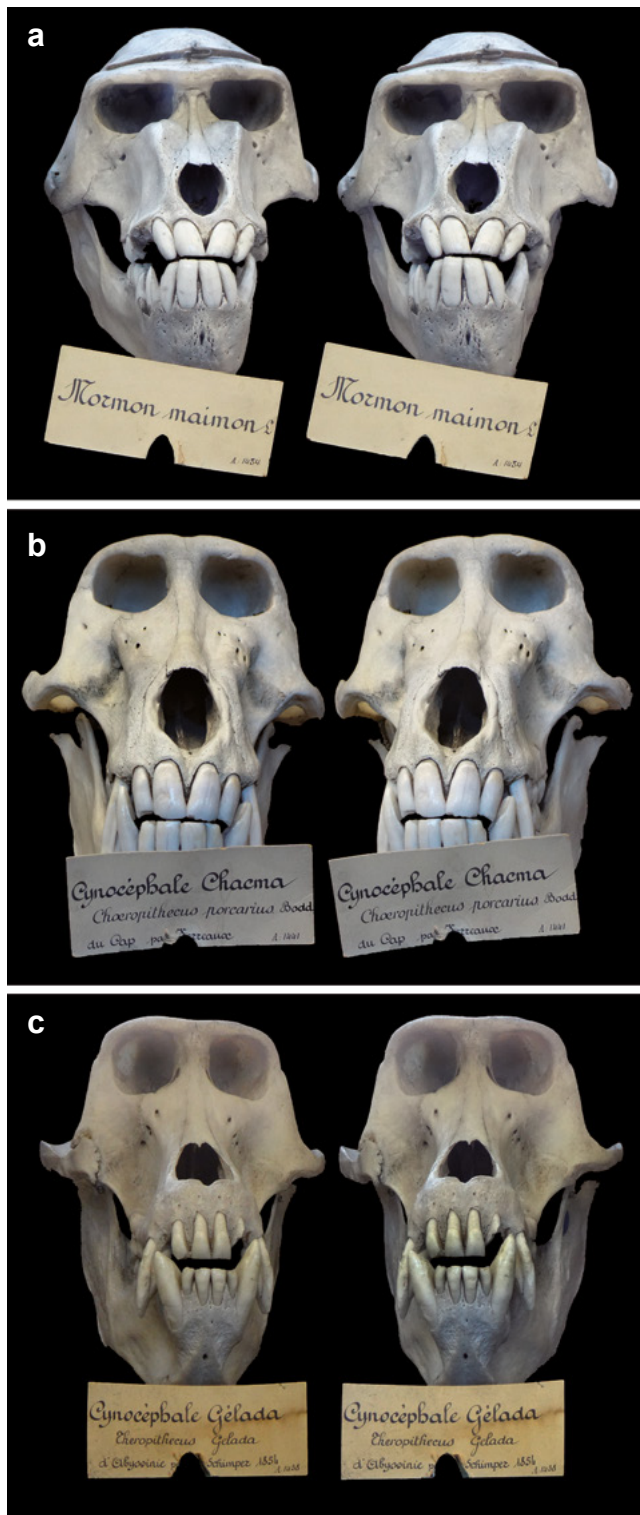
beaded metastylid in the m/3 while the other 'type' specimen from the site (the crushed skull, SB 3) shares the presence of a talon in the M3/, but it is noted that both specimens also show some dental resemblances to teeth of theropithecines such as broad flexus and flexid in the molars, and 2) these two fossils very probably represent a single species because the upper and lower third molars possess morphological features that are rare in cercopithecids, such as the presence of a detached protostyle in the M3/ and a detached protostylid in the m/3, each of which is in a mesio-distally broad flexus or flexid respectively.

The Schurweberg fossils show fewer dental similarities to *Gorgopithecus* and, as Broom (1937) stressed, the molars are markedly divergent from those of *Papio*. They also show some similarities to teeth of the genus *Soromandrillus* GILBERT, 2013, an observation that raises questions about the possibility of synonymy between *Mandrillus*, *Dinopithecus* and *Soromandrillus*. In this paper, however, *Soromandrillus* is considered to be more closely related to geladas than to mandrills (Pickford and de Matos 2026). However, such a study is not the intention of this paper.

The biogeographic implications of the mandrill-like fossils from southern Africa are of interest because, until recently, the origin of mandrills was poorly understood, mainly due to the fact that for a long time no fossils had been confidently attributed to the clade. With the description of *Soromandrillus* in 2013, that changed, because remains from East Africa and Angola have been attributed to this genus (the record from the latter country contested herein), thereby demonstrating that, during the Pliocene, extinct mandrill-like genera may have been more widely distributed in the continent than drills and mandrills are today, in which they are confined to dense, humid tropical forest areas in Nigeria, Cameroon, Gabon, Equatorial Guinea and the Congo Republic. The hypothesis that *Dinopithecus* could possibly be related to extant drills and mandrills (not supported by the present study), suggests that, during the Plio-Pleistocene, the clade may have been more widespread than previously thought. A question that arises, concerns the adaptations of *Dinopithecus* and *Soromandrillus*. Were these genera adapted to relatively open woodland to savannah environments, or were the areas that their fossils have been found more densely forested during the past than they are at present?

Material and methods

For 3D images of fossils, access was made to the the DITSONG: National Museum of Natural History Plio-Pleistocene Palaeontology Section Digital Archive (Adams et al. 2015). Images, descriptions and measurements of teeth were obtained from the literature. Specimens from Angola were measured with sliding calipers to the nearest tenth of a mm. Images were captured with a Sony Cybershot Camera, and treated with Photoshop Elements 15 to remove unwanted background, to enhance contrast and to reduce trembling. Skulls of extant baboons, geladas, drills and mandrills were studied at the Department of Comparative Anatomy of the Muséum National d'Histoire Naturelle, Paris and the Collection of Zoology of the University of Lisbon.



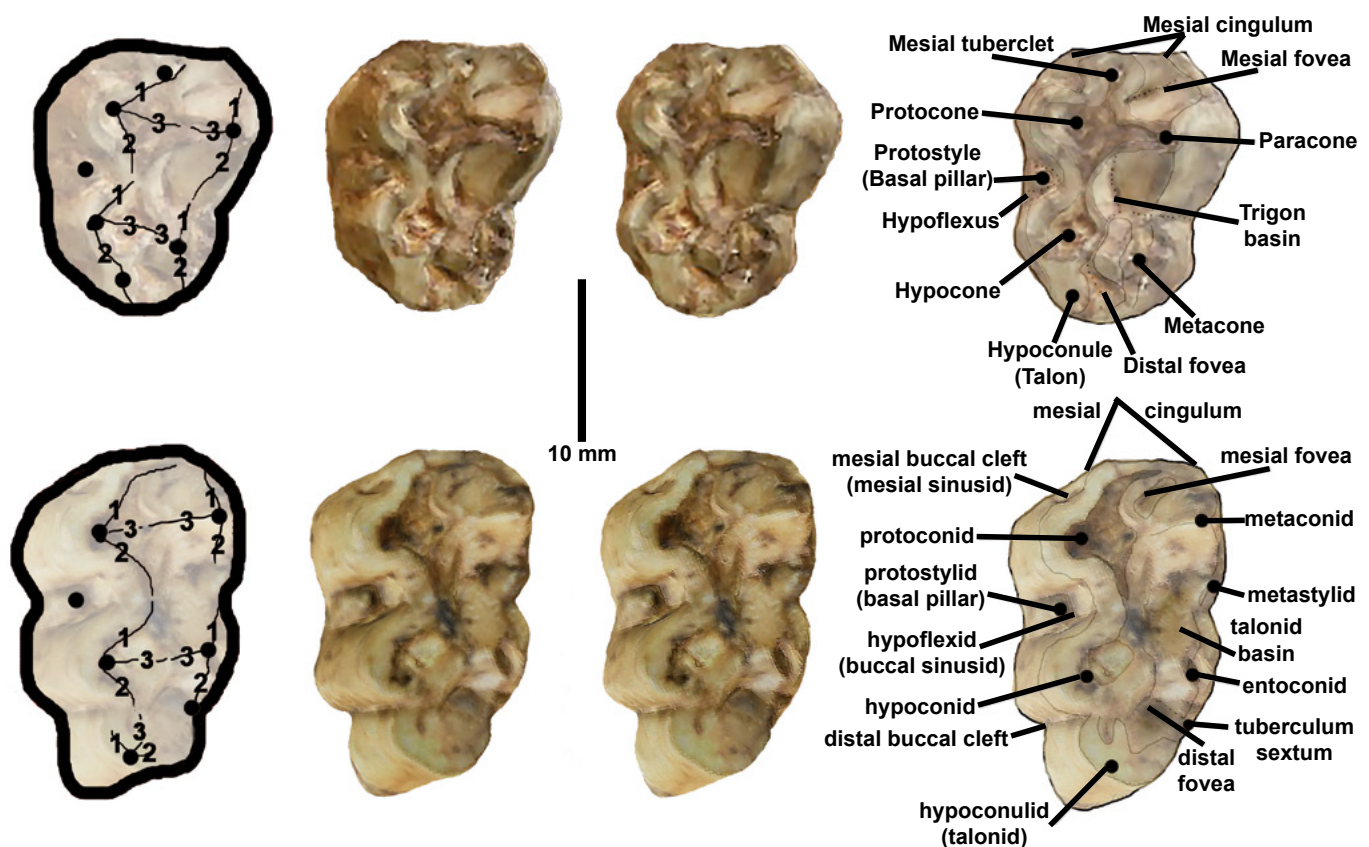
Text-fig. 1. Stereo anterior views of skulls of *Mandrillus sphinx* (LINNAEUS, 1758) (a), *Papio ursinus* (LINNAEUS, 1758) (b) and *Theropithecus gelada* (RÜPPEL, 1835) (c). a – MNHN A 1434, b – MNHN A 1441, c – MNHN A 1438. To which of these genera is *Dinopithecus* most closely related?

List of genera and species mentioned

- Cercocebus* GEOFFROY, 1812
Dinopithecus BROOM, 1937
Dinopithecus ingens BROOM, 1937
Gorgopithecus BROOM et ROBINSON, 1949
Gorgopithecus major (BROOM, 1940)
Lophocebus PALMER, 1903
Macaca LACÉPÈDE, 1799
Mandrillus RITGEN, 1824
Mandrillus sphinx (LINNAEUS, 1758)
Mandrillus leucophaeus (CUVIER, 1807)
Omopithecus DELSON, 1993
Omopithecus brumpti (ARAMBOURG, 1947)
Omopithecus baringensis (R. E. F. LEAKEY, 1969)
Papio ERXLEBEN, 1777
Papio angusticeps (BROOM, 1940)
Papio hamadryas (LINNAEUS, 1758)
Papio rhodesiae (HAAGNER, 1918)
Papio robinsoni FREEDMAN, 1957
Papio speleus BROOM, 1936
Papio ursinus (LINNAEUS, 1758)
Parapapio broomi JONES, 1937
Procercopithecus GILBERT, 2007
Rhinocolobus M. G. LEAKEY, 1982
Rungwecebus DAVENPORT, STANLEY, SARGIS, DE LUCA, MPUNGA, MACHAGA et OLSON, 2006
Simopithecus ANDREWS, 1916 (= *Theropithecus*)
Soromandrillus GILBERT, 2013
Soromandrillus quadratirostris (IWAMOTO, 1982)
Theropithecus GEOFFROY, 1843
Theropithecus danieli (FREEDMAN, 1957)
Theropithecus gelada (RÜPPEL, 1835)
Theropithecus oswaldi (ANDREWS, 1916)

Dental nomenclature

Dental nomenclature is defined in Text-fig. 2. Some terms employed in the old literature such as ‘talon’ and ‘basal pillar’ are included for the sake of completeness. The nomenclature of the main cusps of the molars was defined by Kay (1977) (see also Harrison et al. 2025). As explained by Kay (1977: fig. 1) the main cusps possess clear crests on their mesial edges (precrista in upper teeth, precristid in lower teeth) and distal edges (postcrista, postcristid) as well as crests directed towards the midline of the crown that carried a diversity of names (in lower molars: ‘crest a’ for the protoconid, ‘medial protocristid’ for the paraconid, ‘lateral posterior transverse cristid’ for the hypoconid, ‘postentocristid’ for the entoconid; in upper molars: ‘anterior transverse crista’ for the protocone and paracone, ‘medial and lateral posterior transverse crista’ for the metacone and hypocone). For the sake of simplicity, the crests oriented towards the midline of the crown are herein labelled ‘3’ and are called endocrista and endocristid of the respective cusps of the upper and lower teeth respectively.



Text-fig. 2. Nomenclature of upper and lower third molars of *Dinopithecus ingens*. Top row: left M3/, bottom row: left m/3. Crest numbers in left column, stereo occlusal views in the middle, main cusps, cusplets and foveae in right column. For details of crest nomenclature see Kay (1977). Herein, '1' corresponds to the precrista (upper molars) and precristid (lower molars) of the main cusps, '2' corresponds to the posterista and postcristid, and '3' corresponds to the endocrista and endocristid.

Abbreviations

BF	Bolt's Farm
DGUNL	Department of Geology, Universita Nova de Lisboa, Portugal
DNMNH	DITSONG: National Museum of Natural History, Pretoria, South Africa
KA	Kromdraai A
KNM	Kenya National Museum, Nairobi, Kenya
MRH	Museo Regional da Huila, Lubango, Angola
TMP	Transvaal Museum, Pretoria (now the DNMNH), South Africa
SB	Schurweberg (published alternative spellings Schurveberg, Skurweberg, Skurweburg)
SK	Swartkrans
STS	Sterkfontein
UCMP	University of California Museum of Paleontology, Berkeley, USA
UL	University of Lisbon, Portugal
UMMZ	University of Michigan Museum of Zoology, USA

Biochronology of Schurweberg (or Hoogland)

Schurweberg was initially correlated to the Pleistocene by Broom (1937). Subsequently, the breccia deposits at Schurweberg were considered by Adams et al. (2010) to be part and parcel of the karstic deposits at Hoogland, which

they estimated to be Pliocene, equivalent to Makapansgat members 2–4 (ca. 3.03–2.58 Ma; Latham et al. 1999, 2003, Herries et al. 2010, 2013). However, the lower molar from the site, attributed by Adams et al. (2010) to *Theropithecus oswaldi oswaldi*, suggests that (some of) the Hoogland deposits could be considerably younger. According to the biochronological succession of species and subspecies of *Theropithecus* summarised by Getahun et al. (2023: fig. 14), *T. o. oswaldi* ranged in age from ca. 1.4 to 0.4 Ma. Further research is required to determine whether the Schurweberg (and Hoogland) breccias accumulated at different times, and to verify, or otherwise, the identification of the fossil gelada tooth.

Taxonomic rank of *Mandrillus*

Until the mid-1990's, *Mandrillus* was generally classified within the genus *Papio*, either as a direct synonym of it, or it was differentiated from other 'baboons' at the subgenus rank as *Papio (Mandrillus)* (Disotell 1994). One of the effects of this classification was that researchers such as Broom (1937, 1940) and Freedman (1955, 1957) did not include drills or mandrills in their comparisons of the South African cercopithecoid fossils, confining their comparisons to savannah baboons of the genus *Papio* (in its restricted sense). Arambourg (1955) in contrast, did make comparisons of the Angolan fossils with mandrill skulls which were

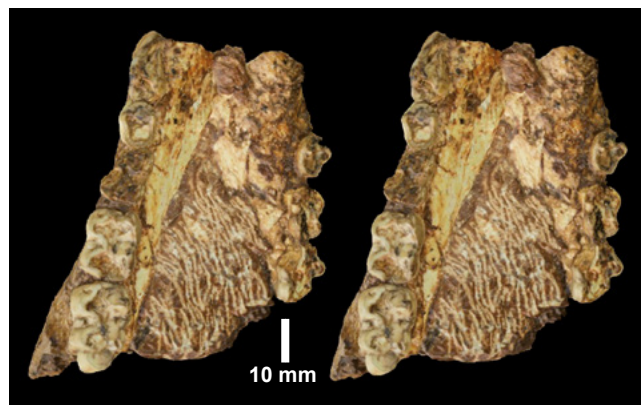
readily available at the Natural History Museum in Paris where he worked. However, despite writing that further publications would be prepared on the said fossil monkeys, he did not complete the project, so we remain in the dark concerning his intentions and findings. Herein the genus *Mandrillus* is accepted as valid.

Historical background

Broom (1937) erected the new genus and species of baboon-like primate, *Dinopithecus ingens*, on the basis of two fossils from Schurweberg, South Africa. In the text, he specified that the type specimen is a mandible with parts of both rami and the damaged symphysis (Text-fig. 3) and that in addition there is ‘a considerable part of a skull, but it is crushed and unsatisfactory. There are, however, well preserved posterior upper molars’. The legend to his figure of the upper molars compared to those of *Simopithecus oswaldi* ANDREWS, 1916, *Papio speleus* (sic) BROOM, 1936, and *Papio rhodesiae* (HAAGNER, 1918) lists all four of the fossils as ‘types’. It is probable that he considered the cranial fragment (Text-fig. 4) to be a co-type (as was often done at the time) or a paratype, but he did not provide any precision. Whatever the case, his writings are clear that he considered the two specimens belong to the same species. These two fossils were later catalogued at the DNMNH as SB 3 for the cranial fragment (Text-fig. 4), and SB 7 for the mandible (Text-fig. 3).

Three years later, Broom (1940) briefly mentioned the discovery of a crushed skull at Schurweberg (sic) that he attributed to *Dinopithecus ingens*, which ‘differs from that of baboons in having a fairly large maxillary antrum’ (i.e., a large maxillary sinus above the roots of the cheek teeth). This skull corresponds to DNMNH SB 2 (Text-fig. 6a). Freedman (1957) considered that ‘it would seem more probably to be a skull of a male *Papio robinsoni*’, an identification accepted by Pugh and Gilbert (2018) and Gilbert et al. (2018, as Skurweberg and Skurweberg).

Arambourg (1947) erected the new species *Dinopithecus brumpti* on the basis of large cercopithecine fossils from the Omo Valley, southern Ethiopia, but it was considered by Freedman (1957) to belong to *Theropithecus*, a view that has

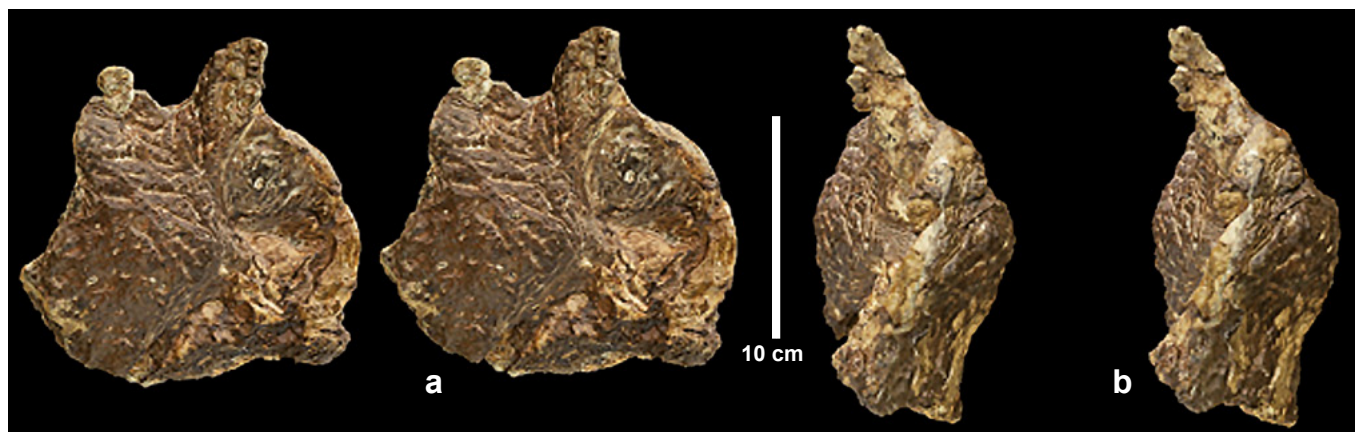


Text-fig. 3. Stereo occlusal view of DNMNH SB 7, the holotype mandible of *Dinopithecus ingens* BROOM, 1937, from Schurweberg, South Africa.

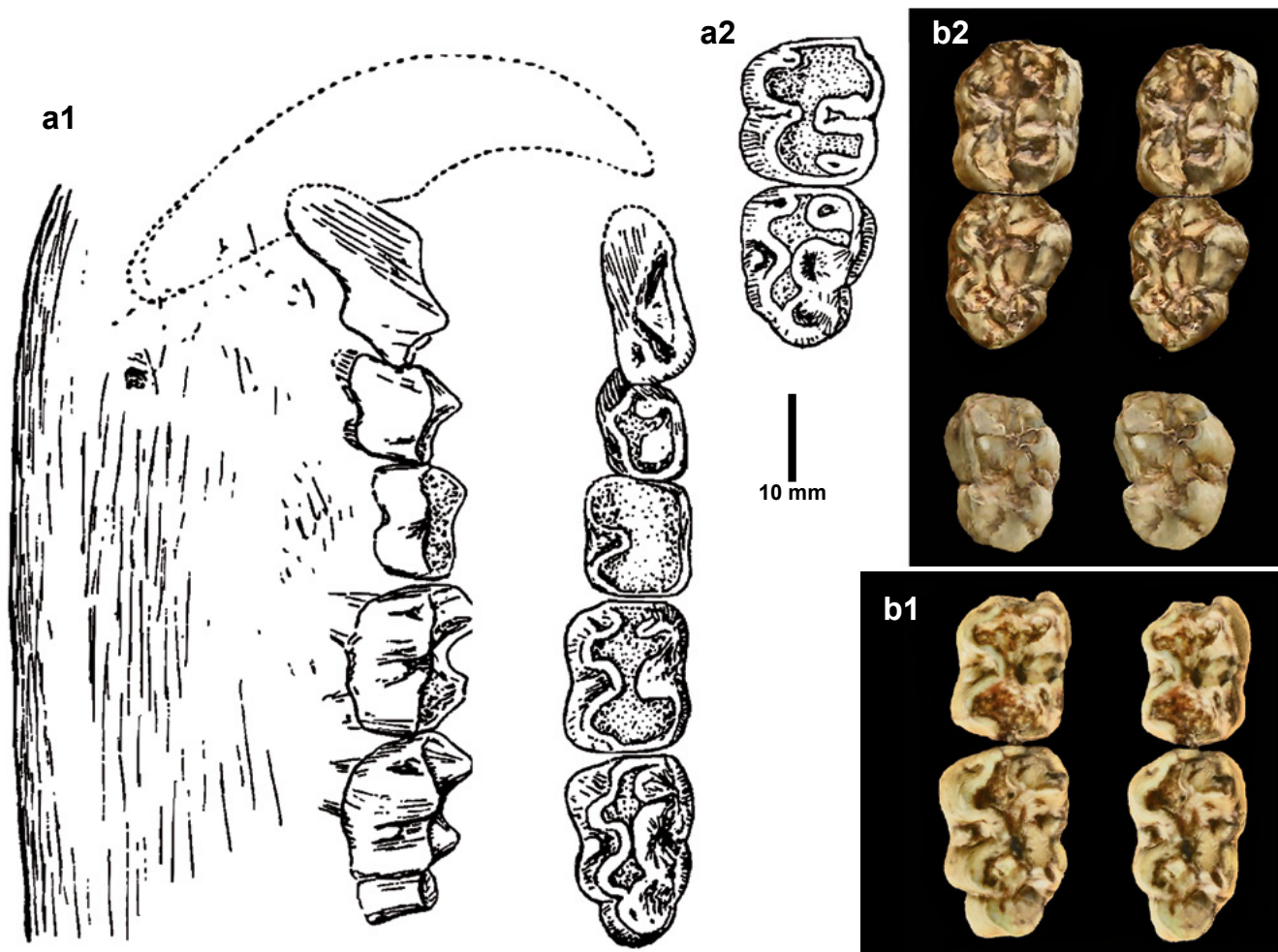
been generally validated by subsequent authors (Jablonski 1993, Jablonski and Frost 2010, Getahun et al. 2023) although Delson (1993) erected the new subgenus *Omopithecus* for this species, a conclusion accepted herein, but raised to the rank of genus, on the grounds that it comprises a distinct lineage within the gelada clade (Getahun et al. 2023, Pickford and de Matos 2026).

Arambourg (1955) attributed a left maxilla with cheek teeth from ‘Leba’, Angola, to *Dinopithecus ingens*, mainly on the basis of the great dimensions of the molars within a cercopithecoid context, and because the M3/ showed a tendency to develop a small talon, and which differed from other ‘*cynocéphales*’ by its degree of brachyodonty. However, the upper third molar in the Angolan specimen (DGUNL LEBA 06; Text-fig. 7) differs somewhat from those in the Schurweberg specimen (SB 3) by being more square in occlusal outline compared with the more elongated outline in SB 3, and by the weak expression of the talon (posterior fovea and its surrounding elongated posthypocrista and cingular structure).

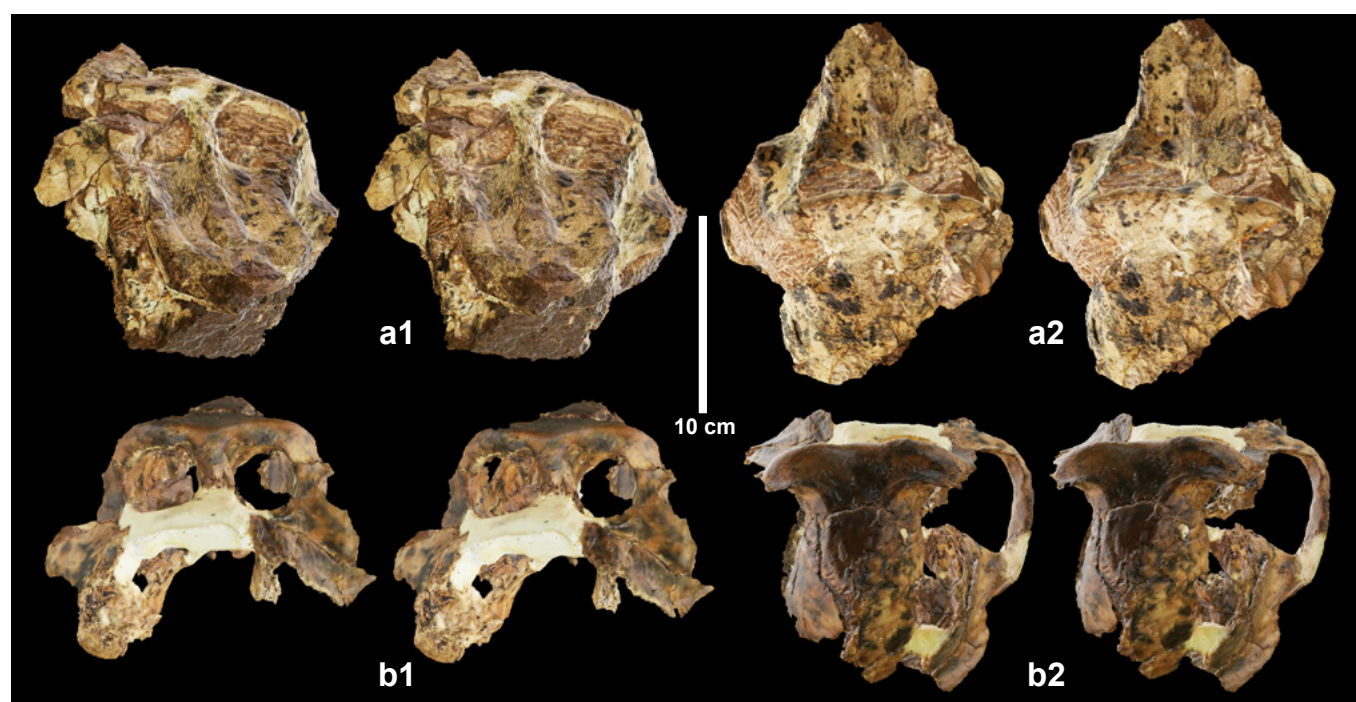
It is possible that Arambourg (1955) confused the morphology of the M3/ of the maxilla with cheek teeth (DGUNL LEBA 06) in which the talon is weak (Text-fig. 8d), with that in a different specimen from ‘Leba’ (DGUNL LEBA 04; Text-fig. 8f) which has a well-developed talon. The latter specimen was attributed to *Papio* sp. by Arambourg (1955) but it is herein attributed to *Omopithecus baringensis* (LEAKEY, 1969) (see also Pickford and de Matos 2026: fig. 79).



Text-fig. 4. Stereo views of DNMNH SB 3, paratype cranial fragment with left M2/–M3/ and right M3/ of *Dinopithecus ingens* from Schurweberg, South Africa. a: inferior view, b: left lateral view.



Text-fig. 5. The original hypodigm of *Dinopithecus ingens*. a1: DNMNH SB 7, mandible; a2: SB 3, fragment of cranium with three upper molars. Drawings are from Broom (1937). b1: stereo occlusal view of the left m/2 and m/3 in SB 7; b2: stereo occlusal views of left M2/-M3/, and right M3/ in SB 3.



Text-fig. 6. Stereo views of (a) DNMNH SB 2, part of the cranium of a large papionine (sensu lato) (*Dinopithecus ingens* or *Papio robinsoni* depending on the author) from Schurweberg, South Africa, and (b) DNMNH SK 599, papionine skull fragment from Swartkrans that has been attributed to *Dinopithecus ingens*. 1 – anterior, 2 – dorsal views.

Whatever the case, DGUNL LEBA 06 differs from *Dinopithecus* from Schurweberg as well as from the fossil (DNMNH SK 604A) that was eventually to become (debatably) one of the reference specimens for the upper teeth of *Dinopithecus* (see for example, Jablonski 2002: fig. 17-12B). In the latter palate, which is from Swartkrans and was first attributed to the species by Freedman (1957), there is no sign of development of a talon in the M3/, there is no development of a protostyle (see discussion below) and the teeth are more bunodont than those in the Schurweberg specimen. Furthermore, in the Swartkrans fossil, the distal loph of the M3/ is not much narrower than the mesial loph, unlike the appreciably narrower distal loph that occurs in *Dinopithecus*. In these respects, the Swartkrans fossil is closer to *Papio* and to *Gorgopithecus* than to any other of the large cercopithecoids (Text-fig. 8). DGUNL LEBA 06 was included in cf. *Mandrillus* sp. by Pickford and de Matos (2026).

Arambourg (1955) mentioned that the ‘Leba’ maxilla differs osteologically from those of mandrills. He wrote ‘la dépression qu’il présente en avant de son apophyse malaire est faible et bien moins marquée que celle des Mandrills adultes’ [the depression that it shows in front of its malar apophysis is weak and much less marked than that of adult Mandrills]. Despite this observation which seemingly differentiates the specimen from *Mandrillus*, he distanced the ‘Leba’ fossil from the more baboon-like *Gorgopithecus major* because ‘le fossile de l’Angola se distingue immédiatement du second (i.e. *Gorgopithecus major*) par son museau allongé et l’absence de fosse infra-orbitaire ainsi que par les dimensions un peu plus fortes de sa denture et la tendance de M3/ à former un petit talon, caractères qui sont précisément ceux de *Dinopithecus ingens*’ [the fossil from Angola is distinguished immediately from the second one (i.e. *Gorgopithecus major*) by its elongated muzzle and the absence of the infra-orbital fossa as well as by its slightly greater dental dimensions and for the tendency of the M3/ to form a small talon, characters that are precisely those of *Dinopithecus ingens*].

As mentioned above, when Arambourg (1955) wrote that the Angolan specimen that he attributed to *D. ingens* showed a tendency to form a talon in the M3/, he was possibly confusing two specimens: DGUNL LEBA 06, that does not clearly show



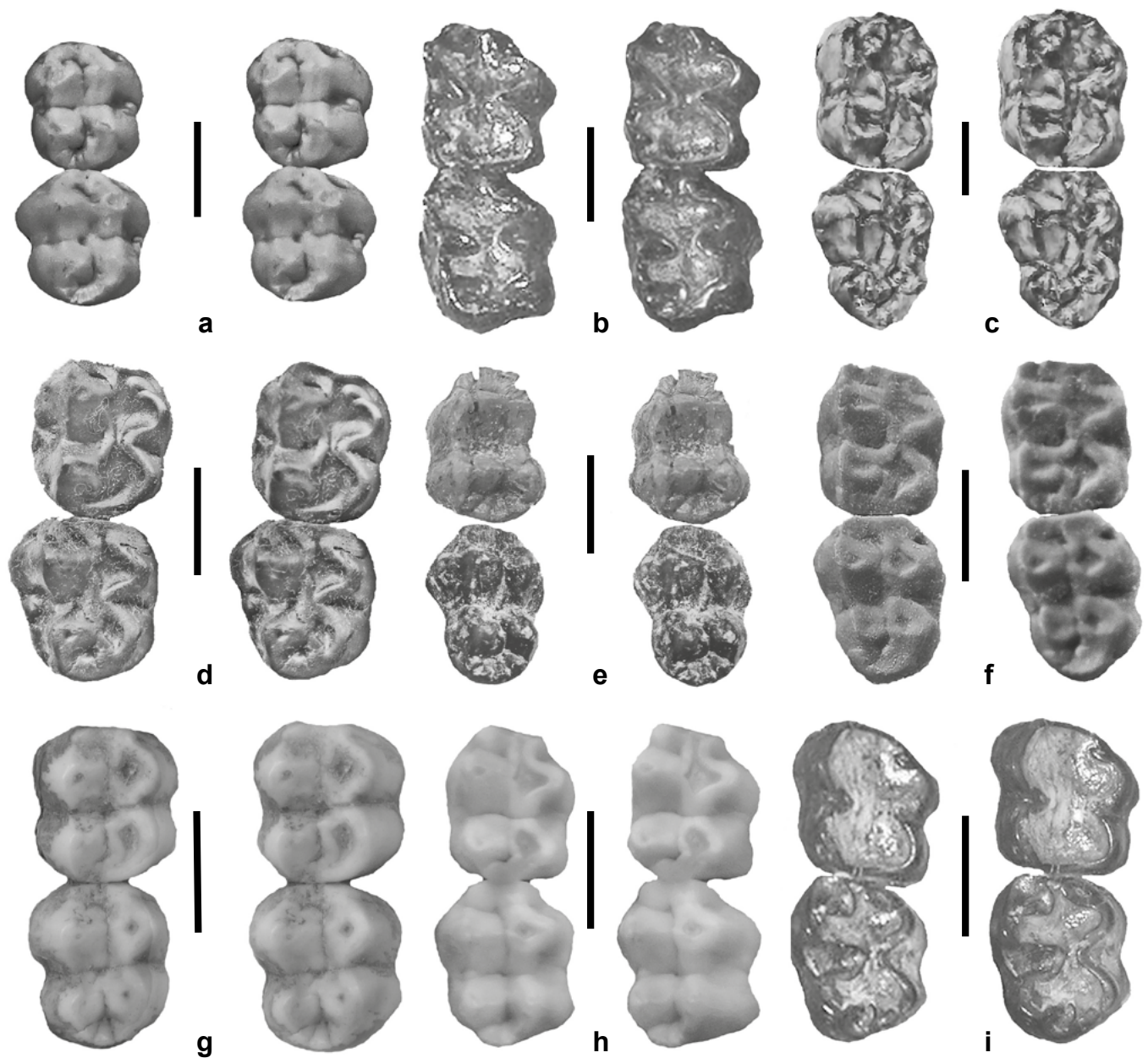
Text-fig. 7. Stereo occlusal views of a cast of DGUNL LEBA 06, left maxilla from Tchiua, Angola, attributed by Arambourg (1955) to *Dinopithecus ingens*, but which was transferred to *Theropithecus baringensis* by Jablonski (1994) and then to *Soromandrillus quadratiostris* by Gilbert (2013). Following Pickford and de Matos (2026) it is herein attributed to cf. *Mandrillus* sp.

such a tendency, and DGUNL LEBA 04, which does. The latter specimen was classified as *Papio* sp. by Arambourg (1955) but was transferred to *Omopithecus baringensis* (LEAKEY, 1969) by Pickford and de Matos (2026: fig. 79).

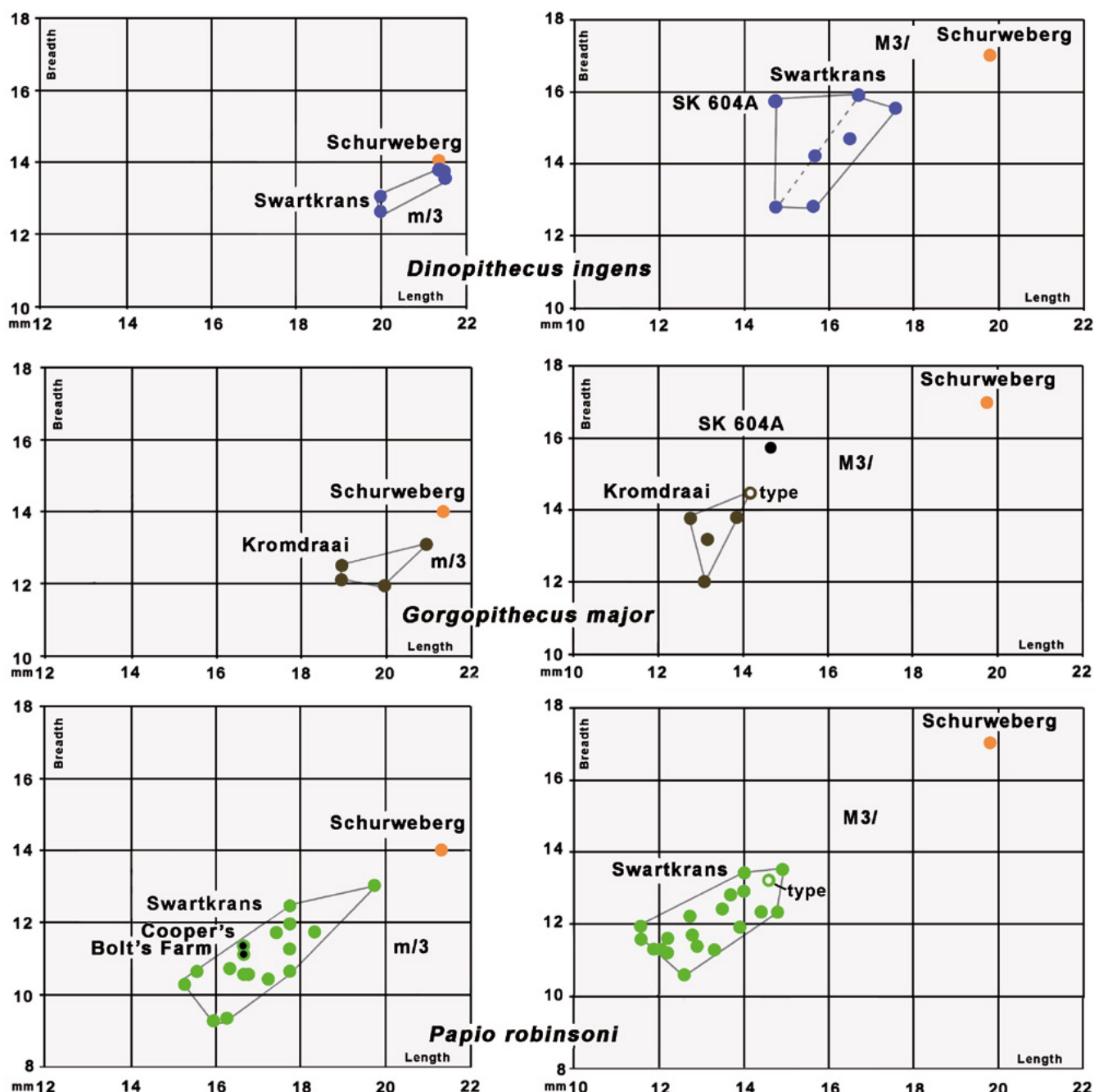
Freedman (1955, 1957) carried out a wide-ranging study of the fossil monkeys from the Transvaal (now Gauteng) South Africa. His discussions concerning the three large ‘baboon-like’ species, *Dinopithecus ingens*, *Gorgopithecus major* and *Papio robinsoni* were extensive and dealt with numerous specimens from Swartkrans and Kromdraai, and a few specimens from Cooper’s, Gladysvale and Bolt’s Farm. He attributed the reasonably well-preserved palate with both cheek tooth rows, SK 604A, to *Dinopithecus ingens*, but it was eventually transferred to *Gorgopithecus major* by Pugh and Gilbert (2018). Thus, for three generations, this fossil was employed as a sort of replacement type specimen (a kind of neo-type or basic reference fossil) for *Dinopithecus ingens* until its taxonomic attribution was changed. The reattribution of the specimen to a different genus and species radically alters interpretations of phylogeny based on the upper cheek tooth rows of the taxa concerned. During their studies many authors marginalised the Schurweberg specimen SB 3 by employing SK 604A rather than SB 3 as the reference for the upper cheek dentition of *Dinopithecus ingens*. As a result, some, if not most of, the maxillary specimens from Swartkrans and Kromdraai attributed to *Dinopithecus ingens*, more likely belong to *Gorgopithecus major* or to another taxon. The available metric and morphological data support the latter possibility.

Freedman’s (1957) opinion that the upper molars in SB 3 are damaged by crushing and expansion is not supported by the evidence (Text-fig. 5). He wrote ‘The two male upper molars (M2/ and M3/) of SB 3 described by Broom (1937) from Schurweberg are badly crushed and expanded and their dimensions may well be too large,’ a description that runs counter to Broom’s (1937) description of the teeth as being well-preserved. Restudy of the fossil reveals that the teeth are indeed well preserved apart from minor damage to the metacone and paracone of the M3/ and the paracone of the M2/, damage that was likely caused subsequent to Broom’s description of the specimen (Text-fig. 5). In addition, there is no serious evidence to support Freedman’s (1957) determination of SB 3 as a male of the species.

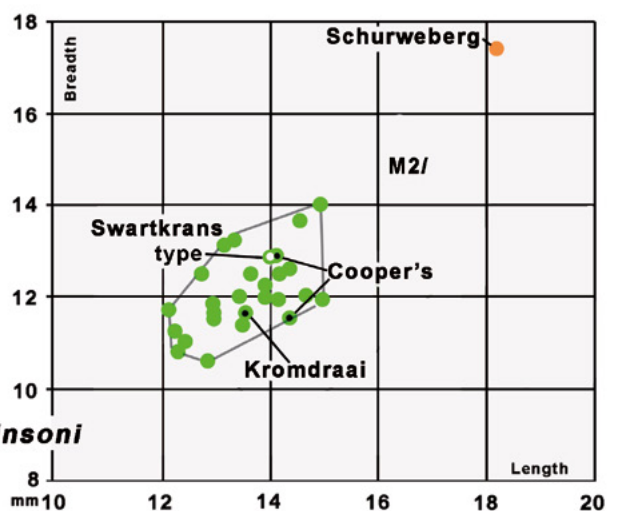
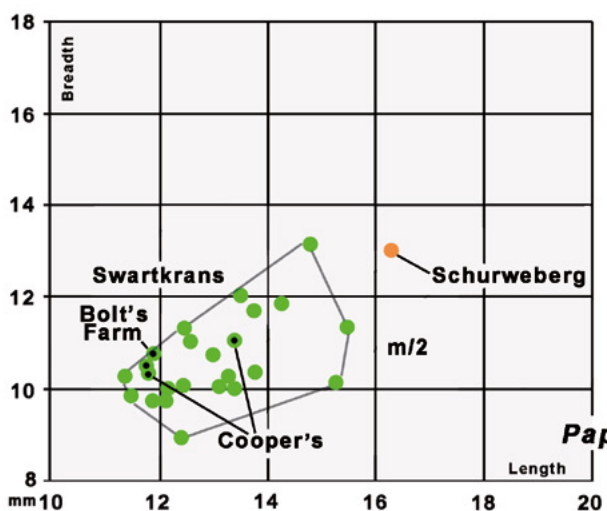
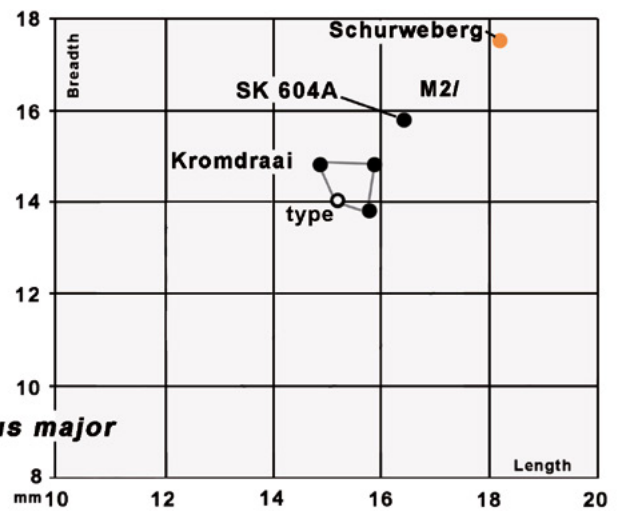
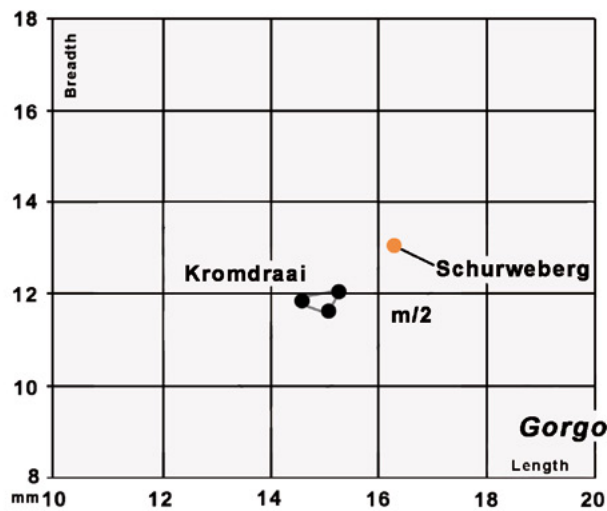
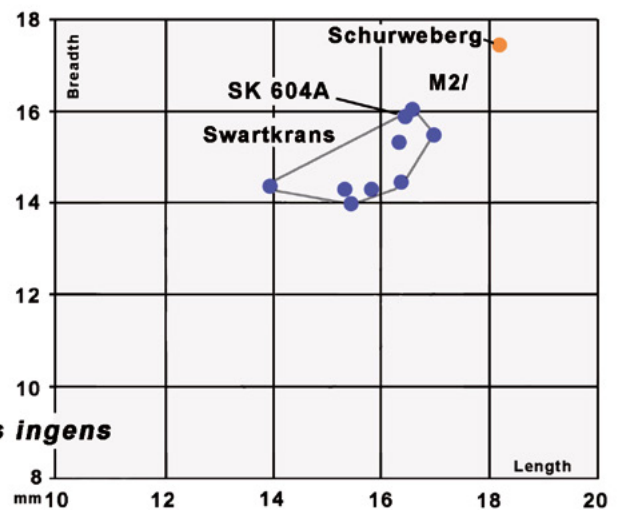
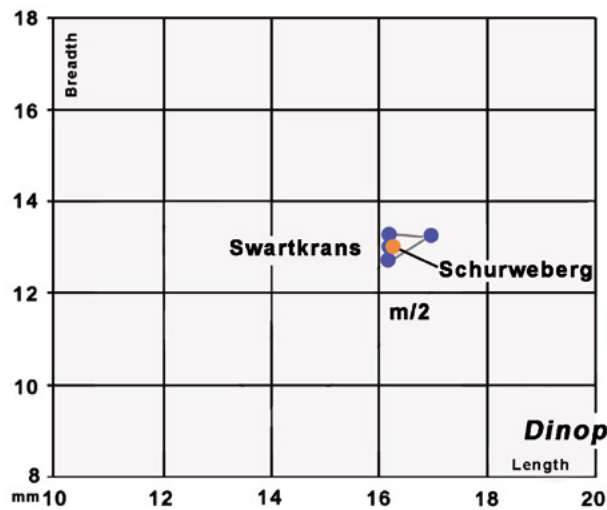
In effect, the molars in SB 3 and SB 7 are the largest cercopithecoid teeth known from Southern Africa, but, counter to the view articulated by Freedman (1957), the size relationship between the upper and lower molars of these two specimens is not highly unusual (Text-figs 9, 10). The m3 is somewhat longer than the M3/ and the M3/ is broader than the m3/, the usual situation in cercopithecoids. Given that only two specimens with cheek teeth are known from the type locality, it is not possible to obtain a realistic impression of the range of metric variation in the species on the basis of fossils from that locality. However, the morphology of the Schurweberg upper and lower teeth suggests strongly that the cranium and the mandible represent the same genus, if not the same species, and that neither of the Schurweberg specimens belongs to *Papio* or to *Gorgopithecus*. The teeth in the Schurweberg specimens (Text-fig. 8) more closely recall those of *Theropithecus* than they do those of the other extant genera of large cercopithecoids (*Papio*, *Mandrillus*) and they share some of their morphology with the extinct genera, *Omopithecus* DELSON, 1993, and *Soromandrillus* GILBERT, 2013.



Text-fig. 8. Comparison of stereo occlusal views of upper M2/ and M3/ (figured as right to simplify comparisons) of (a) *Mandrillus leucophaeus* (MNHN AC 2005-248), (b) *Soromandrillus quadratiostris* from Usno, Ethiopia (type specimen; image reversed, photo credit C. Gilbert), (c) *Dinopithecus ingens* (DNMNH SB 3, paratype; image reversed), (d) cf. *Mandrillus* sp. from Tchiua, Angola (DGUNL LEBA 06; image reversed), (e) *Omopithecus baringensis* from Tchiua (MRH TCH 38'90), (f) *Omopithecus baringensis* from Tchiua (DGUNL LEBA 04), (g) *Papio ursinus* (UL CZ 341), (h) *Theropithecus gelada* (MNHN AC 1972-360), (i) *Omopithecus baringensis* from Chemeron, Kenya (KNM BC 2, holotype; photo credit C. Gilbert). Note the variation in the basal pillar in the buccal flexus and the form of the talon in the M3/ comprised of the thickened union of the postmetacrista and the posthypocrista, completely enclosing the distal fovea in *Mandrillus* (a, d) but not in *Dinopithecus* (c) or *Soromandrillus* (b) or *Omopithecus* (e, f, i). Scale bars: 10 mm.



Text-fig. 9. Bivariate (length-breadth) plots of the third molars of *Dinopithecus ingens* from Schurweberg (the type locality: orange dots) and other large cercopithecoids from South Africa. Freedman's hypodigms: Blue dots – *Dinopithecus ingens*; Green dots – *Papio robinsoni*; Black dots – *Gorgopithecus major*. Lower third molars in left column, upper third molars in right column. SK 604A was included in *Dinopithecus ingens* by Freedman (1957) but was transferred to *Gorgopithecus major* by Pugh and Gilbert (2018). Data from Freedman (1957).



Text-fig. 10. Bivariate (length-breadth) plots of the second molars of *Dinopithecus ingens* (orange dots) from Schurweberg (the type locality) and other large cercopithecoids from South Africa. Freedman's hypodigms: Blue dots – *Dinopithecus ingens*; Green dots – *Papio robinsoni*, Black dots – *Gorgopithecus major*. Lower second molars in left column, upper second molars in right column. SK 604A was included in *Dinopithecus ingens* by Freedman (1957) but was transferred to *Gorgopithecus major* by Pugh and Gilbert (2018). Data from Freedman (1957).



Text-fig. 11. Stereo occlusal views of the palate with left and right cheek tooth rows (DNMNH SK 604A) that was attributed to *Dinopithecus ingens* by Freedman (1957), but was transferred to *Gorgopithecus major* by Pugh and Gilbert (2018).

Freedman (1957) attributed a substantial number of specimens (36) from Swartkrans to *Dinopithecus ingens*, but all of them have upper and lower molars that are smaller than the specimens from Schurweberg. Several times he wrote that male teeth of cercopithecoids are generally larger than female ones. This is so for the canines and anterior premolars, but such is generally not the case for the posterior cheek teeth. Thus, his identification of cheek teeth from Swartkrans as representing females of *Dinopithecus ingens* on the basis of their smaller dimensions, is not strongly supported by the metric evidence. Furthermore, the morphology of the molars that he included in his hypodigm of the species indicates that some of the specimens do not belong to this genus, but to a distinct large papionine. Pugh and Gilbert (2018) already pointed out that SK 604A belongs to *Gorgopithecus major* and not to *Dinopithecus ingens* (Text-fig. 11).

The important point to note is that authors who have compared the Angolan cercopithecoids with *Dinopithecus ingens* from Southern Africa employing the concepts of Freedman (1957) were effectively making comparisons with a taxonomic chimaera. As it happens, because SK 604A is a palate with both cheek tooth rows reasonably well-preserved (Text-fig. 11) it often formed the basis for comparisons as a sort of reference specimen of the genus. However, its posterior molars are markedly different in morphology and dimensions from those of the Schurweberg specimen (Text-fig. 12).

Maier (1970a, b, 1973) proposed that *Dinopithecus* could be related to *Gorgopithecus* and *Papio*, but, in his publication, he did not mention the fossils from the type locality of *Dinopithecus*, instead basing his results on the fossils from Swartkrans and Kromdraai.

In 1977, Freedman and Brain published a paper on the stratigraphic distribution of cercopithecoids from Swartkrans, in which they concluded that there were two assemblages, one each in breccias labelled Member 1 and Member 2 (Freedman 1970, 1976). The authors provided lists of specimens for each taxon, but did not enter into anatomical details other than identifying the fossils as maxillae and mandibles and determining the sex, when possible. Many of the taxonomic

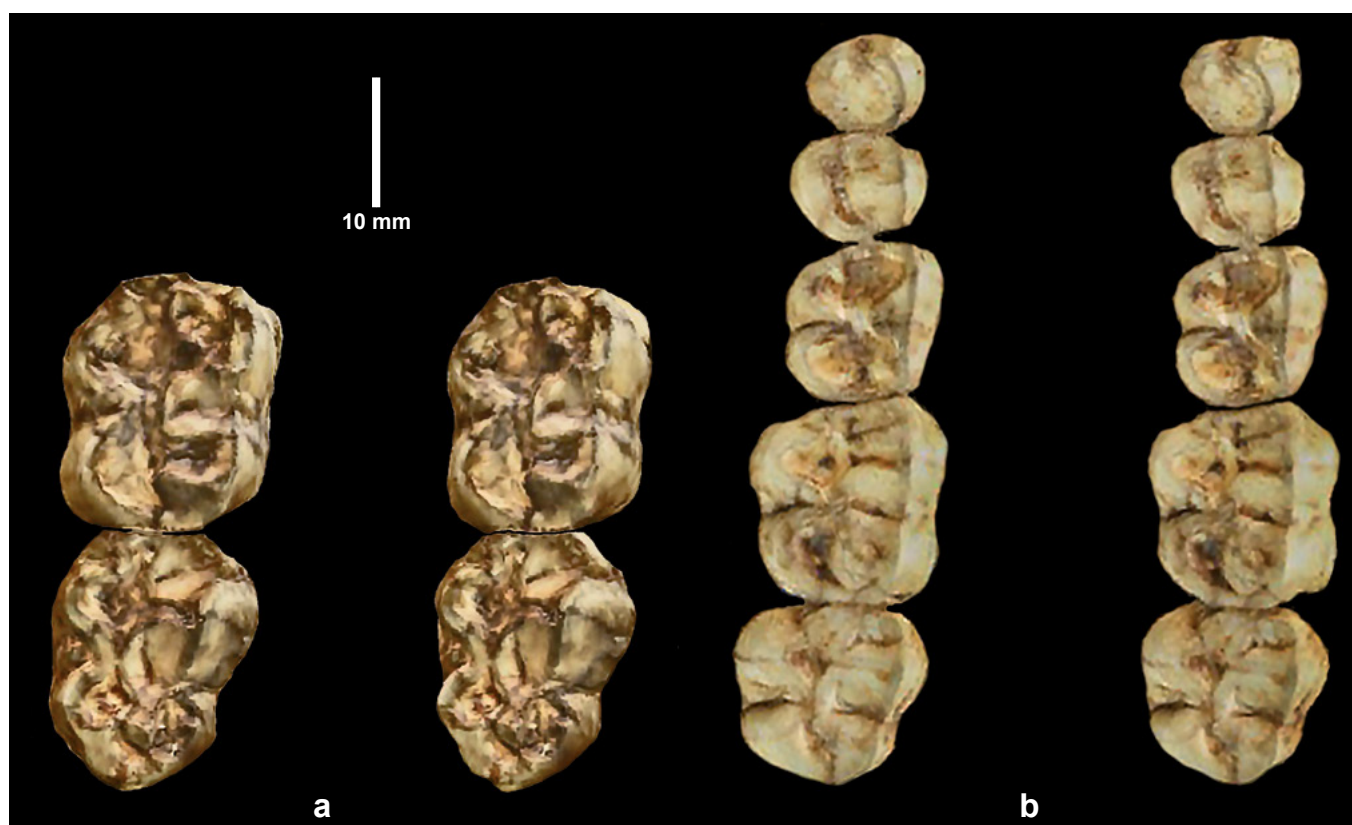
identifications complied with the previous results of Freedman (1957) but there were some changes, and specimens recovered since that work were added. The difficulties of arriving at secure taxonomic identifications of several of the fossils is underlined by the fact that, in this publication, four of the specimens were attributed to two different species, *Papio robinsoni* and *Dinopithecus ingens*. The specimens concerned are the maxillae SK 447, SK 571b, SK 576a and the mandible SK 589. In addition, SK 453 was listed twice, once as a male and the second time as sex unknown. SK 497 was listed as *?Papio robinsoni*.

Brain (1981) listed a minimum of 26 individuals of *Dinopithecus ingens* from Swartkrans, among which there were several isolated teeth that had not been included in the species during previous studies. Among the fossils attributed to *D. ingens*, there are four specimens (SK 503, SK 571b, SK 576a and SK 589) that were attributed to *Papio robinsoni* in prior studies by Freedman (1957) and Freedman and Brain (1977) and one fossil (SK 604A) was subsequently attributed to *Gorgopithecus major* by Pugh and Gilbert (2018). These differences highlight the difficulties that confront researchers working with incomplete fossils.

As concerns *Papio robinsoni*, the tally from Swartkrans listed by Brain (1981) was interpreted to represent a minimum of 38 individuals. Several mandible and maxilla fragments as well as some isolated teeth were added to previous listings, and some specimens previously attributed to the species were omitted.

In contrast to previous researchers, Delson (1984) and Delson and Dean (1993) referred to the Schurweberg fossils as *Papio (Dinopithecus) ingens* and they included the Usno (Ethiopia) species in the same subgenus as *Papio (Dinopithecus) quadratorostris*. This classification implied that the Ethiopian and South African species were closely related (Gilbert 2013).

In contrast to the extensive list of specimens from Swartkrans attributed to *Dinopithecus ingens* by Freedman (1957), Delson and Dean (1993) listed or illustrated only five specimens from Swartkrans in their hypodigm of the species (SK 546, maxilla with P3–M2; SK 553, cranium with P4–M3; SK 577A–B,



Text-fig. 12. Stereo occlusal views of the left upper cheek teeth of SB 3 (a), paratype of *Dinopithecus ingens*, and DNMNH SK 604A (b), herein attributed to *Gorgopithecus major*.

maxilla with P3/–P4/; SK 578, maxilla with P3/–M1/; and SK 599, edentulous neurocranium) and the only specimen from Schurweberg in their list was the holotype mandible (SB 7). A brief mention was made of SB 3, the crushed partial cranium with the posterior molars, to the effect that the holotype mandible ‘may be associated with a large damaged cranium bearing M2/–M3/’. Only one of the Swartkrans specimens that they listed retains the M3/, so it is not possible to make comprehensive comparisons with the upper third molars of the Schurweberg material. The only other tooth in common are the M2/s in SK 546 and SK 553 which reveal that the Schurweberg fossils have significantly larger teeth (more than 20% larger) than SK 553 from Swartkrans (Table 1). Such a degree of size difference is unlikely to be due to sexual bimodality within a single species, but is more likely to reflect differences at the species (or genus) level. In their publication, Delson and Dean (1993: tab. 4.1) provided measurements of the upper teeth of *Papio* (*Dinopithecus*) *ingens*, but the catalogue number of the specimen from Schurweberg was misprinted as SB 7 (the upper teeth are in SB 3).

Concerning the morphology of the maxilla in the area of the malar apophysis and the infraorbital fossa (Arambourg 1955) the only South African specimens discussed by Delson and Dean (1993) that can be compared with SB 3 and LEBA 06, are the neurocranial fragment (SK 599) and the skull (SK 553). The latter fossil shows a shallow infraorbital area (Text-fig. 6).

In their paper on African fossil baboons, Benefit and McCrossin (1990) ‘used the Swartkrans dental material as representative of *Dinopithecus* tooth morphology without ever having looked at material from the type locality’ (Benefit, pers. comm. 2026).

Table 1. Measurements (in mm) of the teeth in the Schurweberg cranium (DNMNH SB 3) and the specimens from Swartkrans included by Delson and Dean (1993) in the species *Papio* (*Dinopithecus*) *ingens*.

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
SB 3	M2/	18.2	17.4
SK 546	M2/	–	16.7
SK 553	M2/	14.0	14.3
SB 3	M3/	19.8	17.0
SK 553	M3/	14.8	12.8

Jablonski (1994) compared the Humpata (Angola) fossil cercopithecoids to material from Eastern and Southern Africa. She accepted that *Dinopithecus* merited full generic status, unlike Delson and Dean (1993) who considered it to be a subgenus of *Papio*. For the hypodigm of *Dinopithecus ingens*, she relied upon the specimen identifications proposed by Freedman (1957), which, as pointed out above, is likely to comprise remains of two or perhaps three different species, if not genera. She concluded that ‘The results of the current study suggest that *T. baringensis* (now including the Humpata papionin sample) and *T. quadratiostris* occupy a position at the base of the *Theropithecus* radiation very close to the origin of *Dinopithecus ingens* and *Gorgopithecus major*. The species of the genera *Theropithecus* (including its Humpata representatives) and *Papio*, along with *D. ingens* and *G. major*,

form a cluster of taxa that are more closely related to each other than they are to other extant or extinct papionins’.

Jablonski’s (1994) attribution of all the large cercopithecoid fossils from Humpata to *Theropithecus baringensis* has not been supported by subsequent studies (Gilbert 2013, Pugh and Gilbert 2018). According to the latter authors, the only specimen in the Angolan collection belonging to this genus is the mandible from Cangalongue (MRH CAN 30’90). The other specimens (from Tchiua) were reclassified by Gilbert (2013) as *Soromandrillus quadratiostris* and he considered that the East African fossils included in the species by Jablonski (1994) could only doubtfully be included in *Theropithecus*, as *?Theropithecus baringensis*. Nevertheless, the morphometric links between some of the large cercopithecoids from South Africa, Angola and East Africa were clear in Jablonski’s (1994) paper, even if the taxonomic details remain debatable.

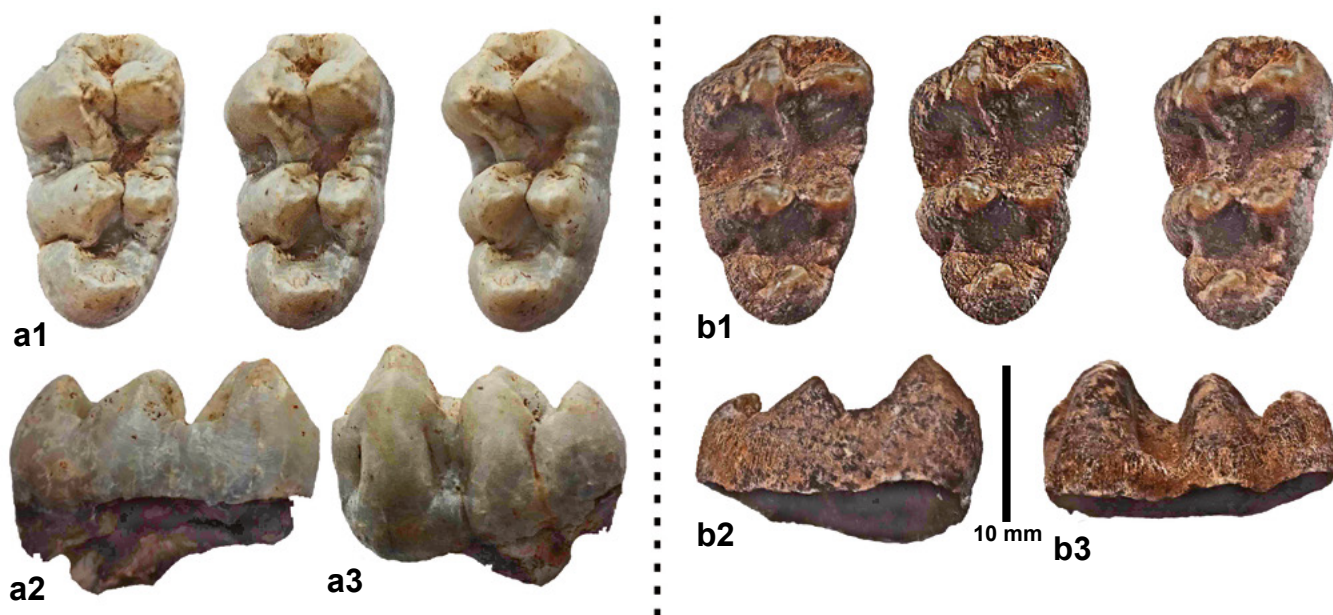
Gautier (1995: pl. 1, figs 5, 6) illustrated two lower third molars from ‘Leba III/IV’ that he attributed to *Papio* sp. (Text-fig. 13). The two specimens are compatible in some aspects of morphology and dimensions to m/3s of *Mandrillus sphinx* and *Mandrillus leucophaeus*, and they differ in morphology from the corresponding teeth of most species of *Papio* in the present-day concept of the genus, notably by their more bundont crowns. After extensive comparisons, it was found that they share some features with the teeth in a male specimen in the collections of the Department of Comparative Anatomy at the MNHN, Paris (CG 1962 N° 1459), enigmatically labelled *Papio papio cynocephalus* and reported as coming from ‘Afrique orientale’. A particular resemblance concerns the presence of a strongly beaded lingual margin between the metaconid and entoconid (lingual margin accessory cusplets; Chapple and Skinner 2023). Gautier (1995) was informed that the Leba III/IV specimens were found in the context of a Middle Stone Age deposit at Leba. His attribution of the specimens to *Papio* sp. reflected the classification widely

employed at the time of his studies (the mid-1980’s) which lumped the mandrills within the genus *Papio*.

Gilbert (2013) accepted that *Dinopithecus* and *Gorgopithecus* were valid genera, distinct from *Papio* and *Theropithecus*, and he erected the genus *Soromandrillus* (type species *S. quadratiostris*). The sample of specimens attributed by him to *Dinopithecus ingens* included two mandibles (SB 7 and SK 401) and ten maxillae (SK 542a, SK 546, SK 548, SK 553, SK 554, SK 574, SK 599, SK 600, SK 603, and SK 604A). The last specimen was removed from the list by Pugh and Gilbert (2018) who attributed it to *Gorgopithecus major* instead. In *Gorgopithecus major*, Gilbert (2013) included one mandible (KA 150) and five maxillae (KA 153, KA 192, KA 524/676, KA 605 and KA 944). Like Heaton (2006) *Papio robinsoni* was considered by Gilbert (2013) to be a subspecies of the extant species *Papio hamadryas*.

In his cladistic analyses, Gilbert (2013) concluded that *Dinopithecus* was not clearly positioned. He explained ‘The overall uncertain placement of *Dinopithecus* is contrary to most authors’ previous hypotheses suggesting that it is a very large ‘baboon,’ closely related to extant *Papio* (e.g., Freedman 1957, Szalay and Delson 1979, Delson and Dean 1993, Frost 2001). Among the MPTs, *Dinopithecus* is sometimes placed at the base of the non-*Theropithecus* crown African papionin radiation (occasionally with *P. angusticeps*), sometimes placed as the ancestor/sister of the *S. quadratiostris*/*Mandrillus*/*Cercocebus*/*Procercocobus* clade, sometimes placed as the ancestor/sister of the *Theropithecus* clade (see SOM), and sometimes placed as a stem African papionin (Analysis 3 only).’ [MPT – Maximum Parsimony Trees, SOM – Supplementary Online Material].

However, the hypodigm of *Dinopithecus* upon which these analyses were based, comprises a taxonomic chimaera. SK 604A, for example, was transferred by Pugh and Gilbert (2018) to *Gorgopithecus major*, and the other maxillae contain teeth that are considerably smaller than



Text-fig. 13. Lower left third molars of cf. *Mandrillus* sp. from Leba, Angola. a: UL TCH 60 (= LEBA III/IV in Gautier 1995), fully formed but unworn tooth with roots (broken), b: UL TCH 61 (= LEBA III/IV in Gautier 1995), incompletely formed germ in which root formation had not started. 1 – stereo occlusal views, 2 – lingual views, 3 – buccal views. These two teeth were identified as *Papio* sp. by Gautier (1995: pl. 1, figs 5, 6). Note the clearly developed lingual margin accessory cusplets (LMAC in Chapple and Skinner 2023) frequently present in *Mandrillus*, but rare in *Papio*.

the Schurweberg fossils, the only specimen with teeth agreeing closely in dimensions with those in the holotype of the species being the mandible, SK 401 (Table 2). The maxillae from Swartkrans belong to a species similar in dimensions to *Soromandrillus quadratiostris*, but differs morphologically from it.

Table 2. Measurements (in mm) of the third molars of material attributed by Gilbert (2013) to *Dinopithecus ingens* (in bold) and *Soromandrillus quadratiostris*. DNMNH SK 604A was subsequently transferred by Pugh and Gilbert (2018) from *D. ingens* to *Gorgopithecus major*.

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
DNMNH SB 7	m/3	21.4	14.0
DNMNH SK 401	m/3	21.5	13.7
DNMNH SB 3	M3/	19.8	17.0
DNMNH SK 574	M3/	15.6	12.8
DNMNH SK 600	M3/	16.5	14.7
DNMNH SK 603	M3/	15.7	14.2
DNMNH SK 604A	M3/	14.7	15.7
NME USNO	M3/	15.5	13.8
NME I. 185-6	M3/	15.9	15.0
DGULN LEBA 06	M3/	15.4	15.0

Beaudet et al. (2016) studied the internal structural organisation of the upper third molar in cercopithecoids and the morphology of the semicircular canal of *Dinopithecus ingens* (two specimens – SK 554, SK 559), *Gorgopithecus major* (two specimens – KA 192, KA 193), *Papio robinsoni* (four fossils – SK 546, SK 555, SK 562, SK 602).

In the ‘heirarchical classification’ based on M3/ structure by Beaudet et al. (2016: fig. 7) the following specimens were mentioned: *Papio* (SK 602, Swartkrans 3, SK 536, SK 562, SK 555 and KA 194), *Theropithecus* (SK 561) and *Gorgopithecus* (KA 192). The M3/s in the Schurweberg cranial fragment (SB 3) were not included in the study. It would be of interest to carry out a study of the latter specimen because, on the basis of the good state of preservation and the moderate stage of wear, a reliable image of the internal morphology of the M3/ ought to be obtainable. The external appearance of the Schurweberg specimen (e.g., the talon development in the M3/) indicates affinities with *Theropithecus*. In the ‘heirarchical classification’ of Beaudet et al. (2016) *Mandrillus sphinx* plotted as the sister of *Parapapio broomi* (STS 544) and *Mandrillus leucophaeus* plotted as the sister of *Theropithecus gelada* and close to *Theropithecus oswaldi* (SK 561).

The taxonomic identification of some of the neurocranial specimens included in the study by Beaudet et al. (2016) is open to debate, so the observation that ‘the condition displayed by *Dinopithecus* approximates that of *Macaca* LACÉPÈDE, 1799, potentially suggesting the retention of a primitive state of the inner ear that is not shared with contemporaneous fossil taxa’ may not apply to *Dinopithecus* but to a different genus, depending on which specimens were attributed to *Dinopithecus* by them.

Monson et al. (2017) studied cranial variation and taxonomic diversity in South African Cercopithecidae, including *Dinopithecus ingens* (SK 553, SK 554, SK 599, SK 600 and SK 604A, all from Swartkrans), *Gorgopithecus major* (KA 153, KA 605 and KA 944, all from Kromdraai) and *Papio robinsoni* (SK 555, SK 557, SK 558, SK 560, SK 562 (from Swartkrans), UCMP 56767 and UCMP 56797 (from Bolt’s Farm) and SWP 31 (from Sterkfontein)). Apart from the material from Bolt’s Farm and Sterkfontein, which were new to their paper, the specimen lists in Monson et al. (2017) accepted the identifications of Freedman (1957) and Gilbert (2013). However, the palate, SK 604A, was later removed by Pugh and Gilbert (2018) from the list of *Dinopithecus ingens* and was transferred to *Gorgopithecus major*.

Pugh and Gilbert (2018) analysed the same fossil sample attributed by Gilbert (2013) to *Dinopithecus ingens* with the exception of the palate, SK 604A, which they transferred to *Gorgopithecus major*. To Gilbert’s (2013) hypodigm of *Gorgopithecus major* were added SK 604A (palate with left and right cheek tooth rows), KA 154 (maxilla with P3/–M2/) and KA 1148 (anatomy not specified) as well as two fossils from Olduvai, Tanzania. They accepted that *Papio robinsoni* was a species distinct from *Papio hamadryas*, including in it 17 specimens from Swartkrans (SK 406, SK 407, SK 408, SK 409, SK 416, SK 421, SK 549, SK 555, SK 557, SK 558, SK 560, SK 562, SK 565, SK 566, SK 571B, SK 602, SK 3211B), two from Schurweberg (SB 2 and M 3147), three from Bolt’s Farm (UCMP 56797, UCMP 56786, BF 38), and one from Swartkrans II (SK II 2). Gilbert et al. (2018) published additional information about the distribution of *Papio robinsoni*, including material from Drimolen (Main Quarry).

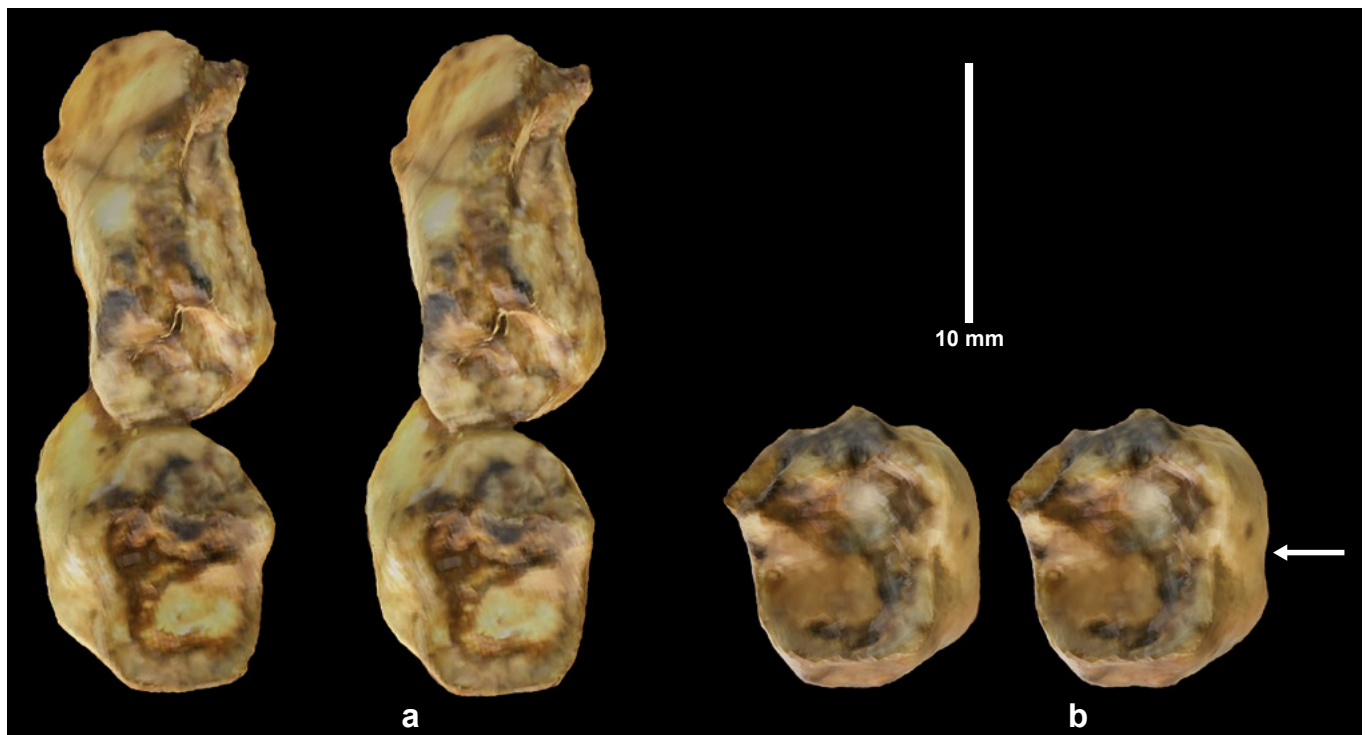
Pugh and Gilbert (2018) summarised the phylogenetic position of *Dinopithecus*, based on molecules and morphology in the following terms ‘*Dinopithecus* and *Gorgopithecus* are also stem or crown P/L/R/T taxa, but their phylogenetic positions remain unstable’. (P/L/R/T: *Papio/Lophocebus/Rungwecebus/Theropithecus*). However, as has been pointed out above, their hypodigms of *Dinopithecus* and *Gorgopithecus* probably contain remains of more than one taxon and, if so, then this would contribute to the unsettled positions of the potentially chimaeric ‘genera’ in the phylogenies. None of their analyses included specimens from the type locality of *Dinopithecus ingens*. Their analyses consistently distanced *Dinopithecus* from *Mandrillus*, but here again, the attribution of the Swartkrans fossils to *Dinopithecus* could be invalid for the reasons outlined above. Dentally, the material from the type locality of *Dinopithecus* recalls, in some features, those of *Mandrillus*, but it shows stronger affinities with *Theropithecus* and *Omopithecus*. The debate about its taxonomic and systematic status remains open.

Systematic palaeontology

Family Cercopithecidae GRAY, 1821
Subfamily Cercopithecinae GRAY, 1821

Genus *Dinopithecus* BROOM, 1937

Type species. *Dinopithecus ingens* BROOM, 1937.



Text-fig. 14. Stereo occlusal views of the premolars in the holotype mandible of *Dinopithecus ingens* from Schurweberg, South Africa. a: left p/3 and p/4, b: right p/4. Note the relatively elongated and broad distal sector of the p/4 behind the buccal flexid (arrow). The p/3 is missing part of its mesial extremity.

Diagnosis. Summarised and modified from Broom (1937); animal nearly allied to the baboons, but differing in a number of important characters, besides being much larger than any baboon ... first lower premolar (p/3) differs from that of typical baboons in having the anterior part relatively shorter and broader ... behind the main cusp are two deep pits, and on the inner side of the anterior cusp another deep pit. The p/4 and molars agree fairly well with those of baboons ... one important difference is that there is only the faintest indication of a posterior cusp ... On the outer side of both m/2 and m/3 there are small subsidiary cusps ... M3/ has a marked inner cusp between the protocone and hypocone and a well-developed hypoconule.

Differential diagnosis. *Dinopithecus* differs from *Mandrillus* by the following features: in M3/ the distal loph is appreciably narrower than the mesial one whereas in *Mandrillus* it is only slightly narrower, and the buccal cusps of the upper molars are taller (less bunodont) than those of *Mandrillus*. *Dinopithecus* differs from *Soromandrillus* and *Omopithecus* by its greater dimensions, its less bunodont buccal cusps in the upper molars and lingual cusps in the lower molars, and the presence of a prominent protostyle in the hypoflexus and of a well-defined protostylid in the hypoflexid.

***Dinopithecus ingens* BROOM, 1937**

Holotype. By original designation, DNMNH SB 7, left and right mandibular bodies with part of the symphysis, containing left p/3–m/3 and right p/4–m/2, part of the right canine root and the left canine alveolus.

Paratype. By original designation, DNMNH SB 3, fragmentary cranium with left M2/–M3/ and right M3/.

Diagnosis. As for the genus.

Type locality and age. Schurweberg, Gauteng Province, South Africa, Late Pliocene (3.03–2.58 Ma) (Adams et al. 2010) or Early to Middle Pleistocene (1.4–0.4 Ma) if the attribution by Adams et al. (2010) of the isolated lower molar from Hoogland to *Theropithecus oswaldi oswaldi* is valid (Getahun et al. 2023).

Descriptions. The honing facet of the p/3 of *Dinopithecus ingens* is relatively shorter than it is in species of *Mandrillus* and *Papio*, and its distal complex is short and quite broad, as was noted by Broom (1937) (Text-fig. 14). The metaconid is small and is closely applied to the protoconid, but its posteristid is enlarged and elongated, reaching the disto-lingual corner of the crown. As a result, the entoconid is reduced in dimensions, and is positioned almost in the midline of the tooth, rather than being in a disto-lingual position as in *Soromandrillus* and *Mandrillus*. A ridge of enamel (the preentocristid) subdivides the distal basin into two, with the lingual half opening linguo-distally. The lingual side of the crown of p/3 has an elongated depression bordered by a cingulum, much as in specimens of *Mandrillus*. This individual (DNMNH SB 7) is evidently a male.

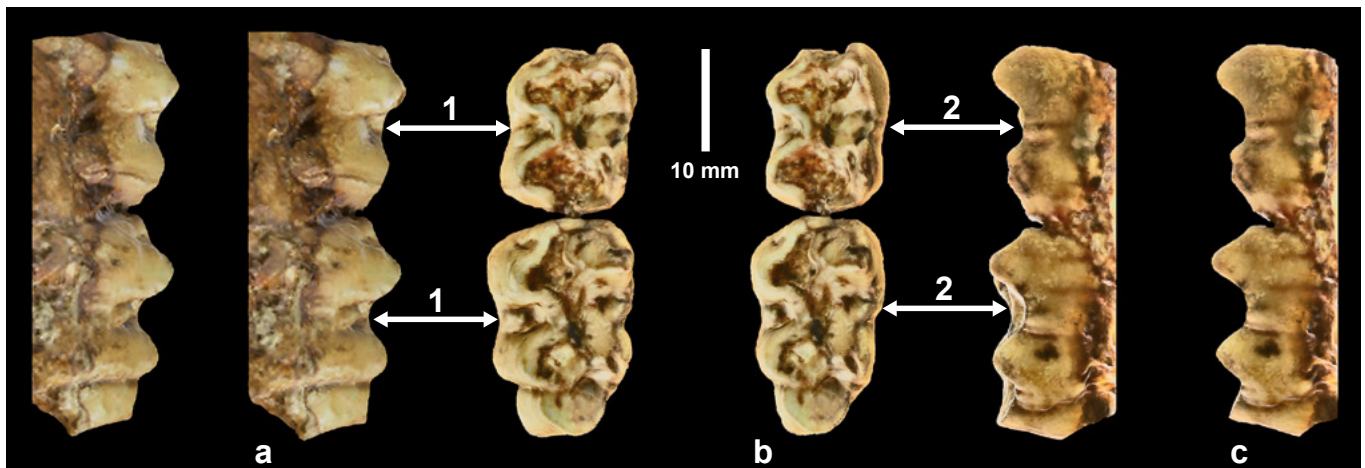
The p/4 of *Dinopithecus ingens* has a relatively elongated and broad distal sector compared to *Papio*, and in this respect it recalls *Mandrillus*. The p/4 is too worn to reveal details of the morphology of the cusps but there are two mesial cusps that form a transverse lophid with a preprotocristid oriented mesio-centrally. The distal basin is broad and shallow.

The lower molars of the Schurweberg holotype mandible of *Dinopithecus ingens* show a marked wear gradient, the

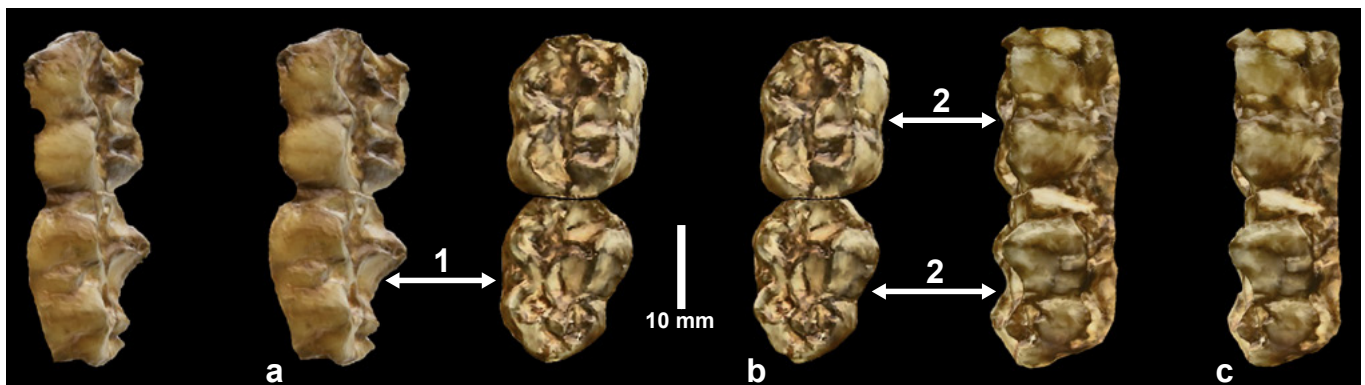
m/1 being worn to a stump, the m/2 having lost much of the apical portions of the main cusps, and the m/3 showing large dentine lakes on the protoconid and hypoconid but none on the metaconid and entoconid. The dentine exposure associated with the postprotocristid has linked to that of the prehypocristid, and the exposure associated with the preprotocristid extends mesio-lingually as far as the mesial cingulum. Dentine beneath the posthypocristid is not exposed, nor is there an exposure of dentine on the hypoconulid. The metaconid and entoconid show planar wear facets sloping mesially and distally, and leaning slightly buccally, but no dentine is exposed by wear, although a small chip of enamel is missing from the tip of the entoconid revealing the dentine beneath it. What remains of the m/2 recalls the first two lophids of the m/3 which are described immediately below. The main difference is that in the m/2, the distal lophid is slightly broader than the mesial lophid, whereas in the m/3, the mesial lophid is the broadest. It is pertinent to note that, in the m/2, as in the m/3, the lingual side of the crown between the metaconid and entoconid shows a beaded morphology, and that the floors of the trigonid basin and the hypoflexid are offset vertically, such that the trigonid basin is well above cervical level and the floor of the hypoflexid is closer to cervical level.

The m/3 consists of five main cusps arranged into three transverse lophids in which the lingual cusps are slightly more mesially positioned than their corresponding buccal cusps. The mesial lophid is slightly broader than the second lophid, and the distal lophid is considerably narrower than the second one, and it is more linguallly positioned, the hypoconulid lying in line with the longitudinal antero-posterior ridge formed by the preprotocristid, postprotocristid, prehypocristid and posthypocristid.

In the m/3, there is a prominent mesial buccal cleft between the buccal end of the mesial cingulum and the column of the protoconid (Text-fig. 15). On the lingual side, the mesial cingulum blends into the premetacristid. The buccal flexid (hypoflexid) is mesio-distally broad and deep and it contains a prominent protostylid (or basal pillar). The distal buccal cleft between the hypoconid and hypoconulid is mesio-distally narrow and bucco-lingually shallow. The tuberculum sextum is small, not very well defined and squeezed between the hypoconulid and the postentocristid. Between it and the mesial edge of the hypoconulid there is a notch forming a distal lingual cleft which extends down to the cervix. The postmetacristid and preentocristid meet each other on the lingual side of the crown, forming a tall beaded wall that closes off the trigonid basin on its lingual side. The floor of



Text-fig. 15. Stereo images of the left m/2 and m/3 in DNMNH SB 7, the holotype of *Dinopithecus ingens* from Schurweberg, South Africa. a: buccal view, b: occlusal view, c: lingual view. Note the deep and mesio-distally broad hypoflexid with its prominent basal pillar (1) and the tall connection between the postmetacristid and the preentocristid which is slightly beaded (2).



Text-fig. 16. Stereo images of the left M2/ and M3/ in DNMNH SB 3, paratype of *Dinopithecus ingens* from Schurweberg, South Africa. a: lingual view, b: occlusal view, c: buccal view. The arrows show (1) the prominent protostyle in the hypoflexus, and (2) the tall beaded connection between the postparacrista and premetacrista that closes the buccal edge of the trigon basin, which is well above cervical level.

the trigonid basin is well above the level of the cervix, in contrast to the floor of the hypoflexid which is much closer to cervical level.

The upper molars in the crushed cranial fragment, DNMNH SB 3, are moderately worn, indicating a fully mature adult (Text-fig. 16). The paracone and metacone of the M2/ have dentine exposures that are continuous with the dentine lakes of the protocone and hypocone. In the M3/ in contrast, the dentine exposure in the paracone is a narrow slit, and there is no exposure of dentine on the metacone. The dentine lakes of the mesial and distal lophids join each other in the middle of the crown in the M2/, but are still separated from each other by a narrow strip of enamel in the M3/.

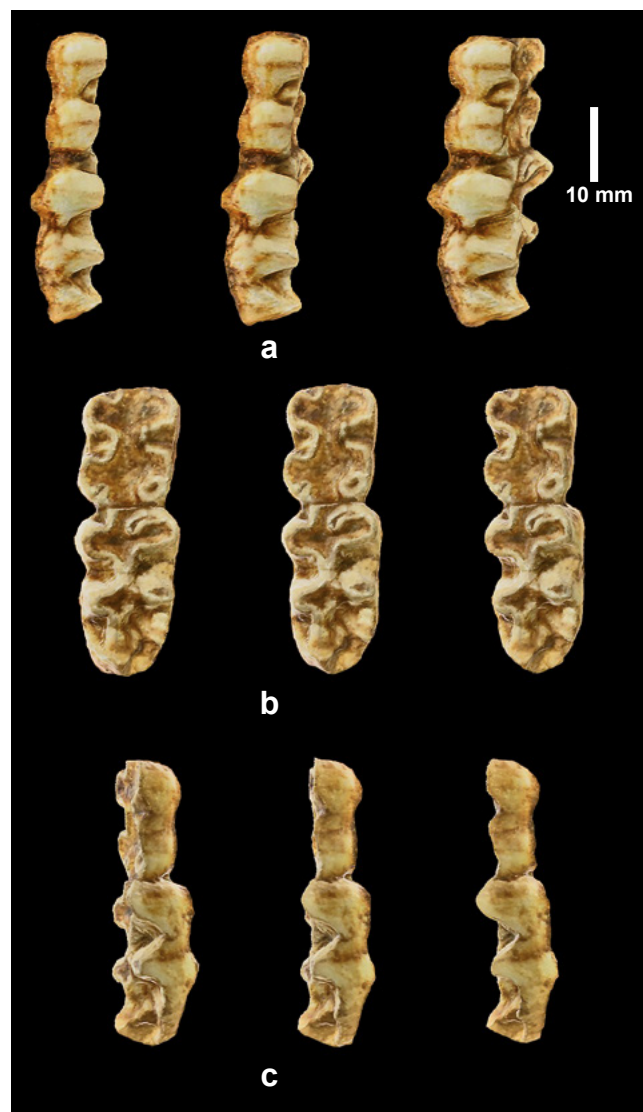
In the M3/ the preprotocrista extends towards the mesial cingulum where it swells to form an anterior accessory cusplet (the mesial tubercle) in the midline of the crown. It separates the mesial fovea from the mesio-lingual cleft. The mesial cingulum is mesio-distally quite broad. The trigon basin is shallow, and is bordered laterally by the postparacrista and premetacrista which are well above cervical level. The distal fovea is shallow with a low cingular margin posteriorly.

The distal loph of the M3/ is somewhat narrower than the mesial loph, and the posthypocrista swells towards its distal end to produce a small hypoconule (distal accessory tubercle or talon; Broom 1937).

Discussion

Among the Cercopithecoidea, the lower molars of *Dinopithecus ingens* are closest in overall morphology to those of geladas, but they show a few characters that recall mandrills. The hypoflexid is deep, U-shaped in lateral profile and is mesio-distally broad as in *Theropithecus*, *Gorgopithecus* and *Mandrillus*, and it differs from *Papio*, in which the hypoflexid is mesio-distally narrow and more V-shaped in lateral profile. A major difference between *Mandrillus* on the one hand, and *Theropithecus* + *Gorgopithecus*, on the other, concerns the zone between the metaconid and entoconid which is tall, beaded and strongly connected between the two cusps in *Mandrillus*, but which has a deep, flexid-like morphology in *Theropithecus* (Adams et al. 2010: fig. 3) and is open buccally in *Gorgopithecus*. This wall closes off the talonid basin in *Dinopithecus* and *Mandrillus*, unlike the lingually open talonid basin in *Theropithecus* and *Omopithecus*. In these respects, *Dinopithecus* recalls *Mandrillus* whereas *Theropithecus* and *Omopithecus* are closer to colobines such as *Rhinocolobus* LEAKEY 1982 (Harrison 2011). Another difference between the lower third molars of *Dinopithecus* and *Theropithecus* concerns the dimensions of the tuberculum sextum, which is greatly reduced in the former genus, but is generally well developed in *Theropithecus* (Text-fig. 17).

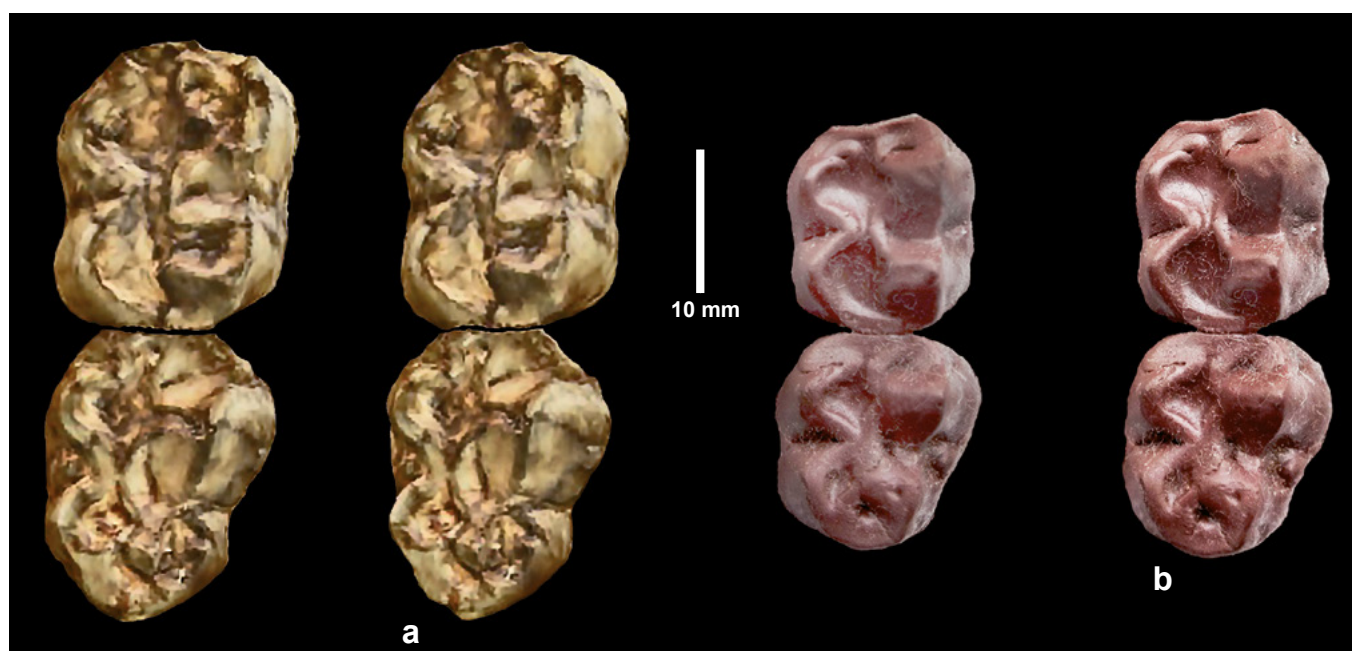
In *Dinopithecus*, the tuberculum sextum in the m/3 is greatly reduced in dimensions being little more than a beaded fold of enamel at the end of the postentocristid, which is itself reduced in dimensions. This morphology is close to that seen in *Mandrillus leucophaeus* and *Mandrillus sphinx*. In *Theropithecus* in contrast, the tuberculum sextum is large and more elongated (Text-fig. 17). In *Dinopithecus*,



Text-fig. 17. Stereo images of the left m/2 and m/3 in SK 405, part of the holotype mandible of *Theropithecus danieli* (FREEDMAN, 1957) from Swartkrans, South Africa, more recently attributed to *Theropithecus oswaldi* by Delson (1993). a: buccal views, b: occlusal views, c: lingual views.

the hypoconulid forms a robust pillar-like cusp at the rear of the m/3 positioned in the mid-line of the crown, as in *Mandrillus*, contrasting with the more laterally positioned hypoconulid in *Theropithecus*. In effect, the positioning of the relatively robust hypoconulid in the midline of the crown in both *Mandrillus* and *Dinopithecus*, leaves little space of the tuberculum sextum which, as a consequence, is squeezed into a small space between the hypoconulid and the postentocristid.

The upper molars of *Dinopithecus* are close in basic morphology to those of *Mandrillus*, but the buccal cusps are slightly taller and less bunodont and the talon of the M3/ is more strongly developed in the former genus. However, the breadth of the distal loph is not as greatly reduced in *Mandrillus* compared to the distinctly narrower distal loph that is present in *Dinopithecus*. In this respect, *Dinopithecus* is similar to *Soromandrillus* and *Omopithecus*, but the main cusps of the latter two genera are slightly more bunodont than those of *Dinopithecus* (Text-fig. 18).



Text-fig. 18. Stereo occlusal views comparing the left M2/ and M3/ of (a) *Dinopithecus ingens*, paratype from Schurweberg, South Africa (DNMNH SB 3) and (b) cf. *Mandrillus* sp. from Tchiua, Angola (DGUNL LEBA 06, cast) that was attributed to *Dinopithecus ingens* by Arambourg (1955) or to cf. *Mandrillus* sp. by Pickford and de Matos (2026).

A major difference between the upper molars of *Dinopithecus* on the one hand and of *Theropithecus*, *Omopithecus* and *Gorgopithecus* on the other (Text-fig. 19), concerns the height of the postparacrista and premetacrista in *Dinopithecus*, which join together to form the buccal margin of the trigon basin well above cervical level, whereas in *Theropithecus* and *Gorgopithecus* the trigon basin opens widely on its buccal side and its floor is closer to cervix level (Jablonski and Frost 2010: fig. 23-14, Gommery and Bento Da Costa 2016: fig. 10).

In summary, the cheek teeth of *Dinopithecus* are close in overall morphology to those of *Omopithecus* with some resemblances to *Soromandrillus* and *Theropithecus* but they also show some resemblances to teeth of *Mandrillus*, a genus that has somewhat more bunodont molars. The cheek teeth of *Dinopithecus* are morphologically more divergent from those of *Gorgopithecus* and *Papio*.

Phylogenetic relationships

The phylogenetic relations flowing from these observations are summarised in Text-fig. 20. In terms of dental morphology, *Theropithecus* and *Omopithecus* are close to *Soromandrillus* + *Dinopithecus*, together comprising a clade distinct from the *Procercocobus* + *Cercocobus* + *Gorgopithecus* + *Papio* + *Mandrillus* clade. The dichotomy between the geladas and the other papionines likely occurred towards the end of the Miocene or during the basal Pliocene. *Papio* and *Gorgopithecus* form a clade distinct from the *Mandrillus* clade. Colobines are not shown in the figure but the split between them, and the theropithecine + papionine clade likely occurred during the Late Miocene. The dental similarities between *Theropithecus* and colobines has been evoked on previous occasions (Leakey 1993).

It is stressed however, that some of the dental resemblances between *Dinopithecus* and *Mandrillus* noted above, open the

possibility that *Dinopithecus* could have been a member of the baboon clade that developed some theropithecine-like dental cusp morphology in parallel with geladas. In that case the phylogeny presented in Text-fig. 20 would require modification. With the currently available fossils from Schurweberg attributed to *Dinopithecus*, it is not possible to resolve the uncertainties. The same uncertainty does not apply to *Soromandrillus*, the type species being a member of the gelada clade as shown by its molar morphology, with a well-developed talon complex in the M3/, among other features.

Biogeographic implications

The possibility that extinct cercopithecoid genera in Ethiopia, Angola and South Africa, could be related to mandrills potentially expands the geographic distribution of this clade of cercopithecoids (Text-fig. 21). Until 2013, no fossils of this group had been recognised as such, the specimens having been attributed to savannah baboons (papionines *sensu stricto*) or to geladas (Gilbert 2013).

Extant mandrills are confined to dense tropical forest environments in western Africa within a zone ca. 7° of latitude north and south of the Equator. Regarding the palaeodistribution of the clade of drills and mandrills (*Mandrillus*) as well as that of *Soromandrillus* (if the systematic attribution of Gilbert 2013 is retained), three possibilities present themselves. The first is that the localities in Ethiopia, Angola and South Africa could have been more densely vegetated during the Plio-Pleistocene than they are today. The second is that species of *Soromandrillus* could have been adapted to more open environments than extant mandrills are. The third hypothesis is that the ancestral group from which mandrills evolved, currently considered to be represented by *Procercocobus* GILBERT, 2007, which has been recorded only from South Africa (Gilbert 2013, Pugh and Gilbert 2018), could have had a relatively wide distribution

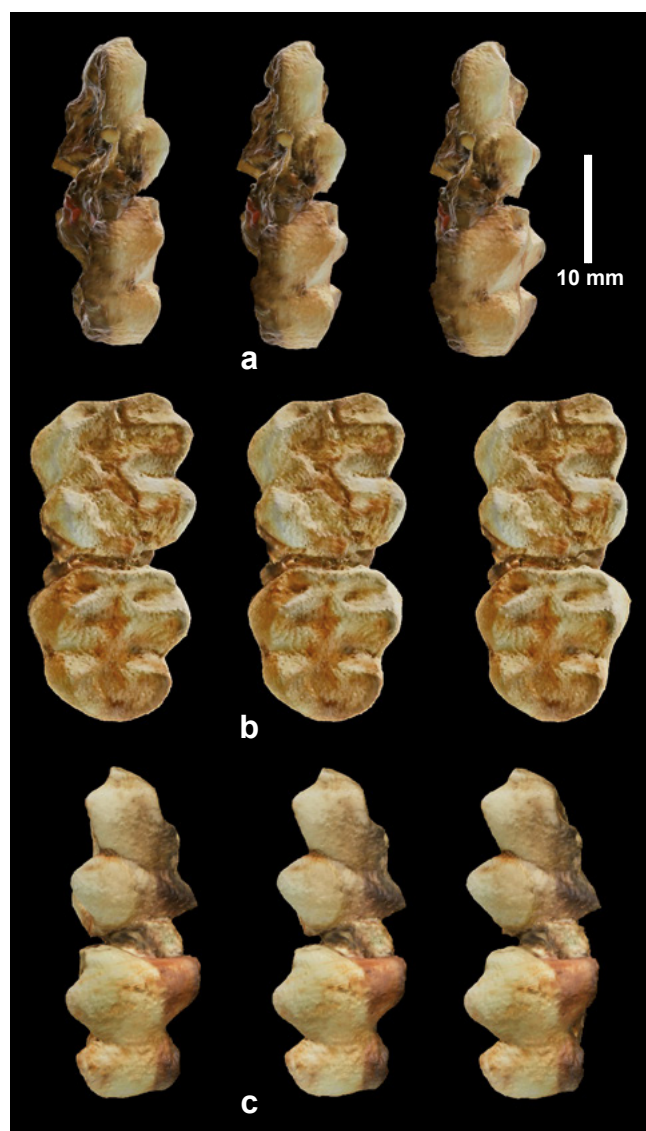
and a broad environmental tolerance during the Pliocene, and that it gave rise to several lineages that occupied different environments, the only ones of which survive today are the drills and mandrills which have a restricted distribution, and the various species of mangabey (*Cercocebus* GEOFFROY, 1812) which are widespread in tropical Africa in gallery forests, mixed woodland/forest as well as forested zones from Senegal in the west to Kenya and Tanzania in the east (Dempsey et al. 2024).

Issues to be resolved

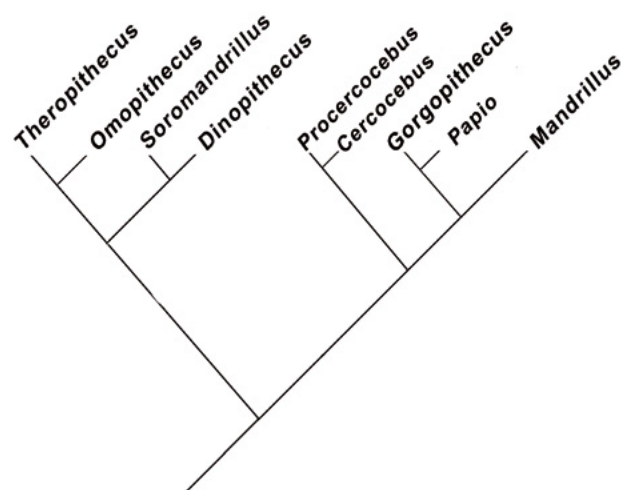
Within the context of the superfamily Cercopithecoidea, the molars of *Dinopithecus ingens* are the largest known from South Africa. First recorded from Schurweberg in the Transvaal, its fossil record (a mandible with nine cheek teeth and a crushed cranial fragment with three teeth) remained extremely scanty for two decades (1937–1957). Numerous fossils from Swartkrans were added to the species hypodigm

in 1957 and subsequently, but it is evident from the literature and from the fossils themselves that, apart from their dimensions, some of the Swartkrans fossils attributed to it do not resemble the holotype and paratype of the species. Indeed, L. Freedman wrote that the large dimensions of the upper molars of the Schurweberg specimen were due to crushing and expansion, with the unstated inference that the Swartkrans specimens are a more reliable guide to the dimensions and morphology of the upper teeth of the species than the fossils from the type locality are. It is clear from the subsequent literature that, for some researchers, the fossils from Swartkrans became the reference for determining the taxonomy and for analysing the phylogeny of the genus and species. One of the better preserved specimens from Swartkrans, a palate with both cheek tooth rows, that was added to the hypodigm in 1957, as a female of the species, played an important role in many subsequent papers that discussed the phylogeny of *Dinopithecus*. However, this specimen was removed from the genus in 2018, thereby radically altering the basis for all the phylogenetic analyses previously carried out on the taxon. But, even after removal of this specimen from the species, the phylogenetic position of *Dinopithecus* continued to remain unstable, probably due to the mixed nature of the hypodigms compiled by the researchers. In effect, they were endeavouring to determine the phylogenetic position of a chimaeric taxon.

Re-examination of the original fossils from Schurweberg, indicate that the molars in the crushed cranium were not radically altered by crushing or expansion, although they have lost small chips of enamel from some of the cusps. Thus, the dimensions of the teeth are reliable and they cannot be excluded from metric analyses as they have been for nearly seven decades. Furthermore, the upper and lower third molars are not deeply worn, such that the morphology of the cusps and crests can be reliably discerned. The conclusion of the study, based on the morphology of the teeth, is that *Dinopithecus* could be more closely related to geladas (genera *Theropithecus*,



Text-fig. 19. Stereo images of DNMNH KA 193, the holotype left M2/ and M3/ of *Gorgopithecus major* (BROOM, 1940) from Kromdraai, South Africa. a: lingual views, b: occlusal views, c: buccal views.



Text-fig. 20. Hypothesis of phylogenetic relationships between geladas (*Omopithecus*, *Theropithecus*, *Dinopithecus*, *Soromandrillus*), mangabeys (*Cercocebus*, *Procercocebus*), mandrills (*Mandrillus*) and baboons (*Papio*, *Gorgopithecus*) based largely on cheek tooth morphology. The positions of *Omopithecus*, *Soromandrillus*, *Dinopithecus* and *Gorgopithecus* are based on the type material, in order to avoid including chimaera in the phylogeny.



Text-fig. 21. Distribution of extant *Mandrillus* and *Cercocebus*, and fossils that in the literature have been interpreted to be related to extant mandrills (cf. *Mandrillus* sp. in Angola (Pickford and de Matos 2026), *Soromandrillus quadratiostris* in Ethiopia (Gilbert 2013; contested herein), *Dinopithecus* in South Africa (contested herein)). The distribution of extant mandrills and mangabeys is based on Dempsey et al. (2024).

Soromandrillus and *Omopithecus*) than to extant drills and mandrills (genus *Mandrillus*) and savannah baboons (genera *Papio*, *Parapapio* and *Gorgopithecus*), although, in a few features it approaches *Mandrillus*. If the latter scenario is correct, then the genus would have evolved its theropithecine-like dental features by convergence with geladas.

Implications of the study are that a fundamental revision of the southern African large ‘baboon-like’ cercopithecoids, including *Gorgopithecus major* and *Papio robinsoni*, is required, especially of the material from Swartkrans, and to a lesser extent that from Kromdraai.

Conclusions

Revision of the large South African cercopithecoid *Dinopithecus ingens*, based on the holotype and paratype from Schurweberg, indicate that it is possibly more closely related to extant geladas (*Theropithecus*) and to the extinct genera *Soromandrillus* and *Omopithecus*, than it is to mandrills (*Mandrillus*) or baboons (*Papio*, *Gorgopithecus*) (Text-fig. 20). Much of the material from Swartkrans and other sites in South Africa that was previously attributed to *Dinopithecus ingens*, belongs instead to other taxa of baboon-like monkeys, such as *Gorgopithecus major*, *Papio robinsoni* and less likely to *Theropithecus* spp.

The history of study of *Dinopithecus* reveals that dental characters tended to be marginalised by researchers in favour of osteological features, but because osteological features vary

greatly during ontogeny as well as a function of gender, the results of such studies have often proved to be contentious. They also vary as a function of life history – the skull of the holotype of *Papio rhodesiae* differs from other specimens of *Papio ursinus* because it developed unusual osteological features during captivity, that Haagner (1918) took to be of evolutionary and taxonomic value (Freedman 1954). The taxonomically mixed nature of the hypodigms of diverse authors who have written about *Dinopithecus ingens* put their cladistic analyses out of focus, which partly explains why the position of the genus in such analyses has remained unsettled (Gilbert 2013, Pugh and Gilbert 2018).

The possible co-existence at Schurweberg (or Hoogland) of *Dinopithecus ingens* and *Theropithecus oswaldi oswaldi* (Adams et al. 2010) suggests either that the breccia deposits could be younger than originally thought, possibly 1.4–0.4 Ma (Early to Middle Pleistocene), or that there are breccias of diverse ages present at the site. Further research is required to throw light on the matter.

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