# TAXONOMIC AND EVOLUTIONARY AFFINITIES OF *PAPIO IZODI* FOSSILS FROM TAUNG AND STERKFONTEIN

Jeffrey K. McKee

*Department of Anatomy and Human Biology, University of the Witwatersrand,*
*Medical School, 7 York Rd., Parktown, Johannesburg, 2193.*

## ABSTRACT

*Papio izodi* is an extinct papionin found at Taung and Sterkfontein. The taxonomic status of southern African fossils sometimes referred to *P. izodi* is clarified here in order to verify the existence of the species at Sterkfontein and define the morphological characteristics distinguishing it from *P. angusticeps*, a later species of similar size. *P. izodi* may be the earliest known species of the genus *Papio* in southern Africa, as the putative contemporary presence of the derived species *Papio hamadryas robinsoni* cannot be confirmed at Sterkfontein. *P. izodi* retains some of the primitive features found in *Parapapio broomi*, suggesting a close evolutionary link between the two species.

KEYWORDS: Cercopithecid taxonomy, faunal correlation, Taung, Sterkfontein.

## INTRODUCTION

*Papio izodi* is an extinct species of baboon named by Gear (1926) on the basis of fossil skulls from Taung cave deposits found near the type site of *Australopithecus africanus* (McKee 1993a). This Pliocene baboon species is among the earliest representatives of *Papio*, and perhaps the earliest member of the genus in southern Africa. It was thought to have been unique to Taung, but the taxonomic status of many early *Papio* fossils from other southern African Plio-Pleistocene fossil sites remains enigmatic (Eisenhart 1974; Szalay and Delson 1979; McKee 1991). Clarification of the taxonomic problems and assessment of the phylogenetic issues concerning the origins of the genus *Papio* are fundamental steps necessary for faunal dating and environmental reconstructions of the australopithecine fossil sites in which the extinct baboons are abundant representatives of the prehistoric faunal community.

A study of fossil cercopithecids from Sterkfontein by Eisenhart (1974) revealed a single cranium of an immature adult female (STS 262) which he felt was representative of *P. wellsi*, a taxon which has since been synonomised with *P. izodi* (Szalay and Delson 1979). STS 262, from Sterkfontein Member 4, had been referred to *Parapapio broomi* by Freedman (1957), but Eisenhart noted that the specimen possessed the distinct morphological features of *Papio*, within the range of *Papio* from Taung.

*Papio izodi* is well represented in the Hrdlička deposits at Taung, with additional specimens emanating from the recent excavations (McKee and Tobias 1990; McKee 1993a). As the complete Taung sample was not studied by Eisenhart (1974), and as *P. wellsi* has been synonomised with *P. izodi*, it becomes necessary to clarify the status of STS 262 within the current taxonomic

framework and to verify its assignment with the additional data.

If STS 262 can be confirmed as a representative of *P. izodi*, then an important link would be established between the fauna from Sterkfontein Member 4 and Taung as one of 20 species that the sites have in common (McKee 1993b). However, Szalay and Delson (1979) referred similar small baboon fossils from the younger sites of Kromdraai (KBE Member 3) and Cooper's to *P. izodi* that had previously been assigned to *P. angusticeps* (Broom 1940, 1946; Freedman 1957). In more recent publications, aimed at establishing a cercopithecid biochronology, Delson (1984, 1988) accepts the specific legitimacy of *P. angusticeps*. It is crucial to clarify the taxonomic status of the Kromdraai and Cooper's small baboons for purposes of faunal dating and phylogenetic reconstructions of the baboons.

Origins of the genus *Papio*, and faunal correlations of southern African cave sites, are even more problematical due to the questionable identification of a much larger baboon species from Sterkfontein Member 4. This large species was originally known as *P. robinsoni* (Freedman 1957), and was recognized from the later sites of Kromdraai, Cooper's and Swartkrans. Eisenhart (1974) argued that some of the Sterkfontein specimens which Freedman (1957) had referred to *Parapapio whitei* showed characteristics of *Papio robinsoni*. Szalay and Delson (1979) agreed with Eisenhart that this taxon, which they saw as a subspecies of *P. hamadryas*, was represented in the Sterkfontein material. Thus Sterkfontein Member 4 is thought to have five species of baboon, including three species of *Parapapio* (*P. whitei*, *P. broomi* and *P. jonesi*) and two species of *Papio* (*P. izodi* and *P.h. robinsoni*). As Sterkfontein and Taung are the earliest known African sites to have yielded specifically identifiable *Papio*, the

baboon fossils from these sites may give clues to the evolutionary origin of the genus, provided that the taxonomic referrals are beyond a reasonable doubt.

Ecological constraints on the number of similarly sized and similarly adapted species has led a number of authors to doubt the probability of five contemporaneous species having existed at Sterkfontein (Freedman 1976; Eisenhart 1974; McKee 1991). Either the environmental parameters are unique or the taxonomic referrals are incorrect. Part of this problem may be resolved with an examination of the fossils referred to *Papio*, demarcation of the diagnostic characteristics of taxa, and an assessment of the evolutionary origins of the genus.

Verification of the taxonomic and evolutionary affinities of fossils referred to *P. izodi* requires an assessment of three key issues: 1) Does *P. izodi* exist in the Sterkfontein Member 4 fossil deposits, as represented by STS 262; 2) what are the definitive morphological differences between *P. izodi* fossils and the similarly sized papionins found at Kromdraai and Cooper's sometimes referred to *P. angusticeps*; and 3) are there two species of the genus *Papio* represented in Sterkfontein Member 4?

## MATERIALS AND METHODS

Odontometric and craniometric variables were compiled into a data base of measurements from published descriptions of fossil baboons (Freedman 1957, 1961, 1962 1976; Freedman and Brain 1972; Eisenhart 1974), as well as from the author's own measurements of the material. The reference sample for this assessment includes 12 *Papio izodi* crania from Taung and 28 *Papio angusticeps* crania from Kromdraai

### TABLE 1

**Cranial Measurements**

GL-IDS Glabella to Alveolare (infradentale superius)
IDS-NA Alveolare to Nasion
IDS-PNS Alveolare to Post-nasal Spine
MAXTEMP Maximum Temporal Breadth
INTORB Inter-orbital Breadth (minimum)
INTFRBR Inter-frontal Breadth (minimum breadth posterior to supraorbital tori)
NAPL Nasal Aperture Length
NAPB Nasal Aperture Breadth
MBM2M Maximum Breadth of Maxilla at Mesial loph of $M^2$
PBM2M Palatal Breadth at Mesial Loph of $M^2$
PBM2D Palatal Breadth at Distal Loph of $M^2$
BA-BREG Cranial Height from Basion to Bregma
ORBHT Orbit Height (maximum)
ORBBR Orbit Breadth (maximum)
MHM2M Maxillary Height at Mesial Loph of $M^2$

**Dental Measurements** (Maxillary)

P3B $P^3$ breadth
M1L $M^1$ length
M1MB $M^1$ breadth, mesial loph
M1DB $M^1$ breadth, distal loph
M2L $M^2$ length
M2MB $M^2$ breadth, mesial loph
M2DB $M^2$ breadth, distal loph

(A and B) and Cooper's. These were used for comparisons with STS 262.

Limitations of the data set and the fossil record led to the exclusion of many possible measurements. The excluded variables were not found to be useful in distinguishing the species in question, or were of an insufficient sample size for analysis. Data on mandibles were excluded as few could be reliably associated with the skulls that show taxonomically diagnostic features.

Variables used in this analysis are listed and briefly described in Table 1; complete descriptions of the methods used in measuring can be found in Freedman (1957) and Eisenhart (1974). The data presented on bilateral traits are the means of the left and right sides where both sides were present, or are derived from unilaterally preserved structures. Some measurements are estimated for cases in which slight damage (e.g. a missing flake of enamel or bone) still allows for a reasonable approximation to be made.

Evaluations of the similarities and differences among species measurements were done on the basis of known ranges. Difference of sample ranges beyond that which one would expect on the basis of intraspecific variations within modern baboons were deemed to be biologically significant. As sample sizes were very small, no statistical tests for significant differences were possible.

Definitive non-metric morphological traits were also observed in the fossils to supplement the data base, as described in the text below. The reference sample for these observations included crania as cited above, as well as crania referred to *Parapapio whitei*, *Parapapio broomi*, and *Papio robinsoni* by Freedman (1957, 1960, 1961, 1962, 1976) and Eisenhart (1974) for comparisons with the Sterkfontein fossils SWP 31 and SWP 3076.

## COMPARATIVE ANALYSIS OF THE FOSSIL DATA

### Taxonomic Affinities of STS 262

Observations of STS 262 show it to be a well-preserved partial cranium of an immature adult female (Figure 1A). It consists of most of the calvarium, missing only the occipital region, and a fairly complete face with damage to the zygomatic arches and lateral orbits. The left $P^3$ is preserved; the $M^1$ and $M^2$ on each side are present, although some enamel has flaked off. Neither $M^3$ had erupted before death.

Nearly all of the features of STS 262 fit within range of size and morphology of *Parapapio broomi*, hence its referral to that taxon by Freedman (1957). Eisenhart (1974: 529) listed four convincing characteristics distinguishing the specimen from *Parapapio*: "1) the large size of the glabella region 2) the steep interorbital drop on the nasals 3) the deep ophryonic groove, and 4) the rise of the calvarial roof posterior to the ophryonic depression". This suite of characteristics is well defined on the better preserved *Papio* crania from Taung, whereas *Parapapio broomi* from Sterkfontein and Makapansgat
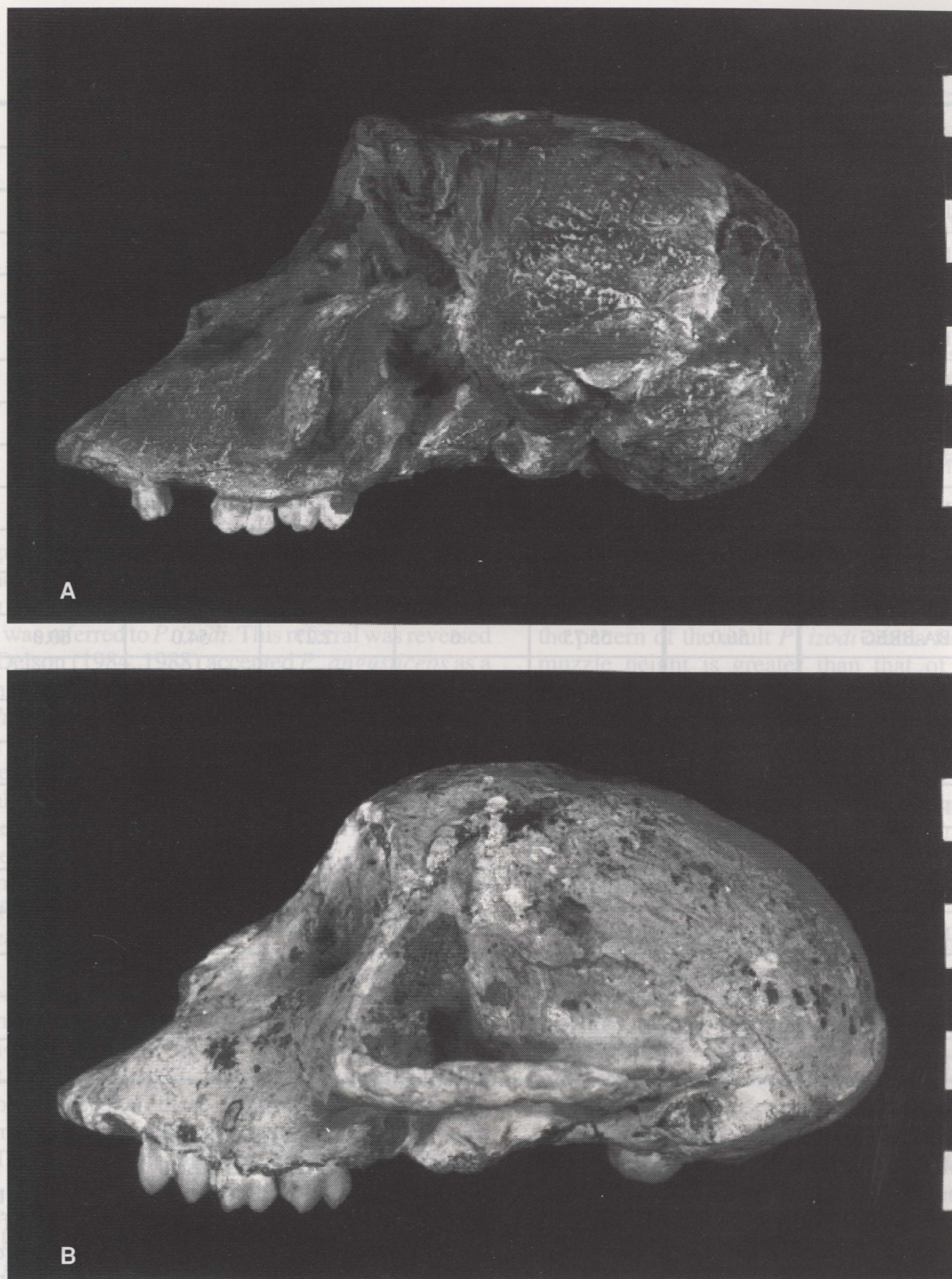
Figure 1. A) STS 262, immature adult *Papio izodi*. B) MP 224, immature adult *Parapapio broomi*. (Scale in centimetres)

never exhibit the steep anteorbital (interorbital) drop of the nasal bone profile or the deep ophryonic groove. The differences are illustrated in Figure 1, which shows STS 262 as compared to a *Parapapio broomi* cranium of a similarly aged individual (MP 224 from Makapansgat).

STS 262 was referred to *P. wellsi* by Eisenhart (1974), a species named by Freedman (1961) on the basis of four specimens from Taung. *P. wellsi* has since been appropriately synonomised with *P. izodi* on the basis of intraspecific variability recognized with an increased sample size (Szalay and Delson 1979). The metric traits of the specimen are compared to the means and ranges of the female sample from Taung in Table 2. Measurements of STS 262 are clearly within or near the known range of the Taung female *Papio* sample for nearly every characteristic for which data are available. Only the

## Table 2

### Measurements of STS 262 compared to female *Papio izodi* from Taung.

|  | STS 262 | Mean | N | Std | Min | Max |
|---|---|---|---|---|---|---|
| GL-IDS | 71.9 | 80.70 | 1 |  | 80.7 | 80.7 |
| IDS-NA | 55.8 | 74.25 | 4 | 9.67 | 67.0 | 88.0 |
| IDS-PNS | 55.8 | 59.23 | 3 | 1.37 | 58.0 | 60.7 |
| MAXTEMP | 68.0 | 69.62 | 6 | 3.58 | 65.0 | 72.0 |
| INTORB | 9.0 | 9.46 | 5 | 1.33 | 7.7 | 10.8 |
| INTFRBR | 51.0 | 51.85 | 4 | 0.60 | 51.0 | 52.4 |
| NAPL | 25.0 | 23.73 | 3 | 1.33 | 22.2 | 24.5 |
| NAPB | 14.0 | 16.12 | 5 | 0.72 | 15.5 | 16.9 |
| MBM2M | 47.9 | 46.0 | 1 |  | 46.0 | 46.0 |
| PBM2M | 20.0 | 20.1 | 1 |  | 20.1 | 20.1 |
| PBM2D | 20.4 | 20.4 | 1 |  | 20.4 | 20.4 |
| BA-BREG | 56.0 | 55.75 | 6 | 2.27 | 54.0 | 60.0 |
| ORBHT | 25.75 | 24.32 | 3 | 2.97 | 22.6 | 27.75 |
| ORBBR | 27.75 | 26.47 | 3 | 1.50 | 25.6 | 28.20 |
| MHM2M | 36.0 | 35.13 | 2 | 1.24 | 34.35 | 36.0 |
| P3B | 7.1 | 6.7 | 1 |  | 6.7 | 6.7 |
| M1L | 10.45 | 10.1 | 2 | 0.57 | 9.7 | 10.5 |
| M1MB | 10.1 | 9.5 | 1 |  | 9.5 | 9.5 |
| M1 DB | 9.1 | 9.25 | 2 | 0.21 | 9.1 | 9.4 |
| M2L | 11.7 | 11.52 | 5 | 0.61 | 10.6 | 12.0 |
| M2MB | 10.75 | 10.43 | 3 | 0.67 | 10.0 | 11.2 |
| M2DB | 9.85 | 9.43 | 3 | 0.67 | 9.0 | 10.2 |

measurements of muzzle length (IDS-NA, IDS-PNS) are low, probably because STS 262 is an immature adult in which the muzzle would have been expected to lengthen with the eruption of the $M^3$. Thus the metric traits support the referral of STS 262 to *P. izodi*.

A survey of available baboon fossils from Sterkfontein Member 4 did not reveal any further specimens that can be referred to *P. izodi* with any confidence. Although many specimens have dental dimensions that fit within the range of *P. izodi*, the key morphological features that would distinguish the faces from the similarly sized *Parapapio broomi* have not been preserved. In this light, it is significant that only the anteorbital drop of the nasal bone profile and the developed supra-orbital torus clearly distinguish *Papio izodi* crania from those of *Parapapio broomi*, suggesting close evolutionary affinities (McKee 1992).

## The status of *Papio angusticeps*

Morphological and metrical assessment of STS 262 makes it very clear that the cranium belongs to the genus *Papio* and that it fits neatly within the range of *P. izodi*. However, another taxon known as *P. angusticeps* also encompasses STS 262 within the general size range of the species. In order to assess the possibility of referring STS 262 to *P. angusticeps*, one must first determine whether or not *P. angusticeps* is a distinct species from *P. izodi*.

Early forms of *Papio* from Kromdraai were first described by Broom (1940) and named *Parapapio angusticeps*. Freedman (1957) provided a complete description of the species, and referred it to the genus *Papio*, largely on the basis of its muzzle profile which exhibits a steep anteorbital drop of the nasal bones.

*Papio angusticeps* has since been through a confusing taxonomic history. Initially, Delson (1975) was unable to

## Table 3

### Maxillary and Cranial Heights of *P. angusticeps* and *P. izodi*

| | *Papio angusticeps* | | | | | *Papio izodi* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Variable | Mean | N | Std | Max | Min | Mean | N | Std | Max | Min |
| MHM2M (Female) | 31.25 | 2 | 0.35 | 31.0 | 31.5 | 35.42 | 3 | 1.01 | 34.25 | 36.0 |
| BA-BREG (Female) | 62.5 | 2 | 0.71 | 62.0 | 63.0 | 55.79 | 7 | 2.08 | 54.0 | 60.0 |
| MHM2M (Male) | 41.0 | 1 | | 41.0 | 41.0 | 41.75 | 2 | 1.77 | 40.5 | 43.0 |
| BA-BREG (Male) | 65.7 | 1 | | 65.7 | 65.7 | 62.0 | 1 | | 62.0 | 62.0 |

distinguish *P. angusticeps* fossils from those of *P. izodi*. This notion was elaborated on in Szalay and Delson (1979) and all small early *Papio* material from southern Africa was referred to *P. izodi*. This referral was reversed when Delson (1984, 1988) accepted *P. angusticeps* as a legitimate species, closer to *P. hamadryas kindae* than to *P. izodi*. Delson (1988) noted that *P. izodi* had a relatively shorter and broader snout as well as larger teeth and orbits relative to *P. angusticeps*.

Analysis of the dentition of *P. izodi* and *P. angusticeps* is difficult, for the metric data are not sufficient to make any clear distinction between the taxa on tooth size. Certainly, however, the dentitions of the small baboon crania from Kromdraai and Cooper's are generally similar to *P. izodi* from Taung in size.

The craniofacial characteristics of *P. izodi* and *P. angusticeps* warrant consideration in taxonomic assessments and may have implications for the respective evolutionary affinities of the taxa. Delson (1988) is correct that the snout of *P. izodi* is relatively broader and the orbits larger than those referred to *P. angusticeps*. Furthermore, the muzzle height of the *P. izodi* specimens from Taung is greater than that of the *P. angusticeps* fossils, whereas the cranial height (basion-bregma) is greater in the latter than in the former sample (Table 3).[1] The relation of the muzzle height to the cranial height allies *P. izodi* much more closely with the genus *Parapapio*, especially *P. broomi*.

Hence *Papio angusticeps* seems to be a legitimate taxon. Although it is in the size range of *P. izodi*, its facial morphology is much closer to that of *P. h. robinsoni*, a somewhat larger species of baboon. *P. angusticeps* and *P. h. robinsoni* share the following characteristics that distinguish them from *P. izodi*: low muzzle height/cranial height ratio, deep maxillary fossae, relatively small orbits,

and long muzzles with straight and parallel post-canine tooth rows.

Although STS 262 is an immature adult female, it fits the pattern of the adult *P. izodi* crania from Taung. Its muzzle height is greater than that of adult female *P. angusticeps*, whereas its estimated cranial height is well within the range of adult *P. izodi*. Judging from data presented by Freedman (1957) on *P. ursinus* at different ages, these dimensions would not be expected to change much with continued growth and eruption of the $M^3$, at least not to the sizes known for *P. angusticeps*.

### On the Putative Presence of Two *Papio* Species at Sterkfontein

Sterkfontein Member 4, like Makapansgat, has yielded three types of *Parapapio*, which many have accepted as three species, the largest of which is *Parapapio whitei*. Eisenhart (1974) referred a number of fossil specimens from Sterkfontein Member 4 to *Papio robinsoni*, a species known from the later sites of Swartkrans, Kromdraai and Cooper's. Some of Eisenhart's specimens had previously been identified by Freedman (1957) and Freedman and Stenhouse (1972) as *Parapapio whitei*. If Eisenhart were correct, then there would be five species of baboon represented within one deposit at Sterkfontein, two of which belong to the genus *Papio*.

Delson accepts Eisenhart's referral, but views "*P. robinsoni*" as a subspecies of *P. hamadryas*, i.e. *Papio hamadryas robinsoni* (Szalay and Delson 1979). There were three specimens in particular identified in the Sterkfontein fossils as *P. h. robinsoni* which Eisenhart (1974: 507) felt were "convincing", including SWP 31, SWP 35[2] and STS 3076. Other fossils, such as STS 263/370B were added on the basis of tooth size. The following key characteristics of these specimens, however, fail to

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[1] On the basis of the relative heights of the muzzle and cranium, a fossil cranium recovered in 1947 by P.V. Tobias from Gladysvale, (a cave site near Sterkfontein), also has strong affinities to *P. izodi*

[2] SWP 35, a single $P^4$ in a left maxillary fragment, cannot be located.

Figure 2. Maxilla of adult male SWP 31 showing shallow maxillary fossa. (Scale in centimetres)

differentiate them from *Parapapio whitei*.

In SWP 31 (Figure 2), a fragmentary maxilla, Eisenhart claims to have noted deep maxillary fossae. On the contrary, this male specimen has a very slight maxillary fossa within the range of *Parapapio whitei*. Adult male *Papio hamadryas robinsoni* invariably have deep maxillary fossae that are excavated under the maxillary crests and back into the roots of the zygomatic arches, a trait that is not present in SWP 31. Likewise, the female STS263/370B has no maxillary fossa, again suggestive of affinities with *Parapapio whitei*.

Dental measurements of the fossils that Eisenhart thought were *Papio h. robinsoni* fall within the size ranges of known *P. h. robinsoni* as well as *Parapapio whitei*. Morphologically, however, the molars are much



Figure 3. Comparison of crown shapes ($M^2$ distal loph, coronal section) of A) *Papio hamadryas robinsoni*, and B) *Parapapio whitei*.

more similar to *P. whitei*. The molar lophs of *P. whitei* have a characteristic flair from the cusps to the cemento-enamel junction. Thus the intercuspal distance is small, and the maximum breadth is greatest at the cemento-enamel junction, giving the molars a 'W'-shaped outline (Figure 3b). This shape is found in all of the well-preserved maxillary molars listed by Eisenhart (1974) as being *Papio robinsoni*, such as STS 263/370B. *P. h. robinsoni* teeth, however, have a different shape due to the greater intercuspal distance and the more vertical buccal and lingual sides (Figure 3a).

Honest taxonomic assessment of a final specimen, STS 3076, is problematical. This calvarium has the distinct characteristics of *Papio*, including well-developed supraorbital tori, a pronounced glabella, and steep anteorbital drop of the nasal bone profile (Eisenhart, 1974). Its pronounced nuchal crest and large size is suggestive of affinities with *P. h. robinsoni*. The maximum bi-temporal breadth is recorded by Eisenhart (1974) as 75.6 mm. However, this breadth is only 3.8 mm greater than the largest known male *P. izodi* from Taung (T89-11-1, with a bi-temporal breadth of 71.8 mm). Moreover, the left side of the STS 3076 cranium is considerably distorted from compression; the breadth of the right half from the sagittal suture is approximately 35 mm, meaning that the total breadth could be estimated at 70 mm, well within the range of known *P. izodi*. Thus only the pronounced nuchal crest looks more like *P. h. robinsoni* than *P. izodi*, and this may also be due, in part, to distortion. In the absence of any other defining criteria or associated fossils, it would be more prudent to defer judgement on the specific referral of the specimen.
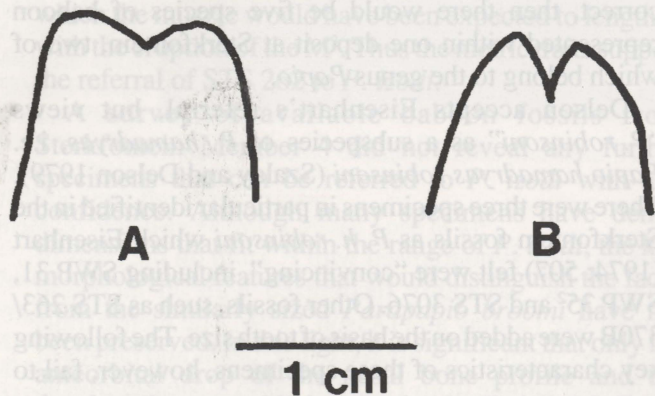
## CONCLUSIONS

Observations on the definitive characteristics of *Papio izodi* from Taung have led to the confirmation of the presence of the species in Sterkfontein Member 4. This allows the species to be used in faunal associations of the two Pliocene sites, especially because *P. izodi* is distinguishable from *P. angusticeps*, a similarly sized species that is known from the later sites of Kromdraai and Cooper's.

*Papio izodi* appears to be the earliest recognized representative of its genus, as the putative presence of *P. hamadryas robinsoni* from Sterkfontein Member 4 cannot be verified. In this light, Delson's (1984, 1988) cercopithecid biochronology may be in need of revision as follows. The *A. africanus* sites of Sterkfontein and Taung are clearly distinguished on the basis of the primitive forms of baboon, *Parapapio* and *Papio izodi*, whereas only the later sites such as Kromdraai, Coopers's and Swartkrans have *Papio hamadryas robinsoni* and *Papio angusticeps*, species which are more similar to the extant baboons of southern Africa.

Origins of the genus *Papio* remain debatable, but the morphological similarities between *Papio izodi* and *Parapapio broomi* may suggest a close evolutionary relationship. Both species are known from deposits at Taung and Sterkfontein, and both share most features of size and morphology, including the greater muzzle height relative to a low cranial vault. All species of *Papio* can be distinguished from *Parapapio* by the presence of a steep anteorbital drop of the nasal bone profile and a well developed supraorbital torus, traits which seem to have their origin in *Papio izodi*.

## REFERENCES

BROOM, R. 1940. The South African Pleistocene cercopithecid apes. *Ann. Transvaal Mus.,* **20**, 89-100.

DELSON, E. 1975. Evolutionary history of the Cercopithecidae. **In:** Szalay, F.S., Ed., *Approaches to Primate Paleobiology. Contributions to Primatology: Vol. 5*, 167-217. Basel, Karger.

------ 1984. Cercopithecid biochronology of the African Plio-Pleistocene: Correlation among eastern and southern hominid-bearing localities. *Cour. Forsch. Inst. Senckenberg* **69**, 199-218.

------ 1988. Chronology of South African australopith site units. **In:** Grine,F.E.,Ed.,*Evolutionary History of the "Robust" Australopithecines*, 317-324. New York, Aldine de Gruyter.

EISENHART, W.L. 1974. *Fossil cercopithecoids of Makapansgat and Sterkfontein*. Unpublished BA thesis, Harvard University.

FREEDMAN, L. 1957. The fossil cercopithecoidea of South Africa. *Ann. Transvaal Mus.,* **23**(2), 122-262.

------ 1961. New cercopithecoid fossils, including a new species, from Taung, Cape Province, South Africa. *Ann. S. Afr. Mus.,* **46**(1), 1-14.

------ 1962. Fossil and subfossil primates from the limestone deposits at Taung, Bolt's Farm, and Witkrans, South Africa. *Palaeont. Afr.,* **9**, 19-48.

------ 1976. South African fossil cercopithecoidea: A reassessment including description of new material from Makapansgat, Sterkfontein and Taung. *J. Hum. Evol.,* **5**, 297-315.

------ & BRAIN, C.K. 1972. Fossil cercopithecoid remains from the Kromdraai australopithecine site (Mammalia: cercopithecidae). *Ann. Transv. Mus.,* **30**, 211-218.

------ & STENHOUSE, N.S. 1972. The *Parapapio* species of Sterkfontein, Transvaal, South Africa. *Palaeont. Afr.,* **14**, 93-111.

GEAR, J.H.S. 1926. A preliminary account of baboon remains from Taungs. *S. Afr. J. Sci.,* **23**, 731-747.

MCKEE, J.K. 1991. Palaeo-ecology of the Sterkfontein hominids: a review and synthesis. *Palaeont. afr.,* **28**, 41-51.

------ 1992. The southern African origin of the genus *Papio*. *S. Afr. J. Med.,* **82**, 193.

------ 1993a. Formation and geomorphology of caves in calcareous tufas and implications for the study of Taung fossil deposits. *Trans. Roy. Soc. S. Afr.,* **48**, in press.

------ 1993b. Faunal dating of the Taung hominid fossil deposit. *J. Hum. Evo.,* in press.

------ & TOBIAS, P.V. 1990. New Fieldwork at the Taung Hominid Site: 1988-1989. *Am. J. Phys. Anthropol.,* **81**(2), 266-267.

SZALAY, F.S. & DELSON, E. 1979. *Evolutionary History of the Primates*. New York, Academic Press.