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Chronology of South African Australopith
Site Units

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Important refinements of the Turkana Basin chronology have recently been presented by Frank Brown and colleagues (Brown *et al.*, 1985; Brown and Feibel, 1986; this volume, chapter 22; Feibel *et al.*, 1988; Harris *et al.*, 1988). These have led to several minor changes in the ages of South African site units I correlated to that sequence, based on the distribution patterns of cercopithecoid monkeys (Delson, 1984). Moreover, through the courtesy of C. K. Brain, I have been able to examine the new sample of cercopithecoid fossils from Members 1 through 3 of the Swartkrans deposits (see Brain, this volume, chapter 20), which permits comments on the relative ages of these Members. In addition, as the result of discussions at the Stony Brook workshop on which this volume is based, some comments can be offered on the relative ages of Swartkrans and Kromdraai and on environmental indications suggested by the monkeys.

Cercopithecoid Fossils from South and East African Site Units

In 1984, I presented a table of taxa known from 17 site units (individual localities or Members or horizons of longer sequences). The data are unchanged for the majority of these units. I have not seen any of the newer material from Sterkfontein or Makapansgat—unfortunately, the sample from undoubted Sterkfontein Member 5 (ST 5) levels remains too minimal to identify, but specimens from ST 1 through 3 will be of great interest. New data provide additional information for several sets of units, while for others only minor clarification is necessary.

Taung

My study of the entire Taung sample is still incomplete, but I continue to infer that the small *Papio* from Taung and ST 4 is a distinct species *Papio izodi*, while the comparably sized population (*P. angusticeps*) known best from Kromdraai and the nearby Cooper's A (COA) site is morphologically and probably taxonomically closer to the living *P. hamadryas kindae* (see Fig. 21.1). About 120 Taung cercopithecoids are now known from the following collections: University of the Witwatersrand Anatomy Department (20), Bernard Price Institute (2), South African Museum (18), Transvaal Museum (29) and the University of California Museum of Paleontology (50, but some matrix is unprepared). Of these, three partial maxillae (all from the Transvaal Museum) are referred to a small cercopithecine, cf. *Cercocebus* or *Parapapio*; 25 crania and mandibles are allocated with reasonable certainty to *Parapapio antiquus*; 20 crania and jaws are identified as *Papio izodi* and the remainder (partial jaws, juvenile crania, neurocrania, endocasts, and post-cranial elements) are as yet unallocated to taxon. The presence of the two common papionins in roughly equal numbers and in both types of matrix discerned in the Berkeley collection suggests that they were contemporaries throughout the span of time represented at Taung.

Swartkrans

Four taxa are well represented in the "Hanging Remnant" of Swartkrans Member 1 (SK 1): *Papio hamadryas robinsoni* (over 100 specimens), *Papio (Dinopithecus) ingens* (48 specimens),

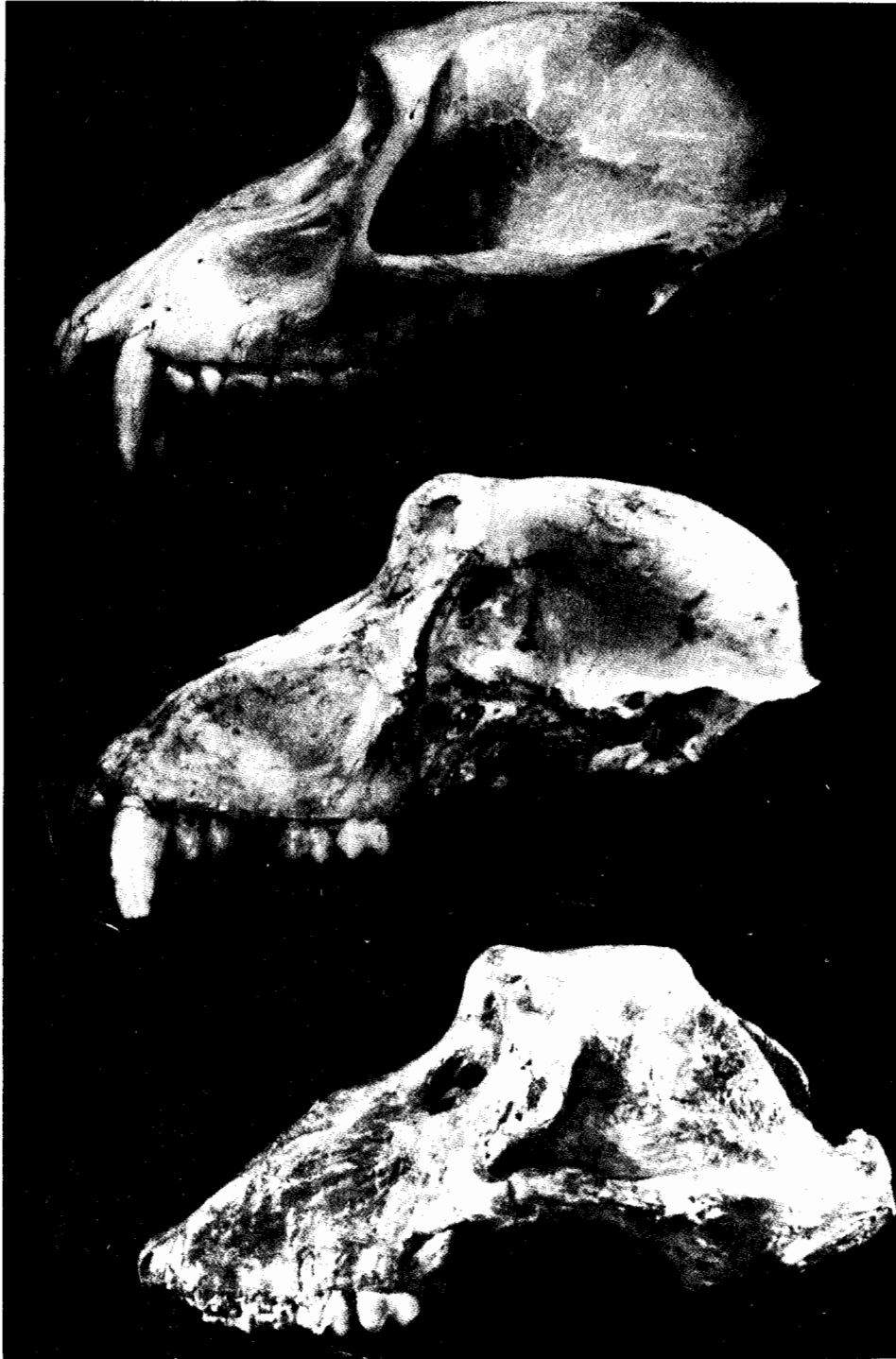


FIGURE 21.1. Left lateral view of three male *Papio* crania, oriented in the occlusal plane and to scale (about two-thirds natural size). Top: modern *P. hamadryas kindae* from Angola; center: *P. angusticeps* from Cooper's A, latest Pliocene?; bottom: *P. izodi* from Taung, late Pliocene. The relatively shorter (and broader) snout and larger teeth and orbits of *P. izodi* suggest it to be distinct from *P. angusticeps*, which may, in fact, best be included within *P. hamadryas*.

Theropithecus oswaldi (25 specimens), and cf. *Cercocebus* sp. (17 specimens). The number of specimens represents identifications of measurable fossils in 1981 and is meant to serve only as a guide to approximate frequency; further analysis is needed to estimate the more meaningful minimum number of individuals. These numbers differ from those of Brain (1981) due to his inclusion of more fragmentary and questionably identifiable fossils, separation of some numbered pieces that fit together, and minor differences in allocation. A "large variant" of *Cercopithecoides williamsi* (4 or 5 specimens, previously termed *C. molletti*) occurs in the Swartkrans deposits, and Brain (pers. comm.) has suggested they may have come from what he then termed Member 2 (but see below). A few specimens comparable to modern *Papio hamadryas ursinus* may be of similar provenance. One crushed palate was identified by Clarke (pers. comm.) as cf. *Gorgopithecus major* on the basis of an apparently large maxillary fossa, and although this specimen is probably correctly allocated, it could have been mislabeled as to origin.

In a sample of several hundred specimens Brain has collected from the Lower Bank of Member 1, as well as Members 2 through 3, only two taxa appear to be present. The great majority of identifiable remains from all three units may be allocated to *P. hamadryas robinsoni*. Several specimens from each of Members 1, 2 and 3 seem to be identical to the *T. oswaldi* material known from the "Hanging Remnant"; they are mostly quite fragmentary, but one partial maxilla is known from Member 2. The lack of any colobine specimens even potentially identifiable as *C. williamsi* and the identity of known taxa from the new and old samples suggest to me that Swartkrans Members 1 through 3 may be more similar in age than Brain (this volume, chapter 20) has inferred. The apparent lack of *P. (Dinopithecus) ingens* in the new sample is surprising, as it is somewhat more common than *Theropithecus* in the "Hanging Remnant"; the smaller papionins *P. angusticeps* and cf. *Cercocebus* sp. also seem absent, but metrical analysis of the dental remains might indicate their rare presence. Perhaps the "Hanging Remnant" is slightly older than the Lower Bank or at least samples a time interval when neither *Papio (Dinopithecus)* nor cf. *Cercocebus* inhabited the Swartkrans area (or died there). On the other hand, if any of Members 1 through 3 were younger than the "Hanging Remnant," I would have expected them to yield the large *C. williamsi*, *P. angusticeps* and/or *Gorgopithecus*, as found at the Kromdraai and Cooper's site units. This may have further implications for the relative age of these units (see below).

West Turkana

Harris *et al.* (1988) have recently presented a summary of the mammalian faunas from the Nachukui Formation on the west side of Lake Turkana. They divided the collection into nine assemblages spanning approximately the 4- to 1-Myr interval. Their tabulated distribution of taxa reveals that no primates at all have yet been collected from the Lokalalei Member, equivalent to Omo Shungura D and E. The Kalochoro Member, equivalent to Shungura F, G and lowermost H (up to the KBS = H2 Tuff level), has yielded only a fragment attributed to *Homo habilis* and a few *Theropithecus oswaldi* specimens (J. M. Harris, pers. comm.). This interval (D through G) is among the most productive of monkeys at Omo, representing my African Cercopithecoid (AC) Zones 3 (upper) through 5. The rarity of both hominid and cercopithecoid material from this interval in the Nachukui Formation is disappointing. It is a time about which more needs to be known. I look forward to further remains from at least the more fossiliferous Kalochoro Member and also to more details on the *Parapapio* material reported from levels in the Lomekwi Member.

Relative Dating and Chronometric Calibration

Taung

The studies by Brown and colleagues have provided a recalibration of the middle part of the Shungura Formation, which results in some differences in the estimated ages of my Zones AC 3 through AC 5. Figure 21.2 indicates the probable placement of those zones and several South African site units in the 2.5 to 2.0 Myr range. Perhaps the most interesting change from my

of *P. humadryas robinsoni* might be intrusive. These specimens were first identified by Eisenhart (1974), and although they are based on fragments from dumps, they appear secure. They are the oldest South African members of the genus, however, and among the oldest in all of Africa (in part depending on the age and generic allocation of *Papio baringensis*).

Kromdraai and Swartkrans

The two sets of site units most relevant to this volume, and about which dating is perhaps least certain, are Swartkrans (Members 1 through 3) and Kromdraai (especially B East, Member 3, but also Kromdraai A and Cooper's A). There is almost no taxonomic overlap among the cercopithecids between the Swartkrans and Kromdraai/Cooper's groups (see Table 21.1). As indicated above, four taxa are known from the SK 1 "Hanging Remnant" (SK 1 "HR"): *P. h. robinsoni*, *T. oswaldi*, *P. (D.) ingens* and cf. *Cercocebus* sp., and a fifth, *G. major*, may also be present but rare. Only the first two are known also in the samples recently excavated by Brain from SK 1 through 3 (not included in the table), and *Theropithecus* is very rare. The Kromdraai A (KA) ("faunal site") assemblage includes about 29 *P. angusticeps*; 2-plus *P. h. robinsoni*; another 13 specimens for which allocation is to either *P. angusticeps* or perhaps *P. h. robinsoni*, 21 *G. major*, and 1 jaw with an M₁ of *Cercocebus* sp. The Kromdraai B, Member 3 East (KBE) ("hominid site") excavations by Vrba have produced an assemblage only slightly different from Brain's previously recovered (KB) sample which crosscut the layers distinguished by Vrba. *Papio angusticeps* and *P. h. robinsoni* are probably both present, with the former predominant; *G. major* is rare; and *C. williamsi* ("large variant") is common. The small sample from nearby Cooper's A (COA) has a few specimens of each of the last two taxa and perhaps a dozen each of the two *Papio* species, but as at KA, no hominid fossils have yet been found.

Of these site units, SK 1 "HR" and KA are the most distinctive; each has unique taxa in some quantity, and they share only rare specimens of each other's most common elements. The KB (including KBE) and COA units are linked by the large *C. williamsi*, but they share some features of each of the two previous units as well. All are clearly younger than AC 4 (meaning Taung and Bolt's Farm in South Africa) due to their lack of *Parapapio*. In 1984, I suggested that this pattern led to the sequence SK 1 ("HR"); KB(E); ?COA; KA. Swartkrans was linked to the older ST 4 assemblage (AC 3 upper) by *P. h. robinsoni*, and to Shungura C through G by *Papio (Dinopithecus)* (albeit a different species). But it was placed in the younger AC 5 Zone due to the presence of *T. oswaldi* (without any earlier *Theropithecus*) and *Cercocebus* (rather than *Parapapio*). The large *Cercopithecoides* and unique *Gorgopithecus* were said to imply a still younger

Table 21.1. Estimated Number of Cercopithecoid Specimens by Taxon for Swartkrans and Kromdraai Site Units

Site unit ^a	Taxon ^b							
	Pa	Phr	Pa/Phr	P(D)i	Gm	To	Csp	Cw(L)
KA	29	2+	13		21		1	
KB	7		14		2			15
KBE			33		2			30
COA	16	10	?		3			2
SK1 "HR"		100+		48	1?	25	17	

^aKA = Broom's original sample from the Kromdraai "faunal site" assemblage; KB = Brain's excavated sample, which crosscut layers discerned in Vrba's later work; KBE = sample from Kromdraai B East of Vrba (Member 3); COA = Cooper's A site; SK 1 "HR" = Swartkrans Member 1 "Hanging Remnant" collection, not including newer collections.

^bPa = *Papio angusticeps*; Phr = *Papio humadryas robinsoni*; Pa/Phr, allocation to preceding taxa uncertain; P(D)i = *Papio (Dinopithecus) ingens*; Gm = *Gorgopithecus major*; To = *Theropithecus oswaldi*; Csp = cf. *Cercocebus* sp.; Cw(L) = *Cercopithecoides williamsi* ("large variant").

age for KB and especially KA, in part because the former taxon also occurred in what was then called SK Member 2.

These interpretations are less secure today, however. If, as noted above, *P. h. robinsoni* is potentially "intrusive" in ST 4, there is little to determine which of the three sites (SK 1 "HR", KA or KB) is the oldest. If KB were older, as suggested by Grine (1982) and followed by Vrba (1982; Vrba and Panagos, 1983) on the basis of the stage of evolution of the australopiths, this would appear to imply discontinuities in the distribution of the Swartkrans taxa *Papio* (*Dinopithecus*) (known at Omo through AC 4 only), *Cercopithecoides* ("typical" form known in AC 3 and in AC 4 at Bolt's), and perhaps *P. h. robinsoni* (known in AC 4 at Bolt's Farm). The first taxon is known only from SK 1 "HR" and does suggest greater age. The provenance of the Swartkrans specimens of *Cercopithecoides* is now unclear, so that its implication for relative age is cast into question. *Papio h. robinsoni* is widespread, but its relative frequency compared to *P. angusticeps* may be important. If this decreases over time, it suggests that Swartkrans is early, but if variation is random, there is obviously no biochronological value in the relative frequency of *P. h. robinsoni*.

Vrba and I now agree that there is no clear indication as to whether KBE is older or younger than SK 1 "HR". However, Vrba (e.g., 1982) has argued that KA is younger than KB from bovid evidence. Although the monkeys do not confirm or reject that hypothesis, I do think that KB and COA are likely to be intermediate in age between KA and SK 1 "HR". Combining these two rather weak views leads me to support my 1984 sequence, but with far less certainty (Fig. 21.2). Overall, I agree with Vrba (1982) and others that these site units probably are between 1.9 and 1.65 Myr old, that is, in the latest Pliocene.

It further appears to me that the consistent nature of the cercopithecoid and hominid sample from Brain's new SK 1 and SK 2 levels contradicts the view that a long time may have elapsed between them. If Brain (this volume, chapter 20) is correct that each level represents a warm interval, perhaps three successive warm phases are being sampled. Prentice and Denton (this volume, chapter 24) indicate that at this time perhaps only 50 kyr separated warm peaks, so that all of the lower Swartkrans deposits might have been laid down within as little as a 100 kyr span, with the SK 1 "HR" (and the unknown *Cercopithecoides* level) and even the Kromdraai units broadly contemporaneous as well. I wonder if we can yet discern differences on this order of fine structure either in the environment or in evolutionary sequence when dealing with events 2 Myr old. I plan to continue analysis of patterns of species distribution, relative frequency, and phyletic relationship in hopes of clarifying this question.

In other paleontological situations, there is always the possibility that differing environments may have been sampled, but because these site units are so close geographically, the environmental differences must be under temporal control; that is, the site units differ in paleoenvironment because of their age differences, rather than being contemporaneous on a scale of 10 kyr with regionally different climates. Unfortunately, little can be added about these local paleoenvironments. Vrba and Panagos (1983) suggested that increasing aridity was indicated by the decreased presence of *C. williamsi* from ST 4 through KBE to SK 1 "HR" and KA. I responded (1984) that this species was highly terrestrial and may not have required as much environmental water as other colobines. I tentatively postulated an increase of surface water from SK 1 "HR" through KB to KA, but that also is probably too simplistic. All the *Papio* species were probably quite terrestrial, as was *Theropithecus* (and presumably *Gorgopithecus*, which is unknown postcranially), so that there is no clear distinction among these site units.

Summary and Conclusions

New cercopithecoid specimens recovered by Brain from Members 1 through 3 of the Swartkrans deposit are almost all identifiable as *P. hamadryas robinsoni*, with rare elements attributed to *T. oswaldi* in Members 1 and 2. This suggests some differences from the earlier collected SK 1 "HR" sample, which includes many *P. (D.) ingens*, some cf. *Cercocebus* sp. and one probable *G. major*. Other Swartkrans specimens identified as a "large variant" of *C. williamsi* were originally attributed to Member 2, but no similar material has been identified in the new sample.

This suggests that at least Members 1 to 3 of the new sample are similar in age to each other but possibly slightly different in age from the SK 1“HR” sample.

Based on the recalibration of Omo Group members by Brown and colleagues in a series of papers since 1985, my 1984 cercopithecoid zonation must be slightly modified. Taung, in lower AC 4, is probably about 2.3 Myr old. Attempts to chronometrically date the Taung tufas about 1 Myr and explain the cercopithecoid correlation in terms of a relict fauna are tenuous at best. If some of the ST 4 assemblage is mixed, then cercopithecoid candidates for such “intrusion” include the unique *P. izodi* and perhaps the *P. hamadryas robinsoni* specimens, which are now among the oldest members of this genus in Africa.

It is not yet feasible to unequivocally determine the age sequence of the group of site units from Swartkrans and Kromdraai. Few species occur in common, and several of the known taxa are rare elsewhere. A more complete analysis of the relative frequency of taxa may prove helpful in the future, but as yet, neither the bovids nor the cercopithecoids (or hominids) indicate a clear pattern. If Vrba’s (this volume, chapter 25) suggestion is accepted that KA is younger than KB, and if KB (and the similar COA) is intermediate between SK 1“HR” and KA, then my 1984 suggestion of a SK 1“HR”–KB–KA sequence is weakly supported. These site units may be quite close in age, probably between 1.9 and 1.65 Myr. Given my suggestion of age similarity among Members 1 through 3 at Swartkrans and Brain’s idea that each was formed during a warm interval, perhaps several successive warm phases sampled over only 100 kyr are involved in the combined Swartkrans (and Kromdraai?) complex.

The major implication of this work for the evolution of “robust” *Australopithecus* is to confirm the young age of the South African forms by comparison to those of East Africa. It is almost certain that the “robust” clade is monophyletic (Grine, this volume, chapter 30), and if the 2.6 Myr old *A. aethiopicus* is morphologically close to the common ancestor of *A. boisei* and *A. robustus*, it is surprising that no “robust” hominid is yet known in the south older than 2 Myr. The only known site units at which such an earlier “robust” form might be expected are ST 4, Taung and the Bolt’s Farm complex; the latter two have together yielded only one hominid specimen, of course, and despite suggestion in this volume, it is unclear that anything other than *A. africanus* occurs in ST 4. Perhaps the time is right to search for new sites in the Sterkfontein valley in hopes of tying in the Swartkrans and Kromdraai forms to the better-documented line of “robust” *Australopithecus* evolution in the east.

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