

**Cercopithecoid biochronology of the African Plio-Pleistocene:  
Correlation among eastern and southern hominid-bearing localities**

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**Abstract**

The relative age of eastern and southern African localities yielding Pliocene and early Pleistocene hominids is of great interest but still uncertain, despite studies of several faunal groups. Most of the approaches to biochronology suffer from circular assumptions, with concurrent-range or assemblage zonation being least problematic. Cercopithecoids are taxonomically diverse and common to both regions, and analysis of their concurrent-ranges yields a pattern indicative of chronologic ordering. This pattern is calibrated through a reanalysis of chronometric dating in semi-continuous sequences (Omo, Turkana, Olduvai, Hadar and Makapan). The ranges of over 20 cercopithecoid taxa in these sequences permit formulation of a set of seven main African Cercopithecoid (AC) zones defined by joint presence of taxa and their relative frequency; several zones are subdivisible. Over 60 site units are correlated to this zonation scheme. Of special interest are the placement of Taung somewhat older than the 1.9 Myr KBS tuff unit; and Kromdraai B (East) slightly younger. Comparisons are also made with range patterns and zonations for other taxa, including hominids.

**Introduction**

The age of the African localities yielding *Australopithecus* and early *Homo* fossils has long been a matter of great interest and discussion. Although earlier workers considered dates between the early Pliocene and the middle Pleistocene, most modern researchers are in agreement that sites producing these taxa are Pliocene and earliest Pleistocene in age, with estimated dates between 4 and 1.5 million years (Myr) ago. But it is the temporal relationships among the many localities which are in need of clarification. Among the problems central to current discussions of these early humans are the number of known taxa and their contemporaneity, the paleoenvironmental regimes in which they lived and their phyletic relationships to each other, later humans and the Miocene fossil hominoids. Although I have argued against the use of temporal data in phylogeny reconstruction (DELSON, 1977), many authors continue to employ them, and all workers would accept the value of such data in grouping population samples into species, evaluating contemporaneity of taxa and comparing paleoecological data across sites.

As BISHOP (1978), among others, has discussed, such problems are especially thorny in dealing with the African australopithecoid localities, because of a combination of historical and taphonomic factors. The earliest fossils of *Australopithecus* were found in South Africa, in cave deposits where large numbers of relatively complete specimens accumulated over intervals measured probably in tens to hundreds of thousands of years. Specimens from these sites were made the holotypes of the central taxa *Australopithecus africanus* and *Australopithecus robustus*. Despite numerous attempts, chronometric or „absolute“ age determinations for these localities have proved impossible, but correlation by paleomagnetism has been claimed at Makapan, as discussed below. By contrast, a number of areally extensive localities in eastern Africa were found later, along the Rift Valley, where subsidence permitted the development of long sequences of nearly continuous sedimentation which are amenable to chronometric and paleomagnetic dating. These eastern groups of localities, or „fields“ in the vertebrate paleontological sense, have yielded many fragmentary remains as well as quite complete specimens, but usually few are from

**Table 1:** Distribution Chart of African Plio-Pleistocene Cercopithecidae. – Key to Symbols Used: X = Taxon present – uncertain – L = Large ?variant. Abbreviations see Table 2, page 203.

Taxa:	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
<i>Parapapio</i>																													
<i>broomi</i>																													
<i>jonesi</i>																													
<i>whitei</i>																													
<i>antiquus</i>																													
<i>ado</i>	T																												
sp. indet.																													
or <i>Papio</i> sp.		X	X	?	?	?	?				X	X	?	X	X	?					X	?	?				X	X	
or <i>Cercocebus</i> sp.			X								X	?	?	?	?	?					X	X	X	?					
<i>Cercocebus</i> sp.																												X	X
<i>Papio (Papio)</i>																													
<i>hamadr. robinsoni</i>																													
cf. <i>hamadryas</i> ssp.							X																						
<i>izodi</i>																													
„ <i>angusticeps</i> “																													
<i>baringensis</i>																													
<i>P. (Dinopithecus)</i>																													
<i>ingens</i>																													
„ <i>quadratiostris</i> “	T							?	?	X	X	X	X	X	X	X													
? <i>Papio</i> sp. indet.	X	X																											
<i>Gorgopithecus</i>																													
<i>major</i>																													
<i>Theropithecus</i>																													
<i>oswaldi</i>												A	?	?	X	X	X	X	C	C	C	C					X	X	
<i>darti</i>																								C	C	C			
<i>brumpti</i>																													
sp. indet.									X															X			X		
<i>Cercopithecus</i> sp.		X									X				X		X						X				X		
<i>Cercopithecoides</i>																													
<i>williamsi</i>																											X		
<i>kimeui</i>						T	X																				?	X	X
<i>Paracolobus</i>																													
<i>chemeroni</i>																													
„ <i>mutiwa</i> “														X	X	X	X	X	X									T	
sp. (nov.)	X																												
<i>Rhinocolobus</i>																													
<i>turkanaensis</i>		X					X	X		X	X	X	X	X	X	T				X	X						X		
Colobinae sp. „A“		?									?	X	X														X		
<i>Colobus</i> sp.			C		C	C	C														C		C					C	
Colobine indet.																											X		

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T = Type locality – C = Cf.-taxon referred – A = Aff.-presence of similar if not same taxon – ? = Taxon identification

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29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62  
.....

..... X X T ..... X .....  
..... C C ..... C C T .....  
..... X X T .....

..... T .....

..... X X ..... ? ..... X .....

..... X .....

X ..... X ..... X C .....

X ..... X ..... X ..... X X X .....

..... X ..... X X X X X X T A ? X .....

..... X T .....

..... X X ..... T X .....

..... ? ..... T .....

..... T ..... X .....

..... X ..... ? .....

..... X ..... ? T X .....

X ..... X ..... X

. C C C C C C ..... T X .....

..... ? X ..... X X .....

..... X X .....

..... X T X X ..... L ? X X X L L .....

..... T ..... A

. X X ..... ? .....

. X ..... X .....

C ..... C C .....

. X ..... X ..... X .....

a restricted area. Moreover, it is necessary to make taxonomic comparisons with the southern holotypes in many cases. In addition, during the past decade a number of inconsistencies have been demonstrated between chronometric dating and faunal correlation, centering on the East Turkana sequence, which is now finally being clarified by BROWN and CERLING. The most important problem, however, appears to be the lack of generally accepted correlations between the eastern and southern groups of sites.

Several authors have recognized this problem and have approached the answer from faunal correlation studies. The most productive and widely utilized studies since 1972 included COOKE & MAGLIO (1972, on elephantids and suids; extended by MAGLIO, 1973 and COOKE, 1978 a, b; COOKE & WILKINSON, 1978); WHITE & HARRIS (1977) and HARRIS & WHITE (1979) on suids; BEDEN (1979) on elephantids; VRBA (1974, 1975, 1976, 1977, 1979, 1982) and GENTRY (1981; GENTRY & GENTRY, 1978) on bovids; and HOWELL & PETTER (1976) on carnivores. Unfortunately, the suid and elephantid work dealt with only a few South African specimens, mainly from Makapan; the two bovid researchers have concentrated on southern (VRBA) or eastern (GENTRY) localities, respectively, although both have attempted transcontinental comparisons and correlations; and the carnivore work is in its early stages. For the past several years, I have been developing a correlational scheme based on cercopithecids, which have the advantage that many species are known from both eastern and southern sites. This is the first detailed report of my results, which still must be considered preliminary. Many of my findings support those of other workers, but some are novel, which may lead to still more argument in an already near-vituperative field. Nonetheless, the goal of a widely accepted time framework for the Plio-Pleistocene interval across sub-Saharan Africa is worth pursuing. It would permit the fossil samples of many groups, including hominids, from penecontemporaneous localities to be compared taxonomically in studies of variation, phylogeny and evolutionary patterns. Moreover, it would aid researchers studying differences in biological and human cultural adaptations to determine if they reflected temporal or geographical/paleoenvironmental variation.

### **Biochronological Methods**

Any faunal study aimed at temporal correlation must begin with systematic revision or clarification of the taxa involved. My ongoing work in this area has built upon the framework detailed in SZALAY & DELSON (1979), with many additions and some alterations. I considered it of prime importance that a single researcher must have observed, identified and analyzed all of the specimens under study in order to guarantee consistency, and therefore I have examined nearly all of the known fossil cercopithecids from this time period, even though I will not be responsible for primary publication of a number of collections. The current status of my understanding of the pattern of distribution of this group in the Plio-Pleistocene of sub-Saharan Africa is presented in Table 1. Here I recognize 23 distinctive and mostly named species, as well as nine taxon units identified to genus (or group of genera). Seven genera or subgenera, and at least 5 species, are known from both eastern and southern Africa. The locality data are presented in terms of site units, that is members or their equivalent in larger sequences and individual smaller or indivisible assemblages. Sixty-two such units are listed here in Table 2, and I have seen material from all but 3 (Chesowanja (BISHOP & al., 1975) and the two Awash localities (KALB & al., 1982)). When the site-by-site analysis is complete, I will have data on the minimum number of individuals per taxon at each site unit, so that relative frequency information may be added to presence/absence data. In addition, further taxonomic analysis should clarify most of the uncertainties indicated here.

The next step is to determine which approach(es) to faunal correlation will be utilized in the study. Currently, there are a number of alternative, even competing methodologies available: stage-of-evolution, *niveaux repères*, comparison of evolutionary and migrational first (and last) occurrences and assemblage or concurrent-range zonation.

The stage of evolution approach has become the most widely accepted means of correlating mammalian fossil assemblages (see SAVAGE, 1977; TEDFORD, 1970). This concept depends on the gradualist model of species evolution, postulating that if the whole of a given ancestral species A evolves slowly and steadily into its descendant species B, all members of A living at one time will present roughly similar degrees of evolutionary „advancement” as seen in their morphology. This has usually been interpreted in terms of metrical equivalence, with measures of tooth size being the most common indicators of phyletic stages, although qualitative changes have also been employed. This approach was used, at least in part, in most of the major recent studies of Plio-Pleistocene African mammals cited above. GINGE-RICH (e.g., 1979, 1980) has carried it to an extreme in his stratophenetic approach, recognizing as full

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**Table 2. African Plio-Pleistocene Fossil Site Units and Abbreviations for Table 1.**  
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01 Laetoli Beds	32 Hadar Fm., lower KH mbr.
02 Omo upper Usno (Brown/White Sands)	33 Hadar Fm., middle KH mbr.
03 Olduvai Bed I	34 Afar Leadu beds (AL 2)
04 Olduvai lower Bed II	35 Afar Ahmado Beds (AL 100)
05 Olduvai middle Bed II	36 Chesowanja
06 Olduvai upper Bed II	37 Lothagam-3 Beds
07 Olduvai Bed III and above	38 Kanapoi loc.
08 Omo Shungura Fm., Basal mbr.	39 Chemeron Fm., „Basal” locs.
09 Omo Shungura Fm., mbr. A	40 Ekora loc.
10 Omo Shungura Fm., lower mbr. B	41 Kanam East locs.
11 Omo Shungura Fm., upper mbr. B	42 Kaiso Village loc.
12 Omo Shungura Fm., mbr. C	43 Chemeron Fm., loc. JM 90/91
13 Omo Shungura Fm., mbr. D	44 Langebaanweg Quarry E
14 Omo Shungura Fm., mbr. E	45 Makapan mbrs. 2 - 3
15 Omo Shungura Fm., mbr. F	46 Makapan mbr. 4
16 Omo Shungura Fm., mbr. G (lower)	47 Sterkfontein mbr. 4 (ST 4)
17 Omo Shungura Fm., mbr. G. (upper)	48 Leba loc(s).
18 Omo Shungura Fm., mbr. H	49 Taung (fauna)
19 Omo Shungura Fm., mbr. J	50 Sterkfontein mbr. 5 (ST 5)
20 Omo Shungura Fm., mbr. K	51 Schurveburg loc. (SB)
21 Omo Shungura Fm., lower mbr. L	52 Cooper's A loc. (CO A)
22 Omo Shungura Fm., upper mbr. L	53 Cooper's B loc. (CO B)
23 Koobi Fora sub-Tulu Bor unit	54 Bolt's Farm, Pit 6 (BF 6)
24 Koobi Fora sub-Allia unit	55 Bolt's Farm, Pit 23 (BF 23)
25 Koobi Fora sub-Hasuma unit	56 Swartkrans II loc. (SK II)
26 Koobi Fora sub-(& supra) Burgi unit	57 Swartkrans mbr. 1 (SK 1)
27 Koobi Fora sub-KBS unit	58 Swartkrans mbr. 2 (SK 2)
28 Koobi Fora sub-Okote unit	59 Kromdraai A loc. (KA)
29 Koobi Fora sub-Chari unit	60 Kromdraai B loc. (KB)
30 Hadar Fm., SH mbr.	61 Kalaloo Beds, middle Awash
31 Hadar Fm., DD mbr.	62 Matabaietu Fm., middle Awash

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species small samples of isolated teeth which are intermediate in size and stratigraphic horizon between known and better-defined taxa and then linking adjacent „species” of a presumed genus as ancestors and descendants automatically. Migration, evolutionary change outside the restricted sedimentary basins where fossils are common, the reality of species defined by time or stratigraphy rather than morphology and derived vs. ancestral character states are almost completely ignored in this approach, which intertwines systematics and biostratigraphy inextricably and circularly. SCHANKLER's (1980) study of some of the same strata considered by GINGERICH (1980) provides a much more reasonable way of looking at the same biochronological problems, from an approach similar to that followed here. Although I thus consider that the stage of evolution approach may have a poor theoretical basis, it has apparently worked well in some studies. This success may be fortuitous, erroneous or indicative of greater pervasiveness of phyletic evolution (within species) than I am prone to accept.

Another method which has gained favor recently, especially in Europe, is the use of reference assemblages (*niveaux repères*) to define intervals (see, e.g., JAEGER & HARTENBERGER, 1975). In this approach, well-documented local faunas are chosen as references and their relative chronologic position determined by a combination of superposition and stage of evolution. It has been argued that in situations such as the present one, with numerous isolated site units, this approach may avoid some of the pitfalls likely with a zonation based on taxon biochrons, but I find the method circular, due to its emphasis on stage of evolution.

Another approach to biochronology often employed in deep-sea core studies and recently championed for paleomammalogy by WOODBURN (1977) is the use of „evolutionary” or migrational first or last appearances of different species in stratigraphic sequences to determine their correlation. Several problems of assumption occur in most formulations of this concept, but I believe some of the precepts may be applied with suitable modification. For example, „evolutionary” first appearances (or first discoveries, as BURCKLE prefers) depend on the recognition of ancestor-descendant sequences and actual transformations in the fossil record. If, as zoologists widely accept, most species originate allopatrically, it is unlikely that the marginal populations undergoing speciation will be fossilized and recovered, not to mention the difficulties in identifying ancestors at all. WOODBURN (1977) has even argued that arbitrary distinctions between successive species recognized under a gradualist model be made especially in the stratotype of a biostratigraphic unit. In addition, the use of first and last discovery data (FDD’s or LDD’s) does seem to be tied closely to the existence of one or more long semicontinuous sections, which are certainly not available for most of the present study; on the other hand, range zonation may suffer from this lack as well. On the positive side, many FDD’s observed in the fossil record may be considered under a punctuational model as migrational first occurrences, fairly close in time (barring environmental barriers) to the time of speciation, re-establishment of sympatry and expansion of a successful new species. They can thus be employed in much the same way as WOODBURN and others suggest. The questions of reliable and acceptable definitions of species discussed by WOODBURN (1977) have already been echoed above. Finally, although SAVAGE (1977) and others have questioned the value of LDD’s as based on negative evidence (no specimens known younger than datum), migrational FDD’s are equally based on the lack of older known specimens; both types of data may be accorded roughly equal weight. For any of these approaches, species whose range is neither ubiquitous nor restricted to a single site unit, especially those with a biochron of 0.5-1 Myr duration, are most useful.

If the stage-of-evolution and related *niveaux repères* approaches are discarded as circular and dependent on phyletic gradualism, and if the use of FDD’s is to be restricted, with what method of correlation is one left? The principle of superposition is clearly acceptable, but it is balanced by homotaxy, whereby identical species may occur in two rock units of differing ages due to ecological or facies control. Still, the study of successions of assemblages of species in localities or fields with numerous horizons is a prerequisite to interpolation of isolated site units. The study of fossil invertebrates and microorganisms from marine deposits has been inextricably tied to semi-continuous rock-sequences or cores, with large samples from single layers or bedding planes, and thus reasonably may be termed biostratigraphy. For fossil mammals, however, it has long been recognized that, except in rare cases, an assemblage of specimens is drawn from numerous layers, separated by gaps and not necessarily reflecting strict depositional relationships with the rocks in which they are found. Isolated occurrences are frequent, but even in the case of long and apparently continuous terrestrial sequences such as those in the East African Plio-Pleistocene or the Wyoming Paleogene, fossil associations generally do not have the close links to rock successions that characterize aquatic deposits. Instead, many studies of fossil mammals from a geochronological viewpoint have involved the definition of time intervals directly by the temporal ranges of taxa, without the intermediary of measured rock sections characterized by fossil content. The term biochronology was apparently first applied to this approach by THALER (1965), based on the concept of a biochron, or temporal range of a taxon, and I employ it here specifically as opposed to biostratigraphy.

Following ELDREDGE & GOULD (1977) and VRBA (1977), among others, I reason that an acceptable biochronological method must be consistent with the (cladistic) concept that it is only with a probabilistic approach involving explicit tests and requirements that actual ancestral (as opposed to sister) taxa can be identified (DELSON, 1977). Moreover, if the allopatric or punctuational model of a relatively short speciation interval, with most species displaying reasonably consistent (if randomly varying) morphology during their „lifespan” is valid, I would accept that directional phyletic evolution is reasonably common within many species’ lifetimes, but that it is less dominant in terms of total evolutionary change than speciation-linked transformation. These views were at the heart of our rejection of stage-of-evolution and related ideas. Instead, the approach advocated by ELDREDGE & GOULD (1977) and here is a return to the „old-fashioned” system of employing the ranges or biochrons of a set of taxa to define units of time when several taxa coexisted: an assemblage or concurrent-range zonation.

Beginning with the longer, superpositionally controlled sequences, the pattern of species distribution is delineated. This pattern is then examined for instances of apparent alteration in the composition

of assemblages, such as the appearance or disappearance of species or, in this study, changes in relative frequency of taxa. If similar changes in taxon presence or frequency occur in more than one sequence, non-biological indicators of correlation (e.g., tephrostratigraphy, lithostratigraphy, magnetostratigraphy, radiochronometry) may be examined to determine if these alterations are likely to have been penecontemporaneous. With the addition of data from shorter superpositionally controlled sections, a preliminary zonation may be developed with zones defined by the joint presence of a set of species, perhaps within a specified range of proportions. Isolated site units can then be compared to this zonation to determine if they can be allocated to one of the defined zones, and a complete correlation scheme elaborated. Clearly, in addition to an accurate systematics and distribution pattern of the taxa involved, what is required for this method to succeed is a basic framework of geochronology for the long sequences which form the calibration infrastructure.

#### **Building a revised East African geochronology**

Because the Omo sequence is of primary importance as a chronological standard for calibrating other deposits, its own dating must be clear. I have analyzed the most recent studies of magnetostratigraphy, K-Ar dating and tephrochronology (BROWN & NASH, 1976; BROWN & al., 1978; CERLING & al., 1979; DRAKE & al., 1980; and CERLING & BROWN, 1982. as well as much appreciated personal communications and assistance from Frank BROWN), and I offer a slightly revised timescale in Figure 1. Note that here and below, all K-Ar ages have been recomputed following DALRYMPLE, 1979. The main novelties of the Omo calibration are: 1) an age for tuff D estimated at near 2.5 Myr, based on its dates and the magnetically calibrated age of upper mb. C; 2) the ages of several important tuff horizons estimated by the (admittedly unrealistic but only available) assumption of constant sedimentation between the top of submember B2 (magnetically calibrated at 2.92 Myr, the end of the Kaena subchron) and tuff D at 2.5 – this 140 m interval (see BROWN & al., 1978) is marked approximately by tuff B10 at 40 m (2.8 Myr), tuff C at 60 m (2.7 Myr) and tuff C4 at 80 m (2.65 Myr), all quite roughly; 3) the very short member E, bracketed by the correlation of the F2-4 normal as the older Reunion subchron ending about 2.13 Myr ago and the ages of 2.23 Myr for the D4 („X”) normal and/or 2.18 Myr for tuff D3 (if the F2-4 normal were the younger Reunion subchron at about 2.02-2.05 Myr, the large member G would become too short – in fact, it may already be so); 4) the rather long member H, with a base just older than the H2 (=KBS) tuff at 1.9 Myr, the H6/7 magnetic boundary equivalent to the end of the Olduvai subchron at 1.67 Myr and a top between 1.65 and 1.6; 5) the probably short member J, but with somewhat uncertain boundaries (between 1.65 and 1.6 Myr below, 1.55-1.5 Myr above); and 6) the very long member L, with a base about 1.4 Myr, the Jaramillo subchron in submembers 5-6 (0.9-0.98? Myr) and some time represented above that level. BROWN & al. (1978) considered some of these interpretations (especially the last) as alternatives, but did not press for them as I do here.

The relative and chronometric age of many Koobi Fora horizons has long been a problem, but the studies of HARRIS & WHITE (1979) and WILLIAMSON (1982) made it possible to arrange faunal collections in a reasonably systematic fashion, and correlation with the Omo (studies cited above) aided in dating the KBS level at least. Now, the new work of BROWN (1982; BROWN & CERLING, 1982) has clarified a number of other problems and refined the correlations with the Omo sediments, although this work is still ongoing. Because of the incomplete nature of East Turkana locality data generally, it is not possible to reorganize all of the Koobi Fora horizons with mammals into the new stratigraphic pattern, nor are all monkey fossils locatable within this pattern. Nonetheless, after comparing BROWN's tuff correlations with the zonal scheme of HARRIS & WHITE, I have suggested an approximate placement of the collection zones in the new Koobi Fora stratigraphy, indicated nine tuff-separated units (corresponding in name but not content to the pre-1976 terminology) and determined for each unit the included cercopithecids (as yet, none are known from the basal or sub-Suregei or the topmost, sub-Silbo, units). Note that the Toroto tuff is dated at slightly greater than 3.3 Myr after CERLING & BROWN (1982).

The stratigraphy and dating of the two Tanzanian sites, Olduvai and Laetoli, are well established and need little more than inclusion here (see LEAKEY & HAY, 1982). The situation is not so simple for the final East African sequence, at Hadar. As described most recently by WALTER & ARONSON (1982), this formation is divided into four members; no cercopithecids have been recovered from the Basal member, but the upper or Kada Hadar member is here divided into lower and middle sections to reflect a cercopithecoid faunal change (the upper part is barren). The BKT-2 tuff at the top of this member is dated close to 2.9 Myr, in an apparently normal magnetic zone; the middle KH unit, above BKT-1

is in an apparent reversed zone, while the lower KH (with „Lucy“) is again normal. WALTER & ARONSON (1982) revised their earlier estimates (ARONSON & al., 1977) of the age of the Kadada Moumou basalt high in the Sidi Hakoma member from ca. 3 Myr to about 3.65 Myr, which led to uncertainty about the still incomplete magnetostratigraphy. BROWN (1982) then demonstrated the apparent tephrostratigraphic equivalence of the basal Sidi Hakoma tuff to the Tulu Bor and B tuffs in the Koobi Fora and Omo Shungura sequences, respectively. This would make the SHT slightly older than the dated Toroto tuff, at perhaps 3.35 Myr (tuff A at Omo is calibrated at about 3.4 Myr at the Gilbert to Gauss magnetic reversal). BOAZ & al. (1982) mistakenly argued for a Sidi Hakoma tuff date closer to 3.2 Myr on the basis of BROWN's work and suggested other implications discussed below. The reply from the Hadar dating team (ARONSON & al., 1983) is unconvincing, while SCHMITT & NAIRN (1984) have confirmed the original assessment of the Hadar paleomagnetism which further supports BROWN's correlation of the SHT as accepted here.

The relative ages and local stratigraphies of the main Transvaal sites have most recently been reviewed by PARTRIDGE (1982) and VRBA (1982), and further comments on the relative dating will be offered below. Of these sites, the only one whose chronometric age has seriously been discussed recently is Makapansgat, from which McFADDEN & al. (1979) reported paleomagnetic results as follows. The sterile member 1 was reversed; member 2 (the „basal red muds“ of BRAIN, with few monkeys) was normal throughout its 8 m thickness; the thin member 3 („grey breccia“) with most of the *Australopithecus* and many cercopithecids yielded no magnetic results; in member 4 (the „pink breccia“ with many fossils below and „Phase II“ above), single indeterminate and reversed horizons were followed by three normal, another indeterminate and a possibly reversed zone after which no further samples could be analyzed. McFADDEN & al. argued for an interpretation of these data which would place the cercopithecoid-hominid horizons (members 3 and the lower part of 4) mostly older than 3.0 Myr on current age values. They offered two alternatives, another was proposed by WHITE & al. (1981), and I can suggest several more which are equally acceptable on the basis of the known data; this reveals the greatest problem with magnetostratigraphy, its lack of a „fingerprint“ technique for correlation. The most likely correlations of the Makapan sequence range members 2 through lower 4 between about 3.1-2.9 Myr, somewhat younger than suggested by McFADDEN & al. This only allows some 50.000 yr for members 2-3, with included unconformities, but if member 2 (the „basal red muds“) represented slope wash with few bones, at least its upper part might have accumulated rapidly. Moreover, there is no evidence that member 3 was deposited in a time of normal polarity (as assumed by McFADDEN & al.); if it were reversed, even more time would be available for the thick member 2, without a major change in dating. My preferred hypothesis would thus be that mbr. 1 represents the Mammoth reversed subchron between 3.15 and 3.05 Myr; mbr. 2 the succeeding short mid-Gauss normal; mbr. 3 and the base of mbr. 4 (the major fossiliferous layers of interest) equate to the Kaena reversed subchron from 3.0 to 2.92 Myr; and higher levels represent the upper Gauss normal.

On the other hand, WHITE & al. (1981) suggested a correlation of the reversed-normal transition with the Gilbert-Gauss boundary and of the normal-reversed one with the Gauss-Matuyama; this would imply the normal lower part of member 4 equated to the „X“ anomaly, while the Kaena and Mammoth reversed subchrons of the Gauss (where I would place the fossiliferous layers) would have been lost through hiatus or erosion. Finally, VAN COUVERING (personal communication) has reminded me that single magnetic samples (as in lower member 4) are never trustworthy and suggested that the presence of *Equus capensis* in the Makapan assemblage (CHURCHER & RICHARDSON, 1978) indicates a post-Gauss age for the relevant member, based on the FDD of this genus in Eurasia and North America (LINDSAY & al., 1980). This would equate member 1 with the Kaena, member 2 with the upper Gauss and members 3-4 either as with the lower Matuyama as WHITE & al. proposed or with the upper Gauss if the lower member 4 single reversed datum is rejected. Unfortunately, it is unclear from which member the horse (a single tooth?) derives, perhaps high in mbr. 4 or 5, above the magnetic data and the primate fossils. In any case, I will argue below that the cercopithecoid correlations deny these two quite young interpretations for Makapan, fitting better with the ideas I outlined above. Additional data from external sources (or perhaps polarities from mbr. 3) are needed to test this model.

#### **Some notes on cercopithecoid taxonomy and distribution**

As noted, these data are summarized in Table 1, but some explanation may be required here. The most common Hadar monkey has been termed *Theropithecus cf. darti*, smaller and more gracile than the

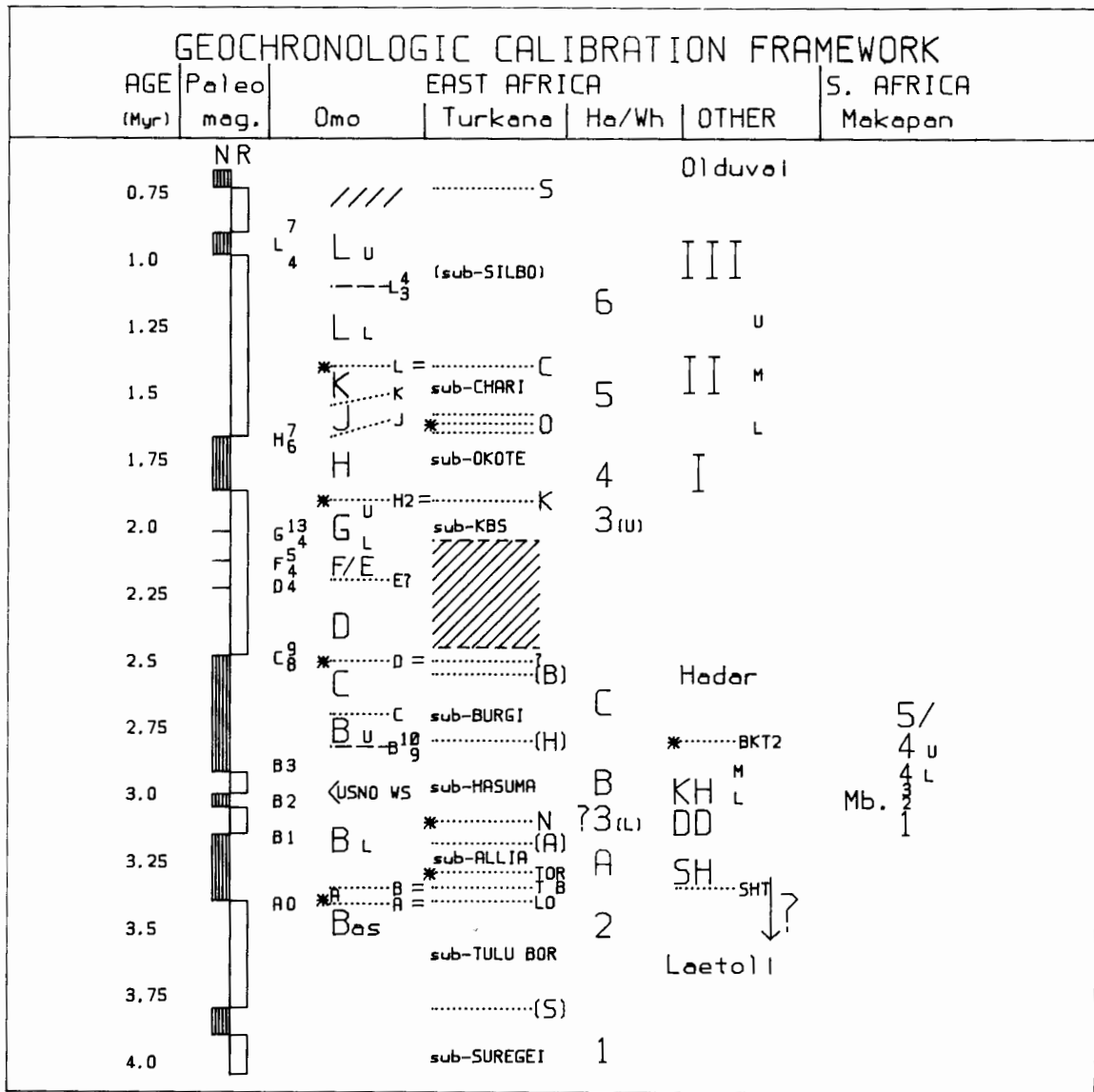


Fig. 1. A geochronologic calibration framework based on a re-evaluation of the radiometric and paleomagnetic dating of several semi-continuous terrestrial sequences (see text for details). The leftmost columns give age in millions of years and the standard paleomagnetic column; the three horizontal lines between 2.0 and 2.25 Myr represent the two Reunion and the „X” normal „events”. The central portion of the Omo column presents the reinterpreted ages of the main tuff layers (dotted lines labeled at right), shown diagonal if their age is unclear; an asterisk indicates a tuff dated radiometrically; several members are divisible into upper (U) and lower (L) moieties, with dashed lines showing the division and the relevant submembers for members B and L. The position of the upper Usno Fm., with the White (and Brown) Sands localities, is shown as an insert. To the left are shown the submembers corresponding to the paleomagnetic transitions correlated to the standard scale. The Turkana column reflects the positions of the major named tuffs (dotted lines labeled at right) and the named sub-tuff units. Tuffs asterisked are dated, those with an = sign at left are correlated to the neighbouring Omo tuff, those labeled in brackets are of uncertain stratigraphic position. The column labeled „Ha/Wh” presents an assessment of the position of the several collection units discussed by HARRIS & WHITE (1978), placed in the current framework. The „OTHER” East African site column places Olduvai Beds I–III, Laetoli and the members of the Hadar Fm. in this framework. Two subsections, middle (M) and lower (L), are shown for the KH or Kada Hadar mbr., while an alternative position is shown for the SHT (Sidi Hakoma Tuff), if it is not equivalent to the Tulu Bor Tuff at Koobi Fora but as estimated by WALTER & ARONSON (1982). The members of the Makapansgat Fm. are shown in positions determined by the reinterpretation of paleomagnetic data proposed in the text.

Makapan type populations, but closest to them of any known sample (other than fragments from East Turkana). *Parapapio* cf. *jonesi* is known from a nearly complete male skull and mandible, a jaw fragment and a referred humerus, as well as some uncertainly allocated other postcranials from the middle levels of the Kada Hadar member at loc. 363 only. It is again most similar to Makapan specimens, which EISENHART (1974) thought were distinctive from the Sterkfontein type sample, although the Hadar fossils are somewhat more complete and the male presents unique nasal morphology; the humeral fragment is the first acceptable allocation of postcrania to this genus. The colobines from this site are comparable to those reviewed recently by LEAKEY (1982). EISENHART (1974) suggested, and I agree, that there is essentially no difference in monkeys from Makapan member 2 (few fossils) through 3 to 4; some rare taxa are present only in one member, but no replacement or significant phyletic evolution is discernable.

From the Omo Shungura (members upper B-lower G especially) comes a large number of specimens (including two female crania, a male muzzle, and five mandibles of both sexes) which have previously been termed *Papio* sp. (e.g., ECK, 1977; SZALAY & DELSON, 1979). In fact, these fossils are most comparable to, but significantly smaller than, *Dinopithecus ingens* from Swartkrans, which in turn is best placed as a subgenus of *Papio*. IWAMOTO (1982) described a new skull from the Usno which he called *Papio quadratirostris*, and which I believe to be the male of the Shungura „*Dinopithecus*“. ECK (1983; ECK & JABLONSKI, in press) has suggested this skull to be a primitive *Theropithecus*, although he agrees that the other fossils are *Papio*-like. Pending complete study, I refer to the Omo large papionin as *Papio (Dinopithecus) „quadratirostris“*. Similar specimens, accompanied by a single mandible of *Cercopithecoides williamsi*, are known from Leba, Angola (ANTUNES & DELSON, in prep.).

Nearly 150 specimens, including a number of well-preserved skulls and mandibles, are now known from Taung. Skulls can be allocated to the two distinct species *Parapapio antiquus* and *Papio izodi*, but isolated teeth and even some mandibles and juvenile crania are not clearly identifiable. A sample of the modern small baboon *Papio hamadryas kindae* shows a number of dental and facial distinctions from *P. izodi*, despite overall similarity in size, thus suggesting species-level difference. The specimens from Swartkrans and Kromdraai termed *Papio angusticeps* are more like modern *P.h. kindae*. It is worth noting that no *Cercopithecoides* is known from Taung, despite numerous citations, and that the material from all three sites cited as *Parapapio jonesi* is in fact best identified as *Cercocebus* (as suggested in SZALAY & DELSON, 1979).

#### A cercopithecoid assemblage zonation of the Plio-Pleistocene

The first-order zonation of Figure 2 is based on the ranges of seven cercopithecoid genera, including 12 specified species or groups of species. The major features are defined by East African semicontinuous sequences, but the replacement of *Parapapio* by *Papio* is really only seen in South Africa and involves some aspects of stage-of-evolution arguments. Each zone will be characterized in terms of its included taxa and then by its typifying site units; finally the correlated site units will be indicated, with reasons for their inclusion. Figure 3 summarizes the resultant chronology of site units, in a framework of time and cercopithecoid zones.

The oldest zone, AC1 (for African cercopithecoid), is loosely defined by the presence of small *Parapapio* and small *Paracolobus*, as at Laetoli (LEAKEY & DELSON, in press). One tooth of a comparably sized papionin and several of *Theropithecus* are present in sub-Tulu Bor beds at Koobi Fora, of similar age. Kanapoi, Ekora and the basal beds of the Chemeron Fm. could also fit here. The lowest Hadar beds (Sidi Hakoma mbr.) do not share these taxa and thus are placed in zone AC2, defined by the joint presence of *Theropithecus darti* (smaller specimens), *Rhinocolobus* and *Papio (Dinopithecus) „quadratirostris“*. The first two taxa occur in all Hadar members, while the last two are present in the Omo Usno (BS/WS localities) and questionably the Omo Basal – lower B members of the Shungura Fm. At Koobi Fora, the interval between the Hasuma and Tulu Bor has yielded a *Parapapio* jaw and several *Theropithecus* cf. *darti* close to those from Hadar, as well as possible *T. brumpti*; the *Parapapio* is older at Turkana (it lies within the Toroto), suggesting the possibility of a northward spread from Tanzania through Ethiopia. Colobines are rare at Turkana, and *Parapapio* is present but rare in most of these levels, but only a site in the middle Kada Hadar member (AL 363) yielded the latter genus, with few other monkeys; this site unit is thus placed in the succeeding zone.

AC3 may be considered the *Parapapio* „acme-zone“, in that this genus is most common here, especially in South Africa. It is accompanied by such taxa as (larger) *Theropithecus darti* or *T. brumpti*, *Papio (Dinopithecus) „quadratirostris“* or *P. hamadryas robinsoni* and rare smaller *Papio* or *Cercocebus*; colobines appear more frequently, with *Cercopithecoides williamsi* (in the south and possibly *C. kimeui*

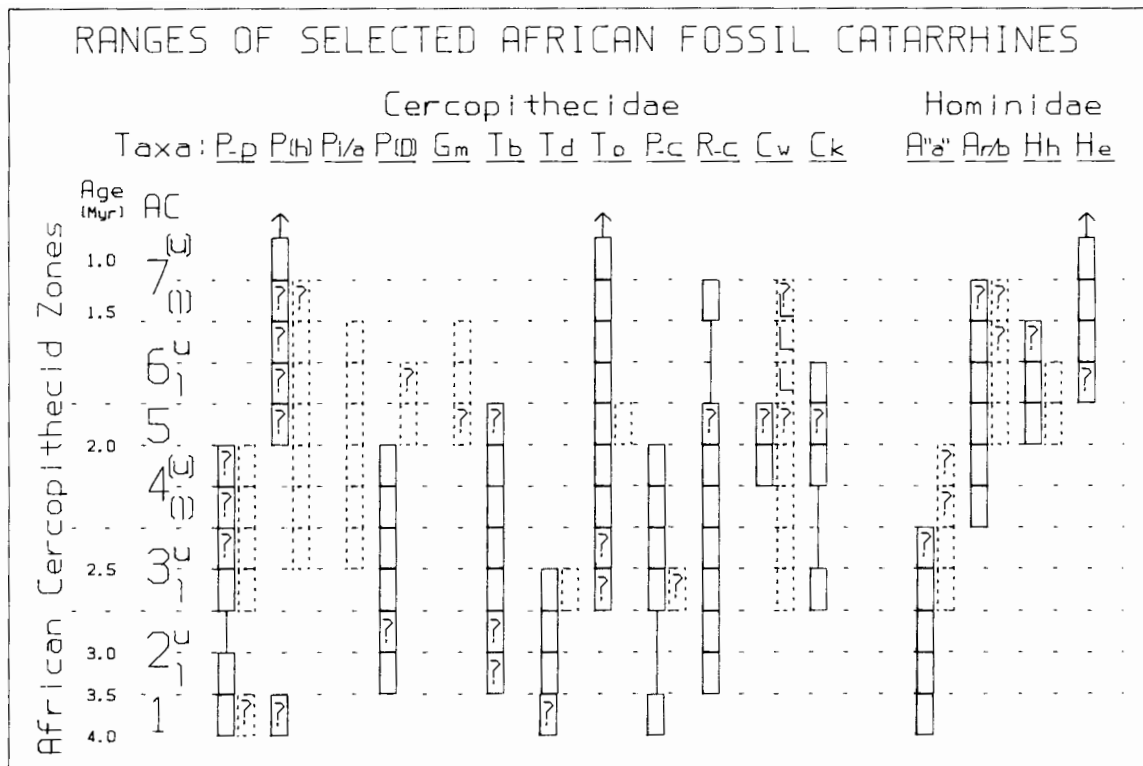


Fig. 2. Ranges of selected African fossil catarrhines and a zonation of Pliocene-early Pleistocene time based on the cercopithecids. The biochronological ranges of 12 cercopithecoid taxa, derived essentially from the site units of Fig. 1 and correlated additions, are shown divided into a series of 12 intervals, as discussed in detail in the text. These intervals or AC zones and subzones, are separated by horizontal dashed lines, and approximate dates have been inserted; note that there is no inherent time scale to this chart. The basic data of this Figure are presented in Table 1. For each taxon, the solid rectangle indicates presence in that interval in eastern Africa, while the dashed rectangle represents a southern African occurrence. A solid vertical line indicates implied continuous presence not yet documented, while a ? inside a rectangle indicates uncertainty as to the taxon identification or the allocation of that occurrence to the relevant interval. The taxa represented are: P-p, *Parapapio* sp. (p.); P (h), *Papio hamadryas* group; P(i/a), *Papio izodi* or *P. „angusticeps“*; P (D), *Papio (Dinopithecus)* sp.; Gm, *Gorgopithecus major*; Tb, *Theropithecus brumpti*; Td, *Theropithecus darti*; To, *Theropithecus oswaldi*; P-c, *Paracolobus* sp.; R-c, *Rhinocolobus turkanaensis*; Cw, *Cercopithecoides williamsi* (L indicates large southern form); Ck, *Cercopithecoides kimeui*. Four hominid taxa are added for comparison (using the same conventions, in zones defined by the cercopithecids): A „a“, *Australopithecus afarensis* and *A. africanus*, not separated because of problems with allocating isolated teeth; Ar/b, *Australopithecus robustus* and *A. boisei*; Hh, *Homo habilis*; and He, *Homo erectus*.

in the sub-Burgi), *Paracolobus „mutiwa“* and *Rhinocolobus turkanaensis*. Important site units include Sterkfontein member 4, Makapan members 2-4, Omo Shungura members B (upper) through D (with the short E equivocal), the middle Kada Hadar member and the Koobi Fora sub-Burgi unit (including the short „supra“ interval above the Burgi but below the major hiatus). Leba, Angola, is placed here or possibly in AC4 because of the presence of *P. (D.) „quadratiostris“* without *Theropithecus*, but the lack of any definite *Parapapio* suggests distinctive ecology or possibly the younger date. It may be that further subdivision of this zone will be possible: Makapan is linked to AC2 by *T. darti* without *Papio*, while the reverse situation links Sterkfontein to AC4.

Zone AC4 appears to represent an important transition in the development of the African Pliocene-Pleistocene cercopithecoid fauna. It also is the best evidence for linkage between eastern and southern African assemblages, which still remains difficult. This zone documents the joint presence of *Theropithecus brumpti* and *T. oswaldi* and of *Papio* and *Parapapio* species with similar numbers of specimens. For example, at Taung, *Parapapio antiquus* is found with *Papio izodi*; at Bolts Farm Pit 23, *Parapapio broomi* occurs (rarely) with common *Papio hamadryas robinsoni*; and in the Omo Shungura members E?, F and G (lower), the two *Theropithecus* species appear to coexist. In addition, *Rhinocolobus* and

*Paracolobus* continue in the Omo and appear in the Koobi Fora sub-KBS unit (late in the zone?) alongside typical *Cercopithecoides williamsi*, also present in South Africa (Bolts) and *C. kimeui*; the diversity of colobines here is quite fantastic, with at least one smaller form usually known as well.

Zone AC5 is characterized by a more „modern“ type of cercopithecoid assemblage, which M. LEAKEY (1982) has tied to climatic change in the Turkana Basin, at least; BONNEFILLE (1983) has presented evidence of a cooling in the central Ethiopian highlands about 2.4 Myr ago, which may represent the onset of this change. *Theropithecus* is represented in AC5 only by *T. oswaldi*, with regional variation appearing. *Parapapio* is extremely rare if present at all, possibly replaced by *Cercocebus*. *Papio h. robinsoni* (but not *P. angusticeps* or *P. izodi*) occurs in the south, accompanied by *P. (Dinopithecus) ingens*; the latter lineage is no longer found in the east, but typical *Papio* may occur rarely. Typical *Cercopithecoides williamsi*, *Rhinocolobus* and probably *Paracolobus* last occur in AC5. This zone includes the sub-KBS unit at Koobi Fora, as well as the short and poorly fossiliferous upper member G at Omo. The Awash Matabaietu beds with *T. oswaldi* and *Paracolobus* cf. *chemeroni* and possibly Chemeron Fm. Loc. JM 90/91 (with the holotype of the latter species) belong in AC5. In the south, Swartkrans member 1 seems to fit clearly here, with *T. oswaldi*; although younger than AC4 (no *Parapapio* or *C. williamsi*, rare *Gorgopithecus*), the presence of large *P. (Dinopithecus)*, *P.h.robinsoni* and numerous *Cercocebus* (instead of *P. angusticeps*) link Swartkrans back to that zone and prevent referral to AC6. Moreover, Schurveberg is tentatively placed late in AC5 because it contains *P. h. robinsoni* and the holotype of *Papio (Dinopithecus) ingens*, although the latter is larger than the Swartkrans material. Swartkrans II (a small, nearby site, not member 2) and Bolts Farm Pit 6, with *P.h. robinsoni* and typical *Cercopithecoides williamsi* may fit early in AC5 or late in AC4 (younger than BF 23 but older than SK 1, apparently). These southern distinctions within zone 5 are flimsy at best, but a true separation may be possible eventually.

Zone AC6 may span the Pliocene-Pleistocene boundary, if the above correlations are valid. This interval is poorly productive of cercopithecids in East Africa, but *Cercocebus* is fairly frequent and *Papio* and *Colobus* may occur, alongside common *Theropithecus oswaldi*. *Cercopithecoides kimeui* may continue, but only one fragment of uncertain horizon is known at Koobi Fora. Olduvai beds I and lower II define this zone, with the major part of the Koobi Fora sub-Okote unit and Omo Shungura members H (nearly devoid of cercopithecids) and probably J referred. The Komdraai/Coopers complex may fit in here, differing from AC5 and Swartkrans by the presence of *Gorgopithecus*, rather than *P. (Dinopithecus)*, and a large variant of *Cercopithecoides williamsi*. I have shown elsewhere (DELSON, 1983) that the latter species is essentially uniform in size throughout all other southern and eastern site units, with only this apparently youngest population significantly larger; this may relate to the common presence of *C. kimeui* at Koobi Fora slightly earlier and in upper Olduvai Bed II-III contemporaneously or slightly later. The same colobine seems to occur also in (the older?) part of Swartkrans member 2, which is otherwise indeterminate. More detailed analysis of the relative frequency of the papionin species is under way and should provide a better relative age inference. For now, I suggest that if Swartkrans 1 represents AC5, Kromdraai B (with rare *Gorgopithecus* and *Cercocebus*, large *Cercopithecoides* and two *Papio* species) is best placed in early AC6. Kromdraai A, with much *Gorgopithecus* and *Papio angusticeps*, but fewer *Cercocebus* or *Papio h. robinsoni* and no *Cercopithecoides* could be later AC6. Coopers A has the same four large species as Kromdraai B, but the total assemblage is small; it might fit with KB or between KA and KB. Coopers B has only the two *Papio* species and is least securely ranked of the four. In fact, any or all of these southern site units conceivably could fit into AC5 as ecological variants.

A final early Pleistocene zone (AC7) may be represented in Omo members K-L and Beds II (middle-upper) and III at Olduvai, as well as by the sub-Karari unit at Koobi Fora. *Cercopithecoides kimeui* is absent at Koobi Fora, but the type cranium is from the upper half of Bed II and one tooth probably derives from Bed III; *Rhinocolobus* reappears briefly at Omo; two smallish papionins (*Cercocebus* and small *?Papio*) co-occur; and *T. oswaldi* is relatively common. This zone is poorly defined as yet, and has no upper limit, but like zone AC1, I include its contents for the record. It may be roughly divided into lower and upper between Beds II and III and submembers L3 and L4.

#### Comparisons of results based on other taxa and studies

It is first interesting to compare this zonation with the other common primate group in these deposits, the Hominidae. Based especially on data presented in HOWELL (1978) and WHITE & al. (1981), supplemented by my own additions and interpretations of taxa (see DELSON, 1981), the ranges of four

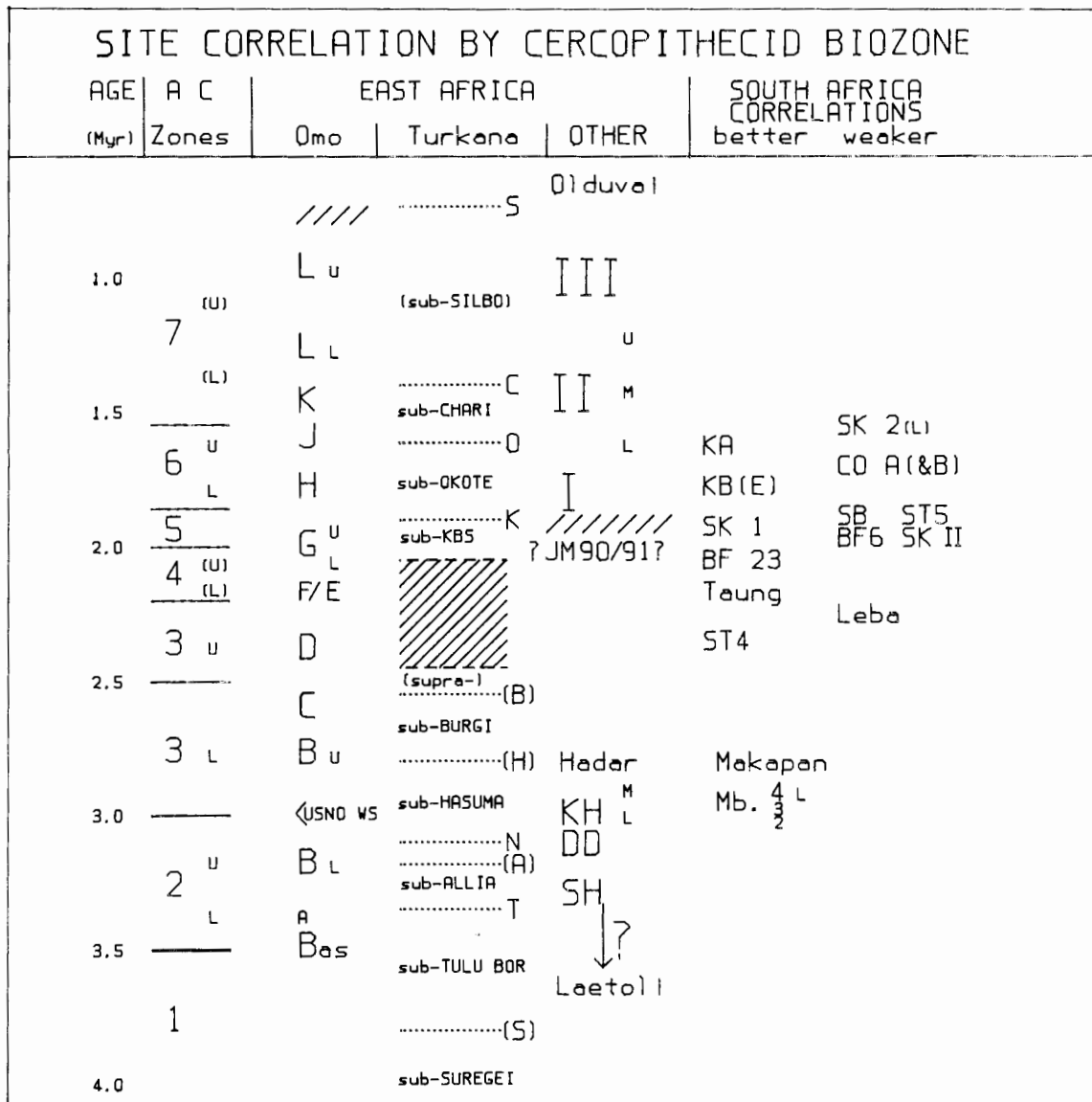


Fig. 3. Correlation of Plio-Pleistocene African site units by cercopithecoid biozones. The framework of Fig. 1 is simplified and to it have been added the Chemeron Fm. locality JM 90/91 and a number of southern African site units whose position is determined (more or less securely) by reference to the AC zones of Fig. 2. Abbreviations used here are identified in Table 2.

species (taking *A. afarensis/affricanus* together due to problems in identifying partial dentitions) are included in Figure 2. It appears that the change from „gracile” australopiths to robusts takes place in zone AC4, as is true for other primate species; *Homo cf. habilis* may occur rarely at the end of this interval. AC5-6 is the major zone of overlap between robusts and *habilis*, with the „transition” to *Homo erectus* occurring within AC6, near where I have divided it into lower and upper subzones. Thus, the cercopithecoid zonation fits well with hominid data, and the hominids may some day be includable in a primate zonation.

In terms of broader correlation, the Plio-Pleistocene boundary (about at the top of the Olduvai normal magnetic subchron or „event”) approximates the intra-AC6 interface as well. This means that, as now understood, *Homo erectus* and perhaps *Gorgopithecus* are effective markers for the start of the Pleistocene. On the other hand, the presence of *Parapapio*, *Paracolobus*, *Papio (Dinopithecus)* and probably *Homo habilis* are indicators of Pliocene time (as well, of course, as are those taxa which disappear earlier in the record, such as *Theropithecus darti*, *T. brumpti* and probably „gracile” *Australopithecus*).

Most of the groupings of site units in this zonation are in agreement with evidence from other faunal and geochronologic dating. Makapan is placed in zone AC3 (lower) because its *Theropithecus darti* is slightly larger than and perhaps derived compared to that from Hadar, although this makes it younger even than my reinterpreted paleomagnetic age. I look forward to fossils from southern site units older than Makapan (perhaps Sterkfontein members 1 - 3?), as well as more definitive dating of the several known units, in hope of clarifying this problem (see most recently PARTRIDGE, 1982).

I have also examined the studies of other taxa from the Shungura Fm. (in part as the result of a much-appreciated suggestion by Bill KIMBEL) to determine if they also found a „relay” or transition zone as I did. BEDEN (1979) basically looked at only one species, *Elephas recki*, through the Shungura, with its subspecies („stages” for MAGLIO, 1973) indicating chronology. There is one form known from upper member F through mid member G and also the sub-KBS unit at Koobi Fora and Olduvai Bed I and lower II; this is close to my AC4 but with AC5-6 units from Olduvai. Another is not seen at Omo but found in the lower sub-Okote and upper Bed II units. The former „association” of BEDEN was also the first without *Loxodonta*. Of more interest are HARRIS & WHITE’s (1979) suid findings based on more taxa. In lower member G at Omo co-occur the last *Notochoerus euilus* and the first *Metridiochoerus hopwoodi* and *M. modestus* (the latter also occurs first at Olduvai Bed I) – this seems to be a „relay” comparable to that between *Parapapio* and *Papio*. No other East African sequences really preserve this interval well – it lies below Olduvai Bed I and mostly in the Kcobi Fora hiatus. HARRIS & WHITE (1979: 79) indicate that the two *Metridiochoerus* species are rare in their „later unit 3” faunas, but in fact their Appendix I (pp. 94-95) shows that only one such fauna, from area 12, has *M. hopwoodi* while *M. modestus* never occurs. More detailed analyses of bovids and carnivores of this time period from Omo and Koobi Fora will be interesting to compare further.

The South African sequence has most recently been reviewed by VRBA (1982) concentrating on bovids, but utilizing all available data. Most of her results accord well with mine, including her placement of Taung. This site has long been a sore point, especially after PARTRIDGE (1973) and BUTZER (1974) suggested that the hominid skull might be younger than 1 Myr. PARTRIDGE (1982) has essentially retained this view, expanding further upon it in a manner which may help to resolve the confusion. He noted that PEABODY (1954) reported the geology of the area on the basis of the University of California expedition of the late 1940’s, which yielded many primate fossils I am now analyzing. PEABODY distinguished a lower „dry”-phase and an upper „wet”-phase of the Taung deposits, a distinction accepted by both PARTRIDGE and BUTZER. Although the first two authors agreed that the Taung hominid was associated with the upper unit, BUTZER (1974) could not find any distinction among matrix samples from the baboons which I provided him, and thus questioned the dichotomy. In the California material, there is no difference between the monkeys from the two named layers: both have *Parapapio antiquus* and *Papio izodi* in roughly equal numbers, as far as they can be identified. Thus, if the Taung hominid is really associated with the „wet”-phase deposit, it is indeed dated by the Taung monkeys to AC 4. Although some early studies thought Taung the oldest site, it was WELLS (1967, 1969) who first suggested a closer link to the (younger) Swartkrans and Kromdraai units; in this, he was followed by EISENHART (1974) and me (e.g., 1974 and in SZALAY and DELSON, 1979). It may also be noted that the Taung *Cercocebus* seems more similar to that from Makapan than the form at Swartkrans 1 and Kromdraai B. VRBA (1982) discussed the rare Taung bovid sample, indicating similarity to material from Makapan through Swartkrans member 2, with closest links with the younger sites. She suggested that the monkey data supported this, based on older faunal lists. COOKE (1983) agreed with both of us that Taung lies between Sterkfontein mbr. 4 and Swartkrans mbr. 1, but while I consider it to typify an intermediate (and most important) zone, VRBA thought it a bit younger on less distinctive evidence, and COOKE placed it rather older.

Again, VRBA (1982) and I are in general agreement on the age of Swartkrans and Kromdraai, with minor inconsistencies. She found that Swartkrans member 1 bovids are closest to those from Olduvai Beds I and lower II, as well as to Omo G. But she did not indicate whether it was upper or lower G, nor did she say from where the comparable Koobi Fora specimens derived. HARRIS & WHITE (1979) also correlated the Swartkrans mbr. 1 suid with Koobi Fora sub-Okote fossils, thus in agreement with VRBA. But the Swartkrans monkeys, as noted above, show strong ties to zone AC4: *T. oswaldi*, large *P. (Dinopithecus)*, clear *Cercocebus* and large *P. (Papio)*. It is separated from that zone by the lack of either *Parapapio* or *C. williamsi*, and not likely to be part of the younger AC6.

Similarly, VRBA (1982) equivocated on the relative temporal placement of the Kromdraai B (member 3) fauna, but in VRBA & PANAGOS (1983), she reviewed this assemblage in more detail, reaching several new conclusions. Chief among these was that the site was clearly not a hominid camp, but merely an accumulation trap. As she had indicated previously, VRBA repeated that BRAIN's collection of fossils from Kromdraai B included material from four members now distinguished from in situ breccia, thus of potentially mixed level and low value; I should note that the four well-known cercopithecoid species are present in both collections, and most also in BROOM's sample, so that only one horizon may have produced all the monkeys (other than the few distinctive ones from VRBA's member 4). On the basis of morphological and metrical intermediacy of the *Australopithecus robustus* from Kromdraai B, VRBA & PANAGOS (1983) suggested that the site unit could fall between Sterkfontein mbr. 4 and Swartkrans mbr. 1, rather older than most authors have placed it. As VRBA has rejected this temporal placement on metrical, stage-of-evolution criteria for her own bovid work, I find it unfortunate that she should use it with other taxa. I accept the argument that the Kromdraai australopithecoid metrics and morphology may distinguish this population at some taxonomic level from its congeners, but that does not allow us to immediately derive a relative age for the site. Even more intriguing to me is VRBA's use of the occurrence of *Cercopithecoides williamsi* to aid in determining local environments. Assuming that all colobines are arboreal and require availability of much water, VRBA suggested that the presence of the fossil species implies moist conditions, while its absence (as at Swartkrans 1, Sterkfontein 5 and Kromdraai A) indicates relative aridity; this was supported by bovid frequencies as well. Unfortunately, VRBA failed to recognize the *C. williamsi* was probably the most terrestrial colobine ever (SZALAY & DELSON, 1979; BIRCHETTE, 1981; LEAKEY, 1982) and may have had less stringent water requirements than living arboreal forms. I have suggested above that Kromdraai B might better be placed slightly younger than Swartkrans 1, rather than older. The problem is comparable to that between Swartkrans 1 and Sterkfontein 5 (which yielded only a single indeterminate monkey): „The apparently less advanced *Homo habilis* from ST5 ... seems associated with abundant Early Acheulian artifacts and faunal elements indicating a marginally later deposition date [than SK1 with a] more advanced [hominid].“ (VRBA, 1982, p.735). Here it seems that a possibly more conservative australopithecoid at KB lived more recently than the SK1 taxa.

I agree with VRBA (1982, 1983) that Kromdraai B is somewhat older than A. Differences from Kromdraai A are few, mainly the presence of *Australopithecus* and *Cercopithecoides*, and these two units, as well as the nearby Cooper's units, are probably close in age but perhaps of differing micro-environment. I might tentatively suggest that we consider a trend to increasing surface water availability from SK1 through KB to KA, with KA so moist that neither *Australopithecus* nor *Cercopithecoides* was present, while *Gorgopithecus* was the dominant large baboon. Another questionable site is Swartkrans mbr. 2, which BRAIN (1982) showed to contain *Australopithecus robustus*, presumably in the lower levels. Together with the large *Cercopithecoides* cf. *williamsi*, this suggests correlation to upper AC6 or perhaps lower AC7, where I have tentatively placed it on the basis of VRBA's (1982) interpretations. Work in progress by both of us should permit our conflicts to be resolved and a consensus reached on the relative age of all the South African Pliocene-Pleistocene site units, both locally and with regard to eastern Africa as well.

### Summary and conclusions

I have suggested that no currently available temporal framework attempting to correlate eastern and southern African Pliocene and early Pleistocene sites is fully accepted. Thus, I proposed to develop one based on faunal correlation by cercopithecoids, of which numerous taxa are known in many site units, with several in both eastern and southern localities. In seeking a methodology which was acceptable in terms of not violating theoretical constraints supplied by cladistic and „punctational“ views of systematics, I rejected the stage-of-evolution and *niveaux repères* approaches and questioned some of the assumptions inherent in the use of first and last appearance (or discovery) datum planes to define faunal units. Instead, I prefer to work toward a zonation based on co-occurrence of taxa in calibrated sequences, which can then be correlated to external site units.

To that end, I re-evaluated the calibration and correlation of the Omo, Koobi Fora and Hadar sequences, offering the diagram of Figure 1. The South African site of Makapan is also included there, based on an interpretation of partial magnetostratigraphy. Table 1 presents the most complete distribution of all recognized taxa (and morphs) in over 60 site units from the Pliocene and early Pleistocene

of sub-Saharan Africa. Several taxonomic notes are provided to explain novelties of that table. For example, the large papionin from Omo previously termed *Papio* sp. is identified as congeneric with South African *Dinopithecus*, in turn ranked as a subgenus of *Papio*. The type of *Papio quadratiostris* is tentatively considered as representing the same species as the younger Omo fossils, although ECK has suggested it to be an early *Theropithecus*. The small South African baboons *Papio izodi* and *P. angusticeps* appear distinct, with the latter close to living *P. hamadryas kindae* in facial proportions. Specimens previously termed *Parapapio jonesi* from Kromdraai, Swartkrans and Taung (and *Cercopithecoides* at the last site) are all actually referable to *Cercocebus* spp. instead.

In Figure 2, I present a first attempt at a zonation of this time interval based solely on the ranges and associations of fossil cercopithecids. This figure includes the ranges of 12 taxa: seven distinct species, two polytypic genera and three groups of species within *Papio*. The sequence of ranges is defined by East African semicontinuous sites with multiple units, to which other eastern and numerous southern assemblages are correlated. The results of this correlation, combined with the calibration of Figure 1, are presented in Figure 3.

Seven numbered AC (African cercopithecoid) zones are distinguished, of which five are subdivided into upper and lower parts. Zone AC3 permits separation of Makapan (older) and Sterkfontein (younger) within the interval dominated by *Parapapio* species. Zone AC4 is a „relay“ interval during which several Pliocene taxa occur jointly with their Pleistocene replacements, and this allows good correlation between the Omo Shungura members E-G (lower) in the east and Taung (and part of Bolts Farm) in the south. Zone AC5 contains more „modern“ taxa, with a few holdovers, such as a great variety of colobines; Swartkrans 1 fits best here. AC6 seems to span the Pliocene-Pleistocene boundary, as defined by the top of the Olduvai subchron, and may include the Kromdraai B locality below and the A locality above that horizon. Zones AC1 and AC7 are less well defined, as older and younger sites are poorly documented.

Four hominid species or groups („gracile“ and „robust“ australopiths, *H. habilis* and *erectus*) are known in the same interval, and their ranges as seen in Fig.2 fit well into the cercopithecoid pattern. The same „relay“ is observed between the australopiths in AC4, for example. *Homo erectus* and, to a lesser degree, *Gorgopithecus*, serve as primate markers of the start of the Pleistocene, while several other taxa are good indicators of (late or general) Pliocene age. Elephants and especially pigs (as based on HARRIS & WHITE, 1979) from eastern Africa also accord well with the zonation pattern and most correlations based on monkeys; the Omo member G „relay“ is again quite clear.

The major goal of this project, of which this paper represents an interim report, was to better place the southern African site units by comparison to those in the east. I consider that after Makapan (whose magnetostratigraphy is suggestive but still under fire), the Taung monkeys represent the best correlated of the South African sites. Once thought to be the oldest australopith deposit, Taung has more recently been suggested by WELLS, EISENHART, DELSON and now VRBA & COOKE to fall between Sterkfontein mbr. 4 and Swartkrans mbr. 1. VRBA (1982) has found that other Taung taxa are less clearly indicative of age than are the abundant monkeys, which suggest an AC4 age just older than 2 Myr. Although PARTRIDGE & BUTZER have thought the Taung hominid to be much younger than the other fauna, in fact close to 1 Myr in age, PARTRIDGE's latest review (1982) suggests to me that it might well be associated with some of the cercopithecids. Since these do not change through the two or more subdivisions at Taung, I suggest that the monkeys do closely date the type of *Australopithecus africanus*, still the youngest member of its species.

The relative ages of Swartkrans 1 and Kromdraai B (and A) have recently been reconsidered by VRBA & PANAGOS (1983), who suggested the latter to be the oldest of the post-Taung site units. I reject that view, on the basis of a moderately strong argument about replacement and relative frequency of the papionins and *Cercopithecoides* at the three localities; other nearby site units (e.g., Bolts, Coopers and Schurveberg) can also be less securely placed in zones AC4, 5 and 6 on this basis. Similarly, the assemblages from Makapan and Sterkfontein mbr. 4 are both placed in AC3, but linked to AC2 and AC4, respectively. The site of Leba, Angola, is also placed late in AC3 by its monkeys – scarce representatives of two bovids, a carnivore and a hippopotamid offer no chronologic indications whatever.

Thus, the work to date has allowed greater precision in arranging the southern African site units in a relative temporal sequence, as well as some strong to moderate linkages with dated eastern units or horizons. Combined with careful recalibration of the long and better-dated eastern sequences (Omo, Koobi Fora, Hadar and Olduvai), refinement of this approach through taxonomic revision and determi-

nation of relative taxon frequencies should permit an even clearer zonation and correlation in the near future.

### Acknowledgments

I thank Drs. RICHARD TEDFORD, RAYMOND BERNOR and TIM WHITE for helpful comments on versions of this manuscript or its verbal presentation. Dr. FRANK BROWN provided much assistance interpreting his results on the stratigraphy, dating and correlation of the Omo Shungura and Koobi Fora Formations and also checked some of the Koobi Fora locality data. Dr. ELIZABETH VRBA discussed aspects of the stratigraphy, ecology and dating of the several South African sites with me on numerous occasions, while Drs. GERALD ECK, TOM GRAY, CLARK HOWELL, DONALD JOHANSON, MITSUO IWAMOTO, CLIFFORD JOLLY, MEAVE LEAKEY and ERIC MEIKLE shared their views on the fossil monkeys from eastern Africa and their provenance. Mr. WILLIAM EISENHART graciously shared with me his insights into South African fossil cercopithecids and donated to me his metrical data on them after his departure from academe. I gratefully appreciate all of their assistance. My studies of fossil monkeys would not have been possible without the help and facilities provided by numerous curators and other colleagues, especially Drs. BOB BRAIN, ELIZABETH VRBA, PHILLIP TOBIAS, JAMES KITCHING, MIKE RAATH, JUDY MAGUIRE, BRETT HENDEY, MEAVE and MARY LEAKEY, DONALD JOHANSON, CLARK HOWELL, KARL-HEINZ FISCHER and the late BRYAN PATTERSON.

Early phases of this research were supported by a Columbia University Travelling Fellowship, grants from the Wenner-Gren Foundation and the L.S.B. Leakey Foundation and City University of New York Faculty Research Awards (11483, 11862, 12118 and 12985). Major support for the development of the biochronological zonation presented here was provided by the CUNY PSC-BHE grant program (awards 13453 and 13610) and especially by the National Science Foundation, Anthropology program (awards BNS79-15091 and BNS81-13628). Once again, I gratefully acknowledge the support of these agencies.

Finally, I thank Drs. JENS FRANZEN and PETER ANDREWS for inviting me to present these ideas at the symposium honoring Professor G.H.R. VON KOENIGSWALD and to formally set this preliminary version of my work to paper. I dedicate this study to the memory of Professor VON KOENIGSWALD and his work, in gratitude for his generosity to me throughout our association.

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