Lal are helpful in underlining inherent difficulties in the interpretation of population genetic data. The high rate of inbreeding found by the more direct heterozygosity measurement would not have been predicted by linkage analysis of the data set.

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Faunal Evidence and Sterkfontein Member 2 Foot Bones of Early Hominid

Ronald J. Clarke and Phillip V. Tobias (*1*) state that they have found the "oldest South African hominid" in Sterkfontein Member 2, as the STW 573 foot remains demonstrate a mosaic of ape-like and human-like features. Their dating of the deposit, between 3.5 and 3.0 million years ago (Ma), is somewhat tenuous, as it is based largely on presumed sedimentological rates that could vary dramatically with different cave morphologies and environments (*2*). Considerations of the associated Member 2 faunal assemblage suggest the strong possibility of a more recent age.

Chronological seriations of the southern African faunal assemblages (*3*), however, place Sterkfontein Member 2 just prior to Sterkfontein Member 4 and after the Makapansgat and Taung fauna. All of the Sterkfontein Member 2 species appear in Sterkfontein Member 4 (circa 2.6 to 2.5 Ma) or in later sites, or in both, under a variety of environmental and taphonomic conditions. However, three of the species (namely, *Papio izodi*, *Chasmaporthetes siberbergi*, and *Megantereon cultridens*), indeed genera, which commonly appear at these later sites, do not appear at Makapansgat Members 3 (circa 3.2 to 3.0 Ma) or 4 (circa 3.0 to 2.9 Ma). It is possible that all of these species were missed by the accumulating agents at Makapansgat Member 3, but this seems highly unlikely; Makapansgat is the richest southern African fossil source in terms of biodiversity, with more than 40 large mammal species represented (as compared to approximately 40 such species known historically from the area). It would be unexpectedly idiosyncratic for three species to appear in the fossil record before Makapansgat, be totally absent in the Makapansgat assemblage, and then reappear in the Sterkfontein Member 4 and later sites.

Given the variety of later sites at which these species appear, temporal considerations override ecological or taphonomic explanations of the differences between assemblages.

Thus, on the basis of the associated fossil fauna, the Sterkfontein Member 2 foot bones do not appear to be as old as Makapansgat Member 3 at 3.0 Ma, but fall closer in time to Sterkfontein Member 4. If this dating were correct, then STW 573 may belong to *Australopithecus africanus*, a hominid species long known to have had some apelike features in its postcranial morphology.

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3. With the use of time-sensitive species seriation as described by J. K. McKee *et al.* [*Am. J. Phys. Anthrop.* **96**, 235 (1995)] and J. K. McKee [*Palaeont. Afr.* **32**, 1 (1995)].

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Response: The eroded and disconformable contact between Beds C and B and the interdigitating contact between Beds B and A, of Sterkfontein Member 4; and the thick band (0.5 m) of recrystallized mesocrystalline calcite interposed between the top of Member 2 and Bed B of Member 3 (*1*) represent time lapses in the history of deposition, prior to the laying down of Beds B, C, and D of Member 4 from which most fossil remains emanate (*2*). The upper beds of Member 4 have a probable dating of earlier than 2.6 Ma. As a depth of about 15.0 m separates them from Member 2, and as this depth of deposit includes at least four interfaces or flowstone horizons, our claim that Member 2 must be older than 3.0 Ma and probably nearer to 3.5 Ma is modest.

The sequence of Members, originally worked out by Partridge (*1*), has been confirmed by his analysis of cores extracted during diamond drilling of the full thickness of the six Members (*3*).

With regard to the rate of sedimentation, according to Partridge [note 27 in our report (*4*)], the 6.5-m *average* thickness of Member 3 would probably have taken 0.3 to 0.5 Ma to accumulate. McKee questions this and states (in note 2) that McFadden *et al.* (*5*) postulate that "a similar depth of deposit at Makapansgat [would] have accumulated in under 130 thousand years." This is incorrect. At Makapansgat, the depth of deposit from the Gilbert/Gauss transition in Member 2 to the upper of two intervals of apparently reversed palaeomagnetism (Kaena event) in the lower part of Member 4 is 9.5 m (*6*). The lapse of time between these two levels under the earlier calibrated polarity time scale is 0.52 Ma (*5*), but under the recalibrated scale (*7*) it is 0.54 Ma. This is equivalent to 0.37 Ma for the deposition of 6.5 m (not 130,000 years) and to 0.57 Ma for that of the 10-m upper limit of thickness of Member 3 (*1*). These estimates of 0.37 to 0.57 Ma for the time taken for Member 3 to accumulate are close to the 0.3 to 0.5 Ma we cited [note 27 in (*1*)]. Even if we adhere to the earlier calibrated polarity time scale, the estimated time lapse is 0.36 to 0.55 Ma. Thus, the application of the Makapansgat rate of sedimentation to the Sterkfontein Formation corroborates and strengthens our claim that Member 2 is appreciably older than Member 4: our new calculations on this basis indicate that Sterkfontein Member 2 might have been as much as 0.8 Ma older than Beds B and C of Member 4.

The carnivoran species existed in Africa before 3.5 Ma and persisted to end-Pliocene or later. This long time-span nullifies their use for dating Member 2.

As to the primates, *Parapapio broomi* has hitherto been identified not only from Sterkfontein Member 4, but also from the somewhat older Makapansgat Members 3 and 4. The genus *Parapapio* is known in the African fossil record, according to McKee, from 4 to 2 Ma, while White *et al.* (*8*) have identified cf. *Parapapio sp.* among the fauna from Aramis, Ethiopia, dated to 4.4 Ma. The long range of the genus, and the hitherto known span of the species, render this cercopithecoid of little value for resolving the dating of Sterkfontein Member 2. Its presence in Member 2 does not preclude the assignment of a dating of 3.0 Ma or older.

Papio izodi, which McKee identified from Member 2, is at present represented by remains from only two southern African sites, Taung (Hrdlicka Deposits) and Sterkfontein Member 4 (*9*). Although McKee *et al.*

(9) regard this as a "time-sensitive" species, its previous identification at only two sites, which on his analysis are either synchronic or separated by no more than 0.1 to 0.2 Ma, means that it is likely that only a part of this species' range in time has so far been sampled. It cannot thus have any bearing on the dating of Member 2. Its absence from Makapansgat cannot be used as dating evidence, for it may indicate taphonomic or environmental factors, a principle which McKee and others recognized.

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More *Haemophilus* and *Mycoplasma* Genes

The sequencing of two entire genomes of free living organisms by Fleischmann *et al.* and by Fraser *et al.* is an outstanding achievement (*1*) and provides a rich basis for further studies. The methods used in these studies to detect genes, however, are biased toward protein coding genes and ribosomal and transfer RNAs. These methods do not reflect the significance of additional RNA species that vitally contribute to the functioning of a cell. In the 0.54- and 1.83-megabase *Mycoplasma genitalium* and *Haemophilus influenzae* genomes, several small stable RNA species remained undetected (*1*): I have located (*2*) the *M. genitalium* and *H. influenzae* genes encoding 4.5S RNA [part of the SRP homolog of Bacteria (*3*)], ribonuclease (RNase) P RNA (*4*), 10*Sa* RNA, and the *H. influenzae* 6S RNA (Table 1). The cellular roles of the latter two RNAs are still unknown [10*Sa* RNA may be involved in the COOH-terminal extension of protein (*5*)]. The proposed half-tRNA–like structure for a portion of 10*Sa* RNA (*6*) is conserved and further supported by compensating base changes in the *M. genitalium* and *H. influenzae* orthologs. In *M. genitalium*, the RNase P RNA gene is tightly linked with the 10*Sa* RNA gene (divergently transcribed), while in *H. influenzae*, the two genes are about 400 kb apart (*7*). The two RNA genes are so close in proximity that their putative −10 promoter regions (TATAAT) overlap by four nucleotides. This may imply a concerted gene regulation.

Very likely, there are more hidden RNA treasures in the genomes of *M. genitalium* and *H. influenzae*. Analysis of the many gaps between open reading frames (ORFs) may reveal undiscovered functional RNA species.

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Table 1. RNA species detected in *M. genitalium* and *H. influenzae*. RNA sequences are available on the World Wide Web at URL <http://www-ifi.uni-muenster.de/xpath/mge-hin-rna.html>.

RNA	Bacterial species*	Query sequence†	Position‡
4.5*S*	Mge	Mpn (S76009)	325,924–326,002§
	Hin	Eco (X01074)	1,223,295–1,223,408
6*S*	Mge	Eco, Hin, Pae (M12965, U32767, and Y00334)	None‖
	Hin	Pae (Y00334)	905,485–905,683
10*Sa*	Mge	Mca (D13067)	406,541–406,928
	Hin	Eco (D12501)	1,356,974–1,357,339§
RNase P	Mge	Mhy (X69982)	406,137–406,518§
	Hin	Eco (U18997)	1,745,841–1,746,216§

*Abbreviations: Eco, *Escherichia coli*; Hin, *Haemophilus influenzae*; Mca, *Mycoplasma capricolum*; Mge, *Mycoplasma genitalium*; Mhy, *Mycoplasma hyopneumoniae*; Mpn, *Mycoplasma pneumoniae*; and Pae, *Pseudomonas aeruginosa*. †Searched with the accession number listed. ‡The exact 5′ and 3′ ends of the mature *M. genitalium* and *H. influenzae* RNAs were not experimentally determined and are inferred from related RNA sequences and secondary structures. §RNA gene is complementary with respect to the numbered sequence. ‖No match was found with the search program applied.

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7. In *M. genitalium*, the 10*Sa* gene is also adjacent to an ORF that has putatively been identified as aminopeptidase P (pepP). In *H. influenzae*, the 10*Sa* gene is in close proximity to $tRNA^{Met}$-C, nusA, and infB. In *Thermus thermophilus*, a portion of the 10*Sa* RNA gene (accession number Z48001, pos. ~220-1) has been sequenced; it is also closely linked to the nusA/infB operon. HI0858 ORF (adjacent to the 6*S* RNA gene) has sequence similarity to the *E. coli* ORF located downstream of 6S RNA.

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The publication of the complete genomic sequences for *H. influenzae* by Robert D. Fleischmann *et al.* (*1*) and *M. genitalium* by Claire M. Fraser *et al.* (*2*) presents the first opportunities to compile complete catalogs of proteins for free-living organisms. It is important that such catalogs be as comprehensive as possible, especially in the case of *M. genitalium*, which is believed to define a "minimal gene content" for a bacterium (*2*). Refinement of the descriptions within the *H. influenza* gene catalog in the study by Fleischmann *et al.* (*1*) has already been attempted by Casari *et al.* (*3*). However, critical examination of these catalogs is an essential prerequisite to their further analysis, as they are incomplete.

We have found an additional 17 protein-coding regions beyond the 1743 reported for *H. influenza* and 3 in addition to the 470 reported for *M. genitalium* using our previously described (*3*) database search strategy (Table 1). These new genes range from proteins ubiquitous to life (three ribosomal proteins, a cold-shock domain-type DNA binding protein, and a DNA repair enzyme) to genes similar only to proteins of unknown function.

In several cases, the close proximity of these new genes to those previously reported or to genes of related function suggests operon structures. For example, in *M. genitalium* the DNA repair enzyme fpg (M2) is preceded by DNA polymerase genes (MG261 and MG262), and the atpB (M4) gene is embedded among nine other genes for the adenosine triphosphatase (ATPase) complex (MG405-