

Neogene African catarrhine primates: climatic influence on evolutionary patterns

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The meeting at Lamont in September last year was a rather informal gathering designed to examine the question of climatic influence on evolution on southern continents from a variety of perspectives. I agreed to present data on the ranges of all African Neogene higher primates and to examine the record of their evolution for evidence of correlation with climatic pulses. For this summary, I have combined data from my own observations with those from a number of recent reports to yield an approximation to the pattern of first and last records of each 'species' published to date. Figure 1 presents this pattern through time, roughly reflecting the cycle of origins and extinctions which actually occurred. The data for Fig. 1 derive mainly from Szalay and Delson,¹ especially for the cercopithecids. Modifications for non-cercopithecoid taxa were based on reports by Andrews (ref. 2 and pers. comm.), Harrison,^{3,4} Ishida *et al.*,⁵ Pickford⁶ and A. Walker (pers. comm.). The dating of sites yielding catarrhine taxa is based especially on Ishida *et al.*,⁵ Pickford⁶ and Delson.⁷ A detailed presentation and analysis of these data is now in preparation.

The Neogene is here taken to include the Pleistocene, in the increasingly accepted view that the Cainozoic may best be divided into the two periods, Paleogene and Neogene, rather than Tertiary and Quaternary. In constructing Fig. 1, lines were drawn between successive data points only when there was continuity of mode. Thus, taxa which occur only at one site or group of penecontemporaneous site units are not connected to others. The plotted data points represent taxa accepted here as morphospecies, although many of them (especially the isolated occurrences) are poorly known and probably do not represent analogues of modern biospecies. Because of the relatively higher temporal resolution of Plio-Pleistocene geochronology (e.g. see ref. 7), the points after 6 Myr are recorded at 0.5-Myr, rather than 1.0-Myr intervals.

It is clear from Fig. 1 that there were two main intervals during which numerous catarrhine species are represented in the African fossil record: the later early and early middle Miocene (20–14 Myr ago) and the Plio-Pleistocene (5–0 Myr). The African earliest and later Miocene are poorly fossiliferous at present, and the few known primates have been studied only in a preliminary fashion. Therefore, it may be somewhat premature to put much reliance on the answers to probing questions about the relationship between evolutionary tempo and climatic patterns which are also just becoming clarified. For the mid-Miocene interval, it is my opinion that the observed pattern of the origin and extinction of catarrhine species is more dependent on the vagaries of site preservation than on climatic influences. On the other hand, the composition of catarrhine (and many other mammalian) assemblages changes greatly between 17 and 15 Myr ago, in a manner suggesting the spread of more open environments and a major climatic shift (see also Pickford⁶ and Bonnefille⁸).

The increase in the number of catarrhine species in the early Pliocene reflects the greater number of site units collected from this interval. However, as I discussed previously (ref. 7; see also Leakey⁹), there is an apparent change in the composition of cercopithecoid assemblages between 2.5 and 2.0 Myr ago (or slightly earlier, given the newest East African geochronological calibra-

tion of Brown *et al.*¹⁰). This interval corresponds to a cooling discerned by Bonnefille^{8,11} after 2.4 Myr ago and may be represented at Koobi Fora based on the continuing work of Vincens.¹²

Vrba¹³ has noted a peak in the number of origins of bovid species around 2 Myr ago and suggested a correlation with global climatic changes which is supported by the primate data. Her implication of a link to the hominid cladogenesis between *Australopithecus* and *Homo* at this date is apparently less valid. The geometry of Pliocene human phylogeny still unclear, but the more conservative *A. robustus* is first known after 2.0 Myr, significantly later than the first appearance of the derived *A. boisei* (~2.5–2.4 Myr in Omo Shungura Member D). *Homo habilis* is first reported between these two data (~2.1–2.0 Myr in the sub-KBS unit at Koobi Fora and perhaps in Omo Shungura Member upper G). This suggests a division of the two main clades well before 2.5 Myr ago, whatever the placement of *A. africanus* and *A. afarensis* with regard to the younger taxa. It would not surprise me if the former species was already on the *Homo* clade, while the latter was near the common ancestry of the *Homo* and 'robust' lineages, given the mosaic of features found in Hadar crania (and postcrania). This would imply a division as early as 3 Myr, with the 'robust' ancestral morphotype similar to *A.*

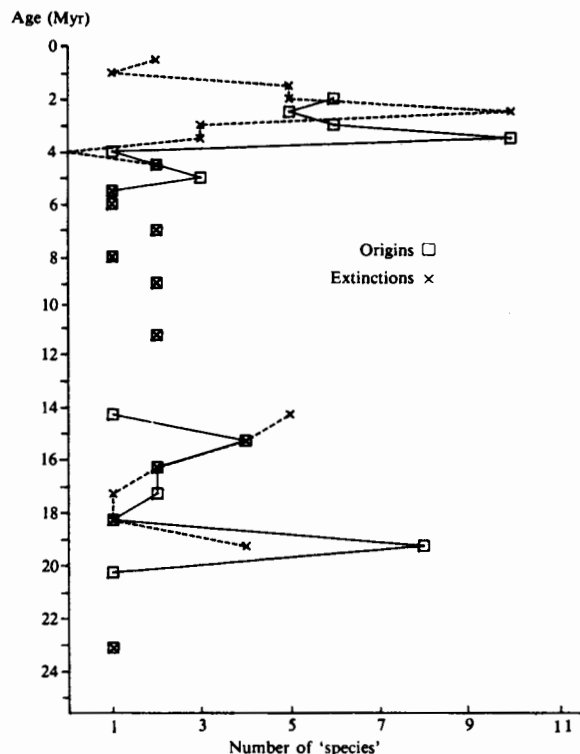


Fig. 1. First and last appearances of catarrhine morphospecies of the African Neogene. Isolated 'x's in boxes indicate species with no known temporal range of any significance. After 6 Myr, taxa are plotted at 0.5-Myr intervals.

africanus gnathically but to the larger Hadar individuals in the neurocranium. Such a splitting time would correlate with Vrba's lowest interval of bovid speciation and a time of climatic stability, but would correspond to the period of greatest catarrhine (essentially cercopithecoid) speciation.

The Pleistocene interval on Fig. 1 is nearly empty, as I have not included information about modern taxa with sparse fossil records. Such data would tend to be more confusing than helpful at this stage of our understanding. The late early and middle Pleistocene in Africa has yielded several good mammalian assemblages, but the small and medium-sized primates, especially those inhabiting forested areas such as the bulk of living taxa do, are not well preserved. Moreover, the dating of such assemblages is notoriously uncertain. Presumably most living taxa originated over the past million years, often as a direct or indirect result of middle Pleistocene climatic fluctuations, for example, in refugia.

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The $\delta^{18}\text{O}$ signal of deep-sea planktonic foraminifera at low latitudes as an ice-volume indicator

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It has been recognized for many years that there is a strong ice-volume component to the deep-sea $\delta^{18}\text{O}$ record. Many workers favour the interpretation of the benthic foraminiferan signal as the 'best' record. This probably stems from Shackleton's¹ elegant success in reversing the story of 'Pleistocene palaeotemperatures' suggested by Emiliani.² Furthermore, benthic foraminifera are less susceptible to dissolution than planktonic foraminifera and therefore tend to be more uniformly available in deep-sea cores.

Unfortunately, there is no *a priori* argument for limits to the temperature fluctuation of bottom water. One can offer the feeble point that bottom water will not freeze, but there are no upper temperature limits. Indeed, comparison of the benthic $\delta^{18}\text{O}$ record with the record of terrace elevation at the time of late Pleistocene glacio-eustasy led Dodge, Fairbanks and Maurrasse³ to propose that the benthic $\delta^{18}\text{O}$ signal is predominantly a temperature indicator which happens to be in phase with the ice-volume signal at isotope stages 5.1, 5.3 and 5.5. It is unfortunate that Dodge *et al.* did not choose compare their data with the $\delta^{18}\text{O}$ record of low-latitude planktonic foraminifera. There is no

Table 1. Summary of new *A. palmata* $\delta^{18}\text{O}$ data from diamond core drill samples of late Pleistocene terraces in Barbados.

Terrace	Average $\delta^{18}\text{O}$ (‰, PDB)	s.d.	n
Worthing (Barbados I) (isotope stage 5.1 equiv.)	-3.28	±0.23	(9)
Ventor (Barbados II) (5.3 equivalent)	-3.28	±0.21	(9)
Rendezvous Hill (Barbados III) (5.5 equivalent)	-3.63	±0.11	(9)

a priori argument for a constant sea-surface temperature in tropical and temperate regions away from upwelling zones. Further, the empirical data of CLIMAP⁴ substantially supports this *a priori* argument. These temperature estimates from faunal analyses indicate some areas as a little cooler, some a little warmer, throughout the tropics and the regions of low latitude. Had Dodge *et al.* compared their terrace data with information on planktonic isotopes from these regions, they would have found

Table 2. Comparison of terrace elevation data with isotope data from corals and low-latitude planktonic foraminifera. [Data reported as (mean Δ) ± (confidence about mean, 95% confidence limits) (number of independent estimates).]

Isotope stage comparison	Terrace elevation data, converted to $\delta^{18}\text{O}$ equivalent ^a $\Delta\delta^{18}\text{O}$ (‰)	Barbados Corals		Low-latitude planktonic foraminifer ^c $\Delta\delta^{18}\text{O}$ (‰)
		Ref. 5 $\Delta\delta^{18}\text{O}$ (‰)	New data ^b $\Delta\delta^{18}\text{O}$ (‰)	
(5.1–5.5)	+0.24 ± 0.1 (3)	+0.54 ± 0.47 (7)	+0.35 ± 0.2 (9)	+0.34 ± 0.2 (5)
(5.3–5.5)	+0.21 ± 0.1 (3)	+0.52 ± 0.1 (15)	+0.35 ± 0.2 (9)	+0.30 ± 0.1 (5)

^aElevation data from Barbados, New Guinea and Haiti converted to $\Delta\delta^{18}\text{O}$ as in ref. 3. ^bTable 1. ^cData from: Emiliani C. (1958). *J. Geol.* **66**, 264; Emiliani C. (1966). *J. Geol.* **74**, 109; Emiliani C. (1978). *Earth Planet. Sci. Lett.* **37**, 349; Shackleton N.J. and Opdyke N.D. (1973). *Quat. Res.* **3**, 39; Thierstein H.R. *et al.* (1977). *Geology* **5**, 400.