

## Evolutionary tempos in Catarrhine Primates

par

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**Résumé.** Afin d'examiner les fréquences relatives de gradualisme versus équilibres ponctués, j'analyse les dossiers fossili-fères des catarrhiniens bien représentés sous forme de stase ou de changement graduel. Les macaques qualifiés comme des « fossiles vivants » à cause de leur rétention de plusieurs traits morphologiques trouvés dans les plus anciens cercopithecines de – 15 M.A. Les colobinés européens *Mesopithecus* et *Dolichopithecus* et le colobiné africain *Cercopithecoides* semblent montrer de la stase relative dans des mesures dentaires pendant 1,5 – 5+ M.A., avec la possibilité des origines des espèces ponctués de plus. Le cercopithecine africain *Theropithecus* paraît indiquer croissance de taille graduelle pendant 3 M.A., mais on trouve la suggestion des périodes de stase aussi. La plupart de l'évolution humaine Plio-Pleistocène est caractérisée apparemment par stase et ponctuation, mais le dossier des derniers quelque cents mille années était dominé par l'évolution phylétique graduelle dans l'espèce *Homo sapiens* (au sens large). Nous devons travailler pour des définitions soigneuses de gradualisme et d'équilibre ponctué comme des modalités prédictives avec des critères convenus pour les éprouver dans des études paléontologiques prochaines.

**Abstract.** In order to assess the relative frequency of gradualism vs. punctational evolution, I analyse the fossil records of well-represented catarrhines in terms of stasis or gradual change. The macaques qualify as "living fossils" in retaining many morphological features seen in the earliest cercopithecines of 15 M.A. ago. The European colobines *Mesopithecus* and *Dolichopithecus* and the African colobine *Cercopithecoides* appear to show relative stasis in dental measures over 1.5 – 5+ M.A., with the possibility of punctational species origins as well. The African cercopithecine *Theropithecus* seems to document gradual size increase over 3 M.A., but there is some suggestion of periods of stasis as well. Most of Plio-Pleistocene human evolution was apparently characterized by stasis and punctuation, but the record of the last few hundred thousand years is dominated by gradual phyletic evolution within the species *Homo sapiens* (in the broad sense). We should work toward careful definition of gradualism and punctuated equilibrium as predictive modes with agreed-upon test criteria for future paleontological studies.

Punctuated equilibria and phyletic gradualism are models of the evolutionary process which make somewhat contrasting predictions about patterns which might be observed in the paleontological (and perhaps neontological) record. As summarized by a number of the participants at this symposium, the contrasts between the two models have reduced recently, as advocates have tried to include more alternatives under their respective banners and as explicit tests have revealed that present data is often inadequate to permit unequivocal distinction. Such a discrete dichotomy is surely unrealistic, as most investigators realize, as the question is more one of relative frequency than of near-absolute dominance of one or other mode of evolution, especially given the problems involved in assigning many cases studied to a particular mode. In the spirit of this colloquium, I present some data and thoughts on evolutionary rates within one restricted but interesting animal group, the higher primates of the Old World.

As Simpson early demonstrated (1944, 1953), rate studies may be taxic or morphologic. Taxic rates involve longevity of species and tempos of origination or extinction, while morphologic rates evaluate changes within species or clades. The study of either sort of rate by literature review is often problematical, as the differing

systematic biases and philosophies of diverse researchers may be incompatible and age estimates may vary widely; these are especially troublesome with taxic rate evaluations. Contributions of original data are thus of higher value than reviews, even if they are more parochial. The matter of time scale is also central to the study of tempos – not only must sample sizes be large, but the interval studied must contain a large number of subdivisions. Schopf has argued in his preprint that 10,000-100,000 specimens are needed, which effectively denies vertebrate paleontologists any voice in the debate, and further that the long duration of most stages results in apparent elongation of species' range. Although the Neogene range of catarrhines is short for most comparisons, this interval may be rather finely divided, so that units of 0.1 or 0.25 million years (M.A.) may be used in my analyses. On the other hand, most taxa must be discarded because they are not represented in a sufficient number of localities (or time divisions) to present a pattern of any kind. Schopf, again, has argued that real paleobiospecies might only have lived 0.1 M.A. in many cases, in which case one locality or time division may represent the real lifetime of the taxon, but this can never be determined securely, or even estimated unless one is dealing with a well-sampled sequence (such as

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the Omo Shungura Fm., for example). Thus, I have ignored all such rare taxa in my search for data suitable for this review.

Most students of this debate have accepted that three aspects of the tempo of evolution may be examined in comparing the two models. 1) Stasis or [gradual] change within species; this may include the study of fossil taxa which have not significantly altered in morphology (often viewed most readily as size) over most or all of their existence, and becomes the question of "living fossils" if the taxon happens to be alive today; 2) species longevities, irrespective of change within the species; and 3) rate of origination and duration of speciation "events". The last of these may be most difficult in practice, as it is always questionable whether "origin" of a new species, punctuational or gradually, is a matter of speciation or of immigration (see Schankler, 1981, by comparison with Gingerich's paper here). I will not consider the matter of species longevities in detail, as Prof. De Bonis has looked at just this point for at least the hominoid catarrhines. Instead, I will concentrate on the first aspect, drawing upon data from four cercopithecoid clades and the hominines.

The question of "living fossils" is one which has scarcely been considered for higher primates, as the traditional definition implies a time scale in the hundreds of Ma. But Eldredge and Stanley proposed to investigate the occurrence of bradytelic rates of evolution through a broad review from many taxa, using the broader definition of living species which are morphologically [nearly] identical to early members of their own clade. In this light, the macaques, genus *Macaca*, may fit the pattern rather well. The earliest cercopithecids are Middle Miocene in age, and early in this subepoch, I have argued, one can distinguish specimens which present some diagnostic features of the two modern subfamilies (see Szalay and Delson, 1979, on this point and

all others not further referenced). In the 15 M.A.-old site of Maboko occur rare remains of a taxon temporarily termed "*Victoriapithecus*" *leakeyi*, which seems to have lower molars indistinguishable from later macaques, and a closely comparable elbow joint as well, although the upper molars are distinctively "primitive". By the Late Miocene and Early Pliocene, dental remains are known from around the Mediterranean which may represent several species best referred to the modern genus, if not to the living species *Macaca sylvanus*. A major radiation occurred in Asia during the later Pliocene and Pleistocene, but most species are distinguished by size and external characters, with little osteological differentiation. Moreover, the cranium of all macaques is quite similar to that of the Plio-Pleistocene *Parapapio*, an extinct sub-Saharan cercopithecine which may have been broadly ancestral to *Papio*, *Cercocebus* and other extinct genera with more derived cranial, postcranial (and dental) character states. The rarity of specimens of fossil macaques prevents metrical study now, but the apparently bradytelic nature of macaque evolution reflects stasis. An even better case for bradytely may be made within the New World platyrrhine higher primates (see Delson and Rosenberger, in prep.). The living *Saimiri* cannot seriously be distinguished at the generic level from *Neosaimiri* of the 15 M.A.-old La Venta locality and is further linked by synapomorphies directly to the late Oligocene *Dolichocebus*. To a somewhat lesser degree, the enlarged orbits of the living *Aotus* are pre-empted by the phyletically related Late Oligocene *Tremacebus*. The "bathyphyly" of some platyrrhine lineages is truly astounding.

Returning to the Mediterranean basin, the European terrestrial colobines *Mesopithecus* and *Dolichopithecus* are known over a 5-6 M.A. span, but with large samples from only a few sites. Thus, it is not possible to interpret the metrical data of Figure 1 without equivoca-

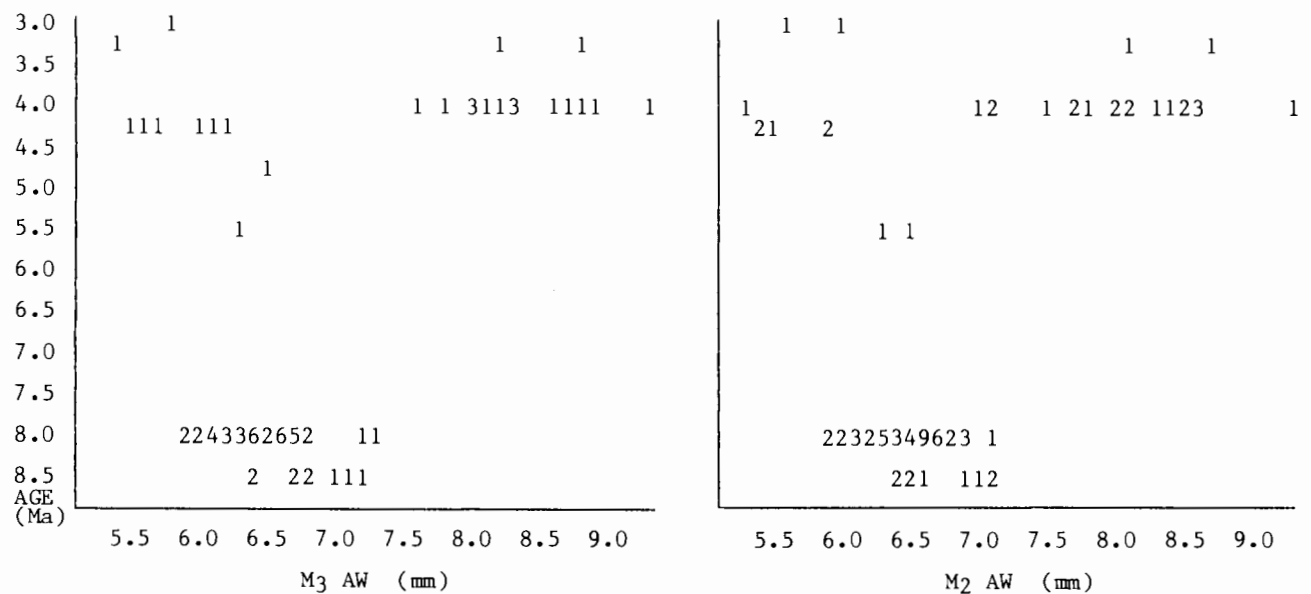


FIG. 1. — Scatterplot of anterior width (AW) of  $M_3$  (left) and  $M_2$  (right) against specimen age in European colobines. The oldest specimens are of *Mesopithecus pentelici*, while the younger groups represent *M. nonspessulanus* (smaller) and *Dolichopithecus rusciniensis*. The plotting symbol indicates the number of specimens with teeth of a given size. See text for interpretation.

tion. Here and later I plot my estimate of locality age against width of selected teeth; the more commonly used length (or area) is not used, as cercopithecoid teeth decrease significantly in length with wear. The two oldest samples in fig. 1 represent *Mesopithecus pentelici*, while the bimodal younger specimens are the smaller *Mesopithecus monspessulanus* and the larger (and significantly more terrestrial) *D. ruscinensis*. Without more fossils from the intervening latest Miocene, which was a period of relative aridity in southern Europe, it is not possible to confirm my view that only minor fluctuation in size and morphology characterized *Mesopithecus* throughout the total span involved. On the other hand, it is suggestive, as I have often argued before, that the earliest fossil of *Dolichopithecus* (a diagnostic ulna) occurs in the Late Miocene of Hungary, on the margin of the range of *Mesopithecus* and in one of the few areas which retained some woodland taxa at that time. With the refilling of the Mediterranean basin and the spread of subtropical forests in the early Pliocene, *Dolichopithecus* became the dominant colobine for a brief time, possibly contributing to the apparent size reduction and greater arboreality of sympatric *M. monspessulanus* through character displacement.

Two genera of African Plio-Pleistocene cercopithecids are wide-ranging in both time and space: the colobine *Cercopithecoides* and the cercopithecine *Theropithecus*. *C. williamsi* is mostly known from southern Africa, but also occurs rarely in the east, where a partial skeleton demonstrates its terrestrial adaptations; a second, larger species is also recognized in East Africa from few specimens (M. G. Leakey, 1982). In Figure 2 are presented data on two teeth over the range of *C. williamsi*. Given the wide variation in size at Sterkfontein (in the middle of the plots), it appears that no significant change in size can be discerned over almost 1.5 M.A., which is reflected also in qualitative morphological characters.

On the other hand, both this data and recent reevaluation of specimens from Kromdraai B (1.6 M.A. here) suggest the possibility that another species may be present there (probably not the same as the older eastern form). The stasis appears meaningful, the punctuation perhaps only wishful. Even more intriguing is the occurrence in the Late Miocene of Algeria of a colobine most similar in morphology to *Cercopithecoides* and of the same size. If what I have previously termed ? "Colobus" *flandrini* is actually *Cercopithecoides* cf. *williamsi*, the resultant stasis would extend over 7 M.A.

*Theropithecus* is often cited as evincing a pattern of gradual size increase through time, and newer large samples suggest that pattern again to Eck (in progress). At least four species are generally recognized, the small and rather conservative living *T. gelada*; the equisized early *T. darti*, the larger *T. oswaldi*, extending into the later Middle Pleistocene; and the mid-sized, cranially autapomorphic *T. brumpti* (which I have ignored for this analysis). Age may be relatively well estimated for most samples, although that of the type sample of *T. oswaldi*, from Kanjera, is questionable (usually thought 0.4 M.A. but possibly 1-2 M.A.). In Figure 3, I plot width of the lower M3 vs. time, revealing what looks broadly like a gradual pattern of size increase, especially if the small Kanjera sample is ignored. On the other hand, if the reader is so inclined, a potentially punctuational pattern may be discerned, with a static (if fluctuating) *T. darti*, mid-sized rather variable *T. oswaldi* (including the Kanjera fossils at an older age) and a large late form possibly meriting separate recognition. Gaps in the Late Pliocene and early Middle Pleistocene facilitate such a distinction and are unlikely to be filled readily (although Omo and Koobi Fora fossils may close the former). If Kanjera is as young as is usually thought, this pattern alters to a variable *T. oswaldi* with large and small morphs persisting through the Pleistocene, im-

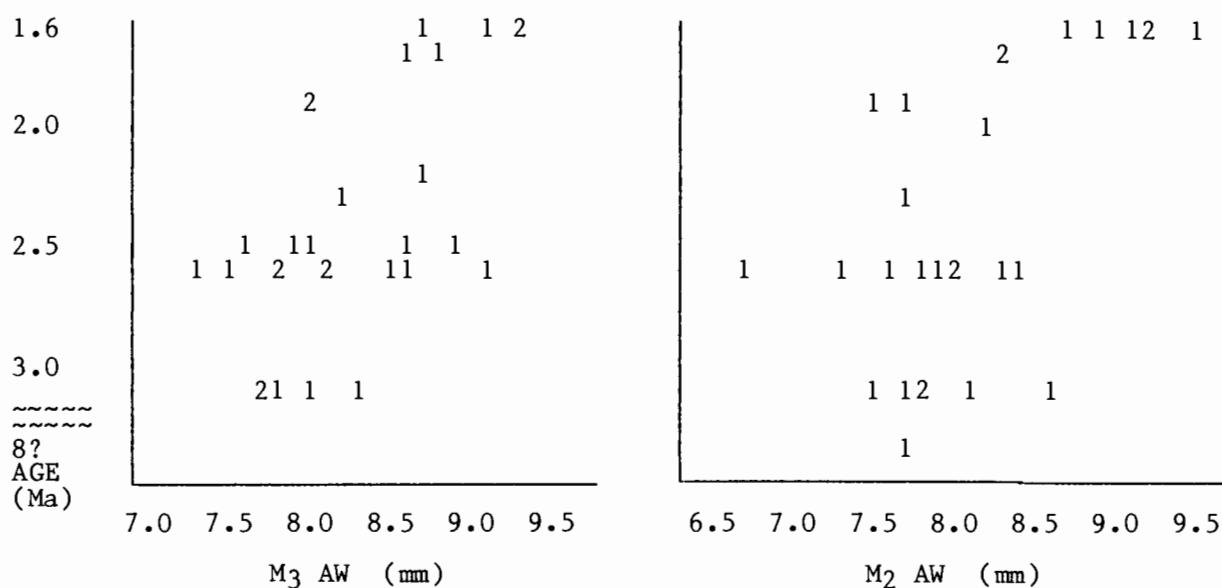


FIG. 2. — Scatter plot of anterior width (AW) of  $M_3$  (left) and  $M_2$  (right) against specimen age in *Cercopithecoides williamsi* and related populations. The plotting symbol indicates the number of specimens with teeth of a given size. Note the single Miocene fossil from Algeria on the bottom line and the larger teeth at the top, with apparent fluctuating stasis inbetween.

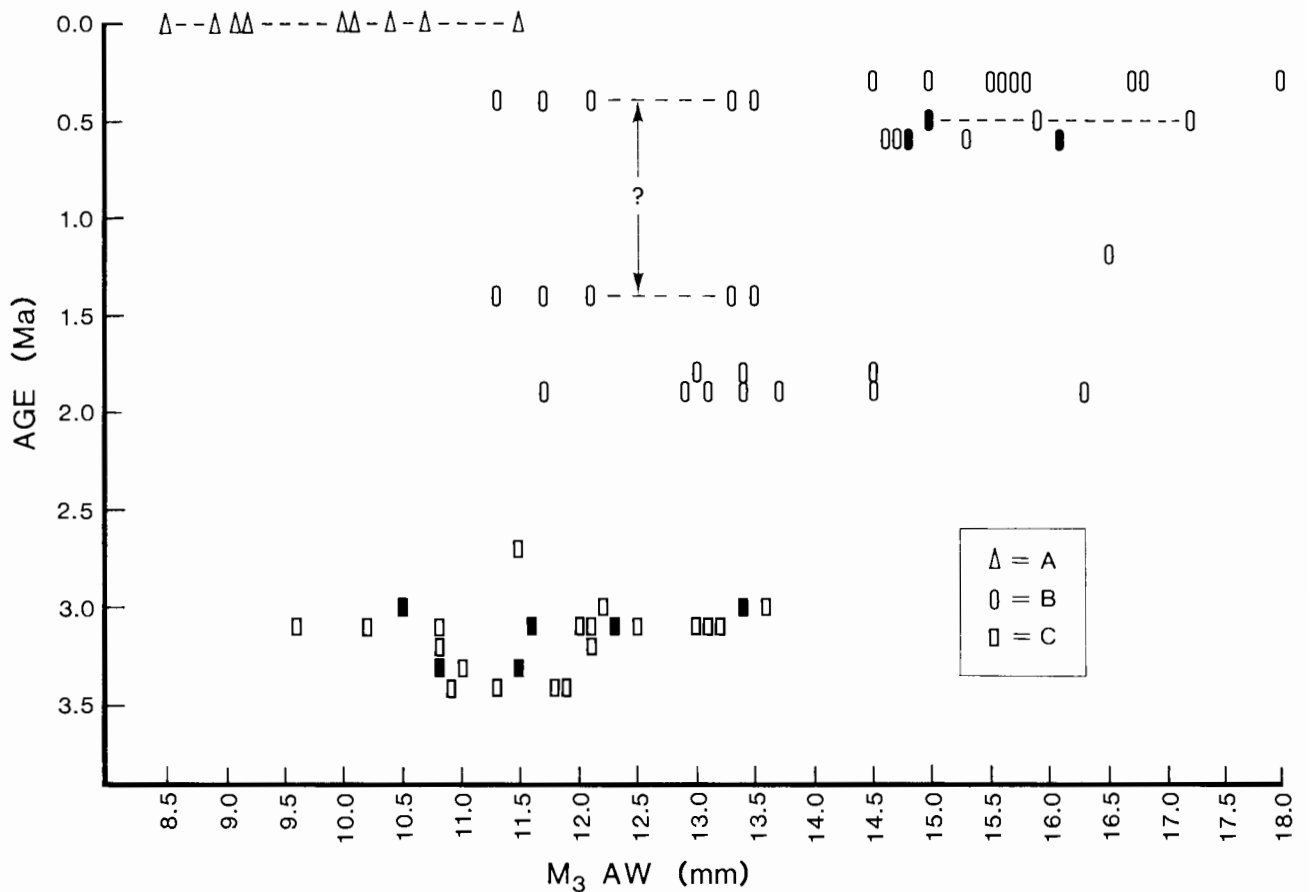


FIG. 3. — Scatter plot of anterior width of lower  $M_3$  in fossil and extant *Theropithecus* species, against specimen age. Symbol A indicates living *T. gelada*; B, *T. darti*; and C, *T. oswaldi* (using standard taxonomy). Open symbols represent single specimens, filled symbols two specimens. Horizontal dashes indicate ranges of known sample variation, where individual measurements are not available. Vertical arrow indicates uncertainty as to the age of the Kanjera population. There is an overall size increase through time with some indication of stasis as well.

plying greater variability than seen in *T. gelada*. Smaller samples of other teeth are as yet less clearly interpreted.

The human fossil record has been even more widely utilized to support both models of macroevolution, mostly by nonspecialists (e.g., Gould, Eldredge, Stanley, Stebbins). Cronin *et al.* (1981; also Stringer, 1982) reviewed the data in more detail and argued for gradualism in brain size increase and overall morphological change, while Godfrey and Jacobs (1981) contrasted several methods of graphical analysis, preferring a punctuational interpretation. Rightmire (1981) concentrated on Early-Middle Pleistocene *Homo erectus*, arguing for relative stasis in brain size and other metrical features, but Thorne and Wolpoff (1981, also Wolpoff, 1982) viewed the pattern gradually with similar data. Taking note of all the most recent publications on cranial capacity by Holloway (1978, 1980 a, b; 1981a, b; also Wolpoff, 1981) and various other sources, I plotted them against my best estimates of site ages (mostly accurate within 0.1 M.A.) in Figure 4.

There is clearly a trend to brain size increase with time, a fact accepted by all involved. But is this increase gradual or tied to other changes recognized by taxonomic distinction of species? The two australopith samples

("gracile" and "robust") show no time-dependent change, just stasis for the former at least. And one of the few widely accepted examples of hominid punctuation is the robust lineage or complex (Cronin *et al.*, 1981). Unhappily, *Homo habilis* is represented by so few crania, most of which are of questioned capacity, that interpretation is clouded. On the other hand, as Rightmire (1981) and I (1981) argued, stasis appears to prevail within *Homo erectus*. Some late specimens had larger brains than the few early ones, but others are quite comparable, and dental features show even less alteration (Rightmire, 1981). Within the broadly defined species *Homo sapiens*, on the contrary, I recognize several infraspecific clades with rather well defined trends in cranial capacity and numerous other morphological complexes. For example, the Neanderthals of Europe were the culmination of a clade stemming from the archaic, pre-Holstein *Homo sapiens*, with derived character states slowly being fixed in successive populations. Contemporaneously, the ancestry of modern humans was developing elsewhere, perhaps in sub-Saharan Africa, with a different combination of traits, trends and tempos. Thus, within the past 4 M.A. of human evolution, there was a mosaic pattern of "moderniza-

tion" in such complexes as the gnathic, cerebral, exocranial and locomotor systems, with most species apparently originating rapidly and often characterized by relative morphological stasis (that is, individual, sexual and geographic variation was more important than temporally-controlled trends), although the last few hundred thousand years give evidence of more gradual change within what I consider a single species but other colleagues may split into several mostly allopatric species (Delson, 1981; Eldredge and Tattersall, 1982).

To review, in five examples of taxa with reasonably continuous and lengthy fossil records in the small group of catarrhine primates, I have discussed the following: the macaques, a modern genus which shows no definite alteration since the Late Miocene and retains some features seen in the earliest 15 M.A.-old cercopithecines, a conservative "living fossil"; the European colobines which seem to show stasis during each species' rather short range and also origin of one new form on the ecological range of its ancestor; an African extinct colobine in relative stasis for 1.5 M.A. with a possibly new species arising (from it?) rapidly; African *Theropithecus* with either gradual size increase in two time-successive species over almost 4 M.A. or a mixture of gradualism and punctuation/stasis; and Plio-Pleistocene

humans showing mainly stasis and punctuational speciation, inferred from brain size, but also gradual phyletic evolution (not phyletic speciation) within the species *Homo sapiens*. From this small sample, the punctuated equilibrium model seems more common, but the same data may be interpreted differently given our personal biases, as clearly shown by the human record.

Is there any overall pattern which emerges from this study? One possibility is that size increase may be one of the few features likely subject to constant selective advantage, especially in larger grazing herbivores, which could take advantage of larger size to process a more fibrous diet (see Janis, 1976) and for defense against their predators (which also show size increase commonly). Most primates are at least partly arboreal, but *Theropithecus* is today (and the larger extinct forms presumably were also) fully terrestrial grazers. Thus, the observed tendency toward gradual size increase may have an ecological control. As both Eldredge and Vrba discussed at the Colloquium, eurytopes tend to persist relatively unchanged in a wide variety of habitats without speciating or evolving gradually; macaques, baboons (which persist with little change from their first appearance 2.5-3 M.A. ago) and perhaps the European and African semiterrestrial colobines discussed here

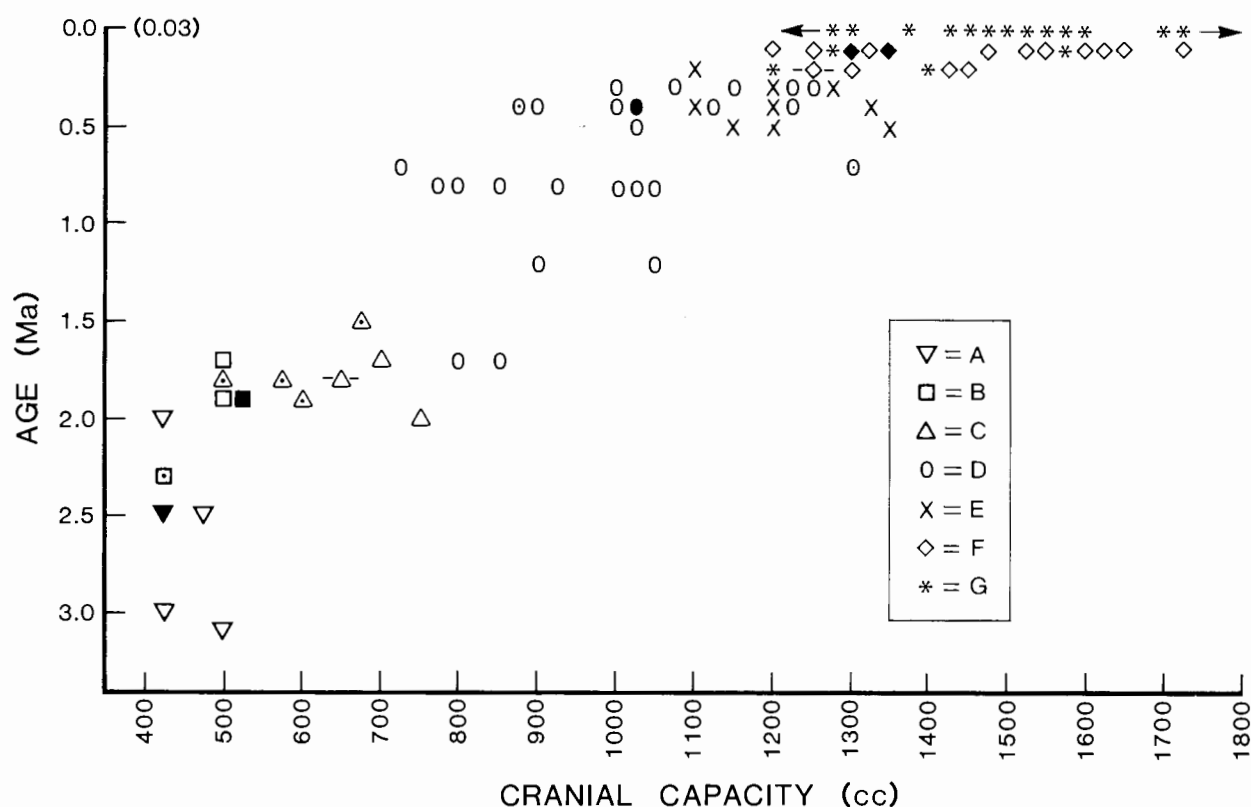


FIG. 4. — Scatter plot of cranial capacity against estimated specimen age in Plio-Pleistocene human fossils. Symbol A represents *Australopithecus africanus*; B, *A. robustus*; C, *Homo habilis*; D, *Homo erectus*; E, archaic *Homo sapiens* (including "Rhodesians", Dali and Elster to early Saale European fossils); F, all Neandertals; and G, Late Pleistocene *Homo sapiens sapiens* fossils. The top line represents specimens 30,000 – 10,000 years old, with arrows symbolizing the greater range of living populations. Open symbols indicate single specimens, filled symbols two fossils of similar capacity: a dot within a symbol indicates some uncertainty about its taxonomic identification. Horizontal dashes indicate capacity uncertainty for those specimens. All ages are probably accurate to within one horizontal line up or down ( $\pm 0.1$  M.A.). This chart indicates a lack of temporally controlled cranial capacity increase in all taxa before *Homo sapiens*, but relatively rapid increase in that species over the past 0.4 M.A.

were probably eurytopes. The controls on human evolution appear to have been more complex, but species like *Australopithecus africanus* and especially *Homo erectus* were also probably rather eurytopic.

I began by considering the expanding definitions of gradualism and punctuation. We must also ask about the underlying theoretical bases for each of these extreme modes and for the probable mixture which represents the course of a typical clade's existence. If this conference could reach a consensus of sorts on the diagnostic differences between the two models and their predictions and propose operational tests which paleontologists could apply in their study of fossil material, it will have served as a true catalyst in this debate.

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