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*Models of early hominid phylogeny*

Fifty years or more after Dart's original recognition and description of *Australopithecus*, we are at last learning enough to propose meaningful hypotheses about the evolutionary history of these early hominids. New sites are being discovered at the rate of nearly one per year, some are producing new specimens at a prodigious speed and interpretive studies of function and variation are providing the data base from which evolutionary studies must build. Today there are at least three major schools of thought about the pattern of evolution and the related systematic placement of the early hominids, as well as a number of variants or nearly discarded prior hypotheses. The purpose of this conference has been to consider the present state of our knowledge of selected aspects of early hominid palaeobiology and to look ahead toward new problems and strategies for their solution. I will try to follow this course with regard to phylogeny and systematics, first briefly describing the main theoretical models of early hominid evolution and then considering how some new trends in general evolutionary and phylogenetic thought may be applied to them. The aim is to determine whether present hypotheses can be tested and compared so as to select the most reasonable and likely among them. I have previously argued (Delson and Andrews, 1975) and still consider that Hominidae should include all living Hominoidea, with Homininae for *Homo* and related fossils, but in the spirit of this conference, I will here use 'hominid' in its more familiar restricted sense.

*Competing models of early hominid evolution*

Perhaps the most recent interpretation of the phylogeny of early hominids to be strongly championed is that known as the single-species hypothesis. The basic conclusion of this school is that the observed variation among Plio-Pleistocene hominids can best be explained as regional and temporal variability within one presumably

culture-bearing species. The brunt of the presentation of this viewpoint has been borne by Brace and Wolpoff, with numerous papers outlining the hypothesis and investigating aspects thereof (e.g. Brace, 1973; Brace, Mahler and Rosen, 1973; Wolpoff, 1968, 1970, 1971a, 1971b, 1971c, 1973, 1975 and this volume). The argument rests on two central postulates: (1) the cultural nature of hominid adaptation; and (2) a rather high degree of variation in early hominids by comparison with variation in the same characters in modern man and modern pongids. In dealing with the first point, Wolpoff (1971c, p.601) wrote that 'because of cultural adaptation, all hominid species occupy the same, extremely broad, adaptive niche. For this reason, allopatric hominid species would become sympatric (leading to) the continued survival of only one hominid lineage'. In that paper, Wolpoff argued that in both canine and summed cheek-tooth size (area), the ranges for 'gracile' and 'robust' australopiths<sup>1</sup> overlapped broadly and were comparable in variability to those of a broad series of modern human populations. Brace (1973) later suggested that sexual dimorphism within a given australopith population might be expected to be larger than that in a single *H. sapiens* population, being more comparable perhaps to that in larger non-human primates. He also indicated that absolute dental size does not clearly distinguish the 'gracile' Sterkfontein form from the 'robust' Swartkrans variety (although the latter argument is weakened when one realizes the 'Telanthropus' mandibles SK 15 and SK 45 were included in the comparisons). Finally, Wolpoff has indicated (1) that there is most probably moderate sexual dimorphism in canine area among australopiths and that it may be possible to sex isolated teeth, albeit with some uncertainty (1975); (2) that absolute size of cheek teeth (P3-M3) in 'gracile' australopiths from South Africa broadly overlaps that in gorillas of much larger body size (1973); and (3) that the absolute dental size differences between 'graciles' and 'robusts' may not be as great as previously thought, with coefficients of variation for pooled samples being only moderately higher in most variates than those for samples divided taxonomically by other authors (this volume). It must be emphasized that the latter two points, namely the large absolute size of 'gracile' australopith cheek teeth and their metrical similarity to those of 'robusts', are observations of great value previously overlooked by many authors. It may also be noted that the origin of the single-lineage idea derives from studies of the South African fossils, with East African specimens discussed only in some of the latest contributions.

The other, by far more common, view of australopith evolution

1. The term 'australopith' is used here, rather than 'australopithecine', as it carries no connotation of the existence of a subfamily (or tribe) 'Australopithecinae'. 'Gracile' and 'robust' are quoted here because the former, as smallish animals of moderate to heavy build, with cheek teeth absolutely as large as those of gorillas, may not fit the usual image of gracility.

recognizes at least two lineages of early hominids. Distinctions can be drawn between 'schools' on the basis of the number of lineages recognized, which this conference has shown to be still an open question, or of other features. I consider the most meaningful basis for comparison to be each model's determination of the character complexes likely to be found in the common ancestor of the known 'graciles' and 'robusts'. In one view, espoused mainly by Robinson (1954, 1956, 1961, 1967, 1971, 1972, this volume; Robinson and Steudel, 1973), the characters observed in 'robust' australopiths or *Paranthropus* are considered to correspond best with those expected in a common ancestor. In his studies, Robinson has attempted to show that the 'robust' form is more ape-like than the 'gracile' in a number of characters, especially in the post-cranial skeleton, the larger cheek teeth, lower skull vault and small brain, while being 'hyper-hominid' in certain other features, such as ischial length, premolar molarization and especially the greatly reduced anterior dentition relative to cheek-tooth size. The dietary model which Robinson proposed to explain these differences suggested that the 'robust' forms were pongid-like vegetarians, while the 'graciles' and their *Homo* descendants incorporated a steadily increasing percentage of hunted or scavenged meat in their diets, with concomitant reduction of the gnathic apparatus required. In his more recent work (since 1967), Robinson has advocated the formal inclusion of *Australopithecus* in the genus *Homo*, while retaining *Paranthropus* for the known 'robust' forms and the presumed much earlier common ancestors of both lineages.

In opposition to this view is the model advocated, in one form or another, by most researchers. This recognizes the distinctions between 'robust' and 'gracile' forms drawn by Robinson and others, but holds that the latter morph represents less divergence away from the ancestral pattern while nonetheless leading broadly to later hominids. On the other hand, the 'robust' forms are seen as a younger, derived offshoot following a separate evolutionary course and leaving no known descendants. The variants in this model depend on the recognition of more than one variety of 'gracile' australopith, such as *Homo habilis* or the taxon represented by KNM-ER 1470 and 1590, etc. Similarly, formal classification schemes vary among supporters of this model, depending upon both taxonomic philosophy and the number of different morphological types recognized (2, 3 or 4). Such authors as Campbell (1972, this volume), Howell (1967, 1972, this volume), Howells (1973), Jolly (1970), R.E.F. Leakey (1973a, 1973b, this volume), Pilbeam (1972, 1973, this volume), Pilbeam and Gould (1974), Szalay (1975), Tobias (1967, 1973a, 1973b, this volume) and Walker (1976) represent a sampling of opinions and interpretations. Some nearly agree with Robinson taxonomically but prefer an *A. africanus*-like ancestor, others accept numerous independent lines from a basically 'gracile' but unspecified common ancestor. Further comment on some views will be presented

at relevant points below. At present, having hastily reviewed the state-of-the-art, it is possible to look farther afield.

### *New developments in systematic methodology*

During the past decade, two schools of systematic philosophy have arisen in opposition to certain views and methods of the 'New Systematics' of the 1940s, which today may be called the accepted or 'classical' school ('evolutionary' to its practitioners; see Hull, 1970 or Simpson, 1975). The 'numerical' or phenetic approach has been concerned with computational reduction of large masses of observational and metrical data in order to indicate the relative similarity among samples without *a priori* weighting of observations. On the other hand, the cladistic or 'phylogenetic' approach has been to concentrate on the distinction between 'derived' versus 'ancestral' characters in the assessment of relationships, which method has been developed along with a number of more controversial, though minor, points. Each of these schools has valuable techniques and methods which can profitably be integrated into the 'evolutionary' approach; the latter in turn must be more widely infused into certain branches of palaeontological study. Forsten's 1973 study, for instance, applies them to *Hipparion*, which exhibits numerous similarities with the australopiths. The application of such methods to the models discussed above may enable us to see ways of testing certain hypotheses and suggest new directions for future, more intensive research.

It is always dangerous to try to isolate one part of a hypothesis or model to test in a short review, because both sides of the argument may feel cheated by the lack of space allowed. Nonetheless, I think it fair to say that proponents of the single-lineage hypothesis, having made a set of assumptions about culture-bearing hominids, spend a majority of their writings in discussion of metrical attributes (i.e., size) of specimens and the overlap between the groups compared. Multi-lineage models, on the contrary, appear to rest on considerations of proportions and 'observational morphology', not directly based on metrical comparisons. It seems best to begin with a consideration of the single-lineage model, primarily because it is the simplest.

### *Metrical phenetics and the single-lineage hypothesis*

#### *Multivariate analyses*

Out of the numerous studies employing a 'numerical taxonomic' approach have developed new types of computational methods which may be applied to metrical and other quantifiable data. Also valuable

has been the realization that these methods must be applied carefully, that the most appropriate statistic should be used to test the precise hypothesis under consideration (see Kowalski, 1972; Pilbeam and Vaišnys, 1975), and that care must be taken with samples of small size added in to the analysis either initially or afterward (see Oxnard, 1972; Andrews and Williams, 1973). The study by Brace, Mahler and Rosen (1973) may in part illustrate a failure to consider these caveats.

In a multivariate discriminant function analysis of fossil and modern hominid mandibular tooth areas, these authors found that Olduvai Hominid 13 always grouped with their *Homo erectus* sample, while OH 7 fell with *Australopithecus* (or with 'gracile' rather than 'robust' forms when that distinction was made). This was interpreted to mean that the linking of OH 7 and OH 13 in the taxon *Homo habilis* could not be substantiated. They did *not* mention certain aspects of these results which render the outcome more equivocal. First, in any discriminant function analysis, the test is inappropriate unless it can be assumed that the unknowns actually were drawn from one of the reference populations. For this reason, the technique is excellent for determining sex and often race. But the question to be investigated here was precisely whether the two fossils belonged to *either* of the 'given' populations, so that a discriminant function was perhaps not the best approach to use. Moreover, their Tables 7 and 8 show that OH 13 was always much further (in terms of the  $D^2$  statistic) from the group mean of *H. erectus* than other specimens listed, while OH 7 was further from the mean of *A. africanus*, although not the furthest from the mean when all australopiths were pooled. This may reflect the composite nature of the combined sample, revealed in the clearer results of the test in which 'graciles' and 'robusts' were separated. The results of this second test would also tend to reject the single-lineage hypothesis on the authors' own criteria, but they discount this conclusion as premature because of sampling problems. Unfortunately, this is true of the whole exercise. The lack of discussion of the 'inconvenient'  $D^2$  values exemplifies the ease with which statistical results may be only partly interpreted and conclusions thus altered. Further, the problem of cranial capacity, dealt with in more detail by Pilbeam and Vaišnys (1975), is not considered at all. It must finally be added that while I disagree with those who claim that use of the computer to analyse 'inoffensive early hominid dental data' is 'statistical overkill' (Brace *et al.*, 1973, p.64) – I would emphasize that the more sophisticated the techniques utilized in any field of study, the greater must be the care taken not to misuse them.

Another aspect of the problem is that the data of both Brace (1973) and Wolpoff (see below) do not reveal a major difference in absolute size between the 'gracile' and 'robust' early hominids, especially those from South Africa. On this point, their data clearly support their interpretations. But the main reason for separating the two forms dentally has not been one of absolute size difference, but one of

proportion within individual specimens (see Robinson, 1971; Robinson and Steudel, 1973), a point which is little discussed by the single-lineage advocates. Wolpoff has discussed canine size, posterior tooth size and for this conference all tooth sizes, but without mention of Robinson's claims of major differences in the proportion of anterior and cheek teeth, especially of C and P3. Robinson's latest dental study (Robinson and Steudel, 1973) reiterated this distinction with the aid of a multivariate analysis, although again utilizing discriminant functions instead of a less 'canalized' technique such as cluster analysis. Wolpoff's data in this volume do not reveal a great distinction between South and East African 'gracile' and 'robust' australopiths in the ratio of C to P3 tooth areas. This, however, may be due to the inclusion of all available isolated teeth, where, as Robinson has long maintained, this comparison applies only to teeth derived from single individuals. The main value of considering all available specimens is obviously to increase sample size, which is important in certain analyses, but not meaningful in the consideration of intra-individual proportions. The examination of individuals, even in limited numbers, does support the comparisons drawn by Robinson in both South and East Africa.

*Models of variation in early hominids*

The matter of sample size and selection is of great importance in the study of variation. In response to Wolpoff's (1971c) review summarized above, Shaklee (1973) argued that the comparison of two samples by means of a *t*-test may yield quite different results depending on sample size and internal variation among other factors. Thus, with a larger sample, or with less variable features chosen, Wolpoff's finding of no significant difference between hominid populations in molar tooth size might be reversed. Bilborough (1972) further noted that Wolpoff has compared variation in australopiths from part of one continent to that in modern (or later fossil) populations from a much larger area (and with very different cultural patterns), thus possibly biasing the comparison: less variability in the modern populations chosen would result in the australopiths appearing more variable, in opposition to Wolpoff's argument. The matter of the 'best' or most reasonable model to use in the evaluation of variability in fossil hominid populations is one which Wolpoff has explicitly discussed only once (this volume). As the choice of model will strongly influence the significance of the results and their effect on the hypothesis under consideration, it is important to consider this matter further.

Wolpoff (this volume) makes several points which indicate his views on the choice of a model for comparing variation in fossil samples. First, he argues that no two fossils can be assumed to have belonged to a single biological population, except in the case of certain late human

burials or other rare cases. This is, of course, true not only of human palaeontology, but for all fossils as well as most museum collections. Vertebrate palaeontologists and other zoologists have long accepted this reasoning. There seems little need to discuss it at length today; one need merely employ the usual cautionary procedures and assumptions.

In direct opposition to *Bilsborough's* comment, *Wolpoff* argues that 'single population samples from populations within the same taxon cannot be used to estimate the mean, variance or range of any individual population, but can only be used to derive such estimators for the taxon as a whole'. More specifically, he reasons that a sample of *N* fossil individuals should be compared metrically to *N* modern populations, not to *N* modern individuals of one (local) population. Following directly from this is *Wolpoff's* further hesitation to utilize fossils from only one site to estimate the statistical parameters of a sample. He suggests employing all the available fossils grouped together, as this will have no effect other than to increase the sample size, for sampling is already being done from the total universe of populations of the taxon. If specimens from one site were no more likely to be related biologically than those from different sites, this argument might be partially valid, but it actually seems more likely that specimens of a single phenon<sup>2</sup> from a single locality will in fact be more closely related biologically than specimens chosen at random from that same phenon (or taxon), even if they did not belong to an single breeding population at a particular time. Furthermore, if the prior step of only comparing *N* fossils with *N* populations is accepted (and I feel this needs more rigorous mathematical and biological proof), the next step only holds true if the comparison is made between the fossils and modern populations. If fossils from one locality or group of localities, all identified as belonging to a single phenon, are compared to an equivalent number of fossils from one or more sites of another phenon, the problem may diminish if not vanish. In fact, a sample from one site may be compared to a sample from another site if both contain sufficient individuals to provide a 'reasonable estimate' of their respective population parameters (but how many is a 'reasonable' number?), or the pooled sample from a number of sites may be compared with a similar pooled sample. This is especially useful if it is known that only one species is represented at the site(s) used as a standard of comparison. It may even be possible

2. The term 'phenon' is used here in the sense of *Mayr* (1969) (not that of the numerical taxonomists) to designate a morphologically relatively uniform sample. As will be seen below, specimens may be sorted into phenon, or morphs, and then grouped into taxa in successive stages of a study. Obviously, one does not wish seriously to compare tooth size in large pigs and small elephants, for example, just to show that they can overlap, nor is the comparison of the more metrically and morphologically similar teeth of peccaries, phenacodonts and dryopiths of any value. Hence the assumption that phenon (or members of single species, genera, etc.) are being compared.

to employ skeletons of modern mammals in this way, but this involves the problem of the equation of temporal and geographic variation treated well by Wolpoff and which I do not wish to discuss at greater length.

Having thus suggested an escape from part of Wolpoff's problem, we can turn to why he did not take such a route, which depends on the taxonomic choice of model. Wolpoff argues that the modern 'baboons are probably the closest ecological counterparts to the early hominids', but rejects them because of their great variability in favour of the modern pongids and hominids, less ecologically comparable but taxonomically closer to australopiths. Moreover, discussion during the course of the conference revealed an attempt to restrict comparison to those groups which are phyletically closest to the animals under study, in order to maximize genetic similarities underlying morphological variation. I agree that comparison is best between closely related forms, but suggest that cercopithecids are close enough to hominids to be used. Moreover, if we are to use fossil populations as models, we must seek situations in which only one species is 'known' to be present in the sample. The African dryopith samples of the Early Miocene would be eminently useful in this case, but they suffer from the same problem as the early hominids – how many species are to be recognized in the samples? (see Andrews, 1974). In fact, modern baboons today are in the same boat, with the results of genetic, behavioural and morphologic studies indicating the possibility of all 'savannah' baboons – *Papio* (*Chaeropithecus*) – being part of an enormously polytypic single species with semi-restricted gene flow in certain areas (Jolly and Brett, 1973). On the other hand, there are some fossil monkeys which meet both requirements: single taxon at a site (not true of Plio-Pleistocene African forms) and apparent open-country adaptations. The most interesting of these for our purposes is *Mesopithecus pentelici* (Delson, 1973, 1975a).

This species is known mainly from southern Europe and south-western Asia during the Turolian mammal age (*c.* 10-5 m.y.). Most localities are in the southern Balkans and associated with an open-country but not intensely arid fauna. A second species referred to this genus, *?M. monspessulanus*, appears to have evolved from *M. pentelici* at the end of the Miocene and continues in approximately the same range through the Pliocene, but with a possible decrease in terrestrial adaptations. This change might in part be due to the spread at this time of the sympatric, large, highly terrestrial *Dolichopithecus ruscinensis*, possibility also derived from *M. pentelici*. Each of these species is known mainly from the sample at its type locality, with smaller numbers of individuals referred from several other localities; *M. pentelici* is the sole cercopithecid at the localities in which it occurs (Delson, 1974). Neither species is polytypic as now understood, but part of the polytypy of australopiths results from the unwarranted pooling of dissimilar phena in Wolpoff's tabulations.

**Table 1** Estimators of variability in molar area of *Mesopithecus* species

<i>Taxon</i>	<i>Locality</i>	<i>Mean</i>	<i>M<sup>1</sup> Area</i> <i>N</i>	<i>CV</i>	<i>RMI</i>	<i>Mean</i>	<i>M<sup>2</sup> Area</i> <i>N</i>	<i>CV</i>	<i>RMI</i>	<i>Mean</i>	<i>M<sup>3</sup> Area</i> <i>N</i>	<i>CV</i>	<i>RMI</i>
<i>M. pentelici</i>													
	Pikermi	46.09	27	7.7	33.3	54.35	26	7.4	26.7	47.16	25	10.1	36.6
	all	46.51	30	7.8	33.2	54.70	32	7.1	21.5	46.96	29	9.6	36.8
<i>M. pentelici</i>													
		<i>Mean</i>	<i>M<sub>1</sub> Area</i> <i>N</i>	<i>CV</i>	<i>RMI</i>	<i>Mean</i>	<i>M<sub>2</sub> Area</i> <i>N</i>	<i>CV</i>	<i>RMI</i>	<i>Mean</i>	<i>M<sub>3</sub> Area</i> <i>N</i>	<i>CV</i>	<i>RMI</i>
	Pikermi	40.11	23	7.7	27.4	48.72	34	7.8	30.6	57.46	32	9.0	38.6
	other	41.20	10	11.7	36.4	53.07	9	5.4	17.3	63.27	9	6.0	20.5
	all	40.44	33	9.2	37.1	49.63	43	8.1	30.6	58.73	41	9.2	37.8
<i>?M. monspessulanus</i>													
	Montpellier					39.73	5	10.8	29.8	52.54	6	9.3	23.2
	other					42.10	5	14.1	35.5	51.90	4	13.3	32.0
	all					40.91	10	12.2	36.7	52.29	10	10.3	31.8
<i>Mesopithecus</i> spp.													
	all					47.99	53	11.3	50.1	57.47	51	10.4	48.6

In order to provide material for comparison with that supplied by Wolpoff on early hominid dental size, calculations of tooth areas were made for the upper and lower molars of these species, grouped in a number of ways. Most data are provided for *M. pentelici*, which has both the largest sample sizes and was probably ecologically most similar to the early hominids. Table 1 lists the mean values (M), sample sizes (N), coefficient of variation (CV = 100 sd/m), and range-mean index (RMI = 100 R/M) for each sample. As regards the CV, Simpson, Roe and Lewontin (1961) note that values between 5 and 10 (especially 5-7) may be average for *linear* variates in a homogeneous sample, while higher values (above 15 for many workers) *tend* to indicate heterogeneity. As this study is made on *areal* variates, a higher score would be expected, especially for the cercopithecids: because of the shape of these teeth, the area was calculated from the formula  $\frac{1}{2}(\text{anterior breadth} + \text{posterior breadth}) \times \text{length}$ .

Interpretation is made more difficult because Wolpoff provides no data on specimens from a single site, but Table 1 reveals that for the six molar teeth, samples of 25 to 34 Pikermi *M. pentelici* have CVs ranging from 7.4 to 10.1 and RMI from 26.7 to 38.6. Samples of 9 or 10 lower molars from up to seven localities show a CV between 5 and 12, RMI from 17 to 37 (values rounded off). Finally, the pooling of all *M. pentelici* specimens results in generally the same values with less inter-tooth variation (N=29-43; CV=7.1-9.6; RMI=21.5-37.8). For M<sub>2-3</sub>, it was further possible to examine values for *M. monspessulanus*, tentatively considered as a distinct species by Delson (1973). With sample sizes about 5 for teeth from Montpellier and from all other localities, CV ranged from 9.3 to 14.1, RMI from 23.2 to 35.5; the pooled samples of 10 had CV=10.3 and 12.2, RMI of 31.8 and 36.7 respectively. This indicates that with small (or perhaps just size-equal) samples, the more variable group from many localities about balanced that from the type locality, which is also the most abundant. Combining all of these specimens for M<sub>2-3</sub> reveals that the greater sample sizes for *M. pentelici* seem to swamp those for the smaller species, with CVs of 10.4 and 11.3, within the range for those from single sites! On the other hand, the RMI clearly stands out here, with values of 48.6 and 50.1, indicating at least a great range of size.<sup>3</sup>

The early hominid data given by Wolpoff indicate a comparable degree of variability for all groupings except 'all East Africa', 'all Australopithecines' and 'all Australopithecines without East African graciles'. The latter three groups have CV above 15 and RMI above 70 (often above 80), while the others have CV mostly between 11 and 15, RMI between 30 and 60. The sample labelled 'robust Australopithecines' was on the borderline between these two groups, suggesting that it is within this group that the cause of the variation

3. It must be noted that such high values of RMI may even occur in single-site samples if one individual is far beyond the mean, although the CV in such cases I observed (in *Dolichopithecus ruscinensis*) was below 13.

may lie. It appears that, while all the South African forms are dentally of similar cheek-tooth size, the difference is great in East Africa, with these 'robust' forms well beyond the average. Perhaps a sample 'total australopith except East African robust' would reveal interestingly low values.

It would also be interesting to see values for samples from single localities, such as the individual South African caves, especially Swartkrans and Sterkfontein. These results suggest that there is more variation in the australopiths than in the *Mesopithecus* samples studied by me, certainly more than accepted by Wolpoff.

By comparing the values for early hominids with those for modern pongids and hominids, Wolpoff has suggested that variability in the fossils is low. Comparison of the CV in his modern populations to *Mesopithecus*, and to values suggested by Simpson, Roe and Lewontin (1961) as acceptable for homogeneous samples, suggests that the modern hominids measured were highly variable, probably because a large number of local populations were sampled. Certainly, this is in line with what Wolpoff has argued should be the method of comparison, but it seems to lead to circularity in interpretation: if a large number of variable populations are used as a model or standard, it is likely that the fossils compared will prove less variable, and thus relatively homogeneous, fitting the single-species hypothesis. But this also can be used to suggest that more fossils should be pooled into the sample, to match the variation in the modern standard. With the use of fossil populations as a standard, the interpretation is reversed, and heterogeneity of the fossils is therefore suggested. Contrary to Wolpoff's argument, if it is clear that only one fossil species is involved, there is no greater probability of error than when using modern morphospecies such as *Pan troglodytes* as a standard.

Wolpoff goes one step further and pools the chimpanzee and gorilla measures to show that very high values of both CV and RMI result (his Table 4). Inspection of the ranges of tooth-crown area in these two species reveal almost no overlap, however, and the result is not truly comparable to the situation for the australopiths – it corresponds to pooling *Dolichopithecus* and *Mesopithecus* samples. On the other hand, the results of pooling orang measures with chimpanzee or even gorilla measures would be more comparable and might prove interesting; the analogy here would be to the pooling of the two 'species' of *Mesopithecus*. Wolpoff complains that *Pan* and *Pongo* are allopathic and thus not comparable to the australopith morphs, but in fact there are few if any cases of the latter being both present at a single site unit or horizon. I hope that the presentation of the data in Table 1 may allow for further comparisons to be made by those with additional data on early hominids and other catarrhine taxa.

*Time and the single species*

A complicated aspect of the single-lineage problem is the role of temporal data in these studies: comparison of temporal and geographic variation, pooling of specimens from widely disparate time levels, and the possibility of recognizing contemporary samples or individuals. Wolpoff argues (this volume) that it is not possible to show clearly that two fossils are contemporaneous. Therefore, he suggests that material from many time horizons can be pooled, again to increase sample size. His argument rests on the errors inherent in the determination of radiometric dates, such that two layers dated at 1.8 m.y., for example, could actually range from 1.6-2.0 m.y. and be nearly half a million years apart. As I will argue below, it is inadvisable to base interpretation too heavily on the age of fossils. But our knowledge of dating can be improved in several ways. First, the use of palaeomagnetic data can limit the possible range of radiometric dates – in the case mentioned, a date of 1.8 m.y. tied to a layer with normal polarity would mean sampling a time horizon within the Olduvai normal event, at most 1.6-1.9 m.y. Secondly, continued refinement of palaeontological correlation would allow other localities to be tied into a standard sequence and at least approximate ranges of time delineated. The present difficulties involved in correlating the East Rudolf and Omo successions show how complicated these problems can be, but the discussions during this conference suggest that, at least for studies of metrical characters, a time scale does exist upon which agreement is sufficiently general to allow more precise comparisons of the sort carried out by Pilbeam and Zwell (1973).

In that work, the hominid fossils thought to be older than 0.75 m.y. were separated into four time blocks, within which selected histograms of tooth size were plotted to determine whether observed variation was high compared with expectation. Their discussion of models for the study of variation is similar to mine, based on modern rather than fossil data. Unfortunately, some of their age determinations do not appear acceptable at present, and some of the following may be altered by new work. However, it does seem quite feasible to suggest replication of their study using three main 'time blocks': (1), specimens between 1.9 and 3 m.y. old, such as those from the Omo Usno Fm. and Shungura members B through F (Howell, this volume; Howell and Coppens, 1974), East Rudolf Lower Member of the Koobi Fora Fm. (Brock and Isaac, 1974; R.E.F. Leakey, this volume), the South African sites of Sterkfontein, Makapan and probably Taung (Cooke and Maglio, 1972; discussions during this meeting), the Hadar Fm. (Taieb, Johanson and Coppens, 1975); (2), specimens falling within the Olduvai normal magnetic event (1.6-1.9 m.y.), such as those from Olduvai Bed I and the Lemuta Member of Bed II (M. Leakey, this volume), Omo Shungura member G, East Rudolf lower part of the Upper Member of the Koobi

Fora Fm. and lower parts of the Ileret sequence, Peninj (Isaac, this volume), possibly Chesowanja and the South African sites of Swartkrans and perhaps Kromdraai; and (3), specimens younger than the above (i.e. 1.0-1.6 m.y.), essentially from the Omo Kalam area, East Rudolf Ileret Mb., and the major part of Bed II at Olduvai.

I would expect that findings similar to Pilbeam and Zwell's would recur with a revised attempt – namely, that variation in tooth size appears to increase upward in time. Pilbeam and Zwell interpreted the increased variability through time to reflect cladogenesis or 'branching' evolution leading to two separate hominid lineages that diverged morphologically. On the basis of data of this type, it is impossible to determine whether the change was due to evolution *in situ* or to the immigration of a more distinct form, possibly descended from a local population related to one sampled in the previous time range. Since we are dealing here with a broad sample over the entire known range, this distinction may not be more than theoretically important. However, the idea that a 'robust' lineage could persist relatively unchanged appears to disturb some workers on theoretical grounds. By way of reply, one interpretation of evolutionary speciation employing an allopatric model suggests that most species remain morphologically constant over long times through the action of homeostatic mechanisms, and that most speciation events (especially those few which 'succeed', or result in a new species surviving to become sympatric with or replace its ancestor), occur on the geographic margin of the ancestor species' range (see Eldredge and Gould, 1972, but also rebuttal by Gingerich, 1974). A long-surviving, conservative lineage of 'robust' australopiths would fit such a model well, especially alongside a more rapidly-changing lineage of progressive 'gracile' types, with a number of rather different local populations separated geographically. At successive times, some of the latter would develop new traits in isolation, then spread back through the previous range to displace the earlier populations and consolidate the new traits. In such a model, it would be possible to consider *Homo habilis*, or something like it, as a species or subspecies which had developed the trait of larger brain size while retaining australopith dentition, although this is, of course, oversimplified.

### *Reconstructing an ancestor in a multi-lineage model*

#### *Theory of cladistic methodology*

The discussion so far has centred on several aspects of the single-lineage hypothesis. Each of these has been seen to be valid under its own assumptions, but less secure when these postulates are called into question. In my opinion, the hypothesis of a single species or lineage including all known early hominids is unsatisfactory. Although there

are questions as to how certain subsamples should be grouped, the need for a multi-species model seems clear. The problem now is to determine how to present this model in clearest form, especially regarding the relationships among the several phena that have been distinguished.

By clarifying these relationships one is essentially making a model of the phylogeny of the group. It must be based mainly on morphological characters, not simply the comparison of metrical variates and their overlap or disjunction, because size may vary within or between lineages, while the development of new traits usually indicates the occurrence of speciation. The best approach seems to be offered by the major principle of the cladistic method: namely, that grouping phena on the basis of morphology must depend only on those characters which can be considered *derived* from the ancestral condition, not merely *inherited* from a common ancestor.

Hennig (1966) has been the leading architect of this approach, although some of his accessory postulates leave much to be desired. Schaeffer, Hecht and Eldredge (1972) have formulated the method as it applies to palaeontology; Eldredge and Tattersall (1975) have reviewed the arguments and offered a summary application to human palaeontology; and I have attempted to apply it more fully to the study of catarrhine evolutionary history (Delson, 1973, 1975a, 1975b, 1977; Delson and Andrews, 1975; Delson, Eldredge and Tattersall, 1977). Phrased most succinctly, the cladistic approach maintains that phena (or taxa) should be linked phyletically only if they share characters which may be termed *derived* by comparison with other members of the larger group to which they belong.

The argument runs as follows. Speciation represents a separation between an ancestral species and two (or more) daughter species. The resulting sisters will share many characters retained from their common ancestor but will also differ in a smaller number of characters. In most cases, it is likely that one of the two daughters will retain the ancestral condition (for a given character), while the other will present a derived condition. In some cases, both daughters may have different derived conditions. The several descendants of these original sister-species can be termed sister-groups, and their members will tend to retain the traits which have been called derived by comparison to the original parent species but which are ancestral for the group as a whole. In general, a new trait is always derived in the first species to present it, by comparison to that species' ancestor, but is ancestral for that species' descendants.

To apply this scheme to a real set of phena with many characters, it is necessary to devise methods to determine which characters in a group are ancestral. Those phena sharing derived characters can then be linked into a subgroup, irrespective of their relative ages. Although this concept is discussed in most works on general systematic theory (e.g. Simpson, 1961; Le Gros Clark, 1971), it is not usually followed in

practice. Palaeontologists tend to accept as ancestral those characters which appear first in the geological record of a group. This may lead to circularity or error, if for example the oldest known member of a group happens to be, in fact, a highly specialized form, while some modern members are more 'generalized', retaining many ancestral characters. To avoid this problem, Schaeffer, Hecht and Eldredge (1972) have advocated that fossil and modern representatives of a group be considered together, without reference to geological age, after grouping specimens into phenons by the usual methods. Thus, one is presented with the total known range of variation within the group, without prejudging which characters were ancestral. Ancestral or derived conditions are best determined by broad comparison of character states throughout the group under study and its close relatives. The most widespread characters or states, especially if also present in related groups (the 'sister(s)' of the total studied group) are likely to be retentions from an earlier ancestor. On the other hand, states which occur only once in a whole group are probably derived, but of no help in linking phenons. Of greatest value are those states occurring relatively few times, enabling the phenons which share them to be linked. A greater number of shared characters linking phenons (if independent) indicate relatively closer phyletic relationship. Schaeffer, Hecht and Eldredge also discussed the concepts of a morphocline, or graded sequence of character states from ancestral to most derived, and of the polarity along this morphocline, which may be used to determine the set of characters to be expected in the ancestor of a group or subgroup.

This set of ancestral characters may be termed the 'morphotype' of such a group. By reconstructing a series of ancestral morphotypes within a large group, one essentially infers or deduces the attributes of some of the actual ancestor species at different points in the group's evolutionary history. On the one hand, it is possible to link modern (and fossil) phenons or taxa into subgroups by comparison of their characters with the ancestral states of the morphotype. This leads to the production of a cladogram, or phylogeny without time dimension. On the other hand, it is also of great interest to compare actual fossils with the postulated ancestral morphotypes at various points along the 'evolutionary tree'. Traditionally, the concept of such a morphotype might have been altered to correspond to a known fossil, but in this method, it is argued instead that the likelihood that a given fossil is a so-called 'structural ancestor' is directly proportional to its possession of ancestral character states. With the addition of the time dimension provided only by fossils, it is possible to suggest the date at which certain derived conditions first were evolved, or the time when basic lineage divisions occurred, because of the presence of such characteristic derived conditions (see also Delson, 1975b, 1977).

*Application to the Australopiths*

Eldredge and Tattersall (1975) have studied some cranial and dental characters of the Hominidae with a number of interesting results. They concluded that the South African 'gracile' australopith corresponds very closely to the ancestral morphotype for Hominidae.<sup>4</sup> In skull shape and lightness, somewhat reduced face and incisors (compared to pongids), broad molars with low cusps and expanded occlusal surface and heavily buttressed jaws, Eldredge and Tattersall found that the known characters of 'gracile' early hominids matched those in the morphotype they postulated. On the other hand, they place the 'robust' forms as a derived lineage sharing great reduction of the anterior dentition, molarization of permanent and deciduous premolars, expanded and flattened molars with reduction or elimination of shearing wear, greater orthognathy and related cranial-vault features. Their analysis agrees well with that of Wallace (1975; this volume), who, in essence, has described a morphocline in early hominid dentition, with the ancestral features being somewhat intermediate between the two end-points. Although part of his determination of polarity rested on temporal evidence, the morphology appears to speak for itself, indicating that South African *Homo* spp. have ancestral conditions, while 'robust' forms and later 'graciles' are derived in different directions. In other words, they follow different trends in morphology, which also match well with their apparent temporal positions.

This interpretation does not correspond exactly to the views of Robinson, who, it must be noted, has at least argued that he is using a somewhat similar methodology. By comparison to Wallace's (and Eldredge and Tattersall's) interpretation, Robinson has seen the morphocline as extending from an ancestral form similar to known 'robusts', through the 'graciles' to later hominids, thus as a single line, rather than a major branching. In terms of actual phylogeny, there would be a branching which left 'robust' forms to persist without much change, but the morphocline would be linear. As Eldredge and Tattersall have said also, there must be further, more detailed analyses of the skull and teeth, as well as inclusion of evidence from

4. By comparison, *Ramapithecus* possessed only one additional ancestral feature: a 'sectorial' or C'-honing P<sub>3</sub>. The very inclusion of *Ramapithecus* in the analysis may be thought to have biased the conclusions, but this is probably untrue. On the other hand, if this analysis had been carried out by Robinson (see below), with the inclusion of *Gigantopithecus* among the Hominidae (and without *Ramapithecus*), it is possible that more 'robust'-like gnathic characters and large size might have been determined as ancestral features of hominids. This contention is hard to prove without actually performing such an analysis, however.

Delson, Eldredge and Tattersall (1977) did undertake a partial study including both of these fossils and other hominoids which agreed with the results of the previous analysis. More recent data on dental characters of later Miocene hominoids suggest alterations in the cladogram, but substantiate the method.

the brain, post-cranium and other systems, before the question can be reconsidered in more detail. But this method seems to offer the most promise.

From the evidence and discussions during this conference, it appears that several different models of early hominid phylogeny can be consistent with present knowledge. I offer the following 'individual variant', based on the preceding arguments.

Whatever the ancestry in the 15-8 m.y. range (see Simons, this volume), the dental pattern seen in Miocene *Dryopithecus* species may have been altered by increase in relative molar size to one similar to that found in South African 'gracile' australopiths. Accompanying this change would have been some relative increase in brain size and the development of a bipedal locomotor system. There is still major disagreement among specialists (as in this volume) as to whether significant morphological or functional differences exist between 'gracile' and 'robust' early hominids in their post-cranium, especially the lower limb, or even if early hominids differ from modern ones. What is required now is a careful determination of polarity along the morphocline whose states include the characteristics of several postcranial complexes in australopiths, *Homo* and modern apes, which are partly derived in their own ways. The australopiths share some features which *may* also be derived among hominids, thus linking them in a clade separate from *Homo*. However, Robinson's (1972; this volume) arguments for a 'primitiveness' of the 'robust' locomotor system still merit full consideration as well.

On the other hand, there is no *a priori* reason to expect that, even if known 'robust' australopiths retain a more 'primitive' locomotor apparatus, their cranio-gnathic complex is also ancestral. Mosaic evolution has long been accepted as functioning for humans as well as other animal groups, and I would expect it to be especially strong in early hominids, as they adapted to new environments locally and perhaps competed with one another in certain niches. Thus, the common ancestor of the early hominids might have possessed the cranium and teeth of a 'gracile', on the body of a (small?) 'robust' form. From this ancestral stock, one or more (sub-)lineages of 'robust' form developed, following the dental trends described by Wallace, increasing absolute brain size as body size increased (and on body size our evidence is most shaky) but showing little overall 'advancement'. Tobias' interpretation (1973b) of a 'robust' superspecies with several semispecies may be a good interim taxonomic assessment.

Another lineage derived from the ancestral early hominid stock appears to have reversed the trend to increase in molar size, resulting in relatively smaller cheek teeth which retained the ancestral shearing functions. At the same time, there was increase of brain size relative to body size and improvement of the locomotor apparatus. These trends, along with some cranial shape changes, proceeded mosaically, perhaps in a set of interbreeding (sub-)lineages which we are as yet

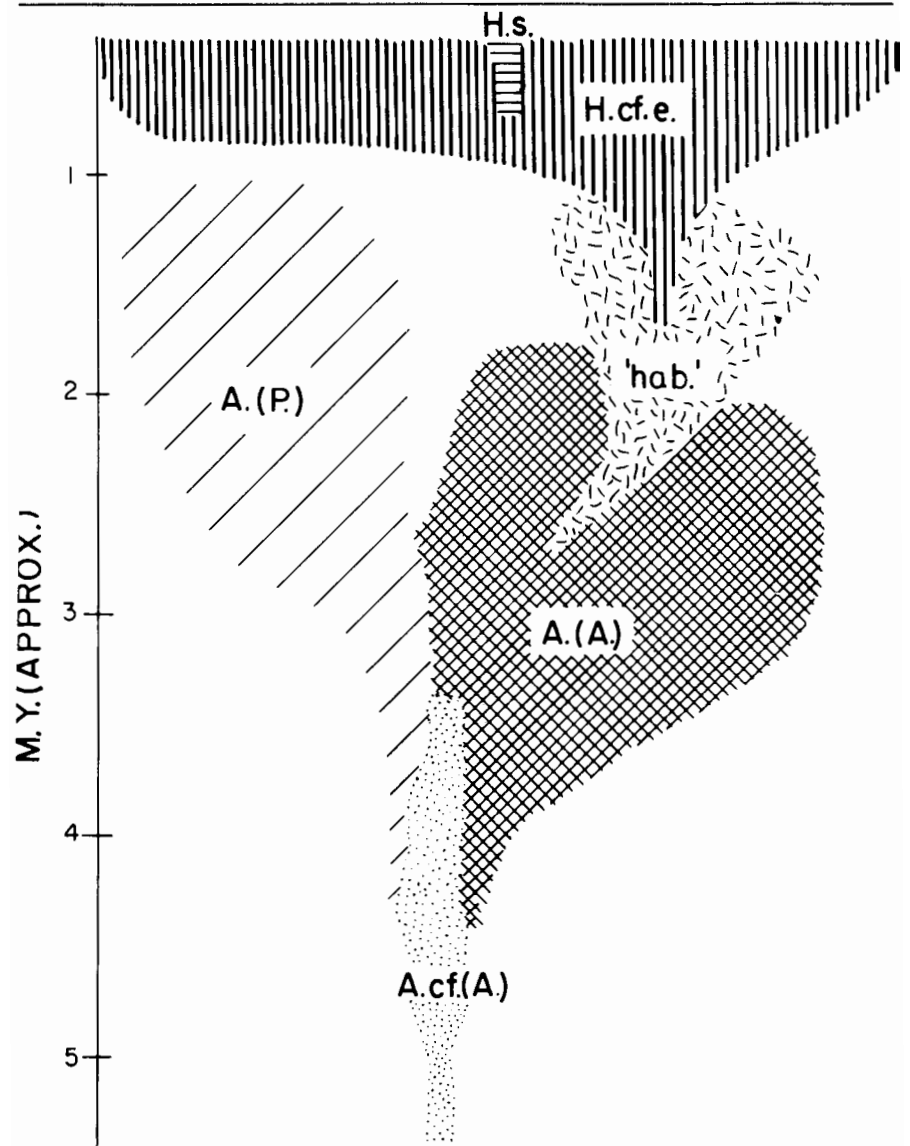


Figure 1. A model of the evolutionary history of the early hominids. The time axis is approximate, and the relative width of the funnel-shaped lineages indicates their range and diversity. Reproductive isolation between species was incomplete at first, later complete. Note that some indicated temporal range data are now incorrect: the oldest known *A. (Paranthropus)* is between 2.0 and 2.25 m.y. in age, while specimens assigned to *Homo habilis* may be older than 3.5 m.y. The latter are less clearly related to *A. (Australopithecus)* than they are to ancestral *Australopithecus*.

Abbreviations: A. = *Australopithecus*  
 P. = *Paranthropus*  
 'hab.' = *Homo habilis*  
 H.cf.e. = *Homo cf. erectus*  
 H.s. = *Homo sapiens* (archaic)

unable to unravel. New developments would thus originate in a peripheral population, allowing it to compete favourably and spread across the total range to replace its ancestor, only to succumb eventually in turn. The pattern is one of successive expanding (sub)species replacing one another through time. This can be illustrated (Figure 1) by a set of nested funnels, rather than by Howell's (1967) pattern of apparently contracting populations or Tobias' picture of each funnel-shaped lineage extending far back in time (1973a, 1973b). The group of 'gracile' populations might also be recognized as a superspecies, or as a set of local subspecies analogous in some ways to Campbell's evaluation (this volume). This reliance on superspecies is perhaps as much a recognition of our own uncertainties as it is a representation of evolution in progress at low taxonomic levels.

Accordingly, it seems best to recognize only two genera in the time period here considered. A strict cladist would consider the 'robust' lineage or lineages, the 'graciles', and their common ancestor as three taxa of equal rank, as Robinson has done, in part. Because what we know as *Australopithecus africanus* is morphologically so 'primitive', so retentive of common ancestral characters, it is still very similar to 'robust' forms in most complexes, as might be expected in diverse species of a single genus. Thus I hesitantly recognize only *Australopithecus* for hominids of moderate body size, with brains of 400-600(?) cc., large cheek teeth, etc. Following Howell (1967) among others, subgenera *A.* (*Australopithecus*) and *A.* (*Paranthropus*) can be distinguished; the unknown common ancestor possibly merits a third.

The morphologically 'transitional' or 'intermediate' specimens from Olduvai, Rudolf, Hadar and other regions testify to the presence of a derived 'gracile' species *Homo habilis*, which is nonetheless still difficult to diagnose or identify consistently. Present evidence suggests its origin from the as yet unknown common ancestor of *Australopithecus* species earlier than is indicated in Figure 1. Still other (later) samples can be identified as *Homo cf. erectus*, whose spread probably coincided causally with the demise of *A. robustus*. Swedlund (1974) found this extinction the most difficult datum to explain in a multi-lineage model under ecological constraints, but the advanced tool kits of *Homo erectus* might have permitted it indirectly to outcompete *A. robustus* in the use of resources, if not more directly. Groves and Mazak (1975) have recently suggested that specimens here allocated to *H. cf. erectus* be named *Homo ergaster*, although no comparison of holotypes or hypodigms was carried out in a paper which professed to apply the methods of mammalian systematics to palaeoanthropology. The description of more complete material from Koobi Fora (Leakey and Walker, 1976) once again underlines the need for the actual application of such methods to the study of fossil man where they continue to be conspicuous for their absence.

I realize that this reconstruction of early hominid evolutionary

history is very speculative, but it may serve as a hypothesis to be tested, one on which I have extended myself when possible in order to be specific. The picture agrees in most respects with Jolly's (1970) well-known two-phase dietary model, especially as we both consider it more likely that the development of increased adaptations to small-object feeding would occur in later or more derived hominid populations ('robusts'), rather than being fully formed in the earliest hominids. Wallace's finding (1975) that there is no clear difference in tooth chipping (and thus grit content of food) between 'gracile' and 'robust' early hominids seems to fit in with Jolly's arguments as well as with the above. Szalay's (1975) suggestion that positively selected incorporation of the canine into the incisor row was coupled with thickened cheek-tooth enamel to facilitate meat-eating is also most valuable, although his inference of bone-crushing by this early hominid dentition requires experimental or behavioral testing.

### *Discussion*

There may seem to be some inconsistency in this analysis with respect to the inclusion of temporal information. In dealing with metrical data, I have argued for the grouping of specimens for consideration into time blocks, so as to avoid blurring potential differences. For example, if an ancestral population had some variate with mean 2 and range  $1\frac{1}{4}$  to  $2\frac{3}{4}$ , and two later populations had values of 1 ( $\frac{1}{4}$ - $1\frac{3}{4}$ ) and 3 ( $2\frac{1}{4}$ - $3\frac{3}{4}$ ), it would be simple to differentiate the two younger phenons considered alone. But if all three were pooled to increase sample size, there would be a spurious indication of a single variable population (see also Pilbeam and Zwell, 1973). With morphological characters, however, the inclusion of temporal data at the wrong stage of the analysis could well be counter-productive. It may be necessary to pool short-period temporal evidence in the first stages of a cladistic study: incomplete specimens from a single site are included in the same phenon to produce a complete picture of the features of that phenon for comparison. What is important is not to employ relative ages in the determination of ancestral characters, so that the time dimension can be added later in order to reconstruct historical events. Time cannot be used in polarity analysis without leading to circularity.

Campbell (this volume) has chosen another route, basing his determination of taxa mainly on the contemporaneity of phenons within a broad group. He has thus separated the East African 'robust' forms as one lineage, but included the South African ones as merely a subspecies of the 'graciles', mostly because it is not easy to see more than one lineage in South Africa. This is too limited an analysis, however: no positive reason is given to link the two South African morphs so closely. Clearly, any two points or clusters in morphological or geometrical space can be connected by a single line

or trend, but, with biological processes, the meaning of that trend also depends on other known points or populations: in the cladistic view, the 'robust' and 'gracile' South African forms may be similar because of shared ancestral features, not having much taxonomic 'weight', while the South and East African 'robusts' share derived conditions (albeit perhaps to different degrees) and thus must be linked phyletically and taxonomically. The phyletic 'lineage' connecting South African 'gracile' and 'robust' australopiths in Campbell's interpretation in fact bypasses the major evolutionary branching point within the group. On the other hand, Tobias (1973a, 1973b) has accepted the arguments of Partridge (1973; see rebuttals by Bishop and by Butzer, this volume) and others (e.g., Butzer) that the Taung hominid is quite recent, and he has suggested, partly because it is late, that it is probably a 'robust' individual. The resulting nomenclatural problems raised by Tobias indicate a disregard for the provisions of the International Code of Zoological Nomenclature.

### *Summary*

I have reviewed several schools of thought on models of early hominid phylogeny: single-lineage and multi-lineage with either 'gracile' or 'robust' form as common ancestor. Data on molar area in single and pooled samples of two species of the terrestrial fossil cercopithecoid *Mesopithecus* are provided to serve as a standard of variability in single species of catarrhines. Consideration of this pattern with that observed in australopiths suggests that the early hominids are more variable than has been thought. Much of this variation may be due to the great size of the East African 'robust' individuals. In addition, studies supporting the single-lineage hypothesis have not considered questions of proportion along the tooth row, as emphasized by Robinson, nor of the effects of pooling specimens from different time periods. I suggest that the work of Pilbeam and Zwell (1973) along the latter lines be repeated, with more accurate delineation of time blocks.

Having determined that a multi-lineage model is required, I have suggested the application of the cladistic methodology, as exemplified by Schaeffer, Hecht and Eldredge (1972) and Eldredge and Tattersall (1975). A theory of relationships among the phena can be formulated by linking those which share derived characters, and a cladogram developed. With the addition of the time dimension, a phylogeny of the group can be drawn up, while comparisons of variation and other criteria may be used to rank the phena into formal taxa.

I have suggested an outline model of early hominid evolutionary history and systematics, developed by applying these methods superficially to published data (especially those of Eldredge and Tattersall, 1975, and Wallace, 1975 and this volume), in order to serve as the basis for further discussion and refinement after more detailed

work. The common ancestor of the known early hominids is reconstructed as possessing cranio-gnathic characters found in early 'graciles', perhaps mosaically linked with a heavy body and the post-cranial features Robinson (1972) has considered distinguish 'robusts' from 'graciles' (assuming such differences do indeed exist). Taxonomically, the known 'graciles' and 'robusts' are perhaps best ranked as subgenera of *Australopithecus*, possibly with a superspecies for the 'robusts'. *Homo habilis* existed as a distinct taxon, morphologically if not phyletically intermediate between *Australopithecus* cf. *africanus* and *Homo* cf. *erectus*. The appearance of the last species probably is closely linked to the extinction of *A. Robustus*. This model or scenario is presented graphically in Figure 1.

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