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Received 20 February 1976
and accepted 25 March 1976

Keywords: cladistics,
classification, fossils,
phylogeny, taxonomy,
primates, Catarrhini.

Catarrhine Phylogeny and Classification: Principles, Methods and Comments

In recent years, zoological systematists have engaged in heated debate over methods of phylogeny reconstruction and classification, but little of this interaction has penetrated the anthropological literature. I have summarized part of it here, concentrating on the cladistic method of phylogeny analysis and the relationship of classification to its underlying phylogeny, with examples and comments from the evolutionary history of catarrhine primates. Phylogeny may be broken down into "cladogeny", the study of branching points and phyletic linkages among taxa, and "scenarios", or interpretive reconstructions of adaptation and ancestry. In cladogeny analysis, fossils are treated in the same way as modern taxa, with their stratigraphic age considered only in special circumstances. In a scenario, the identification of actual ancestor taxa may be attempted in a probabilistic manner only if specific criteria are fulfilled. Classifications must closely reflect the group's cladogeny, but several methods are available to assign ranks to taxa and to vary the final hierarchical pattern. These theoretical postulates are applied to the catarrhines, resulting in several cladograms of intertaxon relationship, a more extrapolative phylogeny diagram and some alternative classifications, including the insertion of new ranks.

1. Introduction

In the evolutionary study of a group of animals, two of the major goals are reconstruction of the phylogeny and development of a classification of the species involved. It will immediately be seen that two different verbs were intentionally employed in the foregoing sentence, and one aim of this paper will be to emphasize that a phylogeny is a sequence of real past events which, with sufficient evidence, can be reconstructed or "discovered", while a classification is one of several ways of transcribing phyletic data into a standardized form.

In recent years, a number of authors have engaged in colloquy (mostly in the pages of *Systematic Zoology*) concerning the methods by which phylogenies and classifications are to be formulated and compared. Much of this discussion has not been generally available to anthropologists in their own journals, although Martin (1968) introduced similar concepts, and several authors in Lockett & Szalay (1975) also considered these questions. Eldredge & Tattersall presented a clear summary of the fundamentals on which this work is based, and I have utilized some of these ideas in works on primate evolution (Delson, 1975*a,c*, 1977; Delson & Andrews, 1975). This essay provides an opportunity to suggest some new variations on the theme. In the first sections, I will discuss some aspects of phylogeny and its relation(s) to classification. In a concluding section, some of these principles will be applied to the catarrhines. Most of the data supporting the statements of relationship have been published in Delson (1975*a*) and Delson & Andrews (1975) and will not be repeated here, nor will all arguments pro and con.

2. Comments on Phyletic Relationships and Paleontology

Phylogeny: scenario versus cladogeny

The term phylogeny has been employed by evolutionary biologists with two overlapping meanings, one implying merely the sequence of branching-points through the evolutionary history of a group, the other also embracing interpretation of the causes of those furcations. This dichotomy is especially clear when the views of cladists such as Hennig (1966) are compared with those of "classical" or "evolutionary" systematists such as Simpson (1961), but these and other authors (including myself) often mix usages of the term even in a single work. This is difficult to avoid, as students of evolution want in most cases to interpret the taxa under study not only as arbitrary sets of specimens or dots on a page to see which one is most closely related to another, but also as (once-) living groups of organisms subject to natural selection and adapting or undergoing speciation. The latter aspects of what is generally called phylogeny have been termed a "scenario" of evolutionary events by Delson, Eldredge & Tattersall (1977), and I here tentatively suggest the new term "cladogeny"* to indicate those aspects which reflect only a sequence of branching points and the complementary concept of determining closest relationships based on recency of common ancestry. This term is not as euphonic as one might hope, but it does clearly call to mind the concept of cladogenesis and the distinctive type of data contained in a cladogram (see below).

Cladistic reconstruction of relationships

"Cladogeny" is the attempt to determine which two of any three known taxa are more closely related to each other (by reason of recent common ancestry) than either is to the third. The solution to this problem must eventually rely on a study of the morphological characters presented by the three taxa, and three currently active schools of thought differ as to the means of weighting characters for comparison. Phenetic systematists (e.g. Sneath & Sokal, 1973) make direct comparison of quantity of characters in common, without weighting, the greater number implying closer relationship. "Evolutionary" systematists (e.g. Simpson, 1961, 1963) weight some characters of greater "utility" but include both "primitive" and "advanced" characters (or states) in determination of relationship. Cladistic ("phylogenetic") systematists (e.g. Hennig, 1966) attempt to make further distinctions, and this view will be argued here (see also Simpson, 1975).

Characters, or states of varying characters, can be possessed in common among animals for one of three reasons as follows. (1) They may be conservative features, retained from the common ancestor of a larger taxon including the specific animals under consideration (ancestral or "plesiomorphic" conditions). (2) They may be convergent features, independently developed by animals which are otherwise not close(st) relatives—also termed parallelisms (see Hecht and Edwards, 1976 on a possible distinction between these

* In an article published after this paper had been completed, Sneath (1975) utilized the term cladogeny several times, but without clear definition. His usage (pp. 360, 364, 365), appears to correspond to the definition I have given here, in that he seems to refer to both an aspect of historical phylogeny and the pictorial representation of that aspect, which might otherwise be called a cladogram. See also Sneath & Sokal (1973).

“sibling” terms). (3) They may be novelties, shared as the result of development in one lineage only of the larger group (derived or “apomorphic” conditions); such derived characters may be shared by a sub-group of taxa (“synapomorphy”) or may occur uniquely in one taxon (“autapomorphy”). It is the argument of cladistic analysis that only derived characters may be used to document relationships within a group. Convergent characters do not indicate special phyletic relationship, although they do provide information on adaptations in common. Ancestral characters merely confirm reference to the larger group, but their conservative retention by two or more sub-taxa in no way indicates ancestry in common later than the original member of the whole group, which would have in turn possessed such features as derived states relative to *its* ancestry. Similarly, autapomorphies are of no use in determining phyletic relationships, but merely serve to *differentiate* sub-taxa from their close relatives.

The theory behind this approach is now accepted at least superficially by many systematists (see Mayr, 1974; Simpson, 1975), but its application is not often accurate. The problem, of course, is that of determining ancestral *vs.* derived states (Gingerich & Schoeninger, in press). Information on this point is drawn from several sources: distribution of character states within the group under study and comparison with distributions in related “outgroups”; functional study of biomechanical and developmental requirements in sets of character states which may be termed “morphoclines” (Maslin, 1952) or “transformation series” (Hennig); and patterns of ontogenetic development and morphogenesis. Certain types of paleontological data may also be employed in special cases, as will be discussed below, but in a manner somewhat different from the data of comparative anatomy. In most cases, however, as Schaeffer, Hecht & Eldredge (1972) have argued, it is important not to employ any relative age information when determining “polarity” of ancestral and descendant characters along a morphocline, so that circular reasoning does not bias the result. Thus, fossils are considered along with modern taxa as if they were lesser-known members of the recent fauna. Morphoclines are then established and polarity determined for each using morphological criteria only.

The development of a set or theory of relationships among the taxa under consideration has been discussed by a number of workers (e.g. Eldredge & Tattersall, 1975, for a clear summary) and will not be detailed here. In brief, one searches for pairs of taxa (not necessarily of the same *apparent* rank) which are each other’s closest relatives among all taxa known to the researcher. These two taxa may be considered sister-taxa, implying descent from a common parent taxon (species). The actual parent may or may not be known (some argue not knowable), and thus the search for ancestor-descendant relationships is unnecessary and often counter-productive (but see below). If one of the two sisters is itself a group of taxa, comparisons must be made with an amalgam of those characters deemed to be ancestral for that group—such a list of features would in a sense characterize the unknown ancestor of the group and has been termed a morphotype (a term sometimes used today by other authors as an equivalent of the pre-Darwinian “archetype”!). The morphotype is not a real animal in itself, but a hypothetical reconstruction of part of one. The end result of a cladistic analysis is a cladogram, a diagram of relationships which has no true time axis, but represents only a sequence of branching events along each lineage involved (see Figures 1 and 2 below). Within a single lineage, older events are below younger ones, but comparisons of the age of nodes is not possible between lineages. All such nodes are characterized by the ancestral morphotypes for the taxa above them.

Following such a cladistic analysis of relationships, a classification can be developed which according to "strict" cladistic methodology must reflect only the information presented in the cladogram. A final step is the development of a scenario of evolutionary history of the group under study, including analysis of (paleo) biogeographical, stratigraphical, functional and adaptational data.

Stratigraphy and polarity

Schaeffer, Hecht & Eldredge (1972) have argued strongly and convincingly for the exclusion of any stratigraphic data in the determination of morphocline polarity. They point out that in many cases geologically older fossils may be more derived in at least some characters than their younger (fossil or modern) relatives. Thus, the acceptance of early appearance in the fossil record as a criterion of "primitiveness" would obviate much of need for morphological comparison in some groups and canalize relationships on the basis of a relatively few data. Moreover, the mosaic nature of evolution is such that few known taxa would be conservative in all features, so that assuming early taxa to be fully "plesiomorphic" would lead to errors in morphocline polarity.

On the other hand, many paleontologists have rebelled at this apparent loss of the "main" value of fossils, their true time placement as ancestors and their place as witnesses of the actual course of phylogeny. And some comparative anatomists (e.g. Le Gros Clark, 1971, esp. pp. 23–30) have accepted the idea that "primitive" *vs.* "advanced" characters differ in phyletic value, while nonetheless according to paleontology the only "direct" role in determination of phylogeny. Even Hennig himself (1966: 142 ff) seems to accept this view in some cases. Despite this, and as a paleontologist, I must accept the reasoning of Schaeffer *et al.* that in almost all cases, the use of stratigraphical data is restricted in relationship determination. They may be employed at the outset, in grouping samples into taxa, so that only those individuals from a relatively narrow time band will be considered as a homogeneous unit from which the "morphotype" of a species can be reconstructed. Age data are then set aside while all species are considered as contemporaneous in determining morphocline polarity. Finally, age data are again important in the formulation of evolutionary scenarios (see below).

Nonetheless, there may often be cases where no clear determination of morphocline polarity can be made by the methods of comparative morphology alone. Some authors (e.g. Nelson, 1970, 1969) would then incorporate biogeographical data, arguing that relict distributions of taxa implies "plesiomorphy" of their characters, but both the joint occurrence of derived and ancestral features in many species and the opportunistic nature of geographical dispersal leads me to reject this view. However, it is obvious that ancestral states must have occurred in the earliest members of a group, if only by definition; and I would argue further that, in general, early fossils are likely to be conservative in more features than are later forms, having had less time to change from the ancestral condition. This of course does not "prove" that states found in early fossil members of a group are ancestral states for that group. But, if we are to obtain the most information from the data available, I think it permissible to argue that in those few cases where it is not otherwise possible to distinguish clear polarity between two (not more) possible character states of a morphocline, the presence of one of them in an ancient fossil would be sufficient grounds to accept that state as ancestral, at least as a working hypothesis, rather than completely to ignore that character as would otherwise be done.

Such a judgement is more probabilistic than one which ignored relative age, as it would be less open to testing, but it does still serve a purpose in building hypotheses, which may then be tested when additional data become available.

3. Scenarios and Ancestors

Identification of ancestors with a probabilistic approach

Once a cladogram has been constructed for known taxa, most systematists, and especially paleontologists, wish to produce a scenario of the evolutionary history of the group. Many authors have engaged in this latter pursuit (including myself: Delson, 1975a), but a good number of these have done so without the important preliminary step of "cladogeny" development. Such work is not based on a testable framework and is not open to question on scientific, rather than purely subjective and interpretational, grounds. But when the best-understood data have been employed in a cladistic analysis of relationships, additional morphological data, as well as factors of time, distribution, ecology, and so forth may be incorporated into a scenario which attempts to explain "why" the observed pattern occurred, rather than merely to document the pattern itself.

The identification of possible ancestors for the various taxa under consideration is one of the most common aspects of a scenario and is unfortunately one which occurs most often when no cladistic analysis has been performed first. Several recent studies by Gingerich (1976b; Gingerich & Schoeninger, in press) typify a common if extreme view of the paleontologist's ability to locate ancestors in the fossil record. The basic argument involved is that if two related phena (groups of morphologically similar individuals or specimens) are sampled from time-successive horizons, it may be most parsimonious to assume that the older is ancestral to the younger rather than to hypothesize an unknown common ancestor of both. Determination of phylogeny thus consists of placing such phena in correct stratigraphic position and allowing the stratigraphy to "reveal" the course of evolution and the linkages between pairs of phena, once it has been shown that all are reasonably close to one another phyletically. In his most detailed study, Gingerich (1976b) has utilized what are apparently derived characters *versus* convergences to delineate seemingly monophyletic lineages among the phena. Unfortunately several of his named taxa consist merely of a few fragments intermediate in time, shape and size between more complete samples. Other workers (e.g. Engelman & Wiley, 1977; Eldredge, personal communication) have commented similarly on this methodology, which is presented most clearly by Gingerich & Schoeninger (in press). Engelman & Wiley, in fact, go so far as to argue that no ancestor-descendant relationships may be accepted in evolutionary studies, as such relationships cannot be tested, and without provision for testing, no hypothesis can be judged scientifically. I essentially agree with these authors (and see also Szalay, 1975b, 1977); that a testable hypothesis is an immediate goal of scientific research, but I am not convinced that the identification of a possible ancestor is untestable, although the development of rigorous falsification tests will be difficult.

Even granting Engelman & Wiley their premise, however, I would reiterate my belief that, within limits, attempts to recognize an actual ancestral species may be considered. As I have already said, it is my feeling that in a scenario of evolutionary events, all reasonable evidence should be included. Thus, even if ancestor-descendant relationships are not fully testable, such hypotheses are important if they throw light on patterns of

evolutionary development and adaptation. It is obvious that all animal species have had a series of successive ancestors stretching back into time, but the question at hand is whether in our paleontological collections there exist any pairs of species such that members of one evolved eventually into the other. These ancestor species did actually live somewhere, and probabilistically, fossils of some of them must have been found. But how do we identify them?

Within a cladistic framework, the identification of potential ancestors may be pursued in a multi-step process involving successively restrictive criteria. As Engelman & Wiley (1977) have argued, it is impossible to objectively test such an identification directly, so that the result is a probabilistic one, depending on plausible inferences and requirements of at least minimum levels of likelihood. Engelman & Wiley have further argued that ancestor-descendant relationships are meaningful only at the level of species, not for higher categories which are merely artificial constructs of species-level taxa; they have specifically denied the morphotype concept any role in this context. I can agree that it is only at the species level where evolution (and thus ancestry) is a real phenomenon, but I submit that judicious use of morphotypes may be the sole means to approach this problem. If species A is the ancestor of species B, it would also be the ultimate ancestor of B's sister taxon, of whatever rank or diversity. But the only way to realistically deal with a group of species is to consider its morphotype, admittedly an abstraction but one based on data analysis. Moreover, for A to be the ancestor of B would require that A be the closest taxon to B, that is, its sister, among known taxa.

Thus, the first step in identifying a potential ancestor would be to examine the cladogram of the group under study (and the character distributions on which it is based) to determine if there exists a taxon which could be ancestral to its own sister. In other words, do the known features of such a taxon correspond completely to the morphotype of the group composed of itself and its sister. This is, of course, not an automatic feature of sister-group relationships, as even a relatively "primitive" taxon might possess one or more autapomorphies which would effectively bar it from further consideration as its sister's ancestor. Only if the purported ancestor is completely plesiomorphic (or identical) by comparison to its putative descendant can the relationship be sustained. It is to be expected that an ancestor would have the same character state as its descendant in several features, namely those which linked them as sisters in the first place. On the other hand, if there were not *some* differences, the two phena would be considered a single species (hopefully), despite any temporal separation. In terms of morphology, however, the proposition of ancestry is rendered more believable if the ancestor is clearly intermediate along at least one important morphocline between the putative descendant and an earlier ancestral condition. It would then be derived with respect to all other taxa, but ancestral relative to its own supposed descendant(s).

Once these primary (i.e. morphological) criteria have been fulfilled, a number of subsidiary tests can be applied, in an effort to increase the probability of (not to prove) the suggested genealogy. For example, I would argue that of several sister species present in a given time interval, the one most likely to give rise to a descendant in a later interval would be a widespread, especially polytypic form. Several models have been proposed to account for the origin of new species, of which the most widely accepted are phyletic evolution, the gradual changeover of a whole ancestor species into its descendant (see Simpson, 1953; Gingerich, 1976a, among others); and allopatric speciation, involving the geographic isolation and subsequent divergence of a small, often peripheral portion of

an ancestor species which may subsequently re-establish sympatry (see Mayr, 1963; Eldredge & Gould, 1972). The former model is often espoused by paleontologists or tacitly assumed, while the latter is generally accepted as the only one broadly observable in the recent biota. Although phyletic evolution may have occurred in specific cases, there does not seem to be any clear way of discriminating in the fossil record between evolutionary transitions and immigration of previously allopatric descendants; I would therefore ally myself with those who argue that most "speciation events" in the past involved geographic isolation. Gould & Johnston (1972) have suggested that this monolithic view may soon be supplanted by a variety of speciation models if support develops for recent concepts of selection—controlled sympatric speciation without gene flow or geographic isolation. In either case, however, it seems most likely that a widespread and polytypic species would have given rise to numerous offshoots, some merely transitory, while a rather rare species would have been more likely to succumb to the very environmental changes which might permit part of a variable species to adapt and speciate. Thus, if one species is widespread and well-known in an interval of the fossil record, it could well be that some population (itself possibly unknown) of that species actually did give rise to a younger related taxon.

On the other hand, a rare or poorly-known species in effect already has at least one handicap: it might be a near relative of a supposed descendant, but only a side branch of a plexus of lineages rather than the actual ancestor. In a character as yet unknown could easily reside a decisive autapomorphy, or in a nearby but as yet unsampled paleoecofacies might be fossils of the true, genealogical ancestor one seeks. If, however, such a postulated ancestor is present in many fossil assemblages, especially if it is the only member of its species group at the given time, and/or if it is known for many character complexes so that autapomorphies would be recognized if present, then it is again more *probable* that its role as an ancestor is reasonably assessed.

Of even lower weight in ancestor determination, because they are farthest from morphology, are questions of comparative temporal and spatial distribution. Nonetheless, both of these factors may help in testing a proposed relationship in certain cases. Thus, in terms of zoogeography, adherents to a punctuated equilibrium model might be impressed with the earliest occurrence of a new species on the margin of its purported ancestor's range, while others might demand "origin" in the heart of a prior distribution. Note again, however, that zoogeographical evidence is not here considered of 'prime importance in polarity determination, while with ancient fossils, it is paleogeography which matters.

Time itself could be even more important. Once again, it is obvious that an ancestor must precede its descendant chronologically. But as Schaeffer, Hecht & Eldredge (1972), among others, have indicated, this may not always be the case in the biostratigraphic record. One can generally hope that a purported ancestor stratigraphically predates its putative descendant, but this can not be a strict requirement, in part depending upon one's model of the speciation process. Fossil evidence is of great importance in extending the range of known variation, especially including extinct autapomorphic "side-branches" as well as in scenario-building, but to employ age to define polarity or ancestry is eminently circular, despite the arguments of Harper (1976).

Finally Hennig (1966) and Nelson (1971), among others have considered the splitting of an ancestral species into two descendants as a methodological principle at least, suggesting that one descendant would tend to remain similar to the ancestor in most cases

(the so-called "deviation rule"). However, they have not fully considered whether a species *A* can give rise to *C* and remain itself unchanged, rather than becoming, say, *A'*. I consider the former is certainly possible in some cases, for example, when a marginal population is isolated and undergoes allopatric speciation. If that deme had simply died out (from whatever natural cause) soon after being isolated or undergoing directional selection, few would argue that the original species had changed. By extension, whenever a small, local fragment of a species becomes distinct, I would claim that the original species continues essentially undiminished in variation, adaptive potential or taxonomy. If that view of speciation is accepted, then when a species *A* "splits" into *A* and *C*, the oldest fossils of *C* might reasonably predate those known for *A*, and yet a true ancestor-descendant relationship might hold. If, on the other hand, one argues that speciation automatically results in two new species (*B* and *C*), even if one (*B*) is indistinguishable from its ancestor (*A*), then fossils of the purported ancestor must represent species *A* and be older than *C* (or *B*). Of course, it would be impossible to differentiate living or fossil samples of *A* and *B* in some cases, rendering the taxonomic interpretation of this pattern rather difficult.

To review, then, ancestor identification would begin with the recognition of a known taxon whose morphology corresponds to the morphotype of the group composed of itself plus its sister taxon. While both taxa might be of any rank, the situation is most readily evaluated when the purported ancestor is a species. Next, the proposed ancestor should be intermediate between the morphotype of its sister (descendant) taxon and their immediate common ancestor in at least one, preferably distinctive morphocline. Additional characters of such an ancestor tending to increase its probable likelihood of acceptance include being widespread, polytypic, anatomically well-known and perhaps of "correct" geographic and chronological range. Fulfillment of all (or most) of these subsidiary criteria does not prove that a taxon is indeed its sister's ancestor, but does allow the scenario-writer to argue that such might reasonably be the case. The application of this stepwise procedure is best considered by means of several examples based on recent literature.

An evaluation of specific cases of ancestor identification

The most important criterion of the sequence laid out above is the first, and failure to meet that would immediately remove the purported ancestor from further consideration. Simons (e.g. 1972, 1974) has suggested that *Parapithecus* was the ancestor of the Old World monkeys, a view which now has wide popularity. I have shown (e.g. Delson, 1975c, 1973; Delson & Andrews, 1975) that there is little congruence between the morphotypes of the two taxa, and a close relationship (much less one of ancestor and descendant) between them was rejected. No other known fossil species was found to conform to the cercopithecoid morphotype, either, although certain forms each seemed to share specific derived features with monkeys, and their common ancestor might also have been ancestral to Cercopithecidae.

On the other hand, Eldredge & Tattersall (1975) determined that in cranio-dental characters South African *Australopithecus africanus* was essentially indistinguishable from the morphotype of the *Australopithecus* + *Homo* group. They were at a loss where to place *A. africanus* in a cladogram because of its apparent "total primitiveness". More recently we (Delson, Eldredge & Tattersall, 1977) have added postcranial evidence

which partly clarifies relationships, but if this species *were* entirely conservative (plesiomorphic) it could be considered as representing the actual genealogical ancestor of its known relatives, even if some of these may be coeval on present evidence.

A more detailed example concerns the single case among fossil cercopithecids in which I would claim to perceive such a relationship (see Delson, 1975a, 1973). *Mesopithecus pentelici* is a colobine monkey known in large numbers from southern Europe at a number of open-country sites about 9–10 million years old and rarely in sites 5–9 m.y. old. It is typically colobine in almost all features, except for a slightly narrow interorbital region for its size and a strong semi-terrestrial adaptation of its postcranium: limb bone robusticity, elbow joint morphology and phalangeal robusticity all indicate at least as much terrestrial adaptation as found in any modern colobine and most closely resemble some macaques. A younger species, *M. monspessulanus*, is present but rare at a number of more forested or well-watered Pliocene localities in southern and central Europe (5–2 m.y.) and differs from its congener in its slightly smaller size, narrower teeth and more “arboreal-seeming” elbow (based on fragments). Generally contemporaneous with *M. monspessulanus*, and found at the same sites, is *Dolichopithecus ruscinensis*, a much larger colobine with an elongated face, narrow interorbital region and even more strongly ground-adapted limbs than *M. pentelici*. Terrestrial adaptation is more pronounced than in any other known colobine and is similar to that of the mandrill. Most interesting is the first occurrence of *D. ruscinensis* (only a partial ulna, but demonstrating the essential terrestrial adaptation) at a site in Hungary contemporaneous with *M. pentelici*, but in a zone which was forested rather than “steppic”. Leaving *M. monspessulanus* aside for the moment, *M. pentelici* and *D. ruscinensis* are sister taxa. They are distinguished from all other colobines by their marked adaptation to terrestrial life, and it is in just this complex that *D. ruscinensis* is derived with respect to *M. pentelici*. There are many localities of the same age range as those yielding *M. pentelici*, and as primates are widely sought, any specimens of another primate taxon would likely be identified even if rare. The model (or scenario) I have proposed thus posits a peripheral population of *Mesopithecus pentelici* forced into the fringes of the forested zone in north-central Europe in the late Miocene, where it became isolated and evolved into *Dolichopithecus ruscinensis*. Each species is represented by rare specimens in this region. Then, in the early Pliocene (as documented by pollen and fauna, see Delson, 1975b), a forest landscape spread over southern Europe, and *D. ruscinensis* spread with it, replacing *M. pentelici*. If *M. monspessulanus* is a distinct species, as now seems the case, it might be the result of character displacement leading to smaller size and less terrestriality in a second descendant of *M. pentelici*. In this scenario, all criteria proposed above have been met, except that *M. pentelici* is not known from present evidence to have been polytypic. In no other case involving a fossil monkey, or perhaps any other fossil catarrhine*, can a clear case for an ancestor-descendant relationship yet be made.

It may be argued that this approach (and result) is little different from the simpler model of Gingerich and others, but in those small distinctions lie the criteria under which

* It is possible that a less definite case could be made for a *Homo erectus* ancestry for *H. sapiens*, but in part this depends on the definition and identification of “intermediate” fossils. If all relevant specimens are indeed conspecific, *H. erectus* would certainly be polytypic, but the possibly autapomorphic feature of skull vault bone thickness has yet to be understood as it affects cladogenetic relationships (see also Delson, Eldredge & Tattersall, 1977).

most "ancestors" would be rejected. Gingerich (1976*a,b*; Gingerich & Schoeninger, in press) has dealt with species of early Tertiary primates and condylarths known from a number of western intermontane basins. Some of these species are widespread, but many are present only in one or a few basins, while neighboring regions have not been fully sampled. These regions may contain other contemporaneous species which were the true ancestors (or descendants) of known forms. More importantly, there is no clear evidence presented that stratophenetically linked "species" are indeed sister taxa, rather than merely broadly related ones, and no consistent attempt is made to delineate morphoclines into which the supposedly linked species fit. Considering one example, Gingerich & Schoeninger (in press) should first be asking not if adapids are ancestral to anthropoids, but whether anthropoids share derived features with adapids rather than with any other taxon. It is thus the relationships of tarsiiiforms which are really the issue here.

Finally, Maglio's (1973) study of Plio-Pleistocene elephant evolution also attempts to document a number of ancestor-descendant relationships in a phyletic evolution model. His method of phyletic analysis is basically similar to that of Gingerich, in that comparisons are not made in terms of derived characters, but some of these can be determined from Maglio's descriptions and interpretations of trends. Most of the younger taxa, at least, are known from tens or hundreds of localities spanning large continental areas and with relatively long time ranges. The application of an allopatric model involving climatic change, migration and feeding-mechanism adaptation suggests that several of Maglio's ancestor-descendant links might well be as meaningful as such hypotheses can be.

4. The Relationship between Phylogeny and Classification

In much the same way as a diagram of phylogeny, a classification is a summary of the main conclusions of a systematic study. In most cases, discussion (especially among primatologists) may center on differences in classificatory schemes without full understanding of the source of those differences, whether due to taxonomic philosophy or phyletic relationship—that is to "subjective" or "objective" distinctions. It is clear to virtually all systematists that a classification must be somehow related to a phylogeny, but the closeness of such relationship is one of the major divergences between the various schools of thought.

"Evolutionary" systematists such as Mayr and Simpson agree that a classification must not *conflict* with the phylogeny (really cladogeny) of a group, and that it should be based upon that cladogeny, but they are willing to admit other criteria, especially in terms of employing such subjective inferences as evolutionary divergence and adaptive difference in ranking taxa. They argue that a classification is more than just a verbal listing of phylogeny, but should be an "information-retrieval" system. Cladistic systematists, on the other hand, desire that a classification essentially be a direct transformation of a cladogram into a formal hierarchy. Nelson (e.g. 1971: 374) has tried to simplify this concept to read: "related species must be classified together," but this is nearly tautological if organic evolution is accepted. In more specific terms, he and other cladists argue that all nodes in a cladogram may (but do not need to be) named at successive levels in a classificatory scheme, but that no groups can be named which do not correspond to the holophyletic (maximally monophyletic) clades of the diagram.

Cracraft (1974) has made a useful comparison of the main differences between these two approaches to classification, emphasizing that the "evolutionary" approach may lead to either the classification of two taxa together on the basis of shared primitive features or the raising in rank of one taxon because of its strong evolutionary divergence from its sister taxon, both of which deviations he decries. He also has responded to the notion of an "information-retrieval" system by asking how data other than phyletic relationships can be "retrieved" from such a classification, once it has been inserted.

Following on the work of Nelson (1973, especially), Cracraft discusses two cladistic approaches to the formal production of a classification, namely the subordination of taxa, such that higher taxa are subdivided into two or more sisters of equal rank; and the phyletic sequencing of taxa, such that each taxon is the sister of all taxa of equal rank which follow it in the classification. The former of these methods leads to a straightforward dichotomous classification as proposed by Hennig (1966) and others, while the addition of sequencing allows the classification of a group with a more complex cladogeny. Drawing upon his work on ratite (flightless) birds, Cracraft offers four alternative classifications based on a single cladogram, the first employing only subordination, the others adding sequencing.

This matter of alternatives may sound reasonable, but the alternative classifications themselves are quite distinctive in matters other than absolute rank of taxa (which may always involve some alternatives—see below). If one argues that cladistic classifications are more scientifically reasonable because they are uniquely linked to a cladogram of phylogeny, it is disturbing at the least to see alternatives in which the relative rank of taxa vary widely. Moreover, if certain agreed conventions are necessary to the interpretation of the classification(s), and to the reconstruction of the original cladogram upon which it is based (as Cracraft agrees is the case here), then almost any set of conventions could be substituted within limits determined by an author. In fact, the concept of phyletic sequencing leads inexorably to the raising in rank of one taxon in a group by comparison to the sister of the whole group. As an example, if there are three families *A*, *B* and *C*, such that *A* is the sister of a group including *B* and *C*, standard subordination would lead to a classification as in 1. Under a sequencing convention, such as in 2,

(1) Superfamily I	(2) Superfamily I
Family <i>A</i>	Family <i>A</i>
Superfamily II	Family <i>B</i>
Family <i>B</i>	Family <i>C</i>
Family <i>C</i>	

however, families *B* and *C* are ranked equally to *A*, which had previously been set off in a separate higher taxon; in addition, reconstruction of the original cladogram without recourse to an agreed convention would result in a trichotomy not implied by the original cladogeny. One might argue in reply that if all workers adopted this convention, as they have others involving the Linnaean system, there would be no confusion. But there may be cases in which a trichotomy is intended, implying either lack of precision or actual double speciation, and such cases could not readily be expressed in this system.

As has been discussed by Delson & Andrews (1975: 437–439), both cladists (e.g., Nelson, 1974) and "evolutionary" systematists (e.g. Mayr, 1974) have cited Darwin as the forerunner of their viewpoints. We showed that in fact (and especially as regards

higher primates), although Darwin (1871) seems to have accepted the theoretical supremacy of a cladistic method of classification, he realized that in some cases it would be most prudent to group together two taxa on the basis of shared ancestral retentions, separating them from a more divergent sister of one. This also could be an agreed convention among classifiers. As with the sequencing convention, it would cause great difficulty in reconstruction of the original theory of relationships, unless there were some indication of where each convention might be applied. A solution might be achieved through the use of an "asterisk convention", obvious to a reader not party to the agreement: each time any convention different from simple subordination is employed, the taxa involved are marked with an asterisk or other footnotational device and the convention explained.

Before considering some examples of classification based on catarrhine phylogeny, it is worthwhile to make one other comment on the subject of ranking taxa. Delson and Andrews noted that in both cladistic and "evolutionary" classification, the assignment of at least one rank *a priori* is necessary unless Hennig's earlier (1966) idea of absolute age of a taxon's origin determining its rank (e.g. genera in the Miocene) were accepted. Cracraft (1974: 83) agrees with this concept, limiting the *a priori* rank to that of the whole group under study and adding that with the adoption of sequencing subordinate taxa will have arbitrary ranks within certain limits. Others have disagreed with these concepts, holding especially that as species are the only taxon whose rank has intrinsic meaning, classifications must begin with species and work up to higher taxa (e.g. A. L. Rosenberger, personal communication). This idea would be valuable in theory, but as some clades or lineages of a large group will often have many more branches than others, there would be no simple way to arrive at a rank for the highest taxa of a group, as this would depend in part on how many nodes are named and along which branch or lineage. All nodes on the most complex clade could be named and these ranks somehow converted to the other clades, but this would perhaps excessively restrict a classifier. In addition, there would be no equivalency of higher ranks among a closely related group not studied by a single individual—for example, some orders of mammals might be raised or lowered in rank by students of an individual order, while a study of all orders might juggle other ranks in order to retain orders constant (see McKenna, 1975 especially). It is also perhaps not necessary that the highest rank be the one defined *a priori*, as Cracraft argues, but this is a reasonable suggestion.

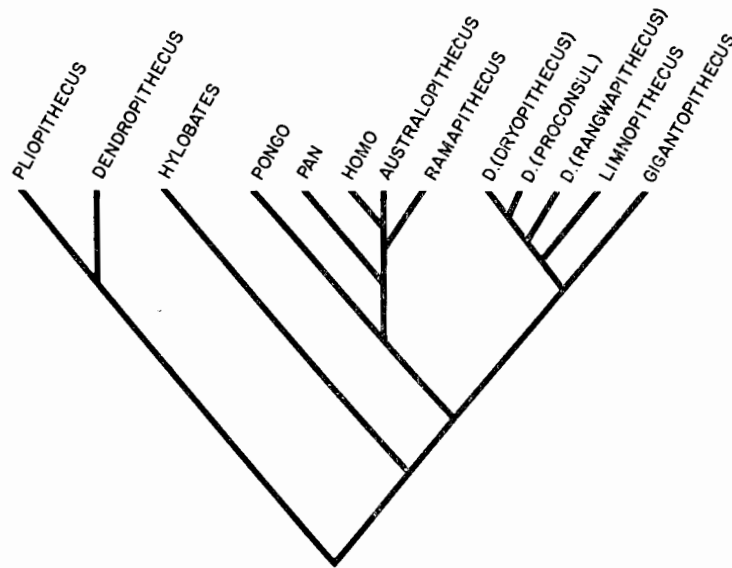
5. Catarrhine Cladogeny and its Expression in Classification(s)

A detailed consideration of catarrhine phyletic relationships including characterization of ancestral morphotypes has recently been presented by Delson & Andrews (1975). This work will not be repeated here, or even fully summarized, but a few points regarding branching patterns of early fossils and higher taxa will be reinterpreted. Andrews and I did not discuss classification in the context of some of the points made above, however, and it seems worthwhile to devote some space to formulating catarrhine classification in their light.

Relationships of major catarrhine groups

Delson & Andrews (1975) considered that the phyletic position of *Hylobates* was critical to the understanding of the cladogeny of anthropomorph catarrhines. Figure 1 corresponds to their illustration of Miocene to recent forms, with the alteration that *Ramapithecus* is more certainly placed as the sister of a *Homo* + *Australopithecus* group (see Delson, Eldredge & Tattersall, 1977). The linkages among the "great apes" (including men) thus appear fairly clear, even if not accepted as such by all workers. The problem is whether the gibbons are phyletically linked to the Miocene fossils *Pliopithecus* and/or *Dendropithecus* (ex-*Limnopithecus macinnesi*), or if *Hylobates* is the sister-taxon of the "great apes", while the fossils represent the sister of all the "modern" apes.

Figure 1. Cladogram of relationships among the Miocene to recent apes and men. In Figures 1-3, there is no simple time axis, but branching points along any given lineage are younger, the closer they are to the top of the page.



Delson & Andrews did not reach a consensus on this point, but I argued then and still consider that the Miocene fossils are essentially conservative, retaining such features as annular auditory meatus, entepicondylar foramen, ancestral facial and molar patterns, typical catarrhine limb proportions and strongly honing canine-premolar complex (all in *Pliopithecus*; *Dendropithecus* is less complete but basically similar). Derived features linking these forms to gibbons are notoriously rare, being confined to such characteristics

as reduced muscle markings on relatively gracile long bones, somewhat shallow mandibular corpus and slightly protruding orbital margins, none of which are particularly convincing. By comparison to the ancestral morphotype reconstructed by Delson and Andrews, *Hylobates* (above the neck) is the most conservative living catarrhine, and thus it is especially difficult to demonstrate relationship based on shared derived characters, while at the same time especially important to do so. In sum, I argue that at present, *Hylobates* is best considered as most closely linked to great apes by virtue of shared characters of the shoulder and thorax (Andrews & Groves, 1975) and thus is the sister-taxon of the latter. *Pliopithecus* is phenetically similar to gibbons in several ways (although a recent morphometric study of the shoulder links it with colobines; Ciochon & Corrucini, in press), but its phyletic ties (and those of *Dendropithecus*?) lie elsewhere.

Including the *Pliopithecus* group, there are three or more sets of early conservative catarrhines whose phyletic relationships require examination. This is not the place for a discussion of alpha taxonomy of the Fayum taxa, so three groups will be considered with the assumption that the members of each are linked by shared derived features, as does seem to be the case: *Pliopithecus* and *Dendropithecus*; *Aegyptopithecus*, *Propliopithecus* and *Aeolopithecus*; and *Parapithecus* and *Apidium*. *Oligopithecus*, although quite fragmentary, can also be included.

Simons (1974 and earlier) has claimed that the *Parapithecus* group is especially related to the Cercopithecidae, but I have previously (Delson, 1975c; Delson & Andrews, 1975) argued that they share no derived features solely with Old World monkeys or their ancestral morphotype except perhaps for a loph-like construction of the upper molars (unpublished at this time). On the other hand, *Parapithecus* and *Apidium* differ from all other catarrhines in such features as the apparent honing development on P₂, a very small metaconid on P₄ and presence of large conules on the upper molars—the latter, which give the loph-like appearance to these teeth, are a derived feature distinctly opposite to what is seen in cercopithecids. *Parapithecus* is distinguished from the cercopithecoid ancestral morphotype by small M₃ and reduced cingulum (especially in *P. fraasi*), although *Apidium* does not share these conditions. The retention of three premolars in the two genera is a conservative holdover which does not in itself disbar these taxa from relationship with other catarrhines, but which does corroborate their distinctness. The *Parapithecus* group must therefore be considered the sister of all other catarrhine primates. The only potential relative of this group among known forms is *Oreopithecus bambolii*, a species whose affinities remain clouded despite a wealth of fossil material.

The remaining early catarrhines except *Oligopithecus* clump together well on the basis of shared ancestral features—annular ectotympanic, postcranium most similar to the *Ateles-Alouatta* group of platyrrhines, canine honing well developed, moderate paraconule development—but without a detailed study of the skull of *Aegyptopithecus* and dentition of all available specimens of the Fayum, taxa linkages are indefinite. There is no clear evidence to link the *Pliopithecus* and *Aegyptopithecus* groups together as opposed to the “modern” apes, but my current interpretation is that the former represent a parallel “radiation” of catarrhines converging toward an ape level of organization. This admittedly introduces an element of scenario into cladogeny reconstruction, but the data are so scarce that even subjective opinion may be worth noting. To develop the scenario, it appears that basic arboreal quadrupedal locomotion was ancestral for the catarrhines, as seen in *Cercopithecus*, most colobines, many platyrrhines and also *Apidium* (Conroy, 1977). The cercopithecids tended to become more eclectic in pattern, developing

terrestriality and leaping ability, while the anthropomorphs* became more arm-dominated, as also did the *Ateles-Alouatta* group of platyrrhines.

A detailed history of Old World monkey evolution is given by Delson (1975a) and summarized in Delson & Andrews (1975); thus the cercopithecoid cladogram of Figure 2 is included here in the interests of reference and completeness. The *Aegyptopithecus-Pliopithecus* group is seen here as the sister-taxon of "modern" apes, sharing some trends which separate the latter from Old World monkeys, shown diverging earlier in Figures 3 and 4. This phylogeny requires some parallel development of features such as the modern ape elbow and shoulder, if the gibbons diverged from great apes at a time (early in the Miocene??) when both had only slightly reduced olecranon processes and conservative shoulder girdles. But if the trend toward ape-like forelimb structure had begun, it might well have continued in the two lineages along similar lines, canalized by their common morphogenetic heritage, leading to the pattern seen today. The underlying cladogeny also implies that the apparently uniform construction of the modern catarrhine auditory region developed at least partly convergently from a pliopithecoid ancestor, perhaps with the beginnings of a tube as in *Pliopithecus*. This view depends on phenetic (ancestral?) similarities between early and late apes which do not necessarily reflect unique common ancestry. However, it is almost equally probable that *Pliopithecus*, *Aegyptopithecus* and allies are the sisters of all modern catarrhines, in which case Figures 3 and 4 (and the resultant classification) would require alteration. *Oligopithecus* appears to be linked to the non-*Parapithecus* catarrhines by such features as the loss of P₂ and concomitant development of C' honing on P₃ (at an early stage, as the premolar enamel has been worn through to dentine; Delson, 1975c) and also the widened molar talonids (see Szalay, 1975a). However, the absence of a distal fovea and of hypocone wear facets (implying a low or absent hypocone) suggests that *Oligopithecus* was more "primitive" than any later catarrhines (Kay, 1977). The resulting cladogeny of all catarrhines is depicted in Figure 3, while Figure 4 presents a more extrapolative scenario, reflecting age ranges and postulated times of divergence.

Comments on alternative catarrhine classifications

There are two main points which require discussion in this section, namely the ranking of catarrhine higher taxa and the classification of *Homo* and its relatives compared to the living great apes. Most other questions have been considered by Delson and Andrews (1975) or by Delson (1975a). The relationships of *Homo* and its closest relatives (*Australopithecus* and *Ramapithecus*) to the next nearest taxa are depicted in Figure 1. In a straightforward cladistic and subordinated classification, *Pan* and the *Homo* group would be sister-taxa, separated only at the rank of, say, infratribe (Delson & Andrews, 1975). The two infratribes would form a subtribe whose sister subtribe would be *Pongo*, and these two taxa would be one tribe of the subfamily Homininae (classification I). This system would permit the precise referencing of any holophyletic taxon, but would drastically alter the rank of the *Homo* group. Today, the latter is generally considered a family, with varying ranks given to gibbons, dryopiths and the *Pan* + *Pongo* group, depending almost on the author's whim. It will be argued below that single-family rank is the most

* This term is employed here to correspond to the Hominoidea of Simpson (1945) and others, in order not to bias a discussion of taxonomic rankings.

Figure 2. Cladogram of relationships among the Late Miocene to recent Cercopithecoidea; notes as in Figure 1.

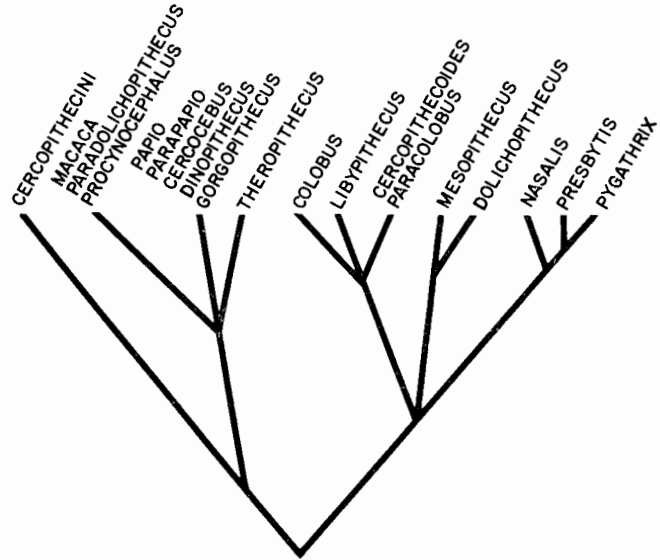


Figure 3. Cladogram of relationships among all catarrhine genera (only family-group taxa of Cercopithecoidea); notes as in Figure 1. The uncertainty as to the phyletic relationships of *Oreopithecus* is indicated by approximate alternative placements marked with *. It is also possible that the *Hylobates/Homo* group should be linked to Cercopithecoidea, rather than the *Pliopithecus/Aegyptopithecus* group, and even more probable that *Oligopithecus* is the sister taxon of all other catarrhines (see text).

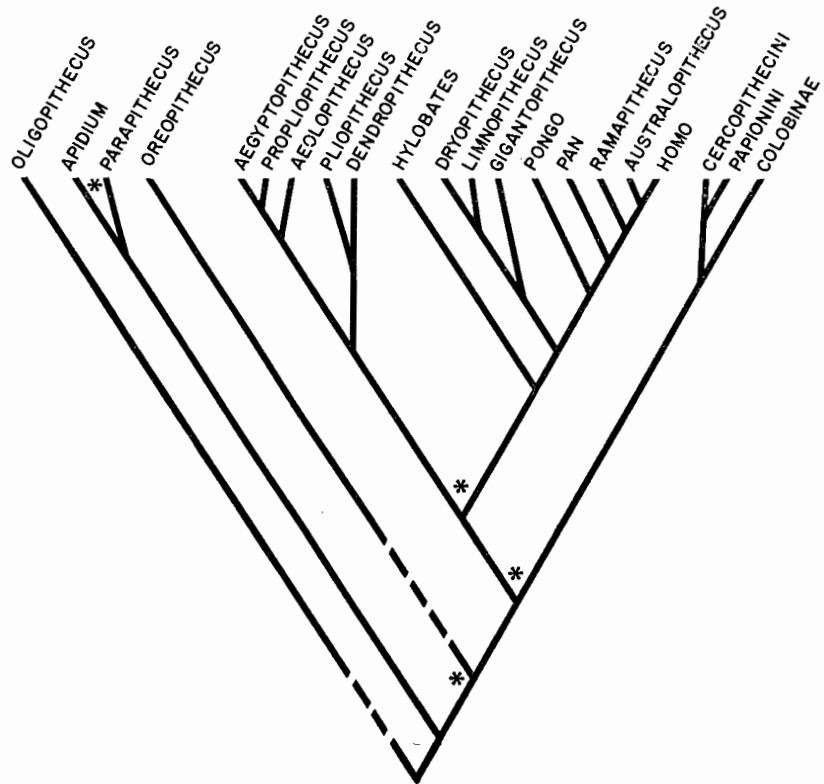
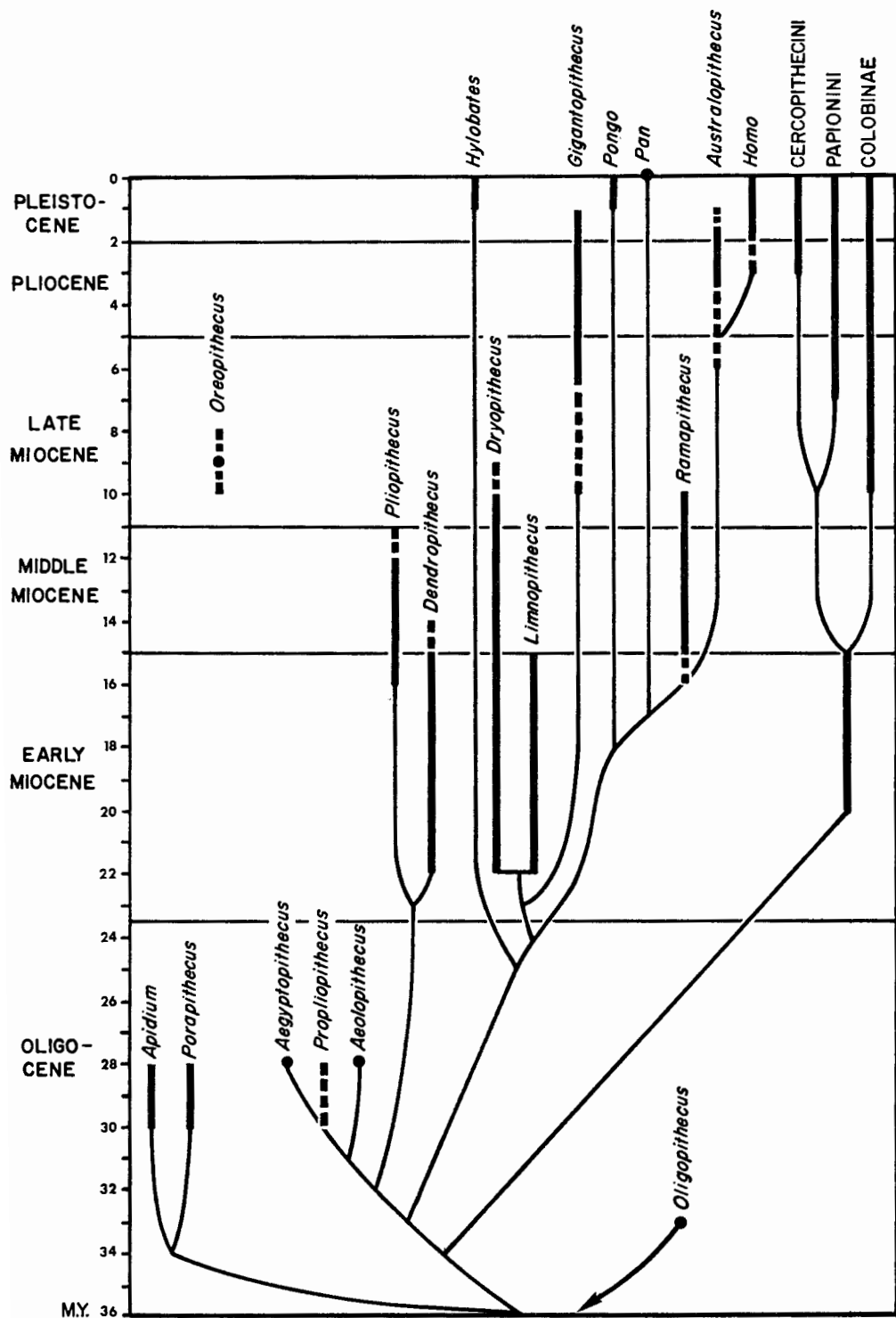


Figure 4. A graphic scenario of catarrhine evolution, combining chronological age range of taxa, postulated relationships and age of branching points. The heavy solid lines represent known ranges of taxa, the heavy dashed lines range uncertainty and the thin lines phyletic linkage (ancestry). All genera are included, except for the Cercopithecoidea, where only family-group taxa are entered. The heavy line for Cercopithecoidea in the early Miocene combines the range of known monkey fossils of *Victoriapithecus* and *Prohylobates*. The uncertain relationships of *Oreopithecus* are indicated by its isolated position. Compare with and see notes to Figure 3.



suitable for the “modern anthropomorphs”; this immediately necessitates some change from the present system, which is clearly outmoded in any case by its anthropocentric motivation.

<i>Classification I</i>	<i>Classification II</i>	<i>Classification III</i>
Family Hominidae	Family Hominidae	Family Hominidae
Subfamily Homininae	“Metafamily Hominacea”	Subfamily Homininae*
Tribe Hominini	Subfamily Dryopithecinae	<i>Homo</i>
Subtribe Hominina	Tribe Dryopithecina	<i>Australopithecus</i>
Infratribe Hominino	<i>Dryopithecus</i>	<i>Ramapithecus</i>
<i>Homo</i>	<i>Limnopithecus</i>	Subfamily Ponginae
<i>Australopithecus</i>	Tribe Gigantopithecini	Tribe Pongini
<i>Ramapithecus</i>	<i>Gigantopithecus</i>	<i>Pongo</i>
Infratribe Panino	Subfamily Ponginae	<i>Pan**</i>
<i>Pan</i>	<i>Pongo</i>	Tribe Dryopithecini
Subtribe Pongina	Subfamily Paninae	Subtribe Dryopithecina
<i>Pongo</i>	<i>Pan</i>	<i>Dryopithecus</i>
Tribe Dryopithecini	Subfamily Homininae	<i>Limnopithecus</i>
Subtribe Dryopithecina	<i>Ramapithecus</i>	Subtribe Gigantopithecina
<i>Dryopithecus</i>	<i>Australopithecus</i>	<i>Gigantopithecus</i>
<i>Limnopithecus</i>	<i>Homo</i>	Subfamily Hylobatinae
Subtribe Gigantopithecina	“Metafamily Hylobatacea”	<i>Hylobates</i>
<i>Gigantopithecus</i>	Subfamily Hylobatinae	
Subfamily Hylobatinae	<i>Hylobates</i>	
<i>Hylobates</i>		

Once a decision is made to rank the whole “modern anthropomorph” group as the family Hominidae, there are a number of ways to go about the process other than the drastic one noted above. If it is so wished, any rank may be arbitrarily assigned to any of the several taxa and through judicious use of new categories and a sequencing convention this rank fit into a complete system. For example, if it were desired to retain the *Homo* group as a subfamily, the Hominidae could be arranged as in classification II. Many other classifications could be similarly formulated, by analogy with Cracraft’s (1974) classifications of the ratites discussed above. But each of these is arbitrary and no more meaningful than any other, as an understanding of the conventions involved is required in order to derive the original cladogram of Figure 1 from such a classification. In fact, there is hardly any real difference between some of these alternatives and the classification I tentatively supported (in Delson & Andrews, 1975) in which the *Homo* group was arbitrarily raised in rank from an infratribe to a subfamily, while not implying sequencing nor changing any other taxon’s rank. Admittedly, this system (classification III) is non-holophyletic and the original cladogram could not be derived from it, but through use of the “asterisk convention”, this problem could again be solved. This result furthermore corresponds exactly to what Darwin (1871) settled on after his discussion of the same points (see Delson & Andrews, 1975: 439). Unfortunately, the classification of *Homo* is still as much a philosophical as a biological problem (see also Simpson, 1945: 187–188), but I would now continue to opt for either classification I or III, and to refrain from those of type II involving a sequencing convention which further confuses the issue.

*This taxon, considered strongly divergent from its ancestral morphotype, is raised in rank relative to its sister-taxon (***) and other taxa—compare with the cladogram of Figure 1.

The second area of classificatory problems within the catarrhines involves the ranking and relative placement of the higher taxa of the group. From the discussion above and the cladogram of Figure 3, the cladistic relationships of these taxa are clear, at least within the framework of this paper. My own previous arguments to the contrary (Delson & Andrews, 1975), it now seems best to classify the *Pliopithecus* + *Aegyptopithecus* group and the "modern anthropomorphs" in a single higher taxon, as they probably shared a common ancestor with each other more recently than either did with Old World monkeys. This "ape" higher taxon would then be linked with an Old World monkey taxon at a still higher rank, as opposed to the highly distinctive *Parapithecus* group. The actual ranks to be assigned to these several higher taxa do cause some problems in light of recent discussions of the still higher level phylogeny of the primates (see especially Szalay, 1977, 1975*b*). According to such researches, it is now fairly certain that the "tarsiers" are the sister-taxon of all "higher primates", the Anthropoidea of Simpson (1945) and most later authors (but compare Schwartz and Gingerich & Schoeninger, in press). The rank generally afforded to the "tarsier + anthropoid" group is that of Suborder Haplorhini, while Anthropoidea is also considered a suborder by those who employ it. There is something to be said for retaining both concepts, as each refers to an important holophyletic assemblage of taxa to which reference is often made in discussions. Unfortunately, this is not possible at present, so long as Catarrhini and Platyrrhini are both retained as infraorders, the only rank between suborder and superfamily. Thus, McKenna (1975) includes these two infraorders and Tarsiiformes in the Haplorhini without any further subordination.

I submit that we have here a situation in which new ranks could be proposed to serve a genuinely useful function (see also McKenna, 1975: 27). If one such rank is inserted between suborder and infraorder, the tarsier group can be set apart from the "higher primates" if so desired. An acceptable name for such a rank might be Hyporder, from the Greek *hypo*, "below" or "under", by analogy with both sub and infra. For the tarsier group, the current term Tarsiiformes might be retained and merely raised in rank if required—as this taxon is monotypic at high ranks, there would never be a need on the basis of present evidence to include two infraorders in the hyporder Tarsiiformes. On the other hand, continued use of Anthropoidea as a hyporder might easily lead to confusion as the concept is often counterposed to a suborder Prosimii, which latter concept must now be replaced by Strepsirhini (excluding Tarsiiformes). Thus, it might be worthwhile to employ Hoffstetter's (1974) term Simiiformes in its place. The latter was proposed explicitly as a replacement for Anthropoidea on grounds which seem to me insufficient, but its translation into the present situation would enable discussions of relationship to avoid the bias inherent in the older term and concept. Goodman (1975) proposed raising Strepsirhini and Haplorhini to his new rank semiorder, but the present suggestion requires fewer changes in total ordinal-group classification, and the new rank may be ignored if so desired.

A second new rank would be required here between infraorder and superfamily, to permit distinction of the *Parapithecus* group from all other catarrhines, while retaining superfamily rank for its more common usages. I follow McKenna (1975) in using Parvorder as the name of such a rank, at which I suggest the new taxa Eucatarrhini (based ultimately on *Homo*) and Paracatarrhini (based on *Parapithecus*). These terms could also easily be employed in the vernacular (eucatarrhines, especially), if their formal recognition is undesirable.

The resulting classificatory scheme carried to subgeneric level is presented below, with the standard Linnaean hierarchy determining the ranks of family-group taxa—fortunately these correspond to widespread usage. As discussed above, it is still not possible to assign *Oreopithecus* unequivocally to either parvorder of catarrhines, but it may be placed *incertae sedis*, although family rank seems a worthwhile if potentially superfluous addition. *Oligopithecus*, on the other hand, now appears correctly referred to the Catarrhini, but *incertae sedis* therein, potentially as the sister-group of all other known catarrhines. Nelson (1972) has argued for the standard placement of fossils of somewhat uncertain affinity as *incertae sedis* within their group, but this implies a different treatment of living and fossil taxa, a procedure which I unhesitatingly deplore as common practice. On the other hand, if *Oligopithecus*, for example, were better known and proved instead to be the sister-taxon of all known eucatarrhines, the present system might require modification by addition of yet another rank below parvorder if that relationship were to be reflected. I do not foresee the need to recognize that branching-point with a name.

Classification of primates, especially catarrhines

Order Primates Linnaeus, 1758

†Suborder Plesiadapiformes Simons & Tattersall, 1972 (in Simons, 1972)

Suborder Strepsirhini E. Geoffroy, 1812

Suborder Haplorhini Pocock, 1918

Hyporder Tarsiiformes Gregory, 1915

Hyporder Simiiformes Hoffstetter, 1974 (or Anthropoidea Mivart, 1864)

Infraorder Platyrrhini E. Geoffroy, 1812

Superfamily Ceboidea Bonaparte, 1831‡

Family Cebidae Bonaparte, 1831

Family Callithricidae Bonaparte, 1831

Infraorder Catarrhini E. Geoffroy, 1812

†Parvorder Paracatarrhini, new

†Family Parapithecidae Schlosser, 1911

†*Parapithecus* Schlosser, 1910

†*Apidium* Osborn, 1908

Parvorder Eucatarrhini, new

Superfamily Hominoidea Gray, 1825

Family Hominidae Gray, 1825

Subfamily Homininae Gray, 1825

Homo Linnaeus, 1758*

†*Australopithecus* Dart, 1925

†*A. (Australopithecus)* Dart, 1925

†*A. (Paranthropus)* Broom, 1938

†*Ramapithecus* Lewis, 1934

‡ Family-group names in Platyrrhini present problems involving both authorship and *nomina oblita*, especially from Gray (1821 and 1825). A proposal is now being prepared for the ICZN to permit conservation of current usage, if not authorship.

*The rank of what is here termed Homininae has been raised arbitrarily relative to that of its conservative sister-taxon *Pan* and other taxa of the "Ponginae"—compare Figures 1 and 3. In addition, the availability of names from Oken (1816, especially *Pan* and *Panthera*) is now under consideration by the ICZN. Thus current usage (which I support in this case) is followed here.

- Subfamily Ponginae Elliot, 1913
 Tribe Pongini Elliot, 1913
Pongo Lacépède, 1799
Pan Oken, 1816*
P. (*Pan*) Oken, 1816
P. (*Gorilla*) I. Geoffroy, 1852
 †Tribe Dryopithecini Gregory & Hellman, 1939
 †Subtribe Dryopithecina Gregory & Hellman, 1939
 †*Dryopithecus* Lartet, 1856
 †*D.* (*Dryopithecus*) Lartet, 1856
 †*D.* (*Sivapithecus*) Pilgrim, 1910
 †*D.* (*Proconsul*) Hopwood, 1933
 †*D.* (*Rangwapithecus*) Andrews, 1974
 †*Limnopithecus* Hopwood, 1933
 †Subtribe Gigantopithecina Greymatskii, 1962
 †*Gigantopithecus* von Koenigswald, 1935
 Subfamily Hylobatinae Gray, 1870
Hylobates Illiger, 1811
H. (*Hylobates*) Illiger, 1811
H. (*Symphalangus*) Gloger, 1841
H. (*Nomascus*) Miller, 1933
 †Family Pliopithecidae Zapfe, 1960
 †Subfamily Pliopithecinae Zapfe, 1960
 †*Pliopithecus* Gervais, 1849
 †*Dendropithecus* Andrews, Pilbeam & Simons, 1977 (still unpublished)
 †Subfamily Propliopithecinae Straus, 1961
 †*Propliopithecus* Schlosser, 1910
 †*Aegyptopithecus* Simons, 1965
 †*Aeolopithecus* Simons, 1965
 Superfamily Cercopithecoidea Gray, 1821
 Family Cercopithecidae Gray, 1821
 Subfamily Cercopithecinae Gray, 1821
 Tribe Cercopithecini Gray, 1821
Cercopithecus Linnaeus, 1758
C. (*Cercopithecus*) Linnaeus, 1758
C. (*Miopithecus*) I. Geoffroy, 1842
Erythrocebus Trouessart, 1897
Allenopithecus Lang, 1923
 Tribe Papionini Burnett, 1828
 Subtribe Papionina Burnett, 1828

*The rank of what is here termed Homininae has been raised arbitrarily relative to that of its conservative sister-taxon *Pan* and other taxa of the "Ponginae"—compare Figures 1 and 3. In addition, the availability of names from Oken (1816, especially *Pan* and *Panthera*) is now under consideration by the ICZN. Thus current usage (which I support in this case) is followed here.

- Papio* Müller, 1773‡
P. (Papio) Müller, 1773
P. (Chaeropithecus) Gervais, 1839
Cercocebus E. Geoffroy, 1812
†*Parapapio* Jones, 1937
†*Dinopithecus* Broom, 1937
†*Gorgopithecus* Broom & Robinson, 1949
Subtribe Macacina Owen, 1843
Macaca Lacépède, 1799
†*Procynocephalus* Schlosser, 1924
†*Paradolichopithecus* Necrasov, Samson & Radulesco, 1961
Subtribe Theropithecina Jolly, 1966
Theropithecus I. Geoffroy, 1843
T. (Theropithecus) I. Geoffroy, 1843
†*T. (Simopithecus)* Andrews, 1916
Subfamily Colobinae Blyth, 1875§
Subtribe Colobina Blyth, 1875
Colobus Illiger, 1811
C. (Colobus) Illiger, 1811
C. (Procolobus) Rochebrune, 1887
C. (Piliocolobus) Rochebrune, 1887
†*Libypithecus* Stromer, 1913
†*Cercopithecoides* Mollett, 1947
†*Paracolobus* R. Leakey, 1969
Subtribe Semnopithecina Owen, 1843§
Presbytis Eschscholtz, 1821
Pygathrix E. Geoffroy, 1812
P. (Pygathrix) E. Geoffroy, 1812
P. (Rhinopithecus) Milne-Edwards, 1872
Nasalis E. Geoffroy, 1812
N. (Nasalis) E. Geoffroy, 1812
N. (Simias) Miller, 1903
Subtribe *incertae sedis*
†*Mesopithecus* Wagner, 1839
†*Dolichopithecus* Depéret, 1889
Subfamily *incertae sedis*
†*Prohylobates* Fourtau, 1918
†*Victoriapithecus* von Koenigswald, 1969
Parvorder *incertae sedis*
†*Oligopithecus* Simons, 1962
†Family Oreopithecidae Schwalbe, 1916
†*Oreopithecus* Gervais, 1872

‡ The status and authorship of *Papio* (from Müller or Erxleben—mandrills or “savannah” baboons, respectively) is now pending before the ICZN—this usage follows Delson & Napier (1976).

§ The problem of the correct family-group name(s) for the leaf-eating Cercopithecidae is also pending before the ICZN—again, this usage follows my proposal to the Commission (Delson, 1976.)

6. Summary

The relationship between phylogeny and classification is one of the major problem areas in current systematic theory. But phylogeny itself, considered as the evolutionary history of a group, comprises two distinct aspects. The study of branching patterns among lineages may be termed "cladogeny", while the more interpretational second stage of phylogeny, involving hypotheses relating function, ecology, selection and the actual course of species evolution and adaptation, has been termed a scenario. Cladogeny is best studied with the methods of cladistic analysis, whereby characters shared by two taxa link them phyletically only if the states are derived by comparison to a preceding ancestral condition. Neither shared retention of ancestral characters, nor, of course, shared states attained convergently offer any information as to the phyletic history of the group under study. The stratigraphic age of taxa is not employed in determining if a character or state is ancestral, but character distribution within the group and comparisons with related groups are important, as may be ontogenetic or functional considerations. However, if two states are equally likely to be ancestral on these grounds, the earlier appearance of one may suggest its "primitiveness", at least as a working hypothesis.

It is unlikely that many actual ancestor-descendant relationships exist among pairs of species known as fossils or living today, but ancestors certainly existed, and some must be represented in collections. It may be possible to identify them by means of a set of successive, probabilistic criteria. First, the morphology of a purported ancestor must correspond to the ancestral morphotype of the group composed of itself plus its sister taxon (the closest relative among all those known, which in this case is the presumed descendant). Moreover, in at least one morphocline, the ancestor should be intermediate between the descendant and their immediate common ancestor. Other features which might increase the likelihood of one known taxon being the genealogical ancestor of another include: being widespread, polytypic, anatomically well-known and of predicted geographic or temporal range. The application of this approach is considered in several examples, especially relating to my work on Old World monkeys (among colobines, documenting *Mesopithecus* as the probable ancestor of *Dolichopithecus*) and Gingerich's on early Tertiary mammals. Translating a cladogeny into a classification involves a decision between "evolutionary" (Simpsonian) weighting of patristic *vs.* genealogical relationships or cladistic use of phyletic links only, followed by questions of which nodes are to be named, whether sequencing as well as subordination is to be employed and how ranks are to be assigned *a priori*.

These principles may be applied to the catarrhines based on data presented previously (especially Delson, 1975a, Delson & Andrews, 1975). The cladogeny of catarrhines is fairly well understood, although relationships of gibbons and their supposed fossil ancestors are still unclear. It now appears that the *Aegyptopithecus* group of Fayum hominoids represents an early catarrhine radiation which persisted into the Miocene as the conservative *Pliopithecus* (and *Dendropithecus*). An earlier radiation led to catarrhine division into monkeys, apes and the very divergent parapithecids, while a third, Miocene, pair of diversifications brought forth the variety of Neogene apes and men on the one hand and monkeys on the other. Cladograms for these groups are presented, as is a more extrapolative phylogenetic tree, including chronologic ranges, possible ancestry indications and suggested ages for these divergences. Three alternative classifications of an enlarged Homnidae (including all gibbons, great apes and men) are contrasted. I prefer

either a cladistic, subordinated pattern or an "evolutionary" classification raising the *Homo* group in rank by comparison to its sister taxon, *Pan*. In a classification of all catarrhines, two new pairs of taxa are proposed: 1) in the new category Hyporder, Tarsiiformes *vs.* Simiiformes (=Anthropoidea) within the Suborder Haplorhini and 2) in McKenna's (1975) category Parvorder, Eucatarrhini *vs.* Paracatarrhini (Parapithecidae) in the Infraorder Catarrhini. *Oreopithecus* (accorded family rank) and *Oligopithecus* are classified as Catarrhini *incertae sedis*.

I thank Dr Ian M. Tattersall, Dr Richard F. Kay, Dr Frederick S. Szalay and Mr Alfred L. Rosenberger for helpful comments on the manuscript, but they are not necessarily in agreement with the ideas propounded here. The illustrations were prepared by Miss Lorraine Meeker. Preparation of this paper was partially supported by research grants from the National Science Foundation (no. BNS74-13258 A01) and the City University of New York's Faculty Research Award Program (no. 11152).

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