

Cladistic Concepts and the Species Problem in Hominoid Evolution 14

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Introduction

Over the past 20 years, since the initial application of Hennigian phylogenetic principles to the study of human evolution, the usage of cladistic concepts has become increasingly popular in paleoanthropology (Eldredge and Tattersall, 1975; Delson *et al.*, 1977; Tattersall and Eldredge, 1977; Bonde, 1977; Olson, 1978; White *et al.*, 1981; Skelton *et al.*, 1986; Wood and Chamberlain, 1986; Stringer, 1987; Chamberlain and Wood, 1987; Kimbel *et al.*, 1988; Tobias, 1988; Groves, 1989). The rigorous operational framework, in conjunction with its potential for the application of Popperian deductive reasoning in testing inferences about character states and morphocline polarities upon which phylogenetic hypotheses are based, has made cladistics an attractive methodological approach, even among some of its initial antagonists (Nelson, 1970, 1971a,b); Bonde, 1977; Bock, 1977; Szalay, 1977; Platnick, 1977, 1978, 1979; Platnick and Gaffney, 1977; Patterson, 1978; Mayr, 1968, 1981; but see Cartmill, 1981 for a critique of the utility of Popper's model of scientific enquiry for testing phylogenetic interpretations).

An early area of contention between cladists and more traditional systematists, however, and one that still persists today, is the nature of the relationship between phylogenetic inference and classification (Hull, 1970; Nelson, 1972,

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1974a,b; Ashlock, 1974, 1979; Mayr, 1974, 1981; Szalay, 1977; Bock, 1977; Martin, 1981; Szalay and Bock, 1991). Hennig's (1966) scheme of ranking taxa according to their absolute time of divergence has been abandoned as impractical, and the majority of cladists today have adopted more flexible classificatory schemes (Crowson, 1970; Nelson 1971a, 1974a; Delson and Andrews, 1975; Farris, 1976; Løvtrup, 1977; Patterson and Rosen, 1977; Eldredge and Cracraft, 1980; Patterson, 1980; Groves, 1989). Nevertheless, in spite of the burgeoning number of seemingly idiosyncratic variants in classificatory methods that have arisen as a response to these problems, the overriding requirement that taxa *must* be monophyletic* is upheld as a basic tenet of all cladistic classificatory schemes (Hennig, 1966; Ashlock, 1971, 1972, 1979; Bonde, 1977; Eldredge and Cracraft, 1980; Mayr, 1981; Ax, 1987).

As a long-term practitioner of cladistics I have had the opportunity to apply cladistic methodology to a range of problems in primate paleontology (Harrison 1981, 1982, 1986, 1987a,b, 1988). Practical experience has served to reinforce my appreciation, based on purely theoretical considerations, that cladistics is the most appropriate (i.e., biologically the most meaningful and scientifically the most rigorous) method to employ in order to attempt to reconstruct phylogenetic relationships. Recent critiques of the use of cladistics in paleoanthropology (e.g., Habgood, 1989; Trinkaus, 1990) have responded more to weaknesses in its application by practitioners than to problems inherent to the method itself. Nevertheless, I do not mean to imply that the theoretical premise of cladistics is not without its limitations. In fact, it has become increasingly evident to me that a number of major theoretical and conceptual difficulties do arise, especially when Hennigian phylogenetic principles are translated into the taxonomic sphere. That these problems impinge directly or indirectly on the question of the species problem in paleontology makes them pertinent to discuss in the context of the present volume.

The aim of this paper is to examine the nature of the interface between cladistic methods of phylogenetic inference and classification. Cladists contend that classification should represent a precise reflection of phylogenetic affinity, while evolutionary systematists argue that additional information, such as the degree of divergence or level of diversification, may be incorporated in the construction of a classification. However, as has been emphasized repeatedly in the literature, phylogenetic inference and classification are two distinct procedures (Simpson, 1961; Bock, 1977; Martin, 1981). The former is a hypothetical representation of actual evolutionary events, while the latter is a human construct that provides a means of conceptualization, communication, and storage of information about taxa (Simpson, 1961; Bock, 1977). As the two processes can be decoupled, there is no intrinsic reason why a cladistic classification need necessarily reflect perfectly the set of relationships expressed in a cladogram, since the latter by itself is the purest expression of such relationships.

A classification is an essential tool, and like all tools, utility is at a premium.

**Monophyly* is used throughout the text in the sense proposed by Hennig (1966), in which a "monophyletic group is a group of species descended from a single (stem) species, and which includes all species descended from this stem species." The term is used as a direct equivalent of Ashlock's (1971) proposed replacement term, *holophyly*.

With this in mind, Simpson (1961) proposed that classifications should fulfil three important principles: (1) the basis of classification should be the most biologically significant relationships among organisms and should bring in as many of those as is practical, (2) classifications should be consistent with the relationships used as its basis, and (3) classifications should be as stable as possible without contravening the two preceding principles. These would seem to be worthwhile and realistic goals for all systematists, regardless of their philosophical persuasion. In fact, cladists, with their uncompromising concern for establishing vertical classifications, are perhaps in the most advantageous position to succeed in applying these principles. This is because cladists, quite rightly, recognize the paramount importance of phyletic information as the most appropriate biological data to employ in constructing a classification.

As will be seen from the following discussion, however, it is the inflexible application of the concept of monophyly in classification, without due regard to empirically based biological research, that is at the root of a number of taxonomic problems. Cladists who adhere, in all cases, to the principles of strict monophyly when attempting to construct classifications are in danger of undermining the utility of a classification by ignoring the first goal of Simpson's principles, which is that classifications should maximize (or more appropriately optimize) their biologically significant content. As I shall discuss in a later section, in certain circumstances other types of biological information may prove to be more appropriate, or at least *more readily accessible*, than phylogenetic data, and the neglect by cladists of this wider array of biological phenomena may impose unnecessary limitation on the usefulness of their classifications. It is an ironic twist, therefore, that the very strength of cladistics—its purported methodological rigor for reconstructing phylogenetic relationships—is one of its weaknesses when it comes to translating the subtle complexities of palaeobiological evidence into a classificatory scheme (see also Bock, 1977).

It should be noted from the outset that this paper is not intended to be a definitive review of the problem. It is simply the presentation of a selection of examples drawn from my own research that serve to illustrate a number of key conceptual difficulties that I have encountered in applying cladistic concepts to taxonomic issues in hominoid evolution. Moreover, I cannot claim that the problems presented here are entirely original, or that I am in a position to offer any real solutions to them, but it is my hope that a reiteration of some of the limitations of cladistic methods of classification, in the context of specific examples, may provoke new attempts by systematists to attain a closer correspondence between what are currently perceived as cladistically correct procedures and observed biological phenomena.

The examples I have chosen are taken primarily from my research on the taxonomy and phylogenetic relationships of the early Miocene catarrhines from East Africa (Harrison 1981, 1982, 1987a,b, 1988). The aims of my research in this area have been threefold: to carry out a detailed taxonomic revision of the fossil primates, to identify their evolutionary relationships, and to make inferences about their natural history. The attainment of these research goals has involved the following discrete procedural steps: (1) the recognition of species groupings based on comparisons of individual specimens, (2) the identification of the species and genus (based on comparison with type specimens) to which

these groupings should be assigned, (3) reconstruction of the paleobiology of each species based on the morphology and inferred functional affinities of their craniodental and postcranial remains, (4) an assessment of the cladistic relationships among the different species, and (5) a wider cladistic analysis involving relevant fossil and extant catarrhines in order to determine the higher taxonomic groupings to which the fossil species may be assigned.

Different conceptual problems with the application of cladistic methodology have been encountered at different phases in the analysis, corresponding with increasing taxonomic level. Specific problems are most easily identifiable at three different levels: (1) at the family-group level and above (corresponding to step 5 in the research design outlined above); (2) at the genus-group and species level, or the alpha-taxonomic level (corresponding to step 4); and (3) at the level of species recognition (corresponding to step 1). It is important, however, to note that the problems are not necessarily exclusive to the taxonomic levels identified. The cases presented here were selected merely because they best highlight the deficiencies of the cladistic method, but they presumably represent individual examples of more wide-ranging phenomena that occur throughout the continuum of hierarchical inclusiveness from the individual to higher order taxonomic categories.

The Family-Group Level and Above

Cladistic analyses have proved to be most effective in resolving relationships among the major groups of living and fossil primates (e.g., Delson, 1975; Rosenberger, 1977; Szalay and Delson, 1979; Schwartz and Tattersall, 1985, 1987; Ford, 1986; Schwartz, 1986; Harrison, 1987a; Groves, 1989), and there has been some measure of success among current workers with regard to the relationships among modern primates at the family-group level and above. This success is due largely to the fact that the last common ancestors of the major groups are sufficiently distantly removed in time to allow the recognition of major adaptive patterns that characterize the extant representatives. Under these circumstances, it is a relatively simple task to identify homologies, to weed out homoplasies, and to delineate more precisely robust transformation sequences in reconstructing ancestral morphotypes. Because of this it is much easier to recognize a member of a major group, regardless of the extent of its convergence on the adaptive pattern of a distantly related group. As I shall discuss in the next section, correct determination of character polarity and the identification of homologies vs. homoplasies become progressively more troublesome as one descends the taxonomic hierarchy to the level of the genus or species.

Despite the apparent success in using cladistic methods for resolving the relationships of the major extant groups of primates, problems occur when the analysis is transferred from the phylogenetic to the taxonomic domain. Especially significant is the way in which fossil taxa, particularly stem groups, are treated in relation to extant higher level taxa. The relative ranking of modern higher level taxa is usually defined by their level of species diversity and/or by their degree of adaptive divergence (Simpson, 1961). This implies that each

taxonomic category of the same rank represents approximately the same absolute level of diversity or divergence. There is an implicit assumption, for example, that the mammalian families Cervidae, Canidae, and Cercopithecidae, and also, for that matter, their less speciose counterparts, the Antilocapridae, Ailuropodidae, and Hominidae, are in some sense biologically equivalent to one another. The purely practical considerations of this approach, in addition to the retarding influence exerted by the desirability to maintain nomenclatural stability, explains why most cladistic classifications of modern primates do not deviate significantly at the family-group level from Simpson's (1945) revision, based on an entirely different philosophical framework, combining cladistic and gradistic concepts.

However, different criteria are commonly used for ranking fossils, particularly stem groups, in a cladistic classification. As noted by Simpson (1975), among others, the strict requirement of monophyly in cladistic classifications may lead to two hardly distinguishable fossil species being classified in widely different taxonomic categories. This is because fossil species, particularly those comprising stem groups, have a *realized* phylogenetic history, while modern taxa, being the contemporary products of their evolutionary history, have only the *potential* to produce major new taxa.

A simple example may serve to illustrate the problem. The phylogram in Fig. 1 depicts a hypothetical situation in which two modern groups of species, here recognized as two separate families, family A and family B, are derived from fossil sister species of an earlier radiation. Following the logic of doctrinaire cladistic philosophy, species A should be classified in family A, while its sister species, species B, should be classified in a different family, family B. Similarly,

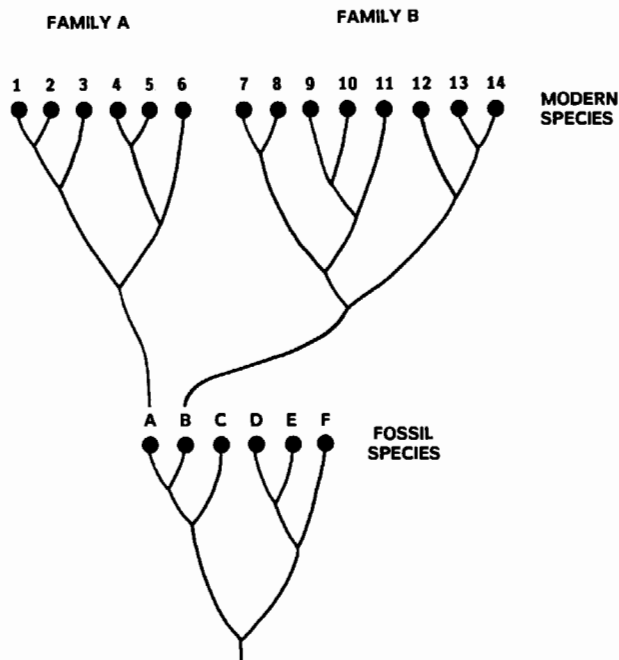


Fig. 1. Hypothetical phylogram illustrating the evolutionary relationships between a stem group and its modern descendants (see text for discussion).

the sister taxon to species A and B, species C, should be classified in a monotypic family, family C. However, species A, B, and C may be very similar to each other, being distinguished by relatively minor morphological difference, such as the structure of the genitalia, pelage color, or molar enamel thickness. After all, it would only require the recognition of a single synapomorphy in each of the fossil species to relate it to a later radiation.

The fossil species in the group depicted in Fig. 1 are clearly related to one another, and they may show a comparable level of adaptive diversity as each of the modern families, but yet they are subdivided into four separate families. In a cladistic scheme, therefore, a paleofamily may not correspond directly with a family composed entirely of modern species. Higher taxa based on paleontological samples will tend to exhibit lower levels of divergence from neighboring groups of equivalent rank and will also tend to be less speciose. In addition, fossil taxa are more likely to be subject to dramatic alterations in their ranking because of the diachronic context and because of the possibility that major new discoveries will influence the level of the diversity. With further, more intensive, research it could be discovered, for example, that each of the individual fossil species in Figure 1 gave rise to a major radiation and that each should be classified in separate superfamilies, or for that matter, even in separate orders.

This type of approach is eminently reasonable from a phylogenetic perspective, but it has less relevance to a paleontologist who is interested in the paleobiology, ecology, and community structure of the individual species. It gives a false impression to those who are less familiar with the biology of the fossil group that they are as different from each other as are representatives of different modern families. Based purely on morphological grounds, and disregarding their relationship to later descendant taxa, we might be tempted, viewing them in a neontological perspective, to consider species A through F as a cluster of closely related species of the same genus. However, in a paleontological scheme, where their descendant relationships may have been realized and subsequently identified by paleontologists, they are given different generic ranks within separate families.

Clearly, there is a discordance here in the way in which cladists view paleontological samples with realized evolutionary history, and modern species that represent the terminal products of this evolutionary history, with only the potential to produce descendant species. An inherent problem in this approach is that paleontologists rarely view the classification of fossil groups in exactly the same way as modern groups. Paradoxically, a paleontologist analyzing species A through F would almost certainly arrive at a very different classificatory scheme from that of a neontologist who was able to study the exact same group of species as living organisms. Similarly, it can be assumed that present classifications of living species will need to be modified in the distant future when the evolutionary history of modern species has been realized. Future (or perhaps I should say futuristic) neontologists may be faced with the perplexing problem of reclassifying species we recognize today as congeneric, such as the closely related Old World monkeys *Cercopithecus nictitans* and *C. mitis*, as members of separate superfamilies or orders, if they happened to give rise to separate adaptive radiations.

When viewed in a diachronic context, taxonomic categories, in a purely cladistic framework, are relative concepts that are determined by descent. They

are, therefore, inherently unstable through time. Taxa would become more or less fixed absolutely only in the unlikely event that all lineages derived from a species have become extinct and that all of the constituent species of this group are known to paleontologists. Surely one of the major objectives of paleontology is to understand and to appreciate past life in a way that is congruent with our view of biological systems as seen today. If our basis for communicating about fossil groups, the classificatory system, is not directly equivalent to that used for modern groups, then it seems logical to conclude that we are presenting a distorted and unnecessarily abstracted view of past life that does not correspond closely to empirically based observations of the relationships that are known to exist among living species today.

The early Miocene catarrhines from East Africa provide an excellent example of the problems concerned. The fossil primates represent a diverse community, comprising 10 genera and 13 species (see Table 1; Andrews, 1978; Harrison, 1981, 1982, 1988; Leakey and Leakey, 1986a,b, 1987). Early workers on the fossil catarrhines from East Africa considered them to be hominoids, with the smaller species linked phyletically to the hylobatids and the larger forms to the great apes (Hopwood, 1933; Le Gros Clark and Leakey, 1951; Le Gros Clark and Thomas, 1952; Simons and Pilbeam, 1965; Simons, 1972; Andrews, 1974, 1978; Delson and Andrews, 1975; Andrews and Simons, 1977).

There is very little evidence, however, actually to link any of the early Miocene catarrhines from East Africa to the extant hominoids (see Harrison,

**Table 1. A List of Currently Recognized Species
of Noncercopithecoid Catarrhines from the Early Miocene
of East Africa Arranged According to Estimated Average Body Size**

	Body weight ^a	Dietary category ^b
Small species		
<i>Micropithecus clarki</i>	4 kg	Frugivore
<i>Limnopithecus legetet</i>	5 kg	Frugivore/folivore
<i>Limnopithecus evansi</i>	5 kg	Frugivore/(folivore)
<i>Simiolus enjiessi</i>	5 kg	Frugivore/folivore
<i>Kalepithecus songhorensis</i>	6 kg	Frugivore
<i>Dendropithecus macinnesi</i>	8 kg	Folivore/(frugivore)
Medium-sized species		
<i>Nyanzapithecus vanconveringi</i>	10 kg	Folivore
<i>Turkanapithecus kalakolensis</i>	12 kg	Folivore/(frugivore)
<i>Proconsul africanus</i>	15 kg	Folivore/frugivore
<i>Rangwapithecus gordonii</i>	15 kg	Folivore
Large species		
<i>Afropithecus turkanensis</i>	30 kg	Folivore/frugivore
<i>Proconsul nyanzae</i>	30 kg	Folivore/frugivore
<i>Proconsul major</i>	50 kg	Folivore/frugivore

^aBody weight estimates are based on comparisons of cranial, dental, and postcranial material with modern anthropoid primates.

^bInferred dietary categories are based on comparisons of cranial and dental material with modern anthropoid primates. Where two categories are separated by a slash, the first is considered to be the primary dietary resource (more than 50% of its diet). A category enclosed by parentheses indicates that it is an important, but relatively minor resource.

1987a, 1988). In fact, assessment of the phylogenetic relationships of the members of this group is severely limited by the lack of adequate material. The dentition of each species is generally well known, and in most cases several good jaw fragments or partial skulls are also represented in the collections. A detailed understanding of the morphology of the dentition and lower face has contributed significantly to the much improved appreciation of the alpha-taxonomy of this group in recent years (Andrews, 1978; Harrison, 1982, 1988; Leakey and Leakey, 1986a,b, 1987). However, important information concerning the morphology of the cranium and postcranium, critical for adequately resolving the relationships of early catarrhine primates, is entirely lacking for most of the species. Good data are only available for *Dendropithecus macinnesi* and *Proconsul africanus* (Harrison, 1987a and references therein).

Comparisons of the partial skeletons of *D. macinnesi* from Rusinga Island, as well as the extensive series of craniodental specimens, provides no clear evidence of close affinities with the modern hominoids. In fact, *Dendropithecus* exhibits a uniform absence of the extensive suite of shared derived traits that unites the extant representatives of the hominoid clade (Harrison, 1982, 1988; Fleagle, 1983; Rose, 1983, in press; Andrews, 1985; Rose *et al.*, 1992). The available evidence therefore suggests that *Dendropithecus*, at least, is not a hominoid in the strict sense and that it is best considered a basal catarrhine that diverged prior to the appearance of the last common ancestor of the hominoids and Old World monkeys (Fig. 2).

In fact, the same conclusion is probably generally applicable to the other small catarrhines from East Africa, such as *Limnopithecus*, *Micropithecus*, *Kalepithecus*, and *Simiolus*. There is little or no morphological evidence to support

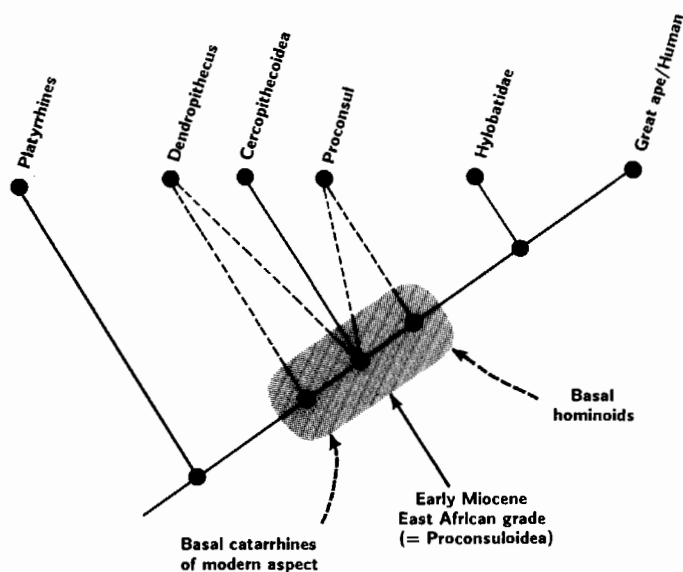


Fig. 2. A cladogram illustrating the inferred phylogenetic relationships of *Dendropithecus* and *Proconsul* to extant anthropoid primates. The shaded area depicts the possible extent of the gradistic zone occupied by the Proconsuloidea.

the contention that any of the small catarrhines (with the possible exception of the oreopithecoid *Nyanzapithecus*) share a particularly close phyletic relationship with extant hominoids (Andrews, 1980, 1985; Harrison, 1982, 1986, 1987a,b, 1988; but see Leakey and Leakey, 1987 for an alternative view). The small catarrhines from East Africa probably represent, therefore, a heterogeneous grade of undifferentiated basal catarrhines that branched off prior to the dichotomy of the two modern superfamilies, the Cercopithecoidea and the Hominoidea (Harrison, 1982, 1987a, 1988; Andrews, 1985; Fleagle, 1988; Groves, 1989; Rose *et al.*, 1992).

Opinion is more deeply divided, however, over the relationships of the large catarrhines from East Africa, such as *Proconsul*, *Rangwapithecus*, *Afropithecus*, and *Turkanapithecus*. Most workers accept that they are hominoids, probably representing a combination of basal hominoids, preceding the appearance of the last common ancestor of the extant hominoids, and hominoids of modern aspect, appearing subsequent to the last common ancestor of the extant hominoids) (Andrews, 1985; Andrews and Martin, 1987; Andrews, 1988; Tattersall *et al.*, 1988; Delson, 1988; Walker and Teaford, 1989). The best known taxon, *Proconsul*, however, conforms in most respects to the ancestral catarrhine morphotype, and in my view the widespread acceptance of its hominoid status is more the product of uncritical supposition than of careful scrutiny (Harrison, 1987a, 1988; see also Feldesman, 1986).

A few possible synapomorphies in the postcranial skeleton have been identified that could be used to support claims that *Proconsul*, and probably also *Afropithecus*, represent conservative basal hominoids (Rose, 1983, 1992, in press; Walker and Pickford, 1983; Andrews, 1985; Senut, 1989; Rafferty, 1990; Rose *et al.*, 1992). I do not believe, however, that a sufficiently strong case has yet been made to assert with confidence that any of the individual genera of early Miocene catarrhines from East Africa should be linked uniquely with the extant hominoids (Fig. 2).

We may infer from the current evidence that the early Miocene anthropoids from East Africa represent part of a larger radiation of conservative catarrhines that probably includes a number of stem taxa that gave rise to the extant hominoids and Old World monkeys. This general conclusion has led most cladists to recognize at least some level of taxonomic differentiation in the group (Andrews, 1985, 1988; Delson, 1988; Tattersall *et al.*, 1988). For example, a recent classification based on cladistic principles (Tattersall *et al.*, 1988) placed the early Miocene catarrhines in four different families and three superfamilies. Taxonomic differentiation may be defensible in terms of a purely phylogenetic perspective of the group, but what about in terms of adaptive diversity?

When compared with extant primates, the level of morphological and adaptive diversity in the early Miocene catarrhines from East Africa could readily be encompassed by a single superfamily. In fact, the fossil taxa are no more different from each other in their craniodental or postcranial morphology than are modern genera classified together in a single family, such as *Lemur* and *Megaladapis* (in the family Lemuridae), *Aotus* and *Alouatta* (in the family Cebidae), or *Presbytis* and *Papio* (in the family Cercopithecidae). If the early Miocene non-cercopithecoid catarrhines from East Africa were classified using the same criteria as neontological taxa, without due regard to their descendant relationships, I

have no doubt that most zoologists would confine the entire group to a single family.

Clearly, there are morphological differences that separate the species, and these provide the basis for recognizing a large number of genera. In addition, it is quite evident that the two best-known species, *Dendropithecus macinnesi* and *Proconsul africanus*, are sufficiently distinct from one another to indicate that they occupied quite different adaptive niches (Fleagle, 1983, 1988; Rose, 1983, 1988; Fleagle and Kay, 1985). Nevertheless, when the group is considered as a whole, they appear to span a quite limited range of diversity, especially when allometric and ecological correlates of species that are known to range in estimated average body size from 4 to 50 kg are taken into consideration (Table 1).

As a scientist interested in issues of paleobiology, such as adaptive diversity, ecological relationships, and community structure, as well as phylogeny, I find that a classification based purely on cladistic criteria is, in this case, much less meaningful, and therefore much less useful, than one based on a combination of cladistic and gradistic concepts. It should be stressed that in most cases a classification based entirely on phylogenetic information will also reflect adequately the level of diversity and other paleobiological factors, and in these instances a cladistic classification is most desirable. The discordance between the cladistic and patristic data only becomes a serious concern when attempting to classify members of a stem group, such as the early Miocene catarrhines from East Africa. This is because stem groups usually exhibit low levels of morphological or adaptive differentiation from the last common ancestor, but yet, in a cladistic analysis, they exhibit high levels of taxonomic differentiation due to the strict requirement of monophyly.

Thus, a cladistic classification of stem groups will reflect only phyletic information, and any inferences about the paleobiology of the group that are usually implied by the classification will be entirely spurious. To recognize three separate superfamilies among the early Miocene catarrhines from East Africa may be justifiable on phylogenetic grounds, but it surely gives a distorted impression about their adaptive diversity, especially when it is considered that all modern anthropoids are traditionally included in only three superfamilies.

For these reasons, stem groups should be considered as a special category in cladistic analyses and should be dealt with in a different way from other groups. In order to maximize the biologically meaningful content of a classification, it might be most appropriate, in certain exceptional circumstances, to consider a combination of cladistic and patristic data. Use of a grade concept is applicable, even within the context of a primarily cladistic analysis, because of the practical benefits and flexibility that it may provide in a classificatory scheme. However, it is important to emphasize that the concept should be employed with extreme caution and should never be applied to a group where good evidence provides indisputable support of paraphyly or polyphyly.

In my recent cladistic analyses of the early catarrhine primates from East Africa (Harrison, 1987a, 1988), I included almost all of the genera in a single superfamily, the Proconsuloidea. The taxon is a patristic group comprising undifferentiated basal catarrhines of modern aspect (Harrison, 1988). The group may also contain *unidentified* basal hominoids, which lack, in their preserved parts, clearly recognizable synapomorphies with the living apes. Until better

material is available, it seems reasonable, for practical purposes at least, to include all East African early Miocene catarrhines that lack clear-cut affinities with either of the two extant superfamilies in the Proconsuloidea (Harrison, 1988).

I feel that this position is justified given the following philosophical and practical considerations: It is certain that the early Miocene catarrhines from East Africa represent a narrow grade, very close to the initial radiation of all recent catarrhines (see Fig. 2). Their general morphological similarity suggests that the various species represent a closely related group that diverged relatively recently from their last common ancestor. However, to demonstrate clear-cut relationships either among them or with other groups of catarrhines has proved exceedingly difficult. The problem arises mainly because the early Miocene catarrhines from East Africa largely retain the ancestral morphotypic pattern defining the extant catarrhines. It is difficult to establish the affinities of the constituent members of a stem group because of their tendency to retain a high frequency of plesiomorphic traits.

In addition, the paucity of material for most of the species makes adequate assessments of their relationships to one another and to other catarrhine groups rather tenuous. It is this combination of phyletic conservatism and the lack of adequate material that makes it impossible at present to determine, with any degree of reliability, the evolutionary relationships of most members of this group. For this reason, I prefer to recognize Proconsuloidea as a useful "waste-basket" category that is not demonstrably paraphyletic or polyphyletic and that includes all those forms from the early Miocene with uncertain affinities to later catarrhines.

In this sense, it is a temporary clustering of species that maintains its integrity only while inadequate material is available or while clear-cut affinities with other groups of catarrhines cannot to be demonstrated. For example, the early Miocene catarrhine *Nyanzapithecus vancouveringorum* is excluded from the Proconsuloidea because it can be shown to have close phyletic affinities to *Oreopithecus*, an undoubted hominoid from the late Miocene of Italy (Harrison, 1986, 1987b, 1991). It may be presumed that other species will be removed from the Proconsuloidea as their relationships to later catarrhines become more securely established.

I do not believe that this approach is such a radical departure from that already employed by most other cladistically oriented paleoanthropologists; the main difference is that I am explicitly acknowledging its practical application within the methodological context. For example, the genus *Australopithecus* (if we exclude those species commonly included in *Paranthropus*) is regarded by most workers as including two species—*A. afarensis* and *A. africanus*. Recent reviews of the phylogenetic relationships of the australopithecines favor the interpretation that *A. afarensis* represents the sister taxon of all later hominids, while *A. africanus* is the sister taxon of *Homo* (e.g., see the contributions in Grine, 1988). If this is the case, then *Australopithecus* constitutes a nonmonophyletic grade of basal hominids.

In order for the classification to reflect these inferred relationships, *A. africanus*, as the type species of the genus, could be retained in *Australopithecus* or be transferred to the genus *Homo*, while *A. afarensis* would need to be removed from *Australopithecus* and subsequently recognized by the prior name *Prae-*

anthropus africanus (Weinert, 1950). In my view this option may prove to be a necessary and desirable course of action, but I can fully appreciate that the majority of workers might prefer to retain *Australopithecus* as a paraphyletic clustering of stem species (just as I do for the Proconsuloidea), at least until such time as the relationships of the early hominids have been more firmly established.

It is important to recall that phylogenetic inference and classification are two discrete operations with quite different functions and properties. For instance, a cladogram, which represents a hypothesis of inferred phylogenetic relationships, is highly labile and is subject to dramatic alterations with the incorporation of new material and information. On the other hand, if the primary purpose of classification is to provide a basis for communication, then some degree of stability is an important requirement if utility is to be maintained. As stem groups tend to exhibit high levels of conservatism, phylogenetic hypotheses tend to be less robust and are subject to repeated revisions, especially if the individual species are rather poorly known.

With our present limited knowledge about the phylogenetic relationships and paleobiology of the early Miocene catarrhines from East Africa, it is likely that we can entertain a wide array of alternative cladograms. This is a necessary and desirable means of exploring the feasibility of different phylogenetic hypotheses, but it is unlikely that concordant changes in the classificatory schemes will be as well received. Until a consensus is reached about the phylogenetic affinities of the early Miocene catarrhines from East Africa, it seems most practical, and in the interests of taxonomic stability, to retain those species of uncertain status in the taxon Proconsuloidea.

The inclusion of the majority of early Miocene catarrhines from East Africa in a single superfamily more realistically reflects the diversity of the group when compared with modern taxa and avoids the unnecessary oversplitting that tends to occur with stem groups. In addition, discussion of the morphological diversity, ecological differentiation, and community structure of the Proconsuloidea can be more readily related to data derived from neontological studies.

In conclusion, the Proconsuloidea should be retained as a taxonomic grouping because it is, at present, the most meaningful way to deal with the constituent members and to communicate information about them. Given the uncertainties surrounding their precise phyletic relationships, it seems much more reasonable to make use of the wealth of paleobiological information that we have accumulated on the group as the primary basis for their taxonomy. In this way we are able to produce a relatively stable, yet biologically meaningful classification, at least as an interim measure, until such time as the uncertainties surrounding their relationships have been resolved.

In conclusion, it is important to point out that I am not advocating that cladists should "soften" their approach as a general rule in order to adopt a more Simpsonian inclination. It is more a matter of allowing greater flexibility within the confines of general cladistic methodology to accommodate the obvious shortcomings of paleontological data and the inherent limitations of the phylogenetic method. I firmly believe that under ideal circumstances it would be most desirable for *all* classifications to reflect cladistic (i.e., monophyletic) relationships *only* and that we should strive, wherever possible, to achieve this objective. Unfortu-

nately, however, our data are rarely perfect, and I would contend that under certain exceptional circumstances formal cladistic classificatory procedures may provide less worthwhile results than those based on other criteria.

As discussed above, the recognition of monophyletic groups based on inadequately known representatives of a stem group may be beyond the resolution of current applications of cladistic method. In these cases, it would be much better to use the more readily accessible and more inherently stable data on adaptive diversity (data that are no less biologically relevant than cladistic evidence) as a criterion for taxonomic attribution. The recognition of a gradistically defined taxon for poorly known stem groups, such as the Proconsuloidea, is therefore recommended for exceptional cases only, and in these instances such groups should be considered to have integrity only until such time as the cladistic affinities of the included species have been more firmly established.

The Genus Group and Species Levels

Cladistic analyses of fossil primates at the alpha-taxonomic level have so far proved to be much less successful than those dealing with higher-level categories. My own attempts, for example, to resolve the inferred relationships among closely related fossil primates, such as the early Miocene catarrhines from East Africa or the Eurasian pliopithecids, have been largely unsuccessful. Perhaps this is hardly surprising when one considers that neontologists, with access to the full range of information from anatomy, ontogeny, behavior, and ecology, have been equally frustrated in their attempts to resolve the relationships among closely related species of modern primates, such as those included in *Cercopithecus* or *Lemur* (Tattersall, 1986, this volume; Tattersall and Schwartz, 1991).

In 1982, I attempted to assess the relationships between the genera of early Miocene catarrhines from East Africa (Harrison, 1982). I constructed a simple cladogram, based primarily on dental characteristics, that purported to illustrate the relationships among the various taxa (Fig. 3 and Table 2). In this scheme, *Limnopithecus*, *Dendropithecus*, *Proconsul*, and *Rangwapithecus* are linked at node 2 by a shared derived character complex, the possession of upper and lower molars with large and well-defined occlusal basins, while *Micropithecus* is excluded by the retention of the primitive catarrhine molar pattern, with restricted occlusal basins (Table 2). *Rangwapithecus* and *Proconsul* are further linked at node 4 by several synapomorphies, such as the development of a moderately elongated lower face and a modified molar pattern (see Fig. 3 and Table 2 for details), and are represented as the sister group of *Limnopithecus* and *Dendropithecus*. The latter share a derived molar pattern that includes a more rectangular occlusal outline, higher and more conical cusps, and further development of crests and occlusal basins. This set of inferred relationships was considered at the time to be a tentative phylogenetic statement only, but one that was consistent with the available fossil evidence.

There is a strong impetus among cladists to generate best-fit cladograms as summary statements, just as I did in my 1982 study, in order to provide hypotheses of possible relationships. However, I believe that too few workers are willing

Table 2. A List of the Characters Used to Define the Nodes in Fig. 3

Node 1:	Nasal aperture ovoid in shape and higher than broad Anterior margin of the orbit situated above P ³ -P ⁴ Palate relatively long and narrow Mandibular symphysis with superior transverse torus only, or dominant over the inferior transverse torus Mandible moderately deep I ¹ slightly higher than broad Upper and lower canines only moderately bilaterally compressed Upper canines with single mesial groove Upper premolars with buccal cusp moderately higher than the lingual cusp Upper and lower molars with the following features: Crowns short and broad, and ovoid in occlusal outline Cusps low and conical Occlusal crests low and quite rounded Relatively restricted occlusal basins Lack of secondary wrinkling M3 relatively large P ₁ longer than broad Lower incisors relatively high crowned
Node 2:	Upper and lower molars with large and well-defined occlusal basins
Node 3:	Upper and lower molars with the following features: Crowns rectangular in occlusal outline High conical cusps Sharp and well-defined crests Large occlusal basins
Node 4:	Position of anterior margin of the orbit above M ¹ Face moderately long Molar cusps high voluminous and rounded
Node 5:	Nasal aperture relatively broad Palate relatively short and broad Mandible relatively deep M3 reduced in size Incisors large relative to the size of the molars
Node 6:	Nasal aperture relatively very narrow
Node 7:	Inferior transverse torus well developed Mandible relatively shallow I ¹ high and relatively narrow Canines bilaterally compressed Upper canines in males with double mesial groove
Node 8:	P ₄ broader than long
Node 9:	Mandible relatively deep I ¹ high and narrow Buccal cusp of upper premolars only slightly more elevated than the lingual cusp Upper molars long and narrow, increasing in size from M1 to M3 Lower molars very long and narrow Molars with secondary wrinkling

Adapted from Harrison (1982).

to concede that some problems are insoluble given the quality of the information that they have at hand. In many cases it is possible to construct a cladogram, even a parsimonious one, that is based on too little information to be a realistic assessment of relationships. In other words, the level of information that is actually required to construct a cladogram is often much less than is required to

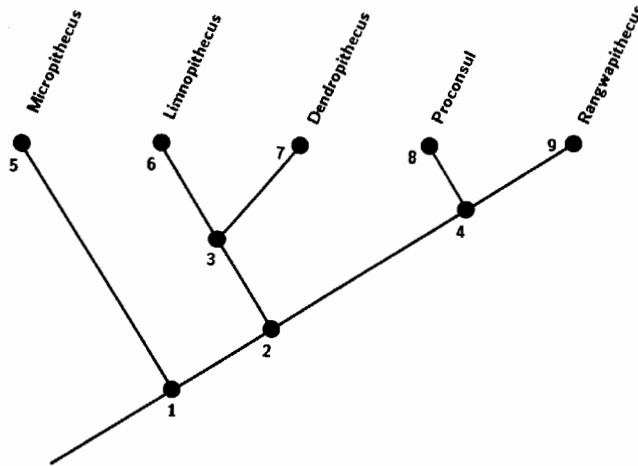


Fig. 3. Cladogram showing the purported evolutionary relationships between some of the genera of early Miocene catarrhines from East Africa, as suggested by Harrison (1982). The characters used to define each node are given in Table 2. [Adapted from Harrison (1982).]

provide inferences about relationships. Cladists commonly ignore the option that no cladogram is preferable to a weakly supported one based on insufficient or conflicting data. This requires that systematists develop a keen appreciation of the threshold at which phylogenetic hypotheses shift from intuitive guesswork to empirically based objectivity.

Recognizing the shortcomings of the data is much less detrimental to future advances in understanding phylogenetic relationships than trying to establish relationships with insufficient support, simply because it is axiomatic that such relationships exist in reality. With hindsight, I now recognize that it is simply not possible, given the quality of the information available, to determine the nature of the relationships among the genera of fossil catarrhines from the Miocene of East Africa. In fact, based on my experience with other fossil groups and my comparative studies of extant primates, I would argue that *most* attempts to assess the relationships among closely related forms are likely to prove inconclusive. If this is true, then the classification of fossil species at the generic level may have to rely much more on the degree of phenetic similarity, rather than on the precise nature of their phylogenetic relationships, as is usually advocated by most cladists.

There are four main reasons why attempts to resolve the relationships among closely related groups of primates may be unsuccessful: (1) Holomorphic insufficiency—there is just not enough morphological information preserved in the fossil record to deduce adequately what relationships exist. (2) The problems of correctly inferring the polarity of character transformations (which, among closely related forms, tend to be based on minor morphological differences, such as the detailed structure of the molars in the case of the East African fossil catarrhines) and the relatively narrow transformational spectrum due to the relative recency of their last common ancestor. (3) It is extremely difficult to establish relationships among closely related members of a stem

groups, such as the early Miocene catarrhines from East Africa, because they tend to retain a high frequency of plesiomorphic characters. Furthermore, the majority of well-established derived traits characterizing the species of fossil anthropoids from East Africa are autapomorphic features, which, although useful for determining species and generic distinctions, are of no value for assessing relationships among the taxa. (4) There is an increased tendency for character complexes in closely related forms to be canalized along identical structural pathways as a result of functional convergence, thereby leading to a high incidence of homoplasies that are indistinguishable from homologies. This is probably true for the East African Miocene catarrhines. I now suspect that the set of relationships depicted in Fig. 3, being based primarily on molar and lower facial morphology, is more likely to be reflecting common adaptive patterns due to similar diets and allometric constraints (see Table 1 for information on estimated body sizes and dietary inferences in the fossils) than the degree of phyletic affinity.

In combination, these problems are likely to obscure any attempts to resolve phylogenetic relationships between closely related species. I should point out that these are not problems uniquely associated with cladistics; they are general theoretical problems encountered by all systematists. However, unlike most other systematists, who usually formulate phylogenetic hypotheses in rather general terms, cladists base their assessments on explicitly identified characters and their inferred morphocline polarities. These represent testable statements that are open to critical scrutiny and reevaluation by other workers. As a consequence, I do not attribute my lack of success in attempts to resolve the relationships among the Miocene catarrhines from East Africa as due to the shortcomings of cladistic methods. On the contrary, the methodological framework prescribed by cladists provides an ideal means by which a scientist can recognize that the reconstruction of relationships is not possible given the data available.

Species Recognition

There has been a noticeable trend among hominid paleontologists in recent years to extend the usage of cladistic methods to encompass the problem of species recognition. In such instances, cladistic concepts have been employed as a basis for diagnosing species and for identifying individual specimens that should or should not be included in the hypodigm. Emphasis is placed on identifying the presence of apomorphies for recognizing samples of hominids as distinct species. Good examples of this type of approach have been set forth in recent reviews of the status of *Homo erectus* (Andrews, 1984a, 1984b; Stringer, 1984, in press; Wood, 1984; Groves, 1989).

From their studies of *Homo erectus*, the above authors draw the following general conclusions: (1) that the Asian sample of *Homo erectus*, containing the type material from Indonesia, is united by a series of autapomorphies; (2) that these autapomorphies essentially exclude *Homo erectus sensu stricto* from direct ancestry to *Homo sapiens*; (3) that all or most of these autapomorphies are lacking in some of the earlier specimens from East Africa traditionally included in *Homo*

erectus; (4) that the lack of synapomorphies in the combined samples from East Africa and Asia implies that *Homo erectus* is a grade concept; and (5) that the autapomorphies in the Asian sample can be considered sufficient grounds to support the possible exclusion of the East African forms (including KNM-ER 3733, KNM-ER 3883, and OH 9, according to Stringer and Andrews, although Wood and Groves retain OH 9 in *H. erectus sensu stricto*) from the hypodigm of *H. erectus*.

These authors are understandably guarded about formally recognizing a separate species for the East African sample. As Stringer (1984) notes, "we must beware of the position of saying on cladistic grounds that *H. sapiens* did not evolve from *H. erectus* but from a different species showing similar characteristics which lived at the same time!" Nevertheless, Clarke (1990) has recently argued that the African material previously attributed to *H. erectus* should be assigned to a separate species, *Homo leakeyi* Heberer, 1963, based on the type specimen OH 9.

However, identification of the valid species name for the hypodigm comprising the African specimens has proved problematic. Most authors include a combination of specimens from North, South, and East Africa that have been associated with the following species group names: *Telanthropus capensis* Broom and Robinson, 1949; *Atlantropus mauritanicus* Arambourg, 1954; *Homo leakeyi* Heberer, 1963; *Tchadanthropus uxoris* Coppens, 1965; *Homo erectus olduvaiensis* Tobias, 1968; and *Homo ergaster* Groves and Mazák, 1975. *Telanthropus capensis* is available and has priority over all other names, but if the species is transferred to *Homo*, then the name is preoccupied by *Homo capensis* Broom, 1917, based on the modern-looking Boskop skull.

Groves (1989) has argued that *Atlantropus mauritanicus* is unavailable because it was proposed as a provisional name only, but this ruling (Article 15 of the *International Code of Zoological Nomenclature*) does not apply to names published before 1961. Nevertheless, as noted by Clarke (1990), *A. mauritanicus* is not available because Arambourg (1954) failed to provide a definition that purports to differentiate it from other taxa [Article 13 (a) (i)]. The name *Homo leakeyi*, accepted as valid by Clarke (1990), is excluded from availability under the provision of Article 15, because Heberer (1963) proposed the name provisionally only (as previously pointed out by Simons *et al.*, 1969, and Szalay and Delson, 1979). An earlier, unrelated reference to *Homo leakeyi* by Paterson (1940), based on the anatomically modern human material from Kanjera, is a *nomen nudum* and is, therefore, unavailable. Similarly, a poorly preserved skull from Tchad, named provisionally as *Tchadanthropus uxoris* by Coppens (1965), is also unavailable.

The subspecies *Homo erectus olduvaiensis* Tobias, 1968, based on the type specimen OH 9, is considered to be the valid species group name for the African sample by Groves (1989). This too, however, can be excluded from availability on the grounds that the name was considered by Tobias (1968) as a conditional proposal only. This leaves *Homo ergaster* as the only possibility as an available name for the African species, although some authors (e.g., Leakey *et al.*, 1978; Stringer, 1986; Groves, 1989) would question whether the type specimen, KNM-ER 992, should really be included in the same species as forms such as OH 9, KNM-ER 3733, and KNM-ER 3883.

A number of authors (Rightmire, 1984, 1987, 1990; Bilsborough and Wood,

1986; Hublin, 1986; Turner, 1986; Turner and Chamberlain, 1989; Habgood, 1989; Bräuer, 1990; Kennedy, 1991) have provided critical responses to this cladistic approach to analyzing *H. erectus*. I must say that as a cladist, which many of the critics are not, I agree with their conclusions. In my view there are good grounds to support the argument that cladistic methods are inappropriate to use in the recognition and definition of species groupings (see also Kimbel and Rak, this volume).

Hennig (1966) was very explicit about the lowest operational unit for cladistic analyses—the species. Species groupings need to be formulated as a prerequisite to cladistic analysis by taking into account all forms of intraspecific variation. Species can only be identified in the fossil record in terms of morphological criteria, and although there are no absolute rules for the recognition of species boundaries, intuitive ideas of the range of well-known extant groups provide models for the inclusion or exclusion of individuals (Hennig, 1966). In other words, fossil species are recognized by employing entirely phenetic concepts, based on analogies derived subjectively from morphological ranges of variation seen in modern species (see also Rose and Bown, this volume).

It is, therefore, important to identify species groupings as an initial step in a cladistic analysis, and not to use cladistics as a method to identify species groupings. After all, cladistics is a method that allows the interpretation of phylogenetic relationships, and phylogenetic relationships cannot be expressed at the infraspecies level. Of course, it is possible to construct detailed cladograms based on subspecies, populations, or individuals of a single species, and to identify synapomorphies and autapomorphies that define the various nodes, but these may contain nothing meaningful about evolutionary relationships.

A detailed cladistic analysis of infraspecific groups could certainly reveal a significant genealogical structure; one that may even indicate that a particular population within a species is the “sister group” of a neighboring species (see the macaque example cited by Jolly, this volume). The reticulate nature of the ancestral-descendant relationships among infraspecies groups, however, rather than the bifurcating relationship among species, serves to confound any attempt at detailed character analysis. This is because species share a common gene pool. Apomorphies, including autapomorphies, being genetically determined, can flow between different populations of the same species. If this is the case, then shared derived traits may not necessarily be the result of common descent, but rather the product of interbreeding. As a consequence, it is not until gene pools become permanently segregated by a speciation event that autapomorphies and synapomorphies can take on any special relevance in phylogenetic interpretations (see Kimbel and Rak, this volume, for further discussion of this issue).

Cladistic analyses below the species level are not comparable to cladistic analyses above the species level. They are, in fact, merely structurally analogous in terms of their operational procedures. As an essential first step in any cladistic analysis of *H. erectus*, it is necessary, therefore, to decide whether the African and Asian samples previously attributed to *Homo erectus* are in fact representative of a single species or not.

One of the key issues in this debate is how one is able to identify which specimens should be assigned to a single species. An extensive series of charac-

ters has been provided in the past to distinguish *H. erectus* from modern humans (Weidenreich, 1936, 1943; Le Gros Clark, 1964; Howell, 1978; Rightmire, 1990). However, as noted by Andrews (1984a), Stringer (1984), and Wood (1984), many of these characters are also found in early *Homo*, and thus may be plesiomorphic for the genus. Although the latter authors acknowledge that a combination of plesiomorphies and apomorphies can be used to define a species in relation to its sister species, they have stressed the particular importance of autapomorphies in recognizing species [see Wood (1984) for the most explicit exposition of this type of approach].

It is important to note, however, that a species diagnosis is merely a phenetically derived morphotype that serves to distinguish the species from all other closely related species. The morphocline polarity of individual characters comprising the list of diagnostic features need not be assessed at this stage. This is done only after the species has been recognized, when its phylogenetic relationships need to be determined, and when variations in character states have been carefully considered. Apomorphies can be used to infer relationships at the species level and above, but not to establish the group identity of individuals within a species. Of course autapomorphies, being uniquely derived traits, are especially helpful in distinguishing species, but synapomorphies can be used to distinguish species from more conservative taxa, and plesiomorphies can be used to distinguish species from more derived taxa.

Definitions containing a combination of apomorphies and plesiomorphies are likely to be the most practical, given the mosaic nature of evolution. For this reason a single list of traits is unlikely to distinguish clearly a species, such as *Homo erectus*, from all other closely related species. This is why a differential diagnosis, in which each species is compared on an individual basis with all other related species, is preferable over a single universal diagnosis. Turner and Chamberlain (1989) and Rightmire (1990) have recently provided a revised set of traits that does, in fact, serve to distinguish *H. erectus* from both *H. habilis* and *H. sapiens*.

In their recent critical essay, Turner and Chamberlain (1989) implied that Tattersall's (1986) review of the species problem in hominid evolution provides support for the view that the African and Asian samples of *H. erectus* should be distinguished at the species level. Although Tattersall (1986) does not address this question directly, based on his empirical studies of modern primate taxa, he argues that separate species should be recognized in the fossil record if distinct morphs can readily be identified from their bony anatomy. I sympathize with Tattersall's viewpoint in this regard. The criteria that I have used to assign individual specimens to species groupings among Miocene catarrhines is also based largely on my experience of the degree of morphological variation seen in modern primate taxa.

These same criteria, however, could not be met by some of the currently accepted taxonomic groupings of hominids. For example, I would have to concur with Tattersall that if I found two morphs as different as Neandertals and modern humans in the Miocene there is little doubt that I would recognize them as two distinct species. Nevertheless, I do not believe that this line of reasoning is necessarily pertinent to the question of *Homo erectus*. The distinction here is simply a matter of degree.

Tattersall contends that separate species should be identified where distinct morphs can *readily* be identified. It may be presumed that he is not arguing that any observable difference constitutes sufficient grounds to distinguish morphs as separate species, or we would soon be reduced to the absurd situation that all individuals are distinct morphs that merit species recognition. Clearly, individual specimens that exhibit low levels of morphological variation should be clustered together to form morphs. One or more morphs can then be combined in such a way that the type or degree of variation does not exceed that considered acceptable for a single species. In my view this is the case for *H. erectus*—the Asian material is not sufficiently different (i.e., readily identifiable enough) from the African sample to merit the recognition of a separate species.

Recently a number of authors have carefully reviewed the extent of the difference between the African and Asian *H. erectus* samples and have noted that there is a good deal of individual variation in the characters that have been purported to separate the two samples (Hublin, 1986; Turner and Chamberlain, 1989; Habgood, 1989; Rightmire, 1990; Bräuer, 1990). This is not to deny that there are identifiable differences between the Asian and African material, it is just that they may not be as profound and consistently clear-cut as was initially believed.

Hublin (1986) has even suggested that many of the individual differences between the two groups may be part of a single functional complex, associated with bone hypertrophy of the cranial vault. The degree of variation observable within the entire sample from Asia and Africa may be considered appropriate for a single geographically widespread species. In fact, Rightmire (1990) has commented that the amount of variation observed is, perhaps, not surprising, given the wide geographical and temporal distribution of the two samples. The weight of the evidence would, therefore, favor the assessment of Rightmire that the *H. erectus* samples from Africa and Asia are morphologically consistent with a single polytypic species that is widely distributed through space and time.

The differences between the Asian sample and the African sample may be explained as populational differences, rather than as a consequence of post-speciational divergence. In this case, Andrews' (1984a,b) and Clarke's (1990) phylogenetic conclusions, that the African species is close to the direct ancestry of *Homo sapiens*, while *Homo erectus* from Asia is a more specialized collateral relative, can still be accommodated with only minor modifications (see Fig. 4). If we exclude the possibility that all *H. erectus* populations across the Old World graded imperceptibly into *H. sapiens* (Eldredge and Tattersall, 1975, 1982; Delson *et al.*, 1977), then the presence of unique specializations in the Asian population may indeed make it more likely that the African population is the ancestral population from which *H. sapiens* was derived (Turner, 1986; Rightmire, 1990).

Conclusions

The examples that I have presented above serve to highlight some of the limitations of the cladistic method. Although not all of them specifically address the species problem *per se*, the underlying theoretical, conceptual, and practical

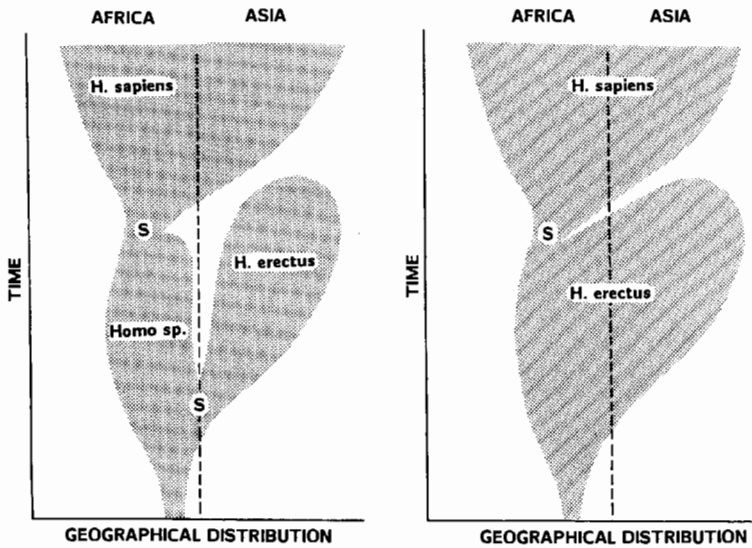


Fig. 4. Phylogenetic tree illustrating the two main competing hypotheses of the relationships between archaic *Homo sapiens sensu lato* and the African and Asian samples of *Homo erectus*. Left: The hypothesis preferred by Andrews (1984a, 1984b) and Clarke (1990). Right: The hypothesis preferred by Rightmire (1984, 1987, 1990), Turner and Chamberlain (1989), and the present author. S denotes a speciation event.

problems that they exemplify do impinge either directly or indirectly on the species concept, and influence the way in which cladists perceive species. The difficulties arise primarily from the fact that the strict operational procedures employed by cladists for inferring phylogenetic relationships tend to pervade all other aspects of their research, including classification and species recognition. A much more flexible approach is required to accommodate the subtle complexities of the natural world.

If our primary objective as cladists is to obtain a better appreciation of phylogenetic affinities and of other biological phenomena, it is clear that utilitarianism must be a guiding principle. If this is so, then systematists should be concerned with applying modified techniques and concepts to suit particular practical problems, rather than dogmatically adhering to rigid procedures that are perceived as theoretically correct.

In this chapter I have identified a number of issues that I feel need more careful consideration by cladists in relation to the species concept in the fossil record. First, diachronicity and descent, unique properties of the paleontological record, create special problems that complicate the direct transfer of concepts and data derived from modern species to the fossil record. However, if systematists are to succeed in making meaningful statements about biological phenomena in the past, it is imperative that they pay close and detailed attention to the use of modern analogues as a basis for determining the limits of palaeospecies.

Second, paleontological data are always much less complete than neontological data. It is, therefore, highly unlikely that paleontologists will be able to

settle issues that have proven to be beyond the capabilities of neontologists. For example, neontologists have been trying for decades to explain and to deal with the widely different levels of intraspecific and interspecific morphological variation seen in modern taxa, while cladistic analyses of closely related extant species have mostly yielded inconclusive results. This is not intended to cast a shadow of pessimism over the entire analysis of the fossil record, but we need to be willing to acknowledge that some key phylogenetic problems are insoluble given the present limitations of the paleontological evidence.

Finally, cladists should aim to maximize the biological content of their classifications. One way to achieve this would be to make fuller use of paleobiological information, which is generally excluded by cladists on the grounds that it is applicable in establishing patristic affinities only.

It is important to emphasize that I am not trying to advocate a complete reformulation of cladistic methods of classification to include more Simpsonian concepts as a general principle. Clearly cladistic relationships should be given priority in any classification, but where this information is lacking or is only tentatively formulated, patristic information may have greater relevance for assessing taxonomic affinity. Cladists contend that mixed classifications of this kind will necessarily lead to misunderstandings, because the criteria upon which the classification is based are not explicitly expressed. However, phyletic relationships are precisely reflected only in the form of a cladogram. A classification, on the other hand, as an entity fully distinct from the cladogram, can incorporate both cladistic and patristic information because it is constrained merely by its usefulness as a means of communication about species.

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