Cambridge University Press
0521580277 - The Mentalities of Gorillas and Orangutans: Comparative Perspectives
Edited by Sue Taylor Parker, Robert W. Mitchell and H. Lyn Miles
Excerpt
More information

PART I

Comparative evolutionary and developmental perspectives on gorillas and orangutans

Cambridge University Press
0521580277 - The Mentalities of Gorillas and Orangutans: Comparative Perspectives
Edited by Sue Taylor Parker, Robert W. Mitchell and H. Lyn Miles
Excerpt
More information

1

Hominid family values: morphological and molecular data on relations among the great apes and humans.

DAVID R. BEGUN

“What we’ve got here is, failure to communicate.” (Cool Hand Luke. Warner Bros., 1967)

INTRODUCTION

Recent fossil discoveries, methodological advances, and ongoing analyses of hominoid comparative molecular biology and morphology have led to dramatic changes in our current understanding of relations among the great apes and humans. The late nineteenth-century view of these relations held that humans and the African apes were most closely related, and that the Asian great ape, the orangutan, was a more distant relative (Darwin, 1871; Huxley, 1959). For most of the twentieth century however, the great apes have been placed not only in their own family (the Pongidae), but also in their own separate evolving lineage, to the exclusion of humans. In the past thirty years, a few molecular biologists have been questioning the evolutionary reality of the pongid lineage, suggesting a return to the Darwin–Huxley view, placing African apes closer to humans, but based on the results of comparative molecular biology. During that time, the techniques of molecular systematics have been greatly improved and refined, to the point where researchers are today actually comparing nucleotide sequences, the fundamental, specific arrangement of DNA molecules, as opposed to overall DNA similarity (hybridization) or the products of DNA metabolism (proteins).

This work in molecular biology has been joined by recent developments in method and theory in palaeontology and comparative anatomy. Foremost among these is the widespread adoption of cladistic methodology, but other developments include more comprehensive analysis of hominoid comparative anatomy, and a more complete hominoid fossil record. One of the outcomes of this revolution in hominoid systematics is the perception that a great divide exists between “traditional” and “modern” hominoid classifications, and that the former has or inevitably will be replaced by the latter. We could switch the words “traditional” with “morphological,” and “modern”

Cambridge University Press
0521580277 - The Mentalities of Gorillas and Orangutans: Comparative Perspectives
Edited by Sue Taylor Parker, Robert W. Mitchell and H. Lyn Miles
Excerpt
More information

with "molecular," reflecting the widely held view, even among some morphologists, that, in systematics, molecules have priority over morphology (e.g., Gould, 1985). The fact is, however, that morphology-based hominoid systematics has progressed enormously during the time in which molecular systematics has been coming into its own. Since the 1980s, new discoveries and the standardization of approaches to phylogeny reconstruction have made morphological systematics quite distinct from earlier research. Unfortunately the "phylogenetic baggage" of a century or more of work in hominoid systematics, often of very high quality, has made some researchers doubtful of their own results (e.g., Groves, 1986; Pilbeam, Rose, Barry, & Shah 1990; Pilbeam, 1996). In contrast, the impressiveness of recent advances in molecular techniques, which currently allow the relatively quick sequencing of nuclear genes and complete mitochondrial genomes in multiple individuals, may have produced some excess of confidence in the potential of molecular approaches to yield the "right" answer (e.g., Gould, 1985; Easteal, Collet, & Betty, 1995). What is needed in this area of research is more communication between the practitioners of both approaches. There is more disagreement within molecular systematics and within morphological systematics than between the two (see below). Compared to the conclusions of hominoid systematics through the 1970s, the conclusions of morphologists and molecular systematists today are much closer than they are divergent. So, rather than focusing on the so-called morphology vs. molecules debate (Patterson, 1987; Cartmill & Yoder, 1994; Shoshani, Groves, Simons, & Gunnel, 1996), this chapter highlights the significant amount of consensus between these fields that has been emerging in the past five years.

In an attempt to move away from the morphology–molecule dichotomy, this chapter is organized along research questions rather than methodology. The main question is, what are the evolutionary relations among living great apes and humans? We can resolve this big question into a series of smaller issues given the results of research over the past century and a quarter. These are, from the phylogenetic perspective: What is hominid, nowadays? What is an orangutan, anyway? How are African apes and humans related to each other? The last question is the most complex, and has generated the most controversy, particularly with regard to the issue of how humans fit in. Before coming to these questions, however, one approach common to both molecular and morphological systematics, cladistics, is outlined, as it has had perhaps the most profound influence on this field of any development in modern systematics.

BACKGROUND TO CLADISTIC APPROACHES

A cladistic approach to systematics is simply one in which the only information considered relevant to the classification of organisms is commonality of descent. Organisms share characteristics of external appearance, genetics, morphology, and behavior for a number of reasons, only one of which is directly attributable to the pattern of their evolutionary relationships (see below). Because a classification of organisms must be derived from phylogenetic conclusions deduced from observations of traits organisms share, the method and theory of classification focuses primarily on distinguishing phylogenetically informative characters, or *shared derived characters* (*synapomorphies*) from others (see below). Systematics is not palaeobiology or neontology. It is simply classification, which helps to organize and standardize the database of organisms known to humans, and allows or facilitates communication among colleagues. It does not seek to characterize organisms in any way beyond their evolutionary relations. The more interesting qualities of organisms are fleshed out in studies of ecology, behavior, evolution, and adaptation.

This view of the role of systematics is not universal (Hull, 1979), but it is becoming more common. Given this limited goal, cladistics can be viewed as a well-defined protocol for determining evolutionary relationships. Although there have been many refinements, the primary reference to cladistic methodology is Hennig (1966). While many of the ideas proposed by Hennig were already part of mainstream systematics (e.g., Simpson, 1961), Hennig standardized the approach to systematics that is nearly universally accepted today, providing a well-defined, if slightly cumbersome, vocabulary (Table 1.1), and a straightforward methodology.

One important limitation of the cladistic approach is the fact that it is incapable of providing evidence for ancestor–descendent relationships. In fact, it seeks only to find what are referred to as sister group relations. Sister taxa are those which share a common ancestor not shared by any other organism, that is, taxa that are more closely related to one another than they are to anything else. Establishing closeness of relationship is a matter of identifying character states[1] shared only by sister taxa, which are most easily explained as having been passed on to these taxa from a common ancestor. Thus, in the process of identifying sister taxa, a set of ancestral character states, or ancestral morphotype, is assembled, but a specific ancestor cannot be identified. At best, one could say that a known taxon does not differ from a reconstructed ancestral morphotype and is a candidate for the ancestry of another taxon. *Ardipithecus ramidus* (White, Suwa, & Asfaw, 1994), for example, appears to conform very closely to the reconstructed ancestral morphotype for the human lineage, but cannot technically be identified as an ancestor using this approach (Figure 1.1). An hypothesis of ancestor–descendant relationship is one that includes a processual component, some statement that involves time, selection, adaptation, environmental change or any combination of these (Figure 1.1). Sister relationships are much simpler hypotheses, involving only pattern recognition. A cladistic approach to systematics thus produces a cladogram, or dendrogram of relations, which can be viewed as the skeleton upon which an hypothesis of phylogeny (including ancestors and descendants) is fleshed out.

In a nutshell, sister relations are determined by identifying shared character states derived from the last common ancestor of the set of taxa under analysis. In order to carry out this type of analysis, taxa must be compared to other taxa known to be outside their evolutionary lineage, that is, an outgroup. This is a necessary initial assumption, but it is usually fairly straightforward. Outgroups are usually taxa most closely related

---

[1] Character states are specific configurations of a character. For example, in hominoids the character ‘‘os centrale’’ has the character states ‘‘separate’’ and ‘‘fused to the scaphoid.’’

Table 1.1 *Cladistic terminology used in this chapter*

Autapomorphy	Uniquely derived characters, having evolved since the divergence of a taxon from its **sister taxon**.
Characters	Units of analysis in phylogeny reconstruction.
Character States	The condition of a character in a taxon (large, small, pronounced, weak, etc.).
Clade	An evolutionary lineage, and the unit of an evolutionary classification.
Homology	Shared characters and/or character states having been inherited from a common ancestor.
Homoplasy	Shared characters and/or character states having been inherited independently from a common ancestor (parallelism) or from different ancestors (convergence).
Monophyletic taxon	A taxon having evolved from a common ancestor. A monophyletic taxon normally includes all descendants of that common ancestor, and is identified on the basis of its **synapomorphies**.
Outgroup	A relative of the group of organisms under analysis, usually the **sister taxon**, used to determine the **polarity** of **character states**.
Paraphyletic taxon	A taxon that excludes some of the descendants of a common ancestor. Paraphyletic taxa are usually identified on the basis of **symplesiomorphies**, and not considered valid evolutionary taxa by cladists.
Polarity	The evolutionary significance of a character state, either apomorphic (derived) because it is not present in the outgroup, or plesiomorphic (primitive) as indicated by its presence in the outgroup.
Polyphyletic taxon	A taxon with multiple ancestors, usually based on homoplasies. Polyphyletic taxa are infrequently identified today.
Sister taxon	The closest relative of a taxon, usually at the same hierarchical level (species, genera, families, etc.).
Symplesiomorphy	Shared primitive character state also found in the **outgroup** and presumed to have been inherited from a common ancestor with the outgroup and not from the last common ancestor of the taxa under analysis.
Synapomorphy	Shared derived characters, not found in the **outgroup** and presumed to have been inherited from the last common ancestor of the taxa under analysis.

Source: Hennig, 1966.

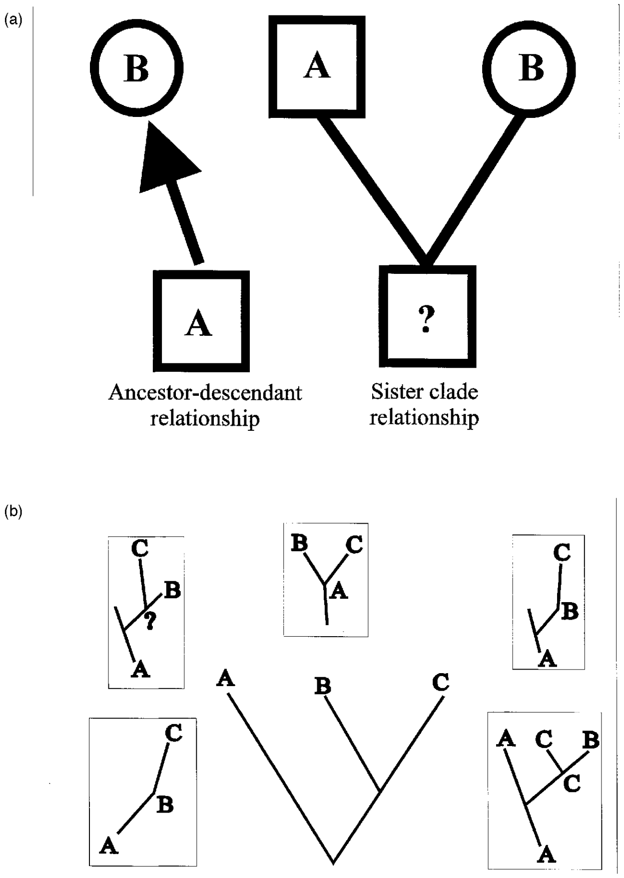


Figure 1.1 Phylogenies and cladograms.
(a) A phylogeny (left) depicts ancestor–descendant relationships. An ancestor–descendant hypothesis requires support from data directly related to the interpretation of evolutionary relationships (morphology, molecular biology, behavior, etc.) as well as information on the process of evolutionary change and the passage of time, represented by the arrow. A cladogram (right) simply represents a hierarchy of evolutionary relationships, without regard to the specifics of the process responsible for the observed diversity. Cladistic hypotheses are thus simpler but less comprehensive than phylogentic hypotheses, and should always precede the latter.
(b) A cladogram surrounded by five alternative phylogenies. Each phylogenetic hypothesis is consistent with the cladogram. Clockwise from the left: a unilinear hypothesis; the ancestors persists following two divergences, with the common ancestor of B and C unknown; B and C diverge for A; A and the common ancestor of B and C are briefly contemporary, and then B evolves into C; A, B, and C persist to the present following a divergence of the common ancestor of B and C from A and then B from C. Many other phylogenies are also consistent with this single cladogram. Deciding among them requires information on adaptation, selection, paleoenvironment, relative dating, and other paleontological variables.

to the set of taxa under analysis, but not included among these taxa. For catarrhines, the outgroup is widely viewed to be platyrrhines, for the Hominoidea, there is little dispute in recognizing the Cercopithecoidea as the outgroup, and for hominids it is widely viewed as hylobatids (see below). In order to identify character states that were present in the last common ancestor of living catarrhines, the outgroup, in this case platyrrhines, is examined for these traits. If catarrhine character states are found in platyrrhines, the most obvious explanation is that they come from a more ancient ancestor shared by both platyrrhines and catarrhines. For example, many catarrhines have tails and fore and hindlimbs of roughly equal length, moderate encephalization compared to prosimians, large canines, well-developed snouts, and divergent halluces. All of these traits are also found in most platyrrhines, and so it can be deduced that these were present in the common ancestor of platyrrhines and catarrhines and do not therefore serve to distinguish catarrhines and platyrrhines. These are *shared primitive characters*, or *symplesiomorphies*. Many or all catarrhines also have two premolars, an ossified ectotympanic tube, some reduction in the tail, and no humeral entepicondylar foramen. These character states are not found or are not common in platyrrhines, suggesting that they appeared in the ancestor of the catarrhines after it diverged from the ancestor of the platyrrhines. These would be shared derived characters of the catarrhines. However, because platyrrhines have also evolved since the appearance of their last common ancestor, it is possible that character states not found in platyrrhines have been lost or modified from their ancestral condition. Thus, it is advisable to look to the next available outgroup to confirm the conclusion that these character states are indeed derived. As it happens, many fossil and living prosimians also resemble platyrrhines in lacking most of these character states, although one of them, tail reduction, is ambiguous. In this case, it seems that catarrhines retain a simpler tail from a more ancient ancestor, while many platyrrhines have evolved more elaborate tails.

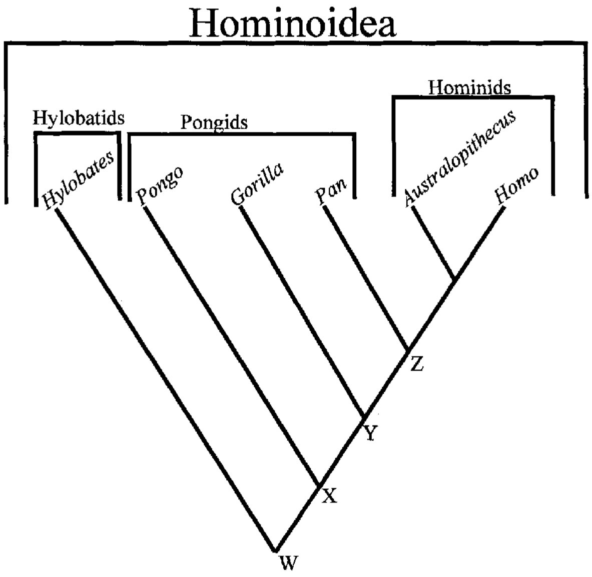
The method outlined above, using an outgroup to establish whether character states typical of the ingroup are primitive or derived (i.e., the polarity of character states), is called the outgroup criterion, and it is by far the most common. This is due to its relative simplicity, though a few assumptions are required. The most important assumption concerns *homology*. It is assumed that character states that are identified as the same in different taxa are homologous, that is, that they are the same character in an evolutionary sense, having evolved once in a common ancestor and having been retained little modified in descendants. This is a necessary initial assumption, and it is also fairly safe, from a methodological standpoint, for two reasons. The assumption of homology is falsifiable. The pattern of derived character states found in ingroup taxa need not conform perfectly to the pattern of relationships deduced from it. A minority of characters will always be inconsistent with the pattern of relationships suggested by most of the characters. These inconsistent characters are considered *a posteriori* to have arisen independently, by convergence or parallelism, and are thus identified as *homoplasies*. The assumption of homology, which was necessary to deduce a pattern of relationships, is falsified for these characters. The other strength of the assumption of homology is parsimony. It is more parsimonious to assume that a character state arose once than to assume that it arose independently more than once. Parsimony, however, is not a description of the evolutionary process. In fact, as just noted, cladistic analyses always reveal homoplasies, which demonstrates the degree to which evolution is not parsimonious, that is, the frequency with which similar character states arise by multiple pathways. Parsimony is a point of logic only. It simply refers to the longstanding preference in science for simpler explanations over more complex ones. All else being equal, a simpler explanation is to be preferred, so long as it does not violate well-established principles. Cladistics has been criticized for representing evolution as parsimonious (most recently in Marks, 1994), but this misunderstanding could not be further from the truth. Cladistic analysis, ironically, has revealed more parallelism and convergence among organisms than had previously been thought possible, reinforcing the notion of the enormous complexity of the evolutionary process.[2]

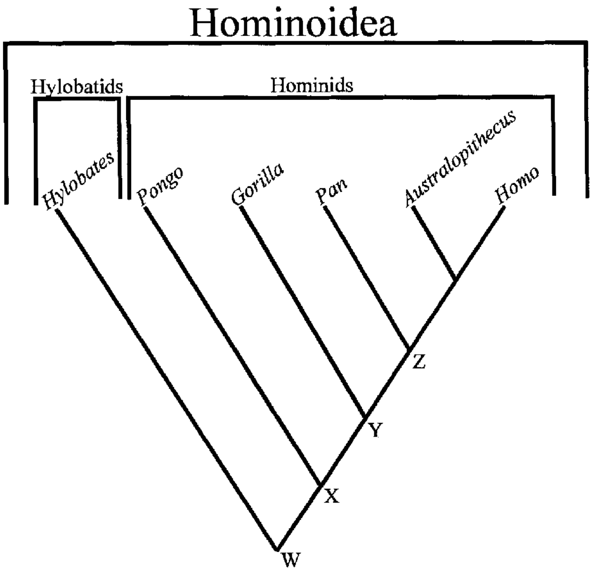
The final goal of a cladistic analysis is the hierarchical representation of *monophyletic* clades, the cladogram. Strictly monophyletic clades are lineages which include all the descendants of a single ancestor. Another way of describing monophyletic clades is that they contain taxa that are all more closely related to each other than to any taxon in another clade. In contrast to monophyletic clades, *paraphyletic* clades exclude some descendants, or they group together taxa some of which are in fact more closely related to outsiders than to others in the clade (Figure 1.2). In the hominoids, for example, Pongidae is paraphyletic when used in the traditional sense because it excludes humans even though humans are more closely related to some pongids (African apes) than these pongids are to other pongids (orangutans). Pongidae would be monophyletic if it included humans, but humans are designated as hominids, which has taxonomic priority[3] over pongids, so that the correct nomen for this monophyletic clade is Hominidae (see below). Recognition of this paraphyly has lead many systematists to reject the nomen Pongidae. In contrast, paraphyly in other hominoids has lead to an increase in nomina. The traditional use of the nomen *Australopithecus* (including all non-*Homo* fossil humans) is also paraphyletic, because it excludes *Homo* despite the fact that *Homo* is more closely related to some *Australopithecus* than some species of this genus are to others in the same genus. The trend here has been to recognize other distinct genera (*Ardipithecus*, *Paranthropus*) thereby removing them from the *Australopithecus* clade.

---

[2] Other methods of identifying derived character states have been proposed. These include palaeontological and ontogenetic criteria, which rely on the order of appearance of character states in the fossil record or in individual growth and development to polarize character states. Because of the additional assumptions these criteria require, concerning the process of ontogeny and the degree to which it accurately reflects evolutionary relations, and the relative completeness and reliability of the fossil record, these approaches are much less commonly used than the outgroup criterion. In this chapter, nearly all the described research proposing various evolutionary relations relies on the outgroup criterion.

[3] Taxonomic priority is a simple but essential rule of taxonomic nomenclature. It requires that taxa considered to be the same be designated by the first used nomen. In this case, since great apes and humans belong in the same family (see below), the first used family nomen Hominidae has precedence. This rule prevents the inevitable confusion that would arise from using different "preferred" nomina to describe the same taxon.


(a)
Hominoidea
Hylobatids
Pongids
Hominids
Hylobates
Pongo
Gorilla
Pan
Australopithecus
Homo
Z
Y
X
W


(b)
Hominoidea
Hylobatids
Hominids
Hylobates
Pongo
Gorilla
Pan
Australopithecus
Homo
Z
Y
X
W

Cambridge University Press
0521580277 - The Mentalities of Gorillas and Orangutans: Comparative Perspectives
Edited by Sue Taylor Parker, Robert W. Mitchell and H. Lyn Miles
Excerpt
More information

Though cladistics was developed and refined by neontological morphologists, it is now widely used by both paleontologists and molecular systematists. The methodology is the same in all areas of research. Character analysis uses the outgroup criterion to polarize character states. Parsimony analysis determines the branching sequence requiring the fewest number of independent origins of character states while still being consistent with the largest number of characters. The remainder of this chapter surveys the recent literature on hominoid systematics, and reviews some of the implications for understanding the evolutionary history of some of the more basic attributes of living great apes and humans.

WHAT IS A HOMINID, NOWADAYS?

A consensus has been achieved among systematists today that the family Hominidae includes more than the genus *Homo*, which was the case when the term was coined. But which additional taxa are allowed to enter the hominid club is the subject of some debate. Although it was not immediately clear to any researcher that *Australopithecus* should be classified as a hominid (Dart, 1925; Woodward, 1925; Keith, 1931), the hominid status of *Australopithecus* soon became widely accepted (Le Gros Clark, 1934). Simpson (1945), in his classic work on mammalian systematics, separated humans and their fossil ancestors, the Hominidae, from all apes, which he placed in the Pongidae. Today, the overwhelming majority of researchers working on hominoid systematics would include some or all of the great apes among the hominids. Widening the definition of hominids was first proposed convincingly based on immunological distances (Goodman, 1963). Goodman (1963) suggested that the African apes should be grouped with humans in the Hominidae, reflecting the closer evolutionary relationship among African apes and humans than between them and either orangutans or hylobatids. As Goodman (1963) noted, this view mirrors that of Darwin (1871), who concluded that it was likely that humans are more closely related to African apes than to

Figure 1.2 (*Opposite*) Monophyletic and paraphyletic taxa.
Pongid is a paraphyletic taxon because it includes the African apes and excludes humans, even though African apes and humans are more closely related to each other than either group is to orangutans. Another way of looking at this is that pongid is paraphyletic because it does not include all the descendants of the common ancestor of included taxa. In this case, Y and Z must be pongids because they are ancestors of the African apes and they postdate the common ancestor of the pongids (X), yet the pongids as defined here do not include all the descendants of Y and Z (the hominids are excluded). Separating hominids and pongids also fails to recognize the close evolutionary relationship among these taxa compared to hylobatids.
A simple monophyletic solution to the paraphyly of the pongids. As defined here, the hominids unites all the great apes and humans in a single family, and also serves to communicate their close evolutionary ties. All hominids have the same evolutionary relationship to hylobatids, and all the descendants of earlier hominids are included in the taxon. Note as well that the stem hominoid (W) is neither a hylobatid nor a hominid, because if it were one of these, that taxon would become paraphyletic. This illustrates one of the methodological limitations of cladistic analysis in recognizing ancestor–descendant relationships.