## Toward a More Reliable Morphological Data Set for Phylogenetic Reconstruction

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For decades, the relationships between different species have been discerned by way of a set of observable characteristics. Based on the similarity of certain observables, two species could be grouped together, along with other organisms that shared the same features. By these methods, scientists constructed a hierarchy of life. *Taxonomy* is the name given to the study and organization of different species. In parallel, relationships between species across time can also be deduced. *Phylogeny* is the study of genetic relationships between different species, and between the species their possible ancestors. These relationships were likewise inferred from observable characteristics present in modern and ancient organisms. The course taken by evolution has thus been charted using these morphological and physiological similarities.

Over the past 10-15 years, there has been much discussion about the validity of these phylogenies. The source of the debate has been the emergence of scientific methods for studying and comparing species at the molecular and genetic level. The human phylogenetic hypotheses that have been around for the last few decades are now being thrown into disarray by the incongruent results of molecular phylogeny. Without a reliable phylogeny as supporting evidence, associated evolutionary hypotheses are on very loose footing.

A recent study by Mark Collard and Bernard Wood finds several discrepancies between morphological and molecular phylogenies for extant higher primates<sup>1</sup>. Cladistic analysis of cranial and dental evidence is commonly used for generating phylogenetic hypothesis about primates and their ancestors. Fortunately, two groups – the hominoids and papionins – have well-established molecular phylogenies. The hominoids are those higher primates most closely related to the fossil hominins, and include *Homo sapiens*. The papionins are an Old World monkey tribe comprising the baboons, mangabeys, and macaques. In comparing phylogenies, the assumption is then made that congruence between those that are morphological and those that are molecular indicates that equivalent hominin fossil evidence yields reliable phylogenies.

The reliability of molecular phylogenies should not be questioned. First, phylogenetic relationships arise purely from genetic grounds, and morphological data is at best a qualitative map of those genes. Second, morphological characteristics can often be influenced by external stimuli and can thus become misleading. Third, molecular phylogenies for the particular groups in this study are supported by several different independent lines of research. Lastly, molecular phylogenetic methods have been successfully tested on groups of organisms that have a well-known phylogeny.

In their study, Collard and Wood focused on the quantitative craniodental data for several hominoids and papionins in comparison with the well-supported molecular phylogenies. The results of the craniodental data analysis were phylogenetic trees that varied significantly from those created through molecular means. What's misleading is that the statistical confidence of the morphological data was very high (97%). So statistical analysis lends support for only small errors in the resulting phylogenetic trees,

while the molecular phylogenies show that they are completely wrong. This is a classic example of precision without accuracy.

The conclusions drawn by Collard and Wood are that craniodental data cannot and should not be relied on for constructing phylogenetic hypotheses for the evolution of hominoids or papionins. They argue not that the morphological methodology is flawed, but that the type of craniodental data that has been employed in past studies is probably not reliable for the reconstruction of the phylogenetic relationships of the higher primate species. The authors do stress the importance of developing new techniques for identifying and evaluating morphological data, and comparative methods for sifting through the data sets and identifying those that are informative and those that are misleading.

Another consideration is the type of tissues employed in the creation of morphological phylogenies. In a second study, Collard and Wood, in collaboration with Sally Gibbs, investigated the use of higher primate soft-tissue characters for reconstructing phylogenetic relationships<sup>2</sup>. They show that these tissues have a robust phylogenetic power and that the associated hypotheses are consistent with those from a molecular phylogeny. Their conclusion is that certain types of morphological data may be more reliable for phylogeny construction.

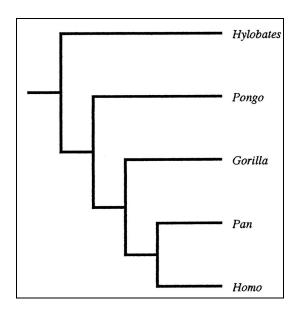


Figure 1: Hominoid molecular relationships<sup>2</sup>

To test their hypothesis, the authors carried out an extensive analysis of a comprehensive soft-tissue data set for the five extant hominoid genera – *Gorilla*, *Pongo*, *Homo*, *Pan*, and *Hylobates* – and then compared the resulting phylogenetic hypotheses against the standard molecular phylogeny (Fig. 1). The data to be analyzed had to meet three criteria: (i) data had to be available for all five genera; (ii) at least two character states had to be available; and (iii) one of these character states had to be present in two

or more species. In all there were 197 different characters that met these criteria, which provided the authors with enough data for statistical significance.

In the end, the authors found experimental support for their hypothesis that hominoid soft tissues provide reliable morphological data for phylogenetic reconstruction. In fact, the resulting phylogenetic tree was not only in agreement with the molecular data, but the statistical confidence level in the outcome was 84%. The five genera were all correctly grouped, something that the craniodental data never provided. In view of the hominoid soft-tissue characters' strong support for the group's true phylogeny, it can be inferred from these results that soft-tissue characters, unlike those of hard tissues, can be relied upon to reconstruct the phylogenetic relationships of the higher primates.

So why are soft tissues more reliable than hard tissues? One explanation may be that hard tissues such as bone and cartilage are more likely to reflect environmental or ecological effects, or simply the wear and tear of everyday life. Bone is a somewhat dynamic tissue in that it can reshape itself according to loads or constraints placed upon it. These slight variances can often be misleading when trying to interpret them for phylogenetic purposes.

The next step in this research would have to focus on extending this methodology to other groups of organisms. It has been shown that for some groups, hard-tissue morphology is somewhat reliable, while for others it is absolutely not. Does the reliability of the soft tissues as a phylogeny sources extend across all species, or is it limited to certain groups a la the hard tissues? Another interesting question is how this soft-tissue reliability depends on the specific systems, organs and tissues involved. Do some soft tissues give a more accurate phylogeny than others? These are just a few questions to be answered in what appears to be a very promising field of research.

<sup>&</sup>lt;sup>1</sup> M. Collard and B. Wood. *Proc. Nat. Acad. Sci.* **97**, 5003 (2000).

<sup>&</sup>lt;sup>2</sup> S. Giibs, M. Collard and B. Wood. *Proc. Nat. Acad. Sci.* **97**, 11130 (2000).