# TIME AND TAXONOMY

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ABSTRACT. A cladistic approach, attempting to reconstruct phylogeny, is the most objective way of depicting relationships; whole-genome comparisons, such as DNA-DNA hybridisation, show that genetic similarity really does increase with recency of common ancestry. But if we aim to represent taxonomically every dichotomy in the cladogram, more and more taxonomic division will be required, and this has led to the current trend towards unranked taxonomies. To preserve the undoubted advantages of a ranked system, I propose that we retain the modified Linnaean ranking system and its associated "subs" and "supers," while inserting unranked taxa at whatever point in the system is required. Moreover, to introduce full objectivity, we should try to link at least the modified Linnaean ranks (order, family, tribe, genus), except for species, to time since common ancestry; these time slots can be determined by looking at available fossil and/or molecular information on separation times of mammalian taxa in general, and applying criteria that do least violence to widely accepted taxonomic ranks.

KEY WORDS. Morphological, molecular, cladistics, unranked taxonomies, linking time to taxonomic rank.

## INTRODUCTION

### THE LOGIC OF PHYLOGENETIC TAXONOMY

Classification is "the ordering of [organisms] into groups (or sets) on the basis of their relationships" (Simpson, 1961). What, then are relationships?

Siblings are more closely related to each other than they are to their cousins; the essence of this is that they share a more recent common ancestor. It seems reasonable to extend this principle to the natural world: taxa sharing a more recent common ancestor are more closely related than they are to taxa which share a more remote common ancestor.

By this logic, taxonomic ranking depends entirely on recency of common ancestry. This is regardless of differing amounts of morphological change occurring in different lineages. *Homo* shares a more recent common ancestor with *Pan* than either do with *Pongo* and so should be

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classified together in a group which excludes *Pongo*, despite the fact that the *Homo* lineage has undoubtedly changed morphologically more than have either the *Pan* or the *Pongo* lineages, so that its modern representatives look very different from modern chimpanzees or orangutans. This apparent anomaly is laid to rest when we turn to the genome.

First, gross morphology is only a small part of any phenotype, which is concerned also with less obvious details: hair and skin structure, patterns of vascularisation, and so on, as well as immunological and biochemical features. So the cladistic analysis of Shoshani *et al*. (1996), based entirely on morphology, succeeded in recovering the same *Homo-Pan* sister-grouping that is indicated by genetics.

Secondly, under 10 percent of the total genome is involved in coding for phenotypic characters at all: the evolution of the 90 percent that consists of pseudogenes, introns, spacers, and repeated sequences, whether truly "junk DNA" or not, appears to depend on time more than on selection. When total genomic resemblance can be calculated, we find that the more recent the common ancestor was, the larger the proportion of the genome that is shared. This adds a new significance to the claim that the interrelationships between organisms are, at least in principle, measurable in a phylogenetic system but not in any other taxonomic system (Hennig, 1966:22-23).

Consequently, recency of common ancestry truly is measuring genetic relatedness.

## THE PLACE OF FOSSILS IN PHILOGENETIC TAXONOMY

One of the criticisms of the phylogenetic scheme is its treatment of fossil taxa: if they are also classified according to recency of common ancestry with respect to other fossil taxa or to living organisms, it is equivalent to saying that Charlemagne was more closely related to his living descendants to than to his mother or his siblings (Mayr and Ashlock, 1991: 226).

There is force in this argument, yet the argument for including them in the phylogenetic system remains compelling because it retains predictive value. To place a fossil taxon in a taxonomic group along with living members of its clade, taxa with which it shares a common ancestor, allows one to make predictions about aspects of its biology that are thus far unknown. Placing it in a "grade" along with other fossil taxa, with which it shares only primitive features, does not allow any predictions to be made.

## STEM-GROUPS AND CROWN-GROUPS

The lineages terminating in modern taxa, including their fossil representatives, back as far as their last common ancestor, are designated the

crown-group; those that branch from the stem from that point back, to its common ancestor with the next major group, are designated the stem-group. The crown-group plus stem-group together make up the total group. So the hominoid crown-group includes the lineages of humans, chimpanzees, gorillas, orangutans and gibbons back to their common ancestor; the hominoid stem-group is from this ancestor back to the branch-point where the Hominoidea and Cercopithecoidea diverged; and the hominoid total group is all the lineages that have ever arisen since this divergence.

Classifying stem-group taxa has problems of the "Charlemagne's descendents" type. Either we insert a whole new rank for a dichotomy between a crown-group and its sister-group that may be a single genus, or we unrank the stem-group taxon in some way. The most convenient way to do this is to adopt the 'plesion' concept of Patterson and Rosen (1977). A plesion is a taxon of any rank, of limited diversity; Groves (1989) proposed to restrict the concept to taxa with few or no known apomorphies and limited time-depth.

## AGES AND TAXONOMIC RANKS

But despite cladistic logic, there is still a great deal of subjectivity in taxonomy: in assigning taxonomic rank. Hennig (1966) proposed that we should link the taxonomic rank of a clade to its time of origin. Thus, among the insects, the different orders are in many cases fairly securely known to have arisen in the Carboniferous or Permian. He realized that by this time the vertebrate class Mammalia (as traditionally defined) had not even appeared, i.e., the vertebrates are over-split from an entomologist's point of view. We could either upgrade the orders of insects to classes, or downgrade the classes of vertebrates to orders, or we could simply accept that different standards apply and link age to rank differently in different groups of organisms. Hennig favored this last solution, but it is fair to say that the consensus of taxonomic opinion was against any such scheme.

The alternative is to abolish taxonomic ranks altogether, and classify with names alone (de Queiroz and Gauthier, 1992). This avoids the anomaly of a given rank having different implications in different phyla, and equally of having to rejig an entire classification when a new and phylogenetically significant fossil has to be interpolated into an existing scheme. In my view, this might perhaps be acceptable whenever the complete classification of a group is being presented, but we lose the ability to refer meaningfully to any given group in isolation.

It may be that the negative reaction to the idea of age-rank linkage was connected to the incompleteness of the fossil record; the time of origin of many groups is simply not known (anyway, should we link age to crown-groups or stem-groups?). The revival by Goodman *et al*. (1998) of

Hennig's proposal pointed out that we can approach the problem by using molecular data, with due caution, and by making it quite clear whether we are talking about crown-groups or total groups. They proposed, among the primates, linking the time of origin of suborders, as total groups, to the Late Paleocene or Early Eocene, 58-50 Ma; and family- and genus-group categories as follows:

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|---|---|---|
| Superfamily | 39-29 Ma | Middle Eocene to Middle Oligocene |
| Family | 28-25 | Middle to Late Oligocene |
| Subfamily | 23-22 | Early Miocene |
| Tribe | 20-14 | Early to Middle Miocene |
| Subtribe | 14-10 | Middle to Late Miocene |
| Genus | 11-7 | Late Miocene |
| Subgenus | 6-4 | Late Miocene to Early Pliocene |

I think we should not reject these proposals out of hand; they represent the only prospect that I can envisage of making taxonomy fully objective. So let me propose some modifications as well as some stipulations:

We must, of course, take all available evidence into account. Some of the splitting times of Takahata and Satta (1997), for example, differ from those of Goodman *et al*. (1998), and those of Easteal and Herbert (1997) are later than those of many other authors, though they were calculated using a global clock. Which splitting times should we use? The problem is not insoluble.

We should start with phyla, and within each one we should concern ourselves mainly, perhaps entirely, with the obligatory ranks: class, order, family, perhaps tribe, genus. The super-, sub- and infra- categories, and intercalated ranks (like cohorts), should be used mainly to split up extensively polytypic taxa, and we need not (at least in the beginning) try too hard to link them to absolute age—indeed, we need not use them at all if fine splitting is not needed.

We do not need to dignify every dichotomous split with a separate rank; sometimes successive dichotomies, if indeed that is what they are, were so closely spaced in time that they are difficult to resolve, and in any case Goodman's *et al*. (1998) proposal is that we adopt a "window of time" approach to ranking. If there are well-attested splits that we want to recognize taxonomically, and we have run out of ranks, then there is nothing wrong with leaving some of these levels indeed unranked.

We should try, as far as possible, to preserve classes, orders, families and genera with the content with which they are widely recognized (if indeed they are): the Principle of Least Violence.

I have collated fossil data from other large mammals, outside the Primates. The families of mammals whose fossil record is well-known go back to the Late Oligocene or Early Miocene, on the whole somewhat later than in Goodman's *et al*. (1998) proposal, while their genera go back to some 6 to 4 Ma, the period within which Goodman *et al.* (1998) placed their subgenera. These, I suggest, are useful guidelines for assigning ranks within the Primates.

If taxonomy, urged so effectively towards greater objectivity by Hennig, is ever to become a fully unbiased and repeatable exercise, then some such criteria as I have suggested should be adopted. I propose that we start by seriously reconsidering the age/rank correlation that for so long appeared to be Hennig's greatest blunder.

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