



Reading Trees

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"A major concern of the systematist, when he devises a classification, is to make one in accordance with probable phylogeny, but first he must assess the characters and determine relationships in a static or nonhistorical sense. Later he may decide on the most likely lines of descent" (Michener & Sokal 1957: 130).

Are birds dinosaurs? Answers to this question yield various responses, depending on a particular viewpoint. From the perspective of a common understanding of recent theories of the origin of birds and their potential precursor (ancestral) animals, then, yes, birds are a kind of dinosaur, having evolved from one or another non-avian dinosaur (Bostwick 2003). From the perspective of public understanding of science (how to inform the general public of biology's latest findings), then, yes, birds are dinosaurs, at least they are a kind of dinosaur, one that young children can actually hold in their hands (e.g., Maugh 2012). These two perspectives, largely derived from phylogenetic reasoning, contrast with the perspective from classification, which asks different questions: What are birds; what are dinosaurs; and how are they related to one another? Addressing these questions raises the issue of trees in classification (phylogenetic or otherwise) and how to read them. This is not as easy a task as is often suggested in the recent literature on tree-reading and tree-thinking (first noted long ago by O'Hara 1988, see Baum and Smith 2012 for a first book-length treatment). The role of tree-thinking in classification is applied after a tree has been constructed and natural groups established. For instance, it would seem premature to infer phylogenies on poorly classified taxa, such as invertebrates, reptiles and so on, as these groupings are artificial. Doing so would only result in erroneous hypotheses that cannot be substantiated. The role of classification, however, is to make sure that the natural groups are justified, and in order to do this it is vital that those groups are understood. Birds represent a monophyletic group, which has series of unique characteristics that it shares with other theropods (i.e., bipedal saurischian dinosaurs). Dinosaurs, as usually conceived, are a group of non-monophyletic organisms that variously share closer characteristics (i.e., relationships) with other taxa rather than uniquely among themselves. In the case of dinosaurs (as Dinosauria) and classification, what is at stake is a taxonomic name, rather than a unique group of character traits. Below we outline and compare two contrasting ways of reading trees, one way, concerned with classification, yielding the view that, no, birds are not dinosaurs.

Reading Trees: Bottom-up and Top-Down Approaches

A branching diagram is essential for depicting evolutionary relationships so that one might, for example, study character evolution. A branching diagram is also essential for deriving overall systematic relationships. These are two very different ways of reading a branching diagram and herein are called *bottom-up* and *top-down* approaches, respectively¹.

The bottom-up approach is commonly used when reading phylogenetic trees. Figure 1a is a branching diagram that can be interpreted as a hypothetical phylogenetic tree.

Here, the nodes represent ancestors or ancestral traits, such as rudimentary wings in insects or avian teeth in birds. Such primitive traits are found at the base of the tree with derived traits found further up. Since character evolution is important in constructing phylogenies, the tree is read from the bottom up. Namely, a rudimentary wing transforms into a developed or even specialised wing. This transformation between primitive and derived traits creates a phylogeny.

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1. Mayr (1982, pp. 158 & 190) also refers to "Downward" and "Upward" classifications. The former term was used by Mayr to describe pre-Darwinian classification by "logical division" (Phylum, Class, Order etc.), while the latter refers to classification by grouping. We do not refer to these classifications, but rather to two valid approaches to reading branching diagrams.

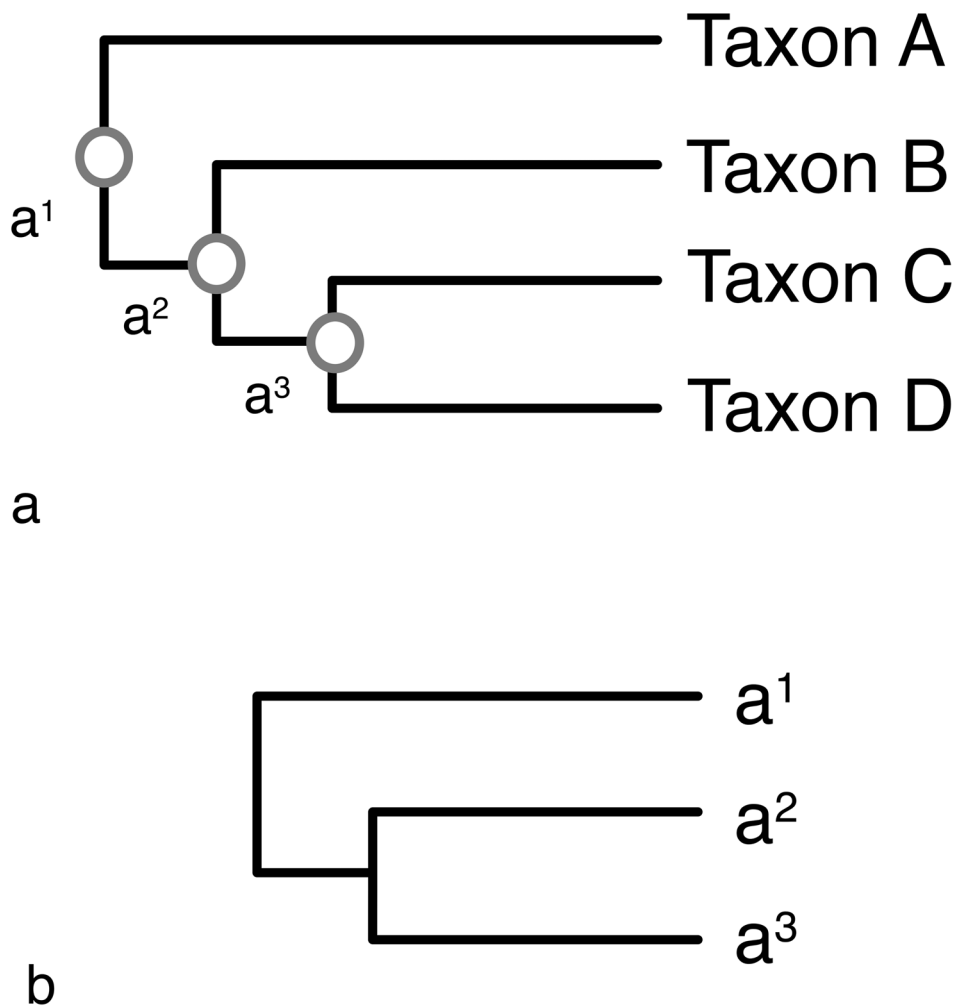


FIGURE 1.

Bottom-up interpretations also make assumptions about character traits. A primitive trait is not dependent on one that is derived; but derived traits are dependent on primitive ones. This dependency becomes important when dealing with a character reversal, which is a transformation of a derived trait back into its primitive version. A flea, for instance, lacks wings, but is derived from a winged ancestor, which in turn was derived from a wingless ancestor. This secondary loss, although primitive in appearance, is actually derived. Without the initial primitive trait, that reversal would be impossible to interpret from a phylogenetic tree. In other words, character traits are dependent in a linear fashion. In the transformation $a^1 \rightarrow a^2 \rightarrow a^3$, both a^2 and a^3 are dependent on a^1 .

In contrast to the bottom-up approach, a top-down interpretation can be made of the same branching diagram (Figure 1). This is synonymous with reading the diagram as a classification. Reading a branching diagram as a classification means that all character traits are treated as derived. Since classification is concerned with topographical relationships, starting at the top of the tree with D, it is first noted that D is more closely related to C than it is to B; and B, C and D are more closely related to each other than they are to A. Unlike B, C and D, it is not known what A is more closely related to in terms of anything else, because that information is missing. Unlike the bottom-up approach, the character traits are also read as topographical relationships. For example, character trait a^2 is more closely related to a^3 than either are to a^1 , which can be drawn as Figure 1b. Given that these approaches read branching diagrams in very different ways, how do they relate? Moreover, do they conflict?

What comes first?

Any phylogenetic interpretation is made after a branching diagram has been created. Statements of relationship can only be made after the branching diagram has been found. It is significant that branching diagrams are created using the top-down approach *and not* the bottom-up approach. It is not necessary to investigate the specifics of numerical methods in any great detail but we will briefly demonstrate how a branching diagram is constructed under the parsimony optimality criterion.

Data are assembled as a binary data matrix. The binary data matrix is converted into network of relationships based on the most parsimonious configuration of character transformations. Our binary data matrix indicates that D and C are more closely related to each other because they share a^3 . What is in doubt is the relationship between A and B. To find the root of the tree (its direction of change), a known and distantly related taxon functions as an out-group. This out-group now roots the tree on character a^1 , placing B, C and D as the in-group taxa, in which C and D are more closely related. While the process is simple in theory, and computationally complex, the character traits are never transformed in an analytical sense. Thus, taxa are grouped on character traits and the transformation is interpreted *after* the analysis. A parsimony program, for example, cannot compute the direction and exact position of all character transformations. It can only be done *a posteriori*.

Clearly the process of creating branching diagrams follows a simple sequence. First a branching diagram is constructed using this top-down approach. Following that, the tree can be interpreted using both bottom-up and top-down approaches: but branching diagrams are never constructed from the bottom-up. Doing so would not result in a branching diagram, but an explicit phyletic history or $A \rightarrow B \rightarrow C \rightarrow D$ for example. Since branching diagrams are not read as phyletic histories, why, then, do we read the character traits as so?

Homologies as Nested Hierarchies

Character traits may be read both as linear transformations and as nested hierarchies as demonstrated above. While both approaches are valid, only top-down interpretations can break the tree into discrete character statements. A combination of these character statements as an aggregated or consensus diagram literally rebuild the branching diagram without the need for character trait dependency, while not deviating from a phylogenetic hypothesis.

For instance, the phylogenetic hypothesis $a^1 \rightarrow a^2 \rightarrow a^3$, in which a^1 is assumed to be the most primitive trait, can be easily represented as $\{a^1 \{a^2, a^3\}\}$ without losing any phylogenetic signal. In doing so a nested hierarchy has been created or independent derived character traits that are interpreted using a top-down approach. While this is useful in classification (determining natural groups), it deviates from phylogenetic assumptions (i.e., ancestor, primitive characters).

Are Birds Dinosaurs?

We ask again, “Are birds dinosaurs?” Birds share characters with other theropods, which are grouped with other dinosaurs. Such a grouping conveys the correct notion that birds and other theropods (classified in Dinosauria) as sharing a common ancestor. But from the point of view of classification, dinosaurs clearly define what birds are via a bottom-up approach. This means that the character traits shared by birds and other theropods are derived from an assumed primitive condition from another ‘dinosaur’ node and so on. In this sense bird traits are dependent on assumed primitive dinosaur traits. Thus birds themselves “complete” dinosaurs as a monophyletic group.

If for the moment all character traits as understood as derived, then the situation reverses and dinosaurs traits are independent from birds. We can demonstrate this as so: birds and other theropods are more closely related to each other than they are to *any other organism* based on the fact that they share derived traits. This means that *some* theropods are birds and birds *are* theropods. But theropods and birds for example are not sauropods, even though they share some character traits. The top-down approach is essential in distinguishing monophyly from non-monophyly. Moreover, nested hierarchies at any level treat all character traits as independent, making it an ideal way to classify at all levels. In addition, phylogenies can be interpreted from existing classifications using a bottom approach if one so wishes.

Within the field of biological classification, dinosaurs are not a unique group of taxa with independently derived character traits. In biological classification such groups are not natural and are discarded. But dinosaurs are different, as they have entered the public conscience as a very distinguishable group of organisms that once roamed the Earth. This is where the catch phrase “Birds are Dinosaurs” is not only useful in communicating the idea of phylogeny, but also capturing the imagination of generations of children.

While such folk taxonomies usefully transmit ideas to the public, they are of no use in taxonomy where such catch phrases create problems, namely the justification of non-monophyletic groups. For instance, if we were to finally revise Dinosauria, it will be synonymised into Aves, an older term that retains priority and anything classed as part of Dinosauria would be designated as Aves. But this does not change the folk taxonomy in any way: birds are still dinosaurs in the popular imagination, but within ornithological systematics the Grey Shrike Thrush (*Colluricincla harmonica*), for example, is a theropod that is classified under Aves. Thankfully, folk taxonomies do not drive scientific classifications, otherwise we would still have *Brontosaurus*, possibly with cavemen sliding down their tails.

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