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MATTERS OF THE RECORD

Ancestor-descendant relationships and the reconstruction of the Tree of Life

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Introduction

The reconstruction of the Tree of Life has been a primary goal in biology since Darwin coined the expression, the ''great Tree of Life'' in *On the Origin of Species*: ''The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during each former year may represent the long succession of extinct species. . . .As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications'' (Darwin 1859: pp. 129–130). Ernst Haeckel was the first biologist who attempted to reconstruct the Darwinian Tree of Life. However, he could not reach his goal because his method of tree reconstruction was deeply anchored in the pre-Darwinian *scala naturae* (Dayrat 2003). A segment of the Darwinian Tree of Life is illustrated in the unique figure published in *On the Origin of Species*. This figure, which Darwin referred to as a ''branching diagram,'' represents ancestor-descendant relationships (ADR).

Pointing out that Darwin's Tree of Life represents ADR is not controversial. It simply is a fact. However, it might be more controversial to point out a paradoxical situation: why does an overwhelming majority of the trees currently published represent sister-group relationships (SGR)? Given that reconstructing the Darwinian Tree of Life is one of today's foremost goals in systematic biology, one would expect that the reconstruction of ADR would arouse greater interest among biologists.

Certainly, only SGR can be reconstructed in many cases, such as among supraspecific taxa, among fossils that belong to distant species, and among living organisms (although molecular studies may reveal ancestral morphospecies and AD pairs of living species [Funk and Omland 2003, and references therein]). However, conditions likely to preserve evidence of ADR are not rare in the fossil record (e.g., Gingerich 1979, 1985; Alroy 1995; Wagner 1995; Foote 1996; Foote and Sepkoski 1999; Fox et al. 1999; Roopnarine 2005). Whether trees could include ADR (e.g., Szalay 1977; Bretsky 1979; Gingerich 1979) or not (e.g., Nelson 1971, 1972; Cracraft 1974; Farris 1976; Platnick 1977) dominated debates in the late 1970s and led to a cladistic orthodoxy according to which reconstructing ADR is not a rigorous scientific task, because ADR cannot be tested in a so-called Popperian sense. This cladistic orthodoxy largely explains why ADR are rarely addressed. However, the fact that the Tree of Life involves ADR fully justifies research on ADR, regardless of Popper's philosophy—or some interpretations of his philosophy. In the present contribution, I discuss the relations between classification and ADR. In

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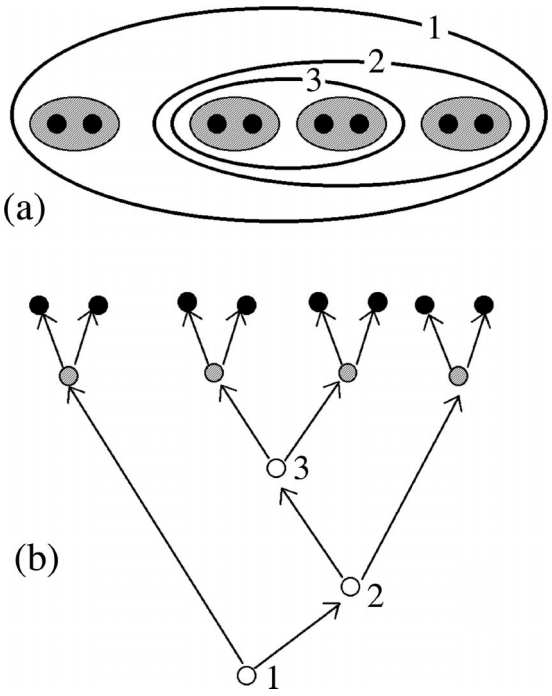

FIGURE 1. Correspondence (according to Hennig) of a Venn diagram representing a classification of recent species with a diagram representing ancestor-descendant relationships among all extinct and recent species. (A and B after Hennig 1966: Fig. 18.)

particular, I argue that classificatory goals have prevented workers from trying to reconstruct ADR.

Cladism or the Triumph of Classification

Several authors noticed the importance of Woodger's (1951, 1952) and Gregg's (1954) works for understanding Hennig's *Phylogenetic Systematics* (e.g., Knox 1998; Reif 2003; Rieppel 2003). However, Knox (1998) is the only one who demonstrated that Hennig's ideas are not the same as Woodger's and Gregg's. This is striking when Hennig (1966) claims that ''Two different graphic representations of a hierarchic system are contrasted in Figure 18 [here Fig. 1]. Comparison shows that they correspond exactly to one another: every fact that can be inferred from I [upper part] is also expressed in II [bottom]; the only difference is the way in which the phylogenetic relationships of the individual species are expressed'' (Hennig 1966: p. 70). Indeed, unlike Hennig, Woodger thought that ''The taxonomic system and the evolutionary phylogenetic scheme are quite different things doing quite different jobs and only confusion will result from identifying or mixing them'' (Woodger 1952: p. 22).

Contrary to Hennig's statement, these two diagrams do not represent the same kind of hierarchy (Knox 1998). The upper part (Fig. 1A) represents a classification of living species, whereas the bottom part (Fig. 1B) represents ADR among the extinct and living species. The entities involved in both diagrams are different: living species and sets of living species (Fig. 1A), extinct and living species (Fig. 1B). The models of organization (relations among entities) also are different: subordination, or containment of sets within sets (Fig. 1A), ADR (Fig. 1B).

Interestingly, Hennig was right when he asserted that ''every fact that can be inferred from I [Fig. 1A] is also expressed in II [Fig. 1B]'' (Hennig 1966: p. 70). Indeed, the information that Figure 1A provides (i.e., subordination of monophyletic groups of living species) is expressed in recency of common ancestry in Figure 1B—note that this figure is not supposed to show branch length. However, Hennig was wrong when he stated that these two diagrams do correspond exactly to one another. Indeed, ADR among extinct and living species (Fig. 1B) are *not* expressed in the classification of living species (Fig. 1A). Obviously, this did not matter to Hennig, otherwise he would have realized immediately that both diagrams do not correspond exactly to one another.

Hennig was a taxonomist. His main goal was to establish classifications, and he adopted the classificatory hierarchy as *the* model of organization. The only way to obtain reciprocal correspondence between classifications and branching diagrams was to consider branching diagrams that would *only* express sister-group relationships, i.e., cladograms. If the bottom part (here Fig. 1B) is reinterpreted as a cladogram (although this is *not* what Hennig illustrated), then both diagrams do correspond exactly to one another: this is what Nelson rightly calls ''cladism as a philosophy of classification'' (Nelson 1971). The problem is that a variety of hierarchies is necessary to represent the complexity of phenomena in na-

ture (Knox 1998), and classification based on subordination cannot represent ADR (e.g., Simpson 1961: p. 63; Nelson 1973; Farris 1976; Hull 1979; Fisher 1991: p. 104; Reif 2003: p. 114). Hennig's work makes sense only if one considers that his deepest goal was to produce classifications: in fact, it is the main reason why Hennig's branching diagrams would represent only SGR.

In current practice, terminals of cladograms are often living organisms and fossils. However, it is less well known that Hennig (1966, 1969, 1981) attempted to reconstruct SGR only among living species. Hennig (1969, 1981) had to classify fossils though: a phylogenetic analysis of extant organisms would provide a series of clades; fossils would be distributed in the clades on the basis of the synapomorphies they would share; stem groups would not be avoided in case of lack of apomorphies.

One of the most important transformations of Hennig's phylogenetic systematics into modern cladistics was Farris's (1976) proposal to treat fossils as possible terminal units, i.e., any differently than if they had existed at a single synchronous level with recent species. Ironically, Farris's contribution made possible the emergence of methods to reconstruct ADR based on cladograms including both fossils and living organisms as terminal units (Fisher 1991, 1992, 1994; Wagner 1995; Polly 1997; Fox et al. 1999; Fisher et al. 2002). Those methods, however, differ from the mainstream practice of cladistics because they use stratigraphic data to infer possible ADR topologies in addition to SGR topologies.

Darwinism or the Triumph of the Tree of Life

Needless to say, Darwin's ideas on classification have caused much ink to flow (e.g., Nelson 1971, 1972, 1974; Ashlock 1979; Mayr 1985; Ghiselin 1985; Padian 1999; and references therein). However, Darwin has been quoted abundantly to arbitrate in a contemporary debate, i.e., whether taxa should only be monophyletic (sensu Hennig) or whether they could be monophyletic and paraphyletic. Haeckel also has been called for help here (e.g., Farris 1990). This issue did not concern whether or not cladograms should be accepted, but rather how a classification should be established from a cladogram (Hennig 1975). The problem is that Darwin did not address this issue, nor did Haeckel, and that our debates have largely prevented authors from considering Darwin's main concern, exactly as they have prevented authors from understanding what Haeckel really meant (Dayrat 2003).

A detailed analysis of Darwin's (1859) use of words such as ''pedigree'' (pp. 422–423, 425, 486), ''genealogy'' (p. 486), and ''tree'' (pp. 129–130, 317, 431–432), in *On The Origin of Species* is critical to understand his ideas on classification. Words such as ''genealogy'' and ''pedigree'' clearly refer to ADR between individual organisms (as in a family tree). However, Darwin used them by extension to refer to ADR between varieties or species along lines of descent of the Tree of Life. Darwin used these words because they conveniently express the idea of descent, although he certainly was aware that descent between individual organisms (which we refer today as ''genealogical nexus'') is different from descent along the branches of the Tree of Life. Also, words such as ''genealogy'' and ''pedigree'' are much less debatable than terms that refer to concepts, such as system and arrangement.

Darwin first mentioned the word ''phylogeny'' in the fifth edition of *The Origin of Species*: ''Professor Häckel in his 'Generelle Morphologie' and in several other works, has recently brought his great knowledge and abilities to bear on what he calls phylogeny, or the lines of descent of all organic beings'' (1869: p. 515). Darwin's use of the word phylogeny was radically different from Haeckel's original meaning: Haeckel's ''whole of phylogeny'' was referring to the main changes in form along the lines of descent of the Tree of Life, and not the lines of descent themselves (Dayrat 2003). It is worth pointing out that referring to trees representing ADR between population-level entities as ''phylogenetic trees'' or ''phylogenies'' (e.g., Eldredge 1979) is in full agreement with Darwin's redefinition of ''phylogeny.'' The problem is that most ''phylogenetic trees'' or ''phylogenies'' currently published simply are cladograms: referring to

the relationships along the actual lineages of the Tree of Life as ''phylogenetic'' relationships might confuse most of today's scientists, but it would be fully appropriate.

Darwin's use of words such as ''pedigree,'' ''genealogy,'' and ''tree'' in *On the Origin of Species* leaves no doubts about his ideas on the relation between classification and ADR:

> As it is difficult to show the blood-relationship between the numerous kindred of any ancient and noble family, even by the aid of a genealogical tree, and almost impossible to do this without this aid, we can understand the extraordinary difficulty which naturalists have experienced in describing, without the aid of a diagram, the various affinities which they perceive between the many living and extinct members of the same great natural class'' (Darwin 1859: p. 431).

This quotation expresses what Darwin clearly stated on different occasions in *On the Origin of Species*: a tree is necessary to represent the ADR of the lines of descent of the Tree of Life.

This helps us reinterpret one of Darwin's most famous statements: ''Our classifications will come to be, as far as they can be so made, genealogies'' (Darwin 1859: p. 486). I think that Darwin meant exactly what he wrote: trees *are* better representations of relationships between all extinct and living forms than a classification. Several quotations corroborate this interpretation, such as

> This natural arrangement is shown, as far as is possible on paper, in the diagram, but in much too simple a manner. If a branching diagram had not been used, and only the names of the groups had been written in a linear series, it would have been still less possible to have given a natural arrangement; and it is notoriously not possible to represent in a series, on a flat surface, the affinities which we discover in nature amongst the beings of the same group (Darwin 1859: p. 422).

One can read Darwin's work on classification by distinguishing two cases: without extinct species versus with extinct species. When Darwin only considered the living species present at the top of his branching diagram, the classification would be obtained from the branching points of the tree:

> Of the eight descendants from (A) the three marked a^{14}, q^{14}, p^{14}, will be nearly related from having recently branched off from a^{10}; b^{14} and f^{14}, from having diverged at an earlier period from a^5, will be in some degree distinct from the three first-named species; and lastly, o^{14}, e^{14}, and m^{14}, will be nearly related one to the other, but from having diverged at the first commencement of the process of modification, will be widely different from the other five species, and may constitute a sub-genus or even a distinct genus'' (Darwin 1859: p. 123).

The most important point, however, is that in this case Darwin did not include extinct species in the classification.

Darwin's proposition for classifying all extinct and living species within the same classification was brief and not convincing:

> These three families [of living descendants of A], together with the many extinct genera on the several lines of descent diverging from the parent-form A, will form an order; for all have inherited something in common from their ancient and common progenitor. . . .If, for instance, the genera a^1, a^5, a^{10}, f^8, m^3, m^6, m^9, were disinterred, these three families would be so closely linked together that they probably would have to be united into one great family (Darwin 1859: p. 331).

Darwin did not explain how the subordination of those genera within the family could represent their vertical and directed relationships. In fact, there is no solution (e.g., Nelson 1973): subordination alone cannot represent the relationships between a^1, a^5, a^{10} and a^{14}, which certainly is why Darwin stated that the best representation of the relationships along lines of descent would be the lines of descent themselves, rather than a classification.

Contrary to Hennig, whose primary goal was to establish classifications and have branching diagrams that could correspond exactly to those classifications (even if the price to pay was the exclusion of ADR from those branching diagrams), Darwin wished to re-

construct ADR along lines of descent, regardless of whether or not they could be represented in a classification: ''We possess no pedigrees or armorial bearings; and we have to discover and trace the many diverging lines of descent in our natural genealogies, by characters of any kind which have long been inherited'' (Darwin 1859: p. 486). Therefore, any method that aims to reconstruct ADR is truly Darwinian. ADR should be studied as often as possible because they are more accurate representations of the evolutionary history than SGR. Also, note that ADR should help address evolutionary questions that require inferences of sampled ancestors, such as richness and gaps in the fossil record (Wagner 2000).

Reconstructing Ancestor-Descendant Relationships

All methods available to reconstruct ADR (ADR methods) consider that fossils are potential ancestors and that stratigraphic data provide temporal information that is crucial for reconstructing ADR. Some methods are based on the reconstruction of cladograms, but they do not reject the possibility of including ADR in the most parsimonious topologies (Fisher 1991, 1992, 1994; Wagner 1995; Polly 1997; Fox et al. 1999; Fisher et al. 2002). Some other methods are based on phenetic approaches (Gingerich 1979, 1985, 1990; Roopnarine et al. 1999; Roopnarine 2005). Alroy's (1995) method uses graph theory to make ADR the null hypothesis relative to SGR (because SGR require adding a separate branch, and graphs with more branches are less parsimonious than graphs with fewer branches). All these methods constitute repeatable treatment of data and are based on hypothesis testing. However, note that Alroy's and Fisher's methods treat ADR as a null hypothesis, whereas Wagner's method uses stratigraphy to reject SGR. I would advocate a simultaneous use of several methods to analyze the same data—comparing these methods by using the same set of data has never been attempted but would certainly generate interesting discussion.

One of the challenges for future research on ADR methods will be to clarify their limits, in particular in terms of both stratigraphic and morphological data. Some issues have been mentioned but need further discussion, such as the quality of the fossil record that is necessary to attempt reconstruct ADR (e.g., Foote 1996; Fox et al. 1999). Also, new practical cases will certainly reveal new issues. One of the major technical constraints on the reconstruction of ADR is the fact that ancestor-descendant series are algorithmically speaking much more difficult, and therefore more computer-time consuming, to reconstruct than SGR. We can hope that progress will step by step help us solve this problem. In this regard, the use of a Bayesian approach and Markov chain Monte-Carlo approximations may offer new opportunities to improve the efficiency of the existing methods or develop additional methods (Roopnarine 2005).

A theoretical question that will need to be discussed and addressed is how continuous lines of descent can be divided in ''species.'' The answer to this question depends on the definition of ADR that is accepted. Darwin, who viewed natural selection as a process producing slow anagenetic changes along lines of descent, thought that species were arbitrary slices. It is particularly striking where Darwin (1859: pp. 118–119) described the lines of descent of his branching diagram constituted by series of ''varieties'' (a^1, a^2, a^3, a^4, and so on). Hennig's species definition as a segment between two speciation events makes perfect sense in the context of his idea of hierarchy (Knox 1998; Rieppel 2003). However, it also has several drawbacks: specimens that would be morphologically identical before and after a budding event would be named differently, whereas specimens that would be morphologically distinguishable in case of a phyletic transformation would receive the same name (Foote 1996). Although I believe that future research should focus on the reconstruction of actual lineages, criteria for delineating and naming ''species'' along them will have to be discussed and selected, in particular because this is necessary to curating museum collections.

When ADR are found, they cannot be represented by a classification based only on subordination. In such cases, Darwin suggested that we consider the tree itself as the best pos-

sible representation of relationships. As a matter of fact, the authors who published trees involving ADR (e.g., Darwin 1859; Gingerich 1985; Alroy 1995; Wagner 1995) represented those relationships by a tree and not by a classification. Several systems of classification based on subordination but not exclusively have been proposed (e.g., Nelson 1973; Craske and Jefferies 1989; Reif 2003). However, such systems are quite complex and unattractive.

Generally speaking, research on ADR is a difficult task. I see this as another illustration of Darwin's genius: he was able to point to a goal although he knew that reaching this goal would be a long and often discouraging process. However, science does not progress by restricting or modifying goals to please practical contingencies. Completing the actual lines of descent of the Tree of Life is an unattainable goal, but we ought to attempt to approach it. Ancestor-descendant relationships should be investigated as often as they can be.

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