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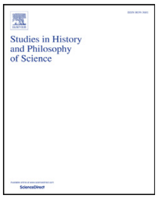

Histories of molecules: Reconciling the past

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ABSTRACT

Molecular data and methods have become centrally important to evolutionary analysis, largely because they have enabled global phylogenetic reconstructions of the relationships between organisms in the tree of life. Often, however, molecular stories conflict dramatically with morphology-based histories of lineages. The evolutionary origin of animal groups provides one such case. In other instances, different molecular analyses have so far proved irreconcilable. The ancient and major divergence of eukaryotes from prokaryotic ancestors is an example of this sort of problem. Efforts to overcome these conflicts highlight the role models play in phylogenetic reconstruction. One crucial model is the molecular clock; another is that of 'simple-to-complex' modification. I will examine animal and eukaryote evolution against a backdrop of increasing methodological sophistication in molecular phylogeny, and conclude with some reflections on the nature of historical science in the molecular era of phylogeny.

1. Introduction

Historical science is often distinguished from experimental science. These distinctions are made on the grounds of differences in the way historical analysis establishes causal relationships (Cleland, 2001; Turner, 2005). Phylogeny, the reconstruction of historical relationships of extant and extinct organisms, appears to be a classic exemplar of standard historical science. Although in its earlier instantiations phylogeny relied exclusively on morphological detail to infer the past, in its current phase molecular data and its analysis are of major importance. The transition from morphological to molecular methods has not been entirely unproblematic, and there are still clashes between phylogenies using different data types. There are also many conflicts between trees built exclusively from molecules, in which different reconstructions of the same era of evolution and the same lineages are discordant. I will suggest that the problems in reconciling different phylogenetic interpretations give some insight into how historical science can be understood philosophically.

To do this, I will look at major disputes in the accommodation of molecular data within the staid and rule-bound discipline of systematics. There are many telling instances of such disputes in animal phylogeny, as traditional morphological approaches were supplemented and then overwhelmed by molecular methods. Ongoing disputes about the earliest metazoans raise some interesting open questions about the epistemic achievements of historical reasoning based on molecular inferences. Another phylogenetic dispute appears even more intractable, but for different reasons. When trying to reconstruct the first eukaryote, the problem is not clashes with morphological data but its very unavailability. Phylogeneticists instead have to extract signal from tremendously noisy molecules, and direct it toward very different competing hypotheses about the origin of eukaryotes. Both cases also challenge the standard story of simple to complex modifications. And both examples shed fresh light on the nature of historical science and its relationship to experimental science.

2. The rise of phylogenetic classification and its molecularization

The ambitious task of representing the historical relationships between all life forms gained its contemporary theoretical impetus from Charles Darwin. He famously used the metaphor of a great tree of life.

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> ‘The affinities of all beings of the same class have sometimes been represented by a great tree. … The green and budding twigs may represent existing species ... this connection of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinate to groups’ (Darwin, 1872, pp. 104-5)

Despite Darwin's influence and the growing acceptance of descent by modification, the relationship between phylogeny and taxonomy remained fraught until well into the twentieth century (Gilmour and discussants, 1940; Stevens, 1984; Winsor, 1995). For systematists, this was primarily because of the difficulties of combining old non-evolutionary classifications with new evolutionary ones.

> ‘We are not going to imagine … that the work of the past is to be thrown aside as worthless, and that the system based on phylogeny will have nothing in common with the older systems’,

said leading plant systematist and evolutionary advocate Charles Bessey (1897, p. 172).

Unsurprisingly, most late nineteenth and early twentieth century efforts to build classifications on the basis of Darwin's theory were not as extensive as Darwin's vision of the great tree of life (apart from Ernst Haeckel's 1866 schematic representation). They were nevertheless large-scale in that these more constrained projects attempted to represent broad phylogenies of major animal and plant groups (e.g., Berry, 1902; Bessey, 1897; Brown, 1938; Campbell, 1928; Herdman, 1886; Matthew, 1930; Tilden, 1928). These representations of evolutionary relationships were feasible due to the morphological detail available to experts in each field, and the deep experience these experts had of investigating their chosen group of organisms and the resemblance relationships between them. However, the accumulation of empirical data and expertise were not the only forces driving the field. Phylogenetic reconstructions also depended on long-held assumptions about which character must have come first (as ‘primitives’) in the evolution and diversification of these lineages. These diversifications were considered to be adaptive as well as ‘progressive’ (Gilmour and discussants, 1940; Schaffner, 1934; Stevens, 1984).

As phylogenetic methods became more entrenched in classificatory practice, some of these preconceptions were overturned—often but not always by evolutionary reinterpretations of existing rather than new morphological data. In some of these cases, ‘simple’ forms could no longer be viewed as the most ancient in the group, but had instead to be interpreted as ‘reduced and greatly specialized’ from ancestrally more complex forms (Sinnott & Bailey, 1915, p. 11). In W. B. Crow's discussion of the problems of reconciling classifications, he laid some of the blame at the foot of trying to bring ‘facts into line with a preconceived simple scheme’ (Crow, 1926, p. 86). Instead, he argued, it had to be recognized that

> ‘Different characters may give different indications of affinities in one and the same organism. Every morphologist knows that a type may be primitive in some respects and advanced in others’ (Crow, 1926, p. 145).

However, even when ‘regression’ (to a more primitive and less complex state) was diagnosed, it could still be interpreted as a ‘special case of increased differentiation’ and thus complexification (Crow, 1926, p. 128).

As the modern synthesis took evolutionary classification to its heart, it too issued warnings about modelling evolution as a simple-to-complex sequence. Systematist Ernst Mayr led the way with cautions about interpreting morphological data.

> ‘We now know that complexity of a structure is not necessarily an indication of evolutionary progress. Cases of secondary simplification are sufficiently frequent to make quite inadmissible the assumption that morphological series from simple to complex are necessarily evolutionary series’ (Mayr, 1959, p. 297).

Despite the growing orthodoxy of the modern synthesis, some background tenets, such as non-progressiveness in evolution, continued to be disregarded. Morris Goodman, whose early protein comparisons of primates transformed their evolutionary placements (see Section 3), believed that ‘the pre-Darwinian concept of the *scala naturae* in which an animal progresses from simple to morphologically simple organisms still operates in post-Darwinian systematics’ (Goodman, 1963, p. 395; see also O'Hara, 1992). That conceptual habit has persisted up to the present day. As contemporary evolutionary zoologist Kenneth Halanych notes (2015, p. 593), ‘many readers will be thinking “Of course evolution does not always go from simple to complex!” Nonetheless, this assumption is often made without realization’. And in some cases, this idea is held with full awareness. For example, ‘one of the basic principles in evolutionary biology [is] that complex life forms derive from more primitive ancestors’ (Schierwater et al., 2009, p. 0037). However, molecular phylogeny in particular has revealed numerous episodes of secondary simplification, in which evolutionary processes are thought to have simplified previously complex states.

Questions about evolutionary processes and the patterns they produce have always been accompanied by deep methodological concerns about making accurate evolutionary classifications. There were many doubts in the late nineteenth and early twentieth century that morphological data[1] and comparative methods were sufficient to resolve the more subtle relationships between organisms (e.g., Bessey, 1897). Some evolutionary biologists openly admitted the ‘speculative’ nature of their classifications because of the sketchy evidence on which their evolutionary inferences were based (e.g., Brown, 1938, p. 570). Gaps in evidence and contradictions between different phylogenetic interpretations led to rather premature conclusions of the failure of phylogenetic classification.

> ‘The general acceptance among biologists that species of animals and plants are related to one another by descent was followed by numerous endeavours to revise the system of classification, and to place it on a genetic relationship [respecting Mendel's rules of inheritance]. Today these endeavours to construct a natural system to a large extent have been abandoned’ (Crow, 1926, p. 85).

Some phylogenetic taxonomists argued the solution lay in new methods and types of data: ‘What is needed most in phylogeny is a method of analysis independent of morphology, to be used in a complementary manner as a check on morphological findings’ (Boyden, 1934, p. 516). One proposal was to use immunological reactions. This method indicated protein similarities across species, and was argued to allow precise and ‘objective’ inferences about evolutionary relationships in the ‘zoological tree’ (Boyden, 1934, p. 517).

When evolutionary classification was morphological, it was necessarily restricted to groups with which the classifier was

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[1] For most of the paper, I will use ‘morphological’ to include fossil, developmental, and comparative structural (anatomical) data. In a few instances I will distinguish fossil data.