

Synthesis and modern techniques of invertebrate phylogeny



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Abstract

Initially designed to infer evolutionary relationships based on morphological and physiological characters, phylogenetic reconstruction methods have greatly benefited from recent developments in molecular biology and sequencing technologies with a number of powerful methods having been developed specifically to infer phylogenies from macromolecular data. This chapter, while presenting an overview of basic concepts and methods used in phylogenetic reconstruction, is primarily intended as a simplified step-by-step guide to the construction of phylogenetic trees from nucleotide sequences using fairly up-to-date maximum likelihood methods implemented in freely available computer programs. While the analysis of chloroplast sequences from various *Vanilla* species is used as an illustrative example, the techniques covered here are relevant to the comparative analysis of homologous sequences datasets sampled from any group of organisms.

Key words: Phylogeny, DNA sequence, Alignment, Phylogenetic tree, Maximum likelihood

Introduction

Robust phylogenetic hypotheses are crucial to understanding many biological processes, ranging from those contributing to population history to those creating macro evolutionary patterns. The development of methods for phylogenetic estimation and high throughput sequencing (HTS) have, in combination, improved our understanding of the relationships among extant organisms. These advances are frequently applied to the estimation of relationships among higher taxa, for example, distantly related animal phyla, families of flowering plants, and orders of birds. While these deeper branches have received significant attention, those at the leaves (e.g., genera and species) often remain largely unresolved, especially for taxa that are under-studied. For the resolution of relationships at lower taxonomic levels, crucial as a backbone for answering many evolutionary questions, a rich and broad species representation is vital. Traditionally, researchers have sequenced relatively freshly collected specimens. However, there is an increasing utilization of historical specimens for molecular phylogenetic reconstruction in the absence of fresh tissue. Historical specimens from museum or other institutional collections are valuable sources of information representing organisms that may be difficult or impossible to sample in contemporary

populations. Most studies that use historical specimens for phylogenetic reconstruction tend to focus on larger-bodied species that are recently extinct, well-studied groups and organisms of economic importance. Only recently have we begun to see an increase in such reports on invertebrate and other small-bodied taxa.

When employing HTS in such historical studies, nucleotide reads are typically mapped to a closely related reference genome, or one from the same species. Alternatively, complete sequences of target regions from related species and/or genera are used to design baits or probes. While these approaches are excellent for groups whose sequences are relatively well-understood, they are unfeasible for clades with low inter-genus sequence conservation, or for those lacking sequence data from closely related reference organisms, such as those we will present here. Here, we use historical and contemporary material from lesser-studied, small-bodied organisms for the purpose of reconstructing robustly supported phylogenetic relationships using molecular data. Our target organisms are cheilostomes, the most species-rich order of the phylum Bryozoa, with ca. 6,500 described extant species, representing about 80% of the living species diversity of the phylum. Cheilostomes are lightly to heavily calcified, sessile, colonial metazoans common in benthic marine habitats. Most species are encrusting, while fewer are erect, and most are small (colony size c. 1 cm², module size c. 500 μm × 200 μm), and live on hard substrates that may be overgrown by other fouling organisms (including other bryozoans, hydroids, foraminifera, and tube worms)

Reevaluating Exclusion from the Modern Synthesis

The assertion that "development was left out of the Modern Synthesis" is one of the most frequently made to support the special importance of evolutionary developmental biology (Evo-devo), which has developed over the past three decades into a distinct but diverse set of research programmes (Müller 2007). Over the course of the last five decades, during which several conceptual and empirical advancements as well as changes in institutional structure and disciplinary organisation have taken place, the issue has been raised often, although in slightly different ways and at various periods. Ernst Mayr's comment demonstrates how these distinctions may be merged in the following sentence: "The synthesis was fiercely opposed by the representatives of various biological fields, such as developmental biology. They just did not want to participate, not because they were excluded from the synthesis as some of them now say. Clear abnormalities emerge when developmental biology is seen as a single, cohesive entity. How can we make

sense of Gavin de Beer's obvious and frequent talks of embryology and evolution? What about the switch from experimental embryology to developmental biology in the middle of the 20th century? What place does comparative embryology have here? What objectives of the Modern Synthesis were pursued: the unification of biology, the clustering of areas around shared issues, or a mix of both? Why would researchers who study embryos have wished to participate? Because of this, even though there is still a real sense in which progress was left out of the Modern Synthesis, the tale is complex and the truism has to be carefully examined. Delineating the numerous developmental studies that may have been omitted, such as comparative vs experimental embryology, is one analytical method I have followed in several settings, with a concentration on Anglophone research environments. Then, by examining fellow passengers (such as morphology and palaeontology) who also seemed to have been left out, one might search for hints as to why one or more of these "embryologies" were excluded (or were not).

After World War II, experimental embryology evolved into developmental biology in part by setting itself apart from comparative embryology, which was more focused on evolutionary issues. This division was further strengthened by the later molecularization of developmental biology. A focus on issues, such as the origin of novelty, that were largely ignored by proponents of the Modern Synthesis because they require higher levels of organization and an understanding of how variation originates in ontogeny, is one reason why comparative embryology, morphology, and palaeontology were excluded). This explains the upsurge in interest in the relationships between evolution and development before the identification of conserved developmental regulating genes and demonstrates how Evo-devo combines novel approaches with age-old issues. Some aspects of this image have recently been contested by Davis et al (2000). They contend that the Modern Synthesis did not entirely ignore development but rather ineffectively incorporated findings from developmental genetics. They provide a strong case for how homeotic mutants were a node for integrating experimental embryology and genetics by looking at studies on homeosis in *Drosophila*. In a tragic turn of events, this finding was acknowledged but rejected as unimportant to evolution. Homeotic mutations were thus neutralised rather than excluded, having little to no impact on the form and organisation of the Modern Synthesis. Others have raised similar objections, saying that the Modern Synthesis' omission of embryology was "far more visible than real". The truism may not be true after all.

Model Organism Exclusion in the Modern Synthesis: The Case of Marine Invertebrates

Two concerns must be addressed in order to prove that model organisms were absent from the Modern Synthesis: What constitutes a component of the Modern Synthesis, in I What are the criteria for identifying model organisms within these components, and (ii) what are they? It is disputed where the Modern Synthesis' borders lie since it was obviously a dynamic process. I utilise an Anglophone circumscription that concentrates on a number of important monographs via numerous editions by various writers during the time when the Modern Synthesis was being developed. 2 In addition, I examine the magazine *Evolution's* early years. In response to the second query, I use a flexible standard: clear citation of specific species or taxa. This does not imply that each of these systems receives equal attention, and the less-mentioned aspect is the more important one. However, revealing the relative lack of marine invertebrates necessitates tediously rehearsing the taxa that were used. I don't take special care to discern between taxonomic ranks or pay attention to systematics advancements that could change specific assessments of groups or their names. Model organisms are often identified by their species names, although higher taxonomic designations (as well as common names) also occur frequently, some of which are now out of date. Since "marine invertebrate" is a miscellany, a category that comprises organisms from several phyla throughout the metazoan tree of life and formally defies current systematic theory, this taxonomic informality is methodologically suitable.

Conclusion

Was the Modern Synthesis missing development? There are two clear answers: "yes" and "no." Although some of the empirical ontogeny from experimental embryology and specific interpretations of heterophony were adopted, the relevance of development for evolutionary thinking was minimized as a result. However, at the same time, empirical substance in the form of embryological phenomena (evolvability, novelty, and variety) illustrative of marine invertebrate larvae and pertinent to specific concerns were disregarded. It is still unclear exactly what led to this predicament, such as why synthesis architects' educational backgrounds did not include coursework in marine invertebrate embryology. The relative absence of marine invertebrates and their larval forms was a fresh viewpoint on the Modern Synthesis that was made possible by differentiating the two distinct historiographical theses and contrasting them with epistemic values. Additionally, it offers information that is crucial to choosing a model organism as well as deciding on research challenges in the present. For our knowledge of history and contemporary scientific endeavors, the details that lie behind the straightforward assertion that "development was left out

of the Modern Synthesis" are crucial. Peeling back the layers of this complex story has been productive, and it may be time to abandon the catchphrase for evolutionary theory and pay closer attention to historical and contemporary patterns of scientific reasoning in terms of epistemic values like theoretical generality and explanatory completeness. A truly enlarged evolutionary synthesis for the twenty-first century would more than make up for the rhetorical strength we lose.

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