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A History of Narrative Phylogenetics

1.1 Why This Book?

In 2007 eminent population geneticist Michael Lynch took equally eminent evolutionary developmental biologist Sean Carroll to task over something he had written in his 2005 popular science book *Endless Forms Most Beautiful*. In the final chapter of his book, Carroll addressed the general public's abysmal understanding of evolutionary biology. To help remedy this problem, he suggested that the teaching of evolution could be made more inspiring by shifting the focus from the dry calculus of population genetics to the evolution of organismal form, because that "is the main drama of life's story... So, let's teach that story" (Carroll, 2005: 294). Lynch didn't like that. He accused Carroll of "two fundamental misunderstandings. Evolutionary biology is not a story-telling exercise, and the goal of population genetics is not to be inspiring, but to be explanatory" (Lynch, 2006: 8597). The story that I tell in this book shows why Lynch is wrong and why and how evolutionary biology is a storytelling discipline.

I have distilled many of my insights from the older phylogenetic literature, supplemented by the literature about the history and philosophy of biology. However, I am neither a historian nor a philosopher. I am a biologist with a long-standing interest in metazoan phylogeny and the evolution of animal body plans, and I have written this book primarily to better understand the conceptual contours and the history of the research agenda of this field. What I report in these pages is therefore my personal intellectual journey, but I believe the book will be of broader interest because it helps plug a gap in the literature. First, although our bookshelves sag with literature on fundamental evolutionary concepts like species and speciation, natural selection, and homology, no recent volume focuses on the concept of ancestors. The recognition and discovery of ancestors pose notorious epistemological challenges, but the power of phylogenetic hypotheses to explain the origin and evolution of organismal traits resides entirely in the traits attributed to hypothetical ancestors. This book shows how hypothetical ancestors came to function as central subjects in macroevolutionary narratives.

Second, much of the recent literature about the history of systematics and phylogenetics has been written with an emphasis on systematics, the science concerned with discovering and describing biodiversity and investigating the relationships between taxa (Willmann,

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2003; Williams and Forey, 2004; Williams and Ebach, 2008; Hamilton, 2014; Rieppel, 2016; Williams et al., 2016). The destination of many of these works is Willi Hennig (1913–1976) and his role in the development of phylogenetic systematics and cladistics. Less attention has been paid to phylogenetics as the science of evolutionary storytelling.

Evolutionary storytelling emerged as a distinct discipline in the second half of the nineteenth century. In 1866 Ernst Haeckel called it *Phylogenie* (Haeckel, 1866a). The origin of phylogenetics ushered in a century of speculative storytelling about evolving lineages before, exactly a century later, Hennig's *Phylogenetic Systematics* appeared in English and transformed systematics and phylogenetics (Hennig, 1966). The ensuing conceptual revolution quashed speculative storytelling, enshrined the epistemological primacy of systematic pattern over evolutionary process, and helped turn phylogenetics into an objective historical science. This, in a nutshell, is the story that you are likely to encounter when you consult the literature. Often little ink is spent on the interval between Haeckel and Hennig.

Ward Wheeler's *Systematics. A Course of Lectures*, for instance, jumps straight from Haeckel to the evolutionary taxonomists of the 1930s and 1940s and thence to Hennig via three paragraphs on the numerical taxonomists, aka pheneticists (Wheeler, 2012: 13–14). In their *Tree Thinking. An Introduction to Phylogenetic Biology*, David Baum and Stacey Smith get from Haeckel to Hennig in just three sentences (Baum and Smith, 2013: 25). Even when the period between Haeckel and Hennig is fleshed out in more detail, these pioneers define the axis of progress, with post-Haeckelian thinkers and ideas chosen chiefly to highlight the road to Hennig (Willmann, 2003; Williams and Ebach, 2008; Rieppel, 2016). Hennig is less of a hero in Joe Felsenstein's *Inferring Phylogenies*, which instead focuses on the development of numerical methods, and reaches the pheneticists of the 1950s and 1960s two sentences after telling readers that phylogenies "were discussed by Darwin and Haeckel" (Felsenstein, 2004: 123). This is all we hear about Haeckel in Felsenstein's book. The relative neglect of work that is not part of the progressive historical arc of systematics and phylogenetics is understandable when the aim is to show where modern concepts and methods have come from. But it does leave one wondering how evolutionary inference worked in the century between Haeckel and Hennig.

Traditional systematic and phylogenetic practices are often pejoratively labelled as "imprecise, authoritarian, and unable to articulate a specific goal other than ill-defined 'naturalness' [of taxa]" (Wheeler, 2012: 14). They are said to rely on "intuition" (Wiley et al., 1991: 1) and "subjective 'artistic' interpretations" (Eldredge and Cracraft, 1980: 189) and to commit the sin of bringing "assumptions derived from process explanations to bear on pattern reconstruction" (Rieppel, 2010a: 487). Traditional practices "lacked optimality criteria for choosing among alternative hypotheses of relationships" (Chakrabarty, 2010: 513), so that "classification and the reconstruction of phylogeny were considered an 'art'" (Reif, 2002: 357). Although these statements ring true enough when one judges traditional approaches from our modern perspective, they don't tell us what our predecessors actually did. Were they just engaged in wild evolutionary arm waving, or did their research strategy have a certain logic and conceptual consistency that allows it to be recognized as a distinctive way of thinking? In this book I argue that it did.

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When Haeckel founded phylogenetics in 1866, he set as its goal the reconstruction of the evolution of lineages. What was new was not the search for taxonomic relationships, which had long been the purview of systematics, but the possibility of tracing lineages of descent of traits and taxa. This required a new type of thinking, which I call *lineage thinking*, that remains at the heart of evolutionary thought today. It focuses the mind's eye on the epistemic hinterland of hypothetical ancestors and character transformations that flow along the branches of phylogenetic trees.[1] The realization that systematic pattern is the product of a phylogenetic process had an important epistemological consequence. The unobservable entities and events of evolutionary history are empirically inaccessible. The visible evidence of the morphologist and the systematist can only provide indirect and imperfect access to this invisible realm. To cross the phylogenetic frontier, biological practice had to float free from pure observation and embrace speculation, inference, and imagination to mentally recreate evolving lineages.

As a result, a new storytelling discipline was born that I propose to call *narrative phylogenetics*. Narrative phylogenetic hypotheses are driven by speculations about the evolutionary process, and they attempt to explain the origin and evolution of traits by linking them to precursors in hypothetical ancestors. The resulting lineage explanations are often little constrained by considerations of relevant systematic relationships. In this book I will outline the history of narrative phylogenetics, show that it continues to play an important role alongside its modern descendants, and reveal that an unrecognized failure to grasp lineage thinking is responsible for a family of conceptual flaws that afflict the professional, popular, and educational literature.

The story I tell in this book is not meant as an alternative to existing historical narratives. The histories of systematics and phylogenetics are intimately entwined, and much of what is relevant to the story told here is covered in the works mentioned earlier and in the expansive literature they represent. My intention is to provide a complementary story with a focus on the type of thinking that evolutionists use to visualize evolving lineages. From among the many sources that influenced my thinking, I want to mention four because together they provided much of the initial inspiration for writing this book.

First, Stephen Jay Gould's *Ontogeny and Phylogeny* (Gould, 1977b) was a challenging, but fascinating read for me as an undergraduate student about 25 years ago. It convinced me that spending a career thinking about evolution would be time well spent. It also taught me that research is greatly enriched when it is illuminated by the history of science, even though I have come to disagree fundamentally with some of Gould's conclusions.

Second, Peter Bowler's *Life's Splendid Drama* (Bowler, 1996) first showed me how evolutionists actually thought in the decades around the turn of the twentieth century in their efforts to understand the evolution of lineages. His study enticed me to engage with the historical literature myself, which set me on the path to writing this book. It remains one of the few modern books dealing with the early history of narrative phylogenetics.

[1] Lineage thinkers interpret cladograms as phylogenies or phylogenetic trees that depict the relationships of diverging lineages. See Chapter 11 for more discussion.

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Third, when Michael Ghiselin kindly sent me a copy of his *Metaphysics and the Origin of Species* (Ghiselin, 1997), he introduced me to the individuality thesis, which holds that taxa and lineages are individuals, not classes. It greatly clarified my thinking, although readers of this book might find that opacities still remain.

Fourth, with *The Changing Role of the Embryo in Evolutionary Thought*, Ron Amundson (2005) excited me with his illuminating marriage of the history and philosophy of biology. He revealed that the explanatory ambition that ties nineteenth-century evolutionary morphology to modern phylogenetics and evo-devo research is the explanation of the evolution of form. With *The Changing Role of Ancestors in Evolutionary Thought*, I aped him for the initial working title of my book. Alas, like any evolving lineage, the book's title and flavor have changed substantially, while still maintaining a thread of conceptual continuity that ties what you are reading today to the first notes that I scribbled, now some years ago.

1.2 Outline of the Book

In Chapter 2 I trace the origin of the idea of evolutionary ancestors back to pre-evolutionary archetype concepts in the thinking of Johann Wolfgang von Goethe, Étienne Geoffroy Saint-Hilaire, and Richard Owen. Ancestors and archetypes were both used to explain unity of type, homology, and the origins of organismal form, but due to their metaphysical dissimilarity, they achieved this in fundamentally different ways. The archetypal thinking of these authors each illuminates a distinctive aspect of this explanatory strategy. I also diagnose and defuse a modern myth that has arisen about the views of Geoffroy Saint-Hilaire, which claims that he thought that the ventral surface of arthropods corresponds to the dorsal surface of vertebrates. When Darwin reinterpreted the archetype as an ancestor, evolutionary storytelling became possible, with hypothetical ancestors becoming the central subjects in phylogenetic narratives. But the emergence of ancestors as actors in evolutionary stories also required reconceptualizing the systematic relationships between taxa to provide pathways along which evolutionary stories could flow.

In Chapter 3 I outline the transformation of systematics into phylogenetics by tracing the emergence of lineage thinking. One of the routes to a realist interpretation of the natural system of systematic relationships was to temporalize it. Lineage thinking emerged when the previously atemporal and symmetrical affinity relationships between collateral relatives were replaced by asymmetrical ancestor–descendant relationships that tracked the arrow of time. This transition was accompanied by a rapid decrease in the diversity of shapes of affinity diagrams published in the systematic literature, and it marked a shift from predominantly reticulating or web-like systems to tree-like figures soon after the publication of Darwin's *On the Origin of Species* in 1859. I argue that this graphic revolution largely records the influence of evolutionary expectations, as biologists redrew their diagrams to fit the theoretical dictates of Darwinian descent with modification. Whereas previous reticulating diagrams had recorded tangles of character conflict, the new evolutionary trees depicted the flow of diverging lineages composed of ancestors and descendants. The current swell of

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enthusiasm for evolutionary networks has driven several recent authors to the peculiar argument that even Darwin disliked the tree of life as an evolutionary metaphor, an argument I will refute. Reconceiving the systematic relationships between taxa as phylogenetic pathways along which body plans evolve had an epistemic corollary as well. The empirical trinity of observation, description, and comparison that had been at the heart of natural history and systematics could not provide access to the invisible realm of ancestors. Speculation became a necessary tool for the evolutionary storyteller, and few employed it so deftly as the founder of phylogenetics.

In Chapter 4 I take a detailed look at the evolutionary storytelling of Ernst Haeckel. He founded phylogenetics as the science dedicated to tracing the evolution of lineages. Although Haeckel's phylogenetic scenarios were nourished from a broad buffet of evidence, the biogenetic law was his favorite shortcut to create lineages of hypothetical ancestors, most famously the tiny cup-shaped Gastraea. A recent consensus has emerged that stigmatizes Haeckel's phylogenies as un-Darwinian constructs that are conceptually stained by teleological thinking and the linearity of the *scala naturae*, the idea that all of God's creations can be arranged in a single, static, ascending chain of being.[2] Instead, I argue that his trees are fully Darwinian and that the linearity present in his trees and thinking is the linearity of evolving lineages that track the arrow of time. Lineage thinking was novel when Haeckel started writing, and his was marred by imperfections. It was up to the following generations of evolutionists to resolve the conceptual tension between the linear and branching aspects of evolution, which is a major theme of this book and an ongoing struggle in today's literature.

In Chapter 5 I discuss the anatomy of evolutionary storytelling. Historical narratives are woven around central subjects that lend them continuity through time. The central subjects of phylogenetic scenarios are lineages of hypothetical ancestors. These define the pathways of homology along which evolutionary change is reconstructed, and they root the power of phylogenetic hypotheses to explain the evolution of form by allowing characters in descendants to be traced back to ancestral precursors. *De novo* origins of novel traits are chinks in the explanatory armory of phylogenetic hypotheses. Hypothetical ancestors have therefore often been deliberately equipped with characters that provide suitable precursors of the traits that await evolutionary explanation. I will argue that the precursor potential of hypothetical ancestors functioned as an early phylogenetic optimality criterion used in the construction and judging of scenarios.

In Chapter 6 I survey how biologists and paleontologists have used their imagination and evolutionary intuitions to animate phylogenetic narratives. Before outgroup comparison and ancestral state reconstruction methods became available, many authors intuited the direction of character evolution from clues provided by the threefold parallelism. The form changes that can be observed during ontogeny, and those inferred from the stratigraphic sequence of fossils, have inbuilt time axes that can be used as shortcuts for proposing lineages of changing forms. But interpreting the polarity of character change suggested by

[2] Unless noted otherwise, all translations from non-English sources into English are my own.

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the systematic leg of the threefold parallelism was less straightforward. Many researchers intuited or imposed the direction of evolutionary change by proposing a smoothly transitional linear series of observed or imagined forms. Some evolutionary intuitions date back to pre-evolutionary times, while others emerged from the search for evolutionary laws, such as Cope's rule of phyletic size increase. Unsurprisingly, evidence and imagination were typically unequal partners in the construction of scenarios, with the latter leading the former wherever it wanted. But when the first molecular phylogenies were published, researchers often muted their once vocal evolutionary intuitions to accept sometimes deeply puzzling results. The complete suppression of the evolutionary imagination is associated with the flawed, but widespread strategy of using observed differences between taxa as prima facie evidence against monophyly and homology. Not asking oneself if such differences could be due to descent with modification rather than convergent evolution signals the death of lineage thinking and diverts phylogenetic debates into fruitless avenues.

In Chapter 7 I take a close look at the early lineage thinking of paleontologists and their attempts to infer evolution from stratigraphic sequences of fossils. Linear thinking with fossils emerged as a core component of the traditional paleontological method in the second half of the nineteenth century. It was taken to extremes by orthogeneticists, and I use the late-nineteenth-century debate between Franz Hilgendorf and Alpheus Hyatt about the famous freshwater Miocene Steinheim snails as a case study for looking at competing forms of lineage thinking. It was in fact the straight-thinking orthogeneticist Othenio Abel who helped resolve the conundrum of how branching evidence can shed light on the evolution of linear lineages.

In Chapter 8 I examine one of the earliest debates about animal body plan evolution. Ernst Haeckel, E. Ray Lankester, Francis Maitland Balfour, Elie Metschnikoff, and Otto Bütschli were the main participants in an international debate about the origins of animals that was triggered by the publication of Haeckel's Gastraea theory in the 1870s. Each author proposed a different hypothetical animal ancestor, which with the exception of Bütschli's, were the products of recapitulationist reasoning. Each of these hypothetical creatures stood at the beginning of a unique scenario with a distinctive explanatory texture, and many of them can still be found in the pages of zoology textbooks today. This late-nineteenth-century clash of scenarios is representative of narrative phylogenetic debates generally. It shows how unique evolutionary stories are produced by authors wielding their personal evolutionary intuitions in the context of unequal attention to available evidence. Unsurprisingly, disagreements quickly became entrenched as dogma, but strikingly, several of these early scenarios, as well as their descendants, continue to inform debates today.

In Chapter 9 I chronicle the emergence of different phylogenetic traditions in invertebrate zoology that coalesced around attractive hypothetical ancestors. The first half of the chapter discusses scenarios for the origin of Bilateria that emerged in the late nineteenth and early twentieth centuries, including the enterocoel and archicoelomate theories, and the importance of the contested character of amphistomy for these scenarios. These scenarios and their associated hypothetical ancestors became phylogenetic totems in different parts of the world, with Gastraea at the core of the European zoological tradition, and Phagocytella rooting both the Russian and American traditions. In the mid-twentieth

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century, an alternative theory was proposed that derived bilaterians directly from ciliate ancestors. Remarkably, this attraction to ciliate ancestors emerged three times independently in quick succession, which illustrates the epistemic importance accorded to the precursor potential of hypothetical ancestors in narrative phylogenetic debates. The second half of the chapter discusses why many authors have felt so strongly attracted to annelid-like ancestors. These were proposed to have crawled at the cradles of many taxa, including molluscs, arthropods, vertebrates, and Bilateria. The arguments used to promote annelid-like ancestors form a conspicuous strand in the history of narrative phylogenetics that can still be traced today.

In Chapter 10 I show that although hypothetical ancestors largely lost their epistemic power as deliberately constructed phylogenetic tools after the spread of modern phylogenetics, narrative phylogenetic reasoning persists. A conspicuous and widespread example of employing narrative shortcuts in evolutionary storytelling today is the attempt to use the phylogenetic position of taxa to predict the presence of ancestral character states. In close analogy to the historical use of the label "lower" to designate taxa that are presumed primitive, modern authors use a range of evocative adjectives to promote the presumed presence of ancestral character states in their favored taxa. "Basal" is the most frequently used label, and many authors think that its link to the phylogenetic position of taxa gives it predictive power over whether these are likely to have retained ancestral states. I explain that phylogenetic and evolutionary theory provide no convincing rationale for this argument and argue instead that basal taxa can be especially misleading about the nature of their character states.

In Chapter 11 I address common flaws in lineage thinking that result from confusing the branching relationships between collateral relatives in the realm of systematics with the linear relationships between ancestors and descendants in the realm of evolutionary descent. The influential voices of the late Stephen Jay Gould and Robert O'Hara, who dubbed the now ubiquitous phrase "tree thinking," have warned readers for decades against the sins of linear evolutionary storytelling and the use of linear evolutionary imagery, with great success. Their works are widely cited and promoted in the professional, popular, and educational literature, but I argue that their impact has been deeply pernicious. Their writings fundamentally misconstrue the relationship between the branching realm of systematics and the linear realm of evolving lineages. Furthermore, I argue that a similar failure to understand lineage thinking is at the heart of the fruitless debate about paraphyletic ancestral taxa. It burned brightly for a while during the early history of cladistics, but it continues to throw out sparks occasionally today. I close with a discussion of the problem that, in the absence of a vocabulary designed to talk about lineages, we are forced to discuss them in the taxic language of systematics. This inevitably causes problems.

Finally, in Chapter 12 I offer a concluding meditation on the inescapability of evolutionary storytelling, if our goal is to go beyond the trees and try to understand what may have happened along life's myriad evolving lineages. As soon as you look at a tree and ask "What does this mean?," you become an evolutionary storyteller. Some dismiss such stories as pure fiction and would prefer not to go beyond the tree. But for those of us who wish to peer over the phylogenetic frontier, these stories are how we generate our understanding of evolution, or at least how we try to.