

The origin of evolutionary storytelling

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Abstract

Phylogenetics emerged in the second half of the nineteenth century as a discipline dedicated to constructing descriptive and explanatory narratives that traced the evolutionary origins of taxa and traits. Because ancestors and evolutionary transformations are empirically inaccessible, phylogeneticists had no choice but to use their more or less informed imagination to gain access to this epistemic hinterland. The explanatory power of phylogenetic hypotheses resides in their ability to trace back traits to their evolutionary origins. Hypothetical ancestors therefore became important epistemic tools as they were deliberately equipped with characters that could function as suitable evolutionary precursors for traits of interest. I argue that the precursor potential of hypothetical ancestors therefore became the first, more or less objective, phylogenetic optimality criterion.

Something missing?

When you read the historical sketches in systematics textbooks, you sometimes get the impression that something is missing. After starting with Aristotle and arriving in the nineteenth century, Wheeler (2012) dutifully praises Ernst Haeckel for coining the word ‘phylogeny’ and drawing such beautiful trees, before vaulting straight to the evolutionary taxonomists of the 1930s and 40s. Baum and Smith (2013) similarly laud Haeckel for his artful phylogenies, but without mentioning that he founded the discipline and coined much of its terminology. They get from Haeckel to Hennig in just three sentences. And although Haeckel figures in the index to Felsenstein’s book *Inferring phylogenies* (2004), this is scarcely deserved as his presence is limited to an uninformative remark where we learn that phylogenies “were discussed by Darwin and Haeckel” (Felsenstein, 2004, p.123). What the first generations of phylogeneticists did around the turn of the nineteenth century is apparently of little interest or relevance to modern readers, and perhaps this is so. You don’t need to know anything about the history of phylogenetics to become a competent phylogenomicist. But there is another explanation for this historical blind spot.

Reconstructing systematic relationships has always been the core business of systematists, both before and after the spread of evolutionism. But the first phylogeneticists developed a different agenda. They were evolutionary biologists, chiefly zoologists studying comparative morphology and embryology, who were interested in the evolution of body plans (Nyhart, 1995; Bowler, 1996;

Amundson, 2005). Like systematists they wanted to discover the relationships between taxa, but not as an end in itself, or to prop up classifications. Systematic relationships could guide phylogeneticists in their attempts to trace evolution, although systematic ignorance was hardly a barrier to phylogenetic speculation. Instead of pursuing the systematists' goal of constructing classifications to crystalize relationships located on the synchronic surface of systematics, phylogeneticists wanted to delve into the diachronic depths of geological time to tell evolutionary stories. Their primary goal was not to sharpen systematic tools, but to discover the phylogenetic events that had produced the natural system. Textbooks can therefore jump straight from Haeckel to Hennig.

Yet, the founding of phylogenetics as a discipline of evolutionary storytelling is a distinctive and noteworthy event in the history of biology, and one that has received comparatively little attention in the historical literature. In this essay I will have a brief look at the kind of storytelling that arose with the origin of phylogenetics, and the epistemic challenges that it posed. What follows is excerpted from a longer narrative that I develop in my forthcoming book on *Ancestors and the science of evolutionary storytelling*, to be published by Cambridge University Press in the Systematics Association Special Volume Series.

The consequences of descent theory

The scientific discipline of evolutionary storytelling originated in the second half of the nineteenth century. Comparative biologists and palaeontologists had long before amassed copious data on the morphology and development of organisms, but they didn't integrate these into historical narratives. Their research produced essentially static syntheses. The first grand narratives of biology only emerged after the advent of evolutionism, especially in the wake of the metaphysical revolution of Darwinism. Before that time systematic relationships didn't have a reading direction that could support a narrative arc. The unity of type that embryologists and morphologists had detected underneath nature's surface diversity was essentially static, and dynamic type concepts, such as Goethe's plant archetype, were based in mental metamorphoses of form, rather than concrete, historical transformations. Even palaeontologists weren't motivated to connect their fossil dots into unbroken genealogies of ancestors and descendants on the canvas of deep time. The theory of common descent changed all that forever.

The science of storytelling was born when the arrow of time penetrated biology. It gave systematic relationships a reading direction from past to present. It brought ethereal archetypes down to earth as concrete ancestors who were linked to modified descendants through the material bonds of ancestry. It turned biological and palaeontological evidence into witnesses of a historical

process, and made evolutionary biology a narrative discipline dedicated to the telling of origin stories. Ernst Haeckel called (t)his new science *Phylogenie* (Haeckel, 1866a). Its foundation was Darwin's key insight that the observable patterns of biodiversity are the products of an unseen process of descent. Edmund Beecher Wilson nicely captured the exciting prospects of the new evolutionary biology:

“The central question in every morphological investigation became twofold: it was no longer simply *what is?* it was also *how came it to be?* And this second question, be it observed, is not properly a speculative matter at all, but an historical one; it related not to an ideal or hypothetical mode of origin, but to a real process that has actually taken place in the past and is to be determined like any other historical event. “Speculative zoology” thus, by slow degrees, became the guide and leader of research, and every morphological inquiry became, in the last analysis, a genealogical one” (Wilson, 1891, p. 54; italics in original).

An important consequence of the realization that biological patterns were produced by evolutionary processes was that it required phylogeneticists to shift their focus to the gaps of the natural system. It became clear that systematic relationships did not map neatly onto the phylogenetic relationships that could explain them. Before the late-nineteenth century systematic diagrams generally depicted relationships between taxa as lines drawn directly between them. However, such lines cannot trace genealogical relationships unless taxa were interpreted as ancestors and descendants. To properly depict phylogenetic relationships systematic diagrams had to be redrawn. Consequently, the range of shapes of systematic diagrams published during the decades following the publication of the *Origin of species* decreased sharply, coinciding with the rise of tree-like branching diagrams (Pietsch, 2012; Morrison, 2014). Importantly, this did not reflect a sudden improvement of systematic tools to better reveal trees, but rather it recorded the imposition of the Darwinian expectation that relationships should generally be branching if descent with modification was indeed the process that produced biological diversity. Hence, in a relatively short period systematic diagrams that directly connected taxa were replaced by branching tree-like diagrams that connected taxa indirectly via hypothetical common ancestors, so that the lines connecting taxa could trace the flow of evolutionary events through time. But gaining access to these events posed an epistemological challenge.

The imagination as an epistemic tool

Haeckel first outlined the goals and procedures of phylogenetics in his *Generelle Morphologie*. He distinguished two branches in the science of morphology: *Anatomie* was the science of the *vollendeten* (completed) form of organisms, while *Morphogenie* was the science of the *werdenden*

(becoming, developing) form of organisms. Within *Morphogenie* he defined two subdisciplines, *Ontogenie* (or *Embryologie*), the science of the embryonic development of organismal form, and *Phylogenie*, the science of the evolutionary history of organismal form. For Haeckel they were intimately related as descriptive and explanatory sciences that aimed, respectively, to uncover the “developmental history of concrete morphological individuals”, and the “evolutionary history of abstract genealogical individuals” (Haeckel, 1866a, p. 60). Their conceptual unity was underlined by Haeckel’s use of the term *Entwicklungsgeschichte* for both. The goal of phylogeny was to “investigate the connected chain of forms of all those organic individuals that have branched off from one and the same shared stemform” (Haeckel, 1866a, p. 30). Phylogeneticists, therefore, were to seek the explanation of evolutionary origins in the lineages of ancestors that underpinned every observable tip in the tree of life.

Like embryology, phylogenetics located its explanatory power in the tracing of origins. As Haeckel put it in the *Generelle Morphologie*, “Jedes Sein wird nur durch sein Werden erkannt” [Every being can only be understood by its becoming”] (Haeckel, 1866a, p. 23). This explanatory ambition further demarcated the emerging field of phylogenetics from systematics, which remained a primarily descriptive discipline strongly rooted in the empirical trinity – observation, description, and comparison – that had been its foundation ever since natural history emerged as a distinct scholarly subject in the sixteenth century (Ogilvie, 2006). However, this three-pronged tool can’t penetrate the phylogenetic barrier. Ancestors and evolutionary processes exist in an epistemic hinterland that is empirically inaccessible. Only by floating free from pure observation and following their more or less informed imagination could phylogeneticists hope to enter this realm with their mind’s eye. Haeckel approvingly quoted his friend and scientific idol Johannes Müller’s defense of the imagination as an epistemic tool: to the nature researcher “fantasy is an indispensable good” (Haeckel, 1866a, p. 74). In the following decades explicit endorsements of the imagination as a phylogenetic tool became commonplace. Haeckel’s student Anton Dohrn put it like this in a letter to E. B. Wilson in 1900: “Phylogeny is a subtle thing, it wants not only the analytical powers of the “Forscher” [researcher], but also the constructive imagination of the “Künstler” [artist], – and both must balance each other, which they rarely do, – otherwise the thing does not succeed” (Dohrn in Groeben, 1985, p. 16).

Hypothetical ancestors as central subjects in scenarios

The phylogeneticist’s job was to imaginatively interpret different sources of evidence to construct evolutionary narratives (scenarios) to account for the origin of focal traits and taxa. The fossil record was of course considered to be the ideal source of evidence since it really was located in the

past. But its promise was compromised by the realization that it was a “completely gappy and torn up patchwork” (“vollständig lückenhaftes und zerrissenes Flickwerk”) (Haeckel, 1866b, p. 307). And even when a fossil was unearthed that seemed to have ancestral traits, one typically couldn’t be sure that it was a lineal ancestor rather than a closely related collateral relative, as Haeckel realized all too well (Haeckel, 1891, p. 466). The primary documents that phylogeneticists could use to guide their mind’s eye into the evolutionary past were therefore the development and morphology of extant organisms. Haeckel’s most distinctive and infamous strategy was to try to replay the tape of evolution from the reel of ontogeny. His biogenetic law declared that ontogeny recapitulates phylogeny, and its application allowed him to turn developmental stages into hypothetical ancestors. The tiny cup-shaped animal ancestor that Haeckel called *Gastraea* was a pure product of recapitulationist reasoning. He identified it from the evolutionary afterimage that he thought was retained as the invagination gastrula found in the development of several animal phyla.

Gastraea anchored one of the most influential, controversial, and enduring phylogenetic hypotheses ever conceived (Haeckel, 1874, 1877). Despite its simple structure *Gastraea*’s morphology was key to its explanatory power. Its invaginated archenteron and its separate ecto- and endodermal cell layers represented the phylogenetic origin of the gut and germ layers of all animals. Haeckel used these homologies to tie together the entire animal kingdom into a single monophyletic clade that he christened Metazoa. This achieved the unification of the four major animal types – Vertebrata, Radiata, Articulata and Mollusca – that had stood in isolation ever since von Baer and Cuvier had declared their incompatibility on developmental and functional morphological grounds. *Gastraea* was the fifth of two dozen ancestors that Haeckel identified as being part of the ancestral lineage of humans (Haeckel, 1895, p. 631). This lineage of hypothetical ancestors represented the central subject in Haeckel’s historical scenario for human origins. Central subjects are the foci around which stories, including historical narratives (Hull, 1975), are organized, and that provide them with unity and continuity. Importantly, lineages of hypothetical ancestors do all the explanatory work in phylogenetic scenarios.

The foundation of phylogenetic explanatory power

Much of the pre-cladistic literature on animal body plan evolution was dedicated to the construction of hypothetical ancestors to explain the origin of novel traits. The explanatory power of hypothetical ancestors resides entirely in their ability to root the evolutionary origins of traits. To accomplish this they need to possess precursors of homologous characters identified in descendant taxa. Traits that cannot be traced back to ancestors necessarily fall outside the explanatory umbrella of phylogenetics. Evolutionary morphologists understood this well. E. Ray Lankester called this

insight “one of the fundamental principles of phylogeny, viz. that new organs do not arise *de novo* as new parts, but by the modification of pre-existing parts” (Lankester, 1881, p. 646). This core principle – as much an ontological commitment as an epistemological necessity – underpins the explanatory power of all phylogenetic morphology (Huxley, 1858, p. 382; Dohrn, 1875, p. 21; Lankester, 1875, p. 480; 1876, p. 54; Hubrecht, 1887, p. 644; MacBride, 1895, p. 342; Meyrick, 1895, p. 10; Patten, 1912, p. 253; Crampton, 1916, p. 2; Bock, 1959, p. 210; Raw, 1960, p. 500; Rensch, 1960, p. 275; Ghiselin, 1969, p. 114; Willmer, 1974, p. 327; Ghiselin, 1991, p. 292; 1994, p. 11; Nyhart, 2003, p. 165; Cracraft, 2005, p. 354; Gudo, 2005, p. 194; Kluge, 2007, p. 217, 224; Arthur, 2014, p. 232; Brunet *et al.*, 2015, p. 836; Havstad *et al.*, 2015; Minelli, 2016, p. 42).

Because phylogenetic explanations require the identification of ancestral precursors, the principle of ‘no *de novo* origins’ points the way to what I think is the first, more or less objective, phylogenetic optimality criterion: the precursor potential of hypothetical ancestors. It specifies what ancestral traits a hypothetical ancestor possesses from which descendant traits of interest could have evolved, and how plausible the necessary evolutionary transformations were thought to be. Because a consensus on higher-level metazoan relationships that could constrain speculations has only emerged during the last few decades, evolutionary morphologists often deliberately chose or designed hypothetical ancestors so as to maximize their precursor potential for explaining the phylogenetic origins of traits. It is in this sense that hypothetical ancestors were used as an epistemic tool in evolutionary narratives.

An example of how this was done is provided by the independent, yet near simultaneous, phylogenetic speculations of turbellarian expert Otto Steinböck, cnidarian expert Jovan Hadži, and protist expert Earl Hanson in the mid-twentieth century. They sharply rejected the widespread consensus that animals had evolved from colonial flagellates, and instead proposed that bilaterian animals had descended from ciliate ancestors (Hadži, 1953, 1958, 1963; Hanson, 1958, 1963, 1977; Steinböck, 1958, 1963). Although their phylogenetic views are complex and do not agree in all details, the crux of their joint preference for ciliate ancestors was their superior precursor potential. The simple morphologies of the *Blastaea*- and *Gastraeta* ancestors conjured by Haeckel’s recapitulationist interpretation of development provided precious few cues to explain the origin of distinctive animal traits such as protonephria, mesoderm, muscles, and more. Hadži, Steinböck and Hanson thought that they could locate homologues of these and other traits in ciliates. Hypothetical ciliate ancestors therefore had the precursor potential needed to explain the origin of simple turbellarian body plans. Alas, despite loud applause in some quarters of the zoological community (de Beer, 1954, 1958), this heterodox hypothesis never found widespread approval.

Because phylogenetic explanatory power resides in the precursor potential of hypothetical ancestors it can be used as a guide for understanding phylogenetic debates. For example, Holland *et al.* (2015) tabulate no fewer than 124 phylogenetic scenarios for the origin of vertebrates, with hypothetical ancestors drawn from many branches of the animal tree. However, they don't discuss why so many scenarios were proposed. Several factors are involved, but a key one is that different workers chose different explanatory foregrounds to which they tried to fit specific hypothetical ancestors. Three early scenarios illustrate these points. Anton Dohrn proposed annelid ancestors because he placed chordate segmentation in the explanatory foreground of his scenario. Annelid segments and segmental appendages provided all the precursors he needed to fashion vertebrate traits, from ribs to penis and post-anal tail (Dohrn, 1875). However, he relegated the notochord to the explanatory background as he could not find any annelid precursor. His scenario also required an inversion of the dorso-ventral axis to maintain homology of the annelid and chordate nerve cords, and the evolution of a new mouth as the old one degenerated. Ambrosius Hubrecht considered such events a “fata morgana” (Hubrecht, 1887, p. 641). He sought the origin of chordates in nemertean (Hubrecht, 1883, 1887) precisely because they seemed to possess a precursor structure for the trait that had earned them their name: he derived the notochord from the coelom surrounding the nemertean proboscis. However, since nemerteans lack segmentation, Hubrecht had to resort to unconvincing arguments to explain the origins of the segmented aspects of the vertebrate body plan. Importantly, it was Hubrecht himself who didn't put too much trust in these aspects of his scenario. Any arguments that went beyond the few characters in his explanatory foreground were “merely the sequel in a train of thoughts” (Hubrecht, 1883). Adam Sedgwick (1884) subsequently placed chordate segmentation back in the explanatory foreground, but considered it “exceedingly improbable that an animal should lose its mouth and **develop** a new one” (Sedgwick, 1884, p. 75). He therefore rejected Dohrn's annelid ancestors, and instead traced chordate somites back to the gut pouches of an anthozoan-like ancestor. These examples show that phylogenetic scenarios were devised as evolutionary origin narratives, each of which is characterized by a specific explanatory focus rooted in a unique combination of hypothetical ancestors and evolutionary intuitions.

Narrative phylogenetics today

The cladistic revolution of the mid-twentieth century delegitimized the use of deliberately fashioned hypothetical ancestors as epistemic tools in phylogenetic narratives. Modern approaches award logical priority to the reconstruction of patterns of systematic relationships, which tightly constrain speculations about ancestors and evolutionary processes. Nevertheless, systematic relationships do

not properly become phylogenetic relationships without explicit hypotheses about ancestors and evolutionary character transformations. Indeed, in research areas where a consensus about systematic relationships is emerging, evolutionary storytelling often makes a comeback.

A recent issue of the *Journal of Experimental Zoology B (Molecular and Developmental Evolution)* (issue 6 in volume 6 in 2015) offers a perfect illustration. It collects together responses to a recent paper (Pyron and Burbrink, 2014) that claimed to have discovered that viviparity evolved early in squamate reptiles, and reversed to oviparity multiple times. Although the study was based on a comprehensive phylogenetic analysis and the use of sophisticated models for ancestral state reconstruction, its results were questioned because they conflicted with the respondents' intuitions about what is and isn't likely to happen during evolution. They used data and ideas from genetics, development, anatomy, physiology and ecology to argue that it is exceedingly unlikely that viviparous ancestors could have re-evolved oviparity. The merit of these arguments isn't important here. What is important is that all authors used their more or less informed evolutionary intuitions to diagnose that something must be wrong with the study of Pyron and Burbrink (2014). In bringing their biological intuitions to bear in this way, biologists today stay true to the original spirit of phylogenetics as a storytelling discipline, whether they realize it or not.

Coda

One of the most important events in my intellectual ontogeny was seeing a copy of Sandro and Fred Schram's 1994 paper titled 'Owen revisited: a reappraisal of morphology in evolutionary biology' on the desk of my undergraduate supervisor André van Loon at the University of Utrecht in 1995. It finalized my resolve to pursue a career in evolutionary biology, which I started by doing a PhD under Fred Schram's excellent guidance at the University of Amsterdam. In the years since I've absorbed Sandro's ideas through the never abating avalanche of papers and books that he continues to produce. Sandro, I hope your fount of inspiration will never run dry. May it long continue to fertilize our thinking about all things evolving.

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