The series, the network, and the tree: changing metaphors of order in nature

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Abstract The history of biological systematics documents a continuing tension between classifications in terms of nested hierarchies congruent with branching diagrams (the 'Tree of Life') versus reticulated relations. The recognition of conflicting character distribution led to the dissolution of the *scala naturae* into reticulated systems, which were then transformed into phylogenetic trees by the addition of a vertical axis. The cladistic revolution in systematics resulted in a representation of phylogeny as a strictly bifurcating pattern (cladogram). Due to the ubiquity of character conflict—at the genetic or morphological level, or at any level in between—some characters will necessarily have to be discarded (*qua* noise) in favor of others in support of a strictly bifurcating phylogenetic tree. Pattern analysts will seek maximal congruence in the distribution of characters (ultimately of any kind) relative to a branching tree-topology; process explainers will call such tree-topologies into question by reference to incompatible evolutionary processes. Pattern analysts will argue that process explanations must not be brought to bear on pattern reconstruction; process explainers will insist that the reconstructed pattern requires a process explanation to become scientifically relevant, i.e., relevant to evolutionary theory. The core question driving the current debate about the adequacy of the 'Tree of Life' metaphor seems to be whether the systematic dichotomization of the living world is an adequate representation of the complex evolutionary history of global biodiversity. In 'Questioning the Tree of Life', it seems beneficial to draw at least four conceptual distinctions: *pattern reconstruction versus process explanation* as different epistemological approaches to the study of phylogeny; *open versus closed systems* as expressions of different kinds of population (species) structures; *phylogenetic trees versus cladograms* as representations of evolutionary processes versus

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patterns of relationships; and *genes versus species* as expressions of different levels of causal integration and evolutionary transformation.

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Introduction

In July of 1837, Darwin opened his 'Transmutation Notebook B', the second in a series of five notebooks that document the development of his thoughts on species transformation. In it, Darwin drew a sketch of a branching diagram, now called a sketch of the 'tree of life', above which he jotted down the line "I think".[1] A few pages before he had mused, in relation to a more rudimentary diagram: "The tree of life should perhaps be called the coral of life, base of branches dead, so that passages cannot be seen" (deBeer 1960). There are several accounts of how the 'tree metaphor' came to represent the evolutionary process of species lineages splitting and splitting again, which will not be rehearsed here (e.g., Barsanti 1992; Bredekamp 2005; Ospovat 1981; Richards 1992, 2002, 2008; Stevens 1994). Many would agree that "the appropriate image for the post-Darwinian system is a much-branched tree, perhaps with some grafting between the branches" (Stevens 1994, p. 5), but this image emerged only after the Great Chain of Being had been broken up and replaced with reticulating systems. In the wake of the 'cladistic revolution' (Hull 1988), phylogeny reconstruction came to be dominated by Hennig's 'principle of dichotomy' (Hull 1979). Whereas Darwin's 1837 'tree of life' still allowed for polytomies, cladists would eliminate those as due to lack of evidence, i.e., as due to ignorance (but see Wagner and Erwin 1995, for a discussion of 'hard polytomies').

The question remains, however, whether phylogeny is universally a process of species lineages splitting and splitting again in a bifurcating pattern, or whether more complex processes can be at work that require representation other than by a strictly dichotomously structured tree? Can the systematic dichotomization of nature deliver a realistic representation of the complex evolutionary history of contemporary biodiversity, or is it embedded in an instrumentalist perspective of phylogenetic systematics (Rieppel 2007a, 2008a)? How did the 'logic' of a hierarchic system, which translates into a strictly dichotomous, tree-like structure, come to represent the historically contingent evolutionary process? What aspect of evolutionary theory predicts a strictly dichotomously branching tree of life, or is it the ease of logically subdividing the world "into dogs and cats, tables and chairs" (Kuhn 1974, p. 17) that gave rise to the picture of species lineages splitting and splitting again in a strictly dichotomous fashion with no reticulation in between them? And what, indeed, is the 'universal Tree of Life' that has recently come under attack? Some would say that it represents the genealogical history of global taxonomic diversity, whereas for Hennig (1966), the phylogenetic system is not a processual hierarchy of species lineages

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[1] Notebook B, p. 36, Cambridge University Library, #DAR121.

splitting and splitting again, perhaps with some meddling here and there, but rather a hierarchical representation of relative degrees of phylogenetic relationships based on recency of common ancestry.

The purpose of the present contribution is to briefly trace the history of how a branching tree diagram replaced the Great Chain of Being as well as reticulated systems to become the standard way to represent phylogeny. With the cladistic revolution, the branching tree changed its meaning from a representation of genealogical processes to a concept rooted in logic and graph theory. Its history can inform recent debates about the validity of the tree metaphor in phylogeny reconstruction by invoking four conceptual distinctions: pattern reconstruction versus process explanation; species as open versus closed systems; the phylogenetic tree versus cladograms; and genes versus species as expressions of different levels of causal integration and evolutionary transformation.

Plenitude and continuity: the Great Chain of Being

There were two principles—rooted in the philosophy of Aristotle and Leibniz (Lovejoy 1936)—that guided natural history in the eighteenth century: plenitude and continuity. The principle of plenitude says that all forms possible are exemplified in nature, while the principle of continuity says that all forms in nature insensibly grade into one another. Consequently, the *scala naturae*, the Great Chain of Being, is the adequate representation of order in nature, one that reflects the Plan of Creation (Lovejoy 1936). The most important eighteenth century advocate of the Great Chain of Being was the self-proclaimed *philosophe et naturaliste* Charles Bonnet from Geneva. In his *Traîté d'Insectologie* (1745), Bonnet commented on the ubiquity of transitional forms so beautifully exemplified by Trembley's (1744) 'polyp', which seemed to combine plant with animal characteristics: "These considerations have led me to try, perhaps too daringly, to sketch a ladder of natural beings (*êtres naturels*)" (Bonnet 1745, p. xxviii). "The polyp links the plant with the animal. The flying squirrel unites the bird with the mammal. The monkey touches the mammal and the human" (Bonnet 1764, p. 29). The kinds recognized in human classifications are nominal kinds; they cannot be natural kinds. The admired empiricist philosopher John Locke[2] had already emphasized that if there is continuity in nature, there cannot be differences in kind, there can only be differences in degree: "Intelligent minds will recognize in the ladder of our world as many rungs as there are individual beings" (Bonnet 1764, p. 29). And if there did appear to be a discontinuity, as between inorganic matter and organic form (Buffon 1749), it would merely reflect ignorance: "Let us not pronounce that there exists a jump, a break here: such a gap is nowhere but in our current knowledge" (Bonnet 1768, p. 191).

Organisms sort into an unbroken ladder of life on the basis of their attributes. The green color and its capacity to propagate by budding were interpreted as plant characteristics of Trembley's 'polyp' (*Hydra viridis*), the *irritabilité* of its fibers and

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[2] Bonnet was introduced to Locke's philosophy by his teacher, the Genevan mathematician and philosopher Gabriel Cramer (Savioz 1948).

its predatory habits revealed its animal nature. But sometimes, characters did not sort that easily, and congruently, into a graded series of forms. "Could the ladder of nature ramify in its ascent" to higher levels of complexity (Bonnet 1764, p. 59)? "Could insects and mollusks constitute two collateral branches of the main stem? … The frogs and the lizards, so close to insects, could they have branched off from the latter? … We cannot at present find satisfactory answers to these questions" (Bonnet 1764, p. 59).

Dichotomies and networks

Bonnet (1769 I: p. 178) reminded his readers "of the fact that as the chicken embryo starts to become visible, its form appears to closely approach that of a very small worm." He further stressed (Bonnet 1769, I: p. 317) that the behavior of small children corresponds less to the well-reasoned behavior of adults than to the playful behavior of higher animals. These were early expressions of the idea that the *scala naturae* is recapitulated during ontogeny. Adding the idea that the *scala naturae* was also reflected in the fossil record resulted in the 'three-fold parallelism', already sketched in Bonnet's (1769) *Palingénésie*, but most forcefully argued by Louis Agassiz (1859; see also Gould 1977; Richards 2008). The *scala naturae* organized natural beings into a linear series of ever increasing complexity and perfection. The same successive unfolding of complexity was believed to characterize embryonic development, and fossils were again thought to document an increasing complexity and perfection of organic beings as they successively appeared through geological time.

In his '*Vestiges of the Natural History of Creation*', a popularization of contemporary geological and biological knowledge, Robert Chambers (1844) invoked a universal 'Law of Development' that drives both embryonic development and the ascent of species through geological time to ever-higher levels of organization along parallel tracks, the rails of the ladder of life. In his equally popular critique of Chamber's views, which he likened to those of the early evolutionist Jean-Baptiste Lamarck, Hugh Miller (1849) pointed to the complex structure of the oldest fossil fish then-known, which he had collected in the Old Red Sandstone of Scotland. The complexity of *Asterolepis* from Stromness seemed to clearly refute, in Miller's view, transformationist ideas associated with the three-fold parallelism. *Asterolepis* was encased in heavy bony armor that is absent in sharks, but it lacked proper teeth, which in turn are abundantly present in sharks. Characters that collectively distinguish groups of organisms did not seem to transform along the ladder of life in equal steps. Ascent to higher levels of organization and perfection had thus to be measured on the basis of selected characters, those that were deemed more important than others. Following the discoveries of the French anatomist and embryologist Etienne Serres (1824, p. 378; see also Millhauser 1959, p. 73), co-author of the 'Meckel-Serres Law of Recapitulation' (Gould 1977; see also Richards 1992), the combatants Chambers and Miller focused their debate on the increasing size of the brain in the ascending series of vertebrates. But where Chambers saw continuity between beast and man, Miller saw humans set off from animals by a distinct hiatus in relative brain size. The important point here is that a linear series, continuous or not, could be reconstructed to

reflect increasing complexity of organs or organ systems, but not for entire organisms (Gould 1977).

The critique of recapitulation theory led to a representation of natural classification in terms of a nested hierarchy (e.g., Ospovat 1981; Richards 1992), depicted by a branching diagram. The embryologist Karl Ernst von Baer (1828) summed up his investigations of development in vertebrates with his argument that the embryos seem to pass through the hierarchical system that had previously been laid out by George Cuvier. Cuvier (1817 I: p. 11) based his classification of the animal kingdom on what he called *une méthode naturelle*: "an arrangement which groups organisms of the same kind more closely to each other than either of them to any organism of another kind." Such classification of organisms was built on Cuvier's principle of character subordination (Cuvier 1817: I, p. 10; Daudin 1926a), according to which characters of greater physiological importance characterize more inclusive groups than characters of lesser physiological importance. Cuvier's *méthode* was put to work in André Marie Constant Duméril's (1806) *Zoologie Analytique*, which presented the whole animal kingdom classified in a series of subordinated dichotomies, each one being based on alternate states of the same character. For example: batrachians, chelonians and saurians were grouped together on the presence of paired limbs, absent in snakes. Saurians and chelonians were grouped together on the presence of claws on hands and feet, absent in batrachians. Chelonians finally differ from saurians in the absence of teeth. As can readily be seen, this method of classification is based on the 'principle of generality', the more general characters marking out more inclusive groups, less general characters marking out subordinated, less inclusive groups (Lovejoy 1959, p. 444).

Comparing the embryonic development amongst vertebrates, von Baer (1828) recognized that the more general characters tend to develop before the less general characters, and that the embryos representing the subordinated groups recognized in the classifications of Cuvier, Duméril and their collaborators successively diverge from one another as they mature: "The development of the embryo relates to the type of organization such as if it [the embryo] passed through the animal kingdom according to the *méthode analytique* developed by French systematists" (von Baer 1828, p. 225).

What Cuvier had called *une méthode naturelle*, von Baer called *une méthode analytique*, as he realized that Cuvier's and Duméril's method seeks a logical dichotomization of the world. Neither Cuvier, of course, nor Duméril, and also not von Baer, would read any temporal dimension, let alone a theory of species transformation, into their hierarchical classifications. Amongst systematists (taxonomists), similar strictly dichotomous tree diagrams were used not to represent genealogical relationships, or 'affinities' of a more general sort, but rather to represent dichotomous analytical keys, each dichotomy again based on alternate states of a key character (Stevens 1994, p. 170). Such dichotomous keys, however, were recognized as artificial constructs, and not held to represent the complex affinities that obtain from a closer study of organismic diversity. Linnaeus claimed that as many plant genera can be recognized as there exist discernible differences in the geometrical arrangement of reproductive organs in plants (Stevens 1994, p. 12). Once the genera have been recognized, two different 'methods' obtain for grouping them into families, orders

and classes. One is to classify the multiplicity of genera by a regulated method of subdivision that enforces and ensures their easy and unequivocal identification. The result is the *artificial* system "which alone Linnaeus flattered himself to have executed in botany" (Daudin 1926b, p. 38). The other method would be to try and represent as closely as possible all the variable degrees of affinities that can be discerned by a close study of plant anatomy. But if that program were faithfully executed, one would end up with a "network of affinities" (Daudin 1926b, p. 47), which Linnaeus expressed in the metaphor of a map-like structure with mutual affinities going in all directions (Müller-Wille 2007).

What was required to sort out the multidimensional multiplicity of characters was a theory about taxonomic characters: what are the characters that are relevant to systematics and classification, and how many characters should be considered relevant in the reconstruction of plant and animal affinities and corresponding classifications? Stevens (1994) traces in detail the development of systematics, particularly in botany, through the nineteenth century, showing how growing insight into plant anatomy rendered the "detection of the natural order" a matter of "growing confusion" (p. 92). Adrien de Jussieu is quoted as having recognized, in his *Cours Elémentaire d'Histoire Naturelle* (1843) that "relationships between groups were very definitively reticulating; it was impossible to form a linear series because emphasizing a relationship in one direction necessarily entailed simultaneously breaking relationships in another" (Stevens 1994, p. 98). This is but one of many examples where attention to a multiplicity of characters broke the linear ladder of life in favor of a network (Stevens 1994, p. 164). To break up the *scala naturae* in favor of reticulating relationships was one thing, to transform a network into a phylogenetic tree another, however. To the extent that organismic 'affinities' were depicted in a tree-like fashion, such dendrograms were simply reinterpreted as phylogenetic trees in the post-Darwinian era: the current morphology, and the systems built on it—such as Cuvier's—"could be taken over, lock, stock and barrel, to the evolutionary camp" (Russell 1916, p. 247). Networks, on the other hand, were turned into tree-like structures by the imposition of a "vertical axis" (Stevens 1994, p. 264), yet to turn a network of relationships into a tree-like structure that represents branching sequences of ancestors and descendants is not an easy task to achieve. Nodes in the network had to be turned into ancestors and descendants, characters had to be sorted into primitive, derived, and possibly convergent. The notions of 'highness' and 'lowness', a shadow cast by the old concept of the *scala naturae*, needed to be shed. Darwin annotated his copy of Robert Chambers' '*Vestiges*' (1844) with a reminder to himself: "Never use word higher and lower" when speaking of organisms and their classification (Bowler 1990, p. 107).

Cleaning up the tree: transgressions and the '*chevauchement des spécialisations*' (L. Dollo)

Tschulok's (1922) influential '*Deszendenzlehre*' sought to deliver the proof for the Darwinian theory of descent, establishing its truth (in the sense of a 'theoretically inferred reality') irrespective of current understanding of the causal factors that

drive species transformation (Steiner 1946, p. 71). The way to do so was to show that biological systematics is an empirical science that is independent from research into the causal factors of species change.

Tschulok (1922, p. 102) credited Linnaeus with the discovery of the "deep difference between an artificial identification key and a natural system"[3] of plants: "The essence of an artificial system lies in the fact that its objects will necessarily be classified as is dictated by the character which has previously been chosen to form the basis of the classification" (Tschulok 1922, p. 103). Having reached that insight, Linnaeus – according to Tschulok (1922, p. 106)—was the first to be equipped with the necessary tool for the recognition that differences between species come in varying degrees. The results are well known: the origin of new plant species through hybridization (within the genus), and the recognition of reticulated relationships, as is documented by his statement that "all taxa of plants have relationships on all sides as do neighboring countries on a map of the world" (Mayr 1982, p. 175; also in Tschulok 1922, p. 151).

The issue, again, is a conflicting character distribution, a nearly ubiquitous phenomenon which Tschulok (1922, p. 145) called the *transgression* of characters. Indeed, Tschulok (1922, p. 145) considered the frequent transgression of characters to indicate the empirical basis of the natural system, thereby clearly distinguishing it from all rational systems, where pre-selected characters intensionally define sharply delimited classes. The transgression of characters renders it impossible to rationally, i.e., *a priori*, assign characters to a fixed taxonomic rank. Which characters, singularly or collectively, mark out which groups at any level of inclusiveness in a classification is a matter of empirical discovery, not one of convention or logic. However, research into the distribution of characters will typically reveal not neatly sorted sets within sets of organisms, but character conflict that—taken at face value—indicates overlapping sets. The consequence, again, is reticulation (Tschulok 1922, p. 149). Reticulation results in a loss of predictability of the hierarchically structured natural system (in a loss of the projectability of taxon names): "In the characterization of a taxonomic group, the reticulated relations force us frequently to say that this and that is the case 'most of the time'—something that is completely unthinkable for a rational system" (Tschulok 1922, p. 151; for a modern discussion of that issue see Griffiths 1999).

In contrast to whole organisms or taxonomic groups, morphological characters can often be ordered into a transformation series, especially if enough transitional forms are known, possibly documented in the fossil record. It is because of the transgression of characters that such character transformation series do not also represent lineages of ancestral and descendant organisms, or taxa. But how, then, is it possible to reconstruct the phylogenetic tree that reflects the branching history of ancestral and descendant lineages? Tschulok's answer (1922, p. 183) was to distinguish the primitive from the derived character or character state. Taxonomic research yields taxonomic groups (taxa), morphological research yields character

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[3] All translations of Tschulok (1910, 1922) are mine.

transformation series, and the "*conditio sine qua non* for the reconstruction of phylogenetic trees is the distinction of primitive and derived conditions of form" (Tschulok 1922, p. 197). The tool to do so was, again, the principle of generality discussed above (Tschulok 1922, p. 187): the more general character (state) that marks out a more inclusive group will be considered the primitive condition, the less generally distributed character (state) that marks out a subordinated, less inclusive group will be considered the derived character state. It might be surprising that such a logical system of subordination, rather than the fossil record, should be used to distinguish primitive from derived character states. The reason is that for Tschulok (1922, p. 242), as also for Hennig (1950), phylogeny cannot be directly inferred from the temporal succession of fossils. Fossils at best document the existence of an organism, or of a taxonomic group, with its mixture of characters at a certain time in a certain place. But that says nothing about the relationships of that organism, or taxonomic group.

Once the distinction of primitive and derived conditions of form is drawn, the mere conflicting distribution (transgression) of characters turns into what Louis Dollo (1895) had called the '*chevauchement des spécialisations*', the '*Spezialisationskreuzungen*' of Tschulok (1922, p. 205) and Hennig (1950, p. 142)—the 'crossing of specializations'. The extensive literature on Dollo's concept of '*chevauchement des spécialisations*' was compiled and summarized by Nelson (2004). Hennig (1965, p. 107) later switched to Takhtajan's (1959, p. 13) term 'heterobathmy of characters' to refer to such 'crossing of specializations'. Abel (1929) provided several compelling examples, one of which involved the mysticete whale families Balaenidae and Balaenopteridae. Amongst other conflicting characters, Abel (1929) found the balaenids to combine a primitive fore-limb skeleton with specializations in the cervical vertebrae, whereas the balaenopterids retain the primitive condition of the cervical vertebral column, but show specializations in the skeleton of the fore-limb. The consequence is that neither family can be derived, phylogenetically, from the other, but both must be derived from a third, unknown taxon, a *hypothetical* common ancestor who retained the primitive condition in both organ systems. At Hennig's (1950) hands, phylogenetic trees thus became strictly bifurcating diagrams (cladograms) that do not represent the historical links between ancestors and their descendants, but only relative degrees of phylogenetic relationships based on the relative recency of common ancestry (Platnick 1977). For Hennig (1965, p. 107), "the mosaic of heterobathmic characters in its distribution over a number of simultaneously living species contains reliable information about the sequence in which the species have evolved from common ancestors at different times—Heterobathmy is therefore a precondition for the establishment of the phylogenetic relationships of species and hence a phylogenetic system."

Popper's demarcation criterion and the 'testing' of phylogenetic trees

Hennig's (1965) optimism might have been justified, if shared derived characters sorted into a neat, clean nested pattern, as they would be expected to do if: (1) the shared derived characters were correctly identified (i.e., if homology could infallibly

be distinguished from homoplasy; see Rieppel et al. 2006); and (2) if the origin of derived characters were associated with strictly dichotomous speciation events (Hennig's deviation rule). Unfortunately, the first requirement is epistemically inaccessible, the second is biologically problematical: there is nothing in speciation theory that mandates dichotomous speciation, necessarily correlated with a particular character transformation that occurs in one, but not the other, daughter species. Brundin (1966), the most important early advocate of Hennig's work (Williams and Ebach 2007), again recognized the generally incongruent distribution of morphological characters, which would seem to support reticulated relationships of species. But "since it is possible to prove that the phylogenetic relationships always form a hierarchy … we have to ask how they can be deduced from reticular morphological relationships of species" (Brundin 1966, p. 22)? The answer for him was provided by the rules that underlie the "argumentation plan of phylogenetic systematics" (Brundin 1966, p. 26) that aims at identifying 'true' synapomorphies.

Hennig (1957) sought an isomorphy of character transformation and species transformation, which translates into an isomorphy in the distribution of shared derived characters (synapomorphies) and the nested hierarchy of monophyletic taxa (Rieppel 2006a, b). The synapomorphies are those 'uniquely shared derived characters' that mark out monophyletic groups, i.e., taxa which include the ancestor and all, and only, its descendants. Convergence, the independent acquisition of the seemingly same derived character (state) in two unrelated lineages, and reversal of a character (state) to its ancestral condition of form, is misleading noise, and needs to be distinguished from synapomorphy, the '*true*' mark of homology. But how can this be achieved in the face of character incongruence?

During the early days of the cladistic revolution Popper's star shone brightly amongst scientists and, indeed, the broader public. The biologist Sir Peter Medawar, for example, declared Popper "the greatest philosopher of science ever" (Magee 1973, p. 9). A collection of essays on the interrelationships of fishes was published by Greenwood et al. (1973) with a "hidden agenda", which "was cladistics, to get as many groups of fishes as possible worked over in the new cladistics framework" (Patterson cited in Nelson 2007, p. 32). A review of the volume (Bonde 1974) highlighted the popularity that Popper enjoyed amongst cladists, who quickly adopted him as their 'patron saint' (Hull 1988). Popper (1959 [1992]) liberated scientific thought from the notion of truth (although he later came back with his concept of verisimilitude to explain progress in science: Popper 1963), as he demarcated science from metaphysics through his principle of falsifiability. Cladists in turn found in Popper's philosophy a way to liberate systematics from "nonscientific (non-testable) elements," such as "tradition, stability, authoritarianism" that they claimed characterized the evolutionary approach to phylogeny reconstruction (Gaffney 1979, p. 104; see also Rieppel 2008b).

Cladists glossed over Popper's requirement that scientific theories must either be formulated in terms of universal laws of nature, or must be subsumable under such laws (Stamos 2007; Rieppel 2008b), as they claimed testability of cladograms and, implicitly, of synapomorphy. The test of cladograms, and synapomorphies, is therefore not properly hypothetico-deductively structured (Rieppel 2008c), falsifiability in systematics hence here referred to as (*quasi-*)Popperian. According to

cladistic theory, there is no need (nor any possibility) to reliably and *a priori* distinguish 'true' synapomorphy from convergence, reversals, or simply observer error, as long as synapomorphy, and through them cladograms, can be tested, and potentially refuted (Kluge 2003). Synapomorphy is thought to be discovered not through a detailed, in-depth analysis of characters prior to phylogenetic analysis, but through the congruence of characters as revealed by phylogenetic analysis (Rieppel 2008a). Miles (1973, 1975) clearly recognized the methodological prerequisites necessary to implement (*quasi-*)Popperian flasificationism (Rieppel 2005) in the test for character congruence (Patterson 1982): a commitment to parsimony, and an acceptance of "Hennig's (1966) principle of the 'dichotomous differentiation of the phylogenetic tree" (Miles 1975, p. 133). The strictly dichotomous cladogram thus became an *a priori* concept for systematic research (Panchen 1992).

The situation is a simple one: both, cladograms and character statements are considered to be hypotheses, testing each other reciprocally (Rieppel 2008a). "By testing, I mean checking with the principle of parsimony" (Miles 1975, p. 133). Assume three taxa, *A*, *B*, *C*, for which obtain—*a priori*, i.e., following Hennig's (1950, 1966) 'principle of dichotomy'—three, and only three, possible hypotheses of relationships: ((*A*, *B*) *C*), ((*A*, *C*) *B*), and ((*B*, *C*) *A*). Assume character *1*, identified as a possible synapomorphy, is shared by *A* and *B*, while character *2*, again a possible synapomorphy, is shared by *B* and *C*. Given their conflicting distribution, none of the three hypotheses of relationships can be chosen as *the* most parsimonious one (although the hypothesis ((*A*, *C*) *B*) implying four character origination events is less parsimonious that the alternative ones, which each imply only three character origination events). What can be known, however, given the historical uniqueness of the evolutionary process, is that characters *1* and *2* cannot both be synapomorphies (homologies). Add character *3*, shared by taxon *A* and *B*, to the analysis. Now, hypothesis ((*A*, *B*) *C*) is supported by two putative synapomorphies (homologies), whereas hypothesis ((*B*, *C*) *A*) is supported by one only. On grounds of parsimony (selecting the hypothesis that implies the smallest number of steps of character transformation, i.e., that which implies the smallest amount of convergence), the hypothesis ((*A*, *B*) *C*) will be accepted, while character *2* will be said to have failed the test of congruence. Add characters *4* and *5*, shared by the taxa *B* and *C* to the analysis: now, hypothesis ((*B*, *C*) *A*) is supported by three characters (*2*, *4*, *5*), hypothesis ((*A*, *B*) *C*) by two only (*1*, *3*). Parsimony rules that hypothesis ((*B*, *C*) *A*) is to be accepted on the basis of the new evidence, which refutes the homology of characters *1* and *3* in *A* and *B*, and hence must now be re-interpreted as instances of homoplasy (convergence).

In other words, the most parsimonious tree is accepted as the preferred one, while the minority of characters that show a conflicting distribution relative to the most parsimonious tee are declared unfit for the discovery of phylogenetic relationships—at least for as long as the weight of new evidence does not shift preference to an alternative tree topology. It is clear that this method will *impose* a strictly nested hierarchy on any data set for any objects, taxa or pasta. What, then is the difference of a taxonomy of taxa, or of pasta? Since it is not the method, it must be the underlying ontology: taxa undergo natural evolution, pasta is—if anything—subject to cultural evolution.

Networks, trees, and nature

Hennig (1950, 1965, 1966) wanted the cladogram to represent the history of species lineages splitting and splitting again, but not in the sense of a phylogenetic tree that depicts 'real' (but epistemically inaccessible) ancestor–descendant relationships (Platnick 1977). Instead, species and species groups were to be related according to recency of common ancestry: the succession of branching points in a cladogram, progressing from its stem towards its terminal branches, represents the relative recency of speciation events that unfolded through the phylogenetic past. To this, Hennig (1950, 1966) added the *formal* requirement that the ancestral species ceases to exist when it splits into two daughter species. Some evolutionary biologists have rejected this requirement as un-biological (e.g., Mayr 1974), but in defending Hennig (1950, 1957) from earlier similar criticism, Günther (1962, p. 279) chastised such objections as "methodically completely irrelevant", emphasizing the "methodological necessity to analyze phylogenetic relationships at least initially in terms of a dichotomous system." Günther (1956, p. 45, emphasis added) praised the "significance and fertility" of Hennig's (1950) "description or *definition* of speciation as a strictly dichotomous process of lineage splitting", to which 6 years later he added a quote from the philosopher Kurt Bloch: "the dichotomy is the most adequate and logically best founded form of classification … it stands at the beginning of analysis, and hence at the beginning of systematics" (Günther 1962, p. 279). Immediately following that statement, Bloch (1956, p. 71) continued: "The law of the dichotomy is, however, not merely a subjective [Kantian category of thought], but is instead grounded in the ontological reality of the polarity of all being." However, speciation through hybridization is a reticulating, not a dichotomous lineage splitting process.

The question thus arises whether the systematic dichotomization of the living world delivers a method of discovery that is adequate to decipher the intricate evolutionary history of biodiversity. In other words: does the strict dichotomization of nature reveal an instrumentalist background of phylogenetic systematics (Rieppel 2007a, 2008a), or is a realist interpretation of such branching diagrams possible? It turns out that leading German evolutionary biologists and systematists of Hennig's time were embedded in a tradition that considered the extra-mental world to be logically structured. In his '*Critique of Pure Reason*', Kant had accepted Hume's conclusion that the universal validity of the causal laws of nature could not be grounded in sensory experience, but he rejected the skepticism that Hume derived from this conclusion. Instead, Kant argued that the regularity of spatial, temporal and causal relations that is manifest in the perceived world of phenomena grounds the fundamental laws of nature, because these laws are part of how we mentally reconstruct the natural world: empirical knowledge of the world is elaborated and expanded by the construction of scientific theories that advance universal laws of nature (Gardner 1999, p. 222). According to Rensch (1968), it was the philosopher Theodor Ziehen (1862–1950) who first explained the correspondence of human rational thought with the extra-mental reality as an evolutionary adaptation. As Rensch (1968), a former disciple and great admirer of Ziehen (Rensch 1979), put it: "Ziehen (1934, §22) was the first to ascertain that thought processes have become adapted to the logical lawfulness of the extra-mental world in the course of

phylogeny" (Rensch 1968, p. 232). In his famous book on trans-specific evolution, which first introduced the term 'cladogenesis', Rensch (1947, p. 374) also discussed the evolution of human powers of cognition, which culminated in the "adaptation of forms of reasoning to the 'material' world determined as it is by universal causal laws", an adaptation that also resulted in Kant's 'necessary categories of thought'. Konrad Lorenz (1941a) likewise turned Kant's *a priori* categories of thought into *a posteriori* evolutionary adaptations, and proceeded to represent the evolutionary relationships of ducks through systematic dichotomization (Lorenz 1941b) in a way that foreshadowed Hennig's argumentation scheme (Craw 1992). The human capacity of cognizing and conceptualizing the 'material world of objects' according to the laws of logic thus was understood to be an evolutionary adaptation of the human mind to the extra-mental world.

Hennig (1950, 1966), who extensively cited the work of Ziehen and Rensch, never explicitly stated that humans are evolutionarily adapted to 'seeing the world aright'; he did, however, consider historical inference to be a strictly logical and scientific endeavor (Dupuis 1984; Rieppel 2007b), praising the virtues of the "logical significance of the hierarchic system" Hennig (1966, p. 21). Brundin (1966, p. 14) again emphasized the isomorphy of Woodger's (1952) definition of hierarchy in terms of symbolic logic with the "structural picture" of a fully dichotomized cladogram, which he ontologically rooted in Mayr's (1963) allopatric speciation model. This was his proof "that the phylogenetic relationships always form a hierarchy", a proof however that ended in a *petitio principii*: "There are many examples in the literature of phylogenetic diagrams demonstrating multiple splitting of an ancestral species. Such a process is theoretically possible, but … must have been a very rare phenomenon."

Logic retained its appeal throughout the later 'cladistic revolution' (Hull 1988). In his address delivered at the 2nd Annual Willi Hennig Society Meeting in 1981, Colin Patterson, a leading cladist (Nelson 2007), recounted how he discovered cladistic methodology: "Then, one day early in 1967, Gary Nelson, who was spending six months in the BM [British Museum (Natural History)], told me that something had just appeared in the library that I might find interesting … it was Brundin's monograph on chironomids just arrived. I was bowled over by it—it was like discovering logic for the first time."[4] Questioning the significance of fossils for phylogeny reconstruction, Patterson (1981, p. 195) again referred to Brundin (1966), still recalling "the excitement with which I realized that there is a logical basis to evolutionary relationships." Patterson (1982) carried the logic of cladistics forward through his formalization of the 'test of congruence', explained in the preceding section using a 'three-taxon statement'. The test is built on set-theoretical considerations, seeking to maximize the relations of inclusion/exclusion and to minimize overlap for sets of characters marking out groups of organisms. Patterson (1982, p. 74) recognized the close similarity of his 'test of congruence' with

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[4] Patterson's talk, delivered at the 2nd Annual Willi Hennig Society Meeting on October 3, 1981, in Ann Arbor, MI, was transcribed and made available by D.M. Williams, Dept. of Botany, The Natural History Museum, London.

E.O. Wilson's (1965) 'consistency test for phylogenies', the latter again based on set-theoretical considerations. E.O Wilson's (1965) test rejects phylogenies that imply overlapping sets of taxa[5]; Patterson's (1982) test rejects incongruent characters as homologies, i.e., as marks of common ancestry. Either way, a strictly dichotomous hierarchy is imposed on the data and taxa.

The logic of cladistic phylogeny reconstruction is bound to clash with the contingency thesis of evolution (Beatty 1995). But even if cladistic analysis based on parsimony and (*quasi-*)Popperian falsificationism is abandoned, and likelihood or Bayesian methods of analysis are adopted instead, the evidence (i.e., the characters) is still evaluated against the scaffold of a strictly dichotomous system and nothing else. Recent critique of the branching diagram as the universal representation of phylogeny may profit from the historical perspective outlined above, as it highlights the need to draw a number of conceptual distinctions.

Conceptual dichotomies

Pattern reconstruction versus process explanation: In the wake of the cladistic revolution, it became generally accepted that pattern reconstruction has logical and epistemological precedence over process explanations (e.g., Lauder 1990; Brooks and McLennan 1991). Evolutionary processes are located in the past, and for that reason epistemically not accessible. Characters used in phylogeny reconstruction, on the other hand, are epistemically accessible. To bring assumptions derived from process explanations to bear on pattern reconstruction is considered to invoke the authoritarianism of traditional evolutionary systematists (e.g., Simpson 1961; Mayr 1969) that cladists attempted to overcome with their appeal to Popper's philosophy of science (see above). Whether carried out under parsimony, likelihood models, of Bayes' theorem, pattern reconstruction in terms of a strictly bifurcated branching diagram is still considered by the majority of systematists to provide the necessary scaffold against which evolutionary process explanations can be legitimately inferred (Brady 1985; Rieppel 2004; Lienau and DeSalle 2009). Critics of the 'Tree of Life' metaphor have begun to challenge such logical and epistemological primacy of pattern reconstruction over process explanation, however. Paraphrasing Wittgenstein's *Tractatus*, Doolittle and Bapteste (2007, p. 2048) claimed: "The TOL was thus the ladder that helped the community to climb the wall of acceptance and understanding of evolutionary processes. But now that we have climbed it, we do not need this ladder anymore … Holding onto this ladder of pattern is an unnecessary hindrance in the understanding of process." According to these authors, it is the processes of gene transmission which need to inform pattern reconstruction, instead of pattern reconstruction elucidating processes of gene transmission. In empirical practice, however, lateral gene transfer is mostly recognized as a violation of hierarchical structure.

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[5] The test was based on the assumption that characters used to infer species relationships are unique (no convergence occurs) and un-reversed (character transformation is irreversible)—two desiderata that are both unwarranted.

Open versus closed systems: Some species can be characterized as open, others as closed, causally integrated processual systems (Rieppel 1986, 2009). Given the fact that many species are genetically open systems, the dichotomous Tree of Life cannot be a universal metaphor. The rejection of the 'Universal Tree of Life' started with research into the complexity of genomic evolution in Bacteria and Archaea (Doolittle 1999; Gogarten 2000; Bapteste et al. 2005), documenting rampant lateral gene transfer, sometimes across vast phylogenetic distances (Gogarten et al. 2002; Gogarten and Townsend 2005). Lateral gene transfer also occurs, but less frequently so, in eukaryotes (Dunning Hotopp et al. 2007; protists: Archibald et al. 2003; Striepen et al. 2004; Loftus et al. 2005; diatoms: Bowler et al. 2008; rotifers: Gladyshev et al. 2008; angiosperms: Bergthorsson et al. 2004; Davis and Wurdack 2004; choanoflagellates: Nedelcu et al. 2008; cnidarians: Denker et al., 2008). It is by now well documented that prokaryote patterns of inheritance have a predominantly reticulated structure (e.g., Doolittle 1999, 2009; Gogarten et al. 2002; Doolittle and Bapteste 2007; Bapteste and Boucher 2008). Boucher and Bapteste (2009) characterize prokaryote and eukaryote lineages subject to lateral gene transfer as 'open lineages' ('fuzzy lineages' in Gogarten et al. 2002; see also the 'fragmented species' of bacteria in Retchless and Lawrence 2007), as opposed to 'closed lineages' with predominantly vertical patterns of inheritance. Among derived metazoans, Darwin's finches provide an example of open species lineages that merge, split, and merge again (Grant and Grant 2002; Grant et al. 2004). The 'Tree of Life', emphasizing a vertical transmission of genes, cannot be a *universal* metaphor, appropriate to capture all complexities of evolutionary processes at all levels of organization, but there are species that form 'closed' lineages that split and split again, forming phylogenetic systems that are appropriately considered tree-like in structure. Conversely, the possibility exists that lateral gene transfer mimics a tree-like structure, which does not correspond to the underlying process (Gogarten et al. 2002). To invoke universality in historical biology is highly problematical (Armstrong 1997; Wilson 1999), because all biological structures have ultimately been formed by historically contingent evolutionary processes (Beatty 1995). Universality imposes necessity on the natural course of events, but no such necessity seems to dominate either evolutionary processes, or taxonomic structures representing the latter. The '*Universal* Tree of Life' is therefore an illegitimate metaphor, as also is Hennig's (1950, 1966) description of speciation as a universally dichotomous process of lineage cleavage.

Trees versus cladograms: Cladistics is not so much about processes of species lineages splitting and splitting again, but rather about the analysis of patterns of character distribution. Hennig (1966, p. 210) emphasized that "if phylogenetic systematics starts out from a dichotomous differentiation of the phylogenetic tree, this is primarily no more than a methodological principle." It is, therefore, important to distinguish the metaphor of a phylogenetic tree ("a much-branched tree, perhaps with some grafting between the branches": Stevens 1994, p. 5), from a strictly dichotomous cladogram that has its root in graph theory (Platnick 1977). Cladistics does not discover ancestor–descendant relationships, but sister-group relationships instead (see Williams, et al. 1996, *contra* Williams 1992). Where species do have multiple or reticulated origins, cladistics is simply not an adequate

method of phylogenetic analysis unless appropriately modified. Lateral gene transfer is not the only cause of reticulation; the origin of species through hybridization is another. The issue of species origins through hybridization was prominently discussed during the early phases of the 'cladistic revolution' already (e.g., Funk 1985), and continues to be discussed today (e.g., Wheeler and Meier 2000). Wagner (1983), for example, defended a program called "Reticulistics" in order to deal with hybridization issues in plants. Humphries (1983, p. 91) rejected this program as one that confounds cladograms with phylogenetic trees, insisting that cladograms have to be taken "for what they are—dichotomizing diagrams showing the most parsimonious expression of character distribution without making any assumptions about the taxa under consideration." This is an ontologically minimalist approach to phylogeny reconstruction (the so-called 'pattern cladism' of Beatty 1982), which bans all processual inferences from influencing pattern analysis. "In other words, evolution may well be true, but basing one's systematics on that belief will give bad systematics" (Patterson 2002, p. 31; see also Brower 2000). From a cladist point of view, the prominent analytical issue at stake is to "eliminate the potentially confounding effects [of] homoplasy", i.e., of conflicting character distribution (Lienau and DeSalle 2009). The method to do so, discussed above, is a (*quasi*-)Popperian falsificationism applied to phylogeny reconstruction. The process assumption that enters through the backdoor, spoiling the proclaimed ontologoical austerity, is the (unwarranted) hope (in fact a *petitio principii*) that "the majority of genetic material is passed from one cell to another vertically" in prokaryotic organisms also (Lienau and DeSalle 2009, p. 2; see also Laurin and Bryant 2009, p. 336). The odd and seemingly misplaced gene, which might indicate lateral gene transfer, is dismissed as mere noise in the overall attempt to dichotomize nature.

Genes versus species: deQueiroz (1999) touted the 'lineage concept' as the most general species concept, applicable to all levels of organization. The question remains whether it is not so general as to be nearly empirically empty. However, at least species of sexually reproducing organisms can be characterized as causally integrated and spatio-temporally located complex wholes (Ghiselin 1974, 1997; Hull 1976, 1989, 1999). For the sake of the argument, let's look at a species of sexually reproducing organisms as they obtain for mammals, say *Homo sapiens*. In such cases, the causal integration and consequent cohesiveness of the processual system that instantiates the species is intuitively easily appreciated. It is also intuitively easily appreciated that such a species would originate through a process of species lineage splitting and splitting again, i.e., through speciation. Assume further that the genome of *Homo sapiens* had a complex origin as a consequence of past hybridization and lateral gene transfer from viruses, intracellular bacteria, endosymbionts, and so on in human ancestors. The question then arises whether the origin of *Homo sapiens* would be described in terms of a branching or a reticulated pattern. At the level of the component genes, the relationships would be reticulated. But at the level of the causally integrated, spatio-temporally located complex whole, the origin of the species *Homo sapiens* would presumably still be described as a branching event. To do otherwise would mean to reduce the 'nature' of the species *Homo sapiens* to the collection of its genes. As with the 'levels of selection' debate

(e.g., Okasha 2006), it seems necessary to peg the discussion and pictorial representation of species origins to levels of complexity in order to avoid confusion. In short, it seems that gene trees, or gene networks, need to be distinguished from species trees (Brower et al. 1996; Maddison 1997).

To reduce species to nothing but spatio—temporally located complex wholes is insufficient: species are spatio-temporally located objects that also instantiate a natural kind, i.e., they are characterized by intrinsic and relational, dispositional properties (Boyd 1999; Rieppel 2007c, 2009; Brigandt 2009). To formulate a species concept for prokaryotes has proven to be notoriously difficult (Konstantinidis et al. 2006; Ereshefsky 2010). Morphological, ecological, and genetic components have been invoked in the characterization of bacterial species (Gogarten 2000; Konstantinidis et al. 2006). If bacterial 'species' are reduced to the sum of their genetic properties, and derivative properties such as proteins, which seems to be the current approach to phylogenetic analysis at the prokaryote level of organization, then their origins and relationships will likely form a network, unless a tree-like structure is enforced (e.g., Bapteste et al. 2005).

Conclusions

Tschulok (1910, p. 236) saw systematics as a tool that allows the investigating mind to master the biological 'multidimensional multiplicity', but recognized that "every attempt to group plants on the basis of as many characters as possible, and at the same time to do justice to every similarity and dissimilarity, had to result in reticulated relationships." It is incongruence, i.e., conflicting character distribution that led to the dissolution of the *scala naturae* into reticulated systems, which were then transformed into phylogenetic trees by the addition of a vertical axis (Stevens 1994). An important component of that vertical axis was the distinction of primitive from derived characters (Tschulok 1922; Hennig 1950, 1966), but Dollo's (1895) '*chevauchement des spécialisations*' persisted. More work was required to structure a classification in terms of a nested hierarchy that corresponds to a branching tree of life, which was the distinction of shared derived characters from convergence or reversal. In cladistic shorthand, this became the distinction between homology and homoplasy, the first a mark of common evolutionary origin, the latter a mark of noise in history. Suppose bacteria, or protists, were to form well-integrated species-lineages that split and split again in a tree-line fashion: is a gene imported from a distant branch into such a species a mark of evolutionary relationship, or merely noise? This is the question that seems to be driving the 'Questioning the Tree of Life' initiative.[6]

In 'Questioning the Tree of Life', it seems beneficial to draw at least four conceptual distinctions: pattern reconstruction versus process explanation as different approaches to the study of phylogeny, open versus closed processual systems as expressions of different kinds of population (species) structures; phylogenetic trees

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[6] For the 'Questioning the Tree of Life' initiative, see http://centres.exeter.ac.uk/eugenis/research/QuestioningtheTreeofLife.htm.

versus cladograms as representations of evolutionary processes versus patterns of relationships; and genes versus species as expressions of different levels of causal integration and evolutionary transformation (keeping in mind that there are intermediate levels of organization between genes and organisms—and beyond—that can be levels of integration and transformation: e.g., Okasha 2006). But even if these distinctions are drawn, the age-old question that troubled Charles Bonnet 250 years ago still stays with us: the conflicting character, or gene, distribution. Given the ubiquity of character conflict—at the genetic or morphological level or any level in between—some characters will necessarily have to be discarded (*qua* noise) in favor of others in support of a strictly bifurcating phylogenetic tree at all levels of organization.

"A tree-thinker may choose to ignore conflicting signal as if it were noise, even if legitimate evolutionary events underlie it [such as lateral gene transfer]. However, if this 'noise' is in fact *bona fide* phylogenetic signal, then may-be tree-thinking is inappropriate" (Bapteste et al. 2005, p. 2). This assessment nicely reflects the conflict between pattern analysis and process explanation. Pattern analysts will seek maximal congruence in the distribution of characters (ultimately of any kind) relative to a tree-topology (Lienau and DeSalle 2009); process explainers will call such tree-topologies into question by reference to incompatible evolutionary processes (Doolittle and Bapteste 2007). Pattern analysts will argue that process explanations must not be brought to bear on pattern reconstruction; process explainers will insist that the reconstructed pattern requires a process explanation to become scientifically relevant, i.e., relevant to evolutionary theory.

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