

## Willi Hennig's dichotomization of nature

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### Abstract

Two formal assumptions implied in Willi Hennig's "phylogenetic systematics" were repeatedly criticized for not being biologically grounded. The first is that speciation is always dichotomous; the second is that the stem-species always goes extinct when its lineage splits into two daughter species. This paper traces the theoretical roots of Hennig's "principle of dichotomy". While often considered merely a methodological principle, Hennig's realist perspective required him to ground the "principle of dichotomy" ontologically in speciation. As a methodological principle, the adherence to a strictly dichotomously structured phylogenetic system allowed Hennig to be unequivocal in character analysis and precise in the rendition of phylogenetic relationships. The ontological grounding of the "principle of dichotomy" in speciation remains controversial, however. This has implications for the application of techniques of phylogeny reconstruction to populations of bisexually reproducing organisms (phylogeography). Beyond that, the "principle of dichotomy" has triggered an intensive debate with respect to phylogeny reconstruction at the prokaryote level.

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In his final assessment of "cladistics", Mayr (1982, p. 229) criticized Hennig's (1950, 1966) theory of phylogenetic systematics for implying two "strictly arbitrary" and "unrealistic" assumptions (see also Mayr, 1974): "The first one is that every existing species is eliminated when a new species originates, and the second one is that every splitting event is a dichotomy." This paper will deal with Mayr's second complaint (his first was dealt with by Rieppel, 2005), an issue that was also addressed by Hull (1979). Although he noted that "no cladist has ever maintained that the 'principle of dichotomy' is an empirical claim about the process of speciation", and registered Hennig's (1966, p. 210) assertion "that dichotomy is 'primarily no more than a methodological principle'" (Hull, 1979; p. 425), he nevertheless questioned the universal validity of the "principle of dichotomy" because synapomorphy cannot be universally and infallibly established: "If a trichotomy represents either a genuine trichotomy or two unresolved dichotomies, then a dichotomy could just as well represent either a

genuine dichotomy, a lumped trichotomy, or a single lineage divided mistakenly into two" (Hull, 1979, p. 426).

In this paper, I propose to trace the theoretical roots of Hennig's "principle of dichotomy", which rules phylogeny reconstruction. The "principle of dichotomy" lies at the root of "tree-thinking", which is currently under attack by representatives of the so-called microbialist point of view that emphasizes reticulate relationships among prokaryotes resulting from horizontal gene transfer (e.g. Doolittle, 2009; see below). Microbialists such as Dagan and Martin (2007) and Boucher and Baptiste (2009) are portrayed as having suggested "that the assumption of a tree-like structure of the relationships of life is a positivist philosophical construct", or that the "construction of the ToL [Tree of Life] is verificationist" (Lienau and DeSalle, 2009a, p. 1)—claims that Lienau and DeSalle (2009a) reject with an appeal to Popper's falsificationism (for an analysis of Popper's relation to logical positivism see Stadler, 1997; for an analysis of the positivist "verification principle" as a "criterion of test" see Godfrey-Smith, 2003). A historical approach to Hennig's writing, and to his reception by contemporary cladists and phylogenetic systematists,

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holds the promise of clarifying some of the issues underlying the current debate.

### Hennig's "principle of dichotomy"

In the revised version of his 1950 book, Hennig (1966, p. 210) stated: "If phylogenetic systematics starts out from a dichotomous differentiation of the phylogenetic tree, this is primarily no more than a methodological principle." This contrasts with his earlier writings, where the "principle of dichotomy" was derived from the dichotomous splitting of the stem-species into two sister- (daughter-) species: "If a species divides into two species as a consequence of the interruption of tokogenetic relations, it ceases to exist. It becomes the stem-species of the two daughter species. The two daughter species stand to each other in a phylogenetic relationship of first degree [...] If both these daughter species split again into two successive species, then the four resulting species stand in a phylogenetic relationship of second degree" (Hennig, 1950; p. 102). This is how Hennig (1950, p. 103) defined "phylogenetic relationship", emphasizing the similarity of his definition to that of Zimmermann (1931 [1937]), yet replacing the latter's criterion of the "relative age of the stem-species" with the number of successive dichotomous speciation events as the correct (i.e. more accurate) measure of degrees of phylogenetic relationships.

Zimmermann (1953) indeed defended a strict dichotomization of the world, yet distinguished conceptual from systematic dichotomization (genus, species), and both of these from genealogical dichotomization. Phylogenetic relationship, to be expressed in a strictly dichotomous (enkaptic) hierarchy, was defined by Zimmermann (1953) as follows: "Those species or other taxa that share a more closely situated ancestor are more closely related to one another than those natural groups that go back to a more remotely situated ancestor." This definition is based strictly on relative degrees of relationships, without the implication of necessarily dichotomous speciation—unlike that of Hennig (1953, p. 7), who refined his definition as follows: "A species *B* is more closely related to a species *C* than to any other species *A* if and only if species *B* shares with species *C* a stem-species that is not also a stem-species of *A*." Rendered in Hennig's (1965, p. 97) own translation, this definition reads: "Definition of the concept 'phylogenetic relationship': under such a concept, species, *B*, is more nearly related to species, *C*, than to another species, *A*, when *B* has at least one ancestral species source in common with species *C* which is not the ancestral source of species *A*."

Replacing the criterion of "relative timing of common ancestry" with a count of dichotomous speciation events as the measure of degrees of phylogenetic relationship,

Hennig (1950, p. 332, emphasis in the original) invoked "*the problem of the dichotomy of the phylogenetic tree: [...] Does this form of systematic dichotomization express a property of the phylogeny of the taxonomic groups under consideration, or is it an artifact that results from a desire for symmetry on the part of the classifying systematist?*" At this point, Hennig (1950) launched into an elaborate discussion of how the nature of speciation processes could ontologically ground his "principle of dichotomy". Hennig (1950) started from d'Ancona's (1939) work on population growth, which he extrapolated to the multiplication of species within a given space. The basic idea is that every species is characterized by a constant species-specific rate of speciation (multiplication). As species multiply, the space that "is available to species of the corresponding adaptational type" (Hennig, 1950, p. 318) will be successively filled, with the consequence that the speciation rate will successively be diminished. Hennig (1950, pp. 317–319) formulated a "logistical law" in mathematical terms that describes this successive reduction of the species-specific speciation rate under spatial constraints. Assuming the validity of that law, Hennig (1950) then introduced two further basic assumptions, one of which harks back to his deviation rule. In addition, for the ancestral species to go extinct upon speciation, this rule also requires that one of the descendant species deviates more than the other from the ancestral one. The first assumption that Hennig introduced (Hennig, 1950, fig. 55, top; reproduced in Hennig, 1966, fig. 64) is that the decrease in speciation rate affects all the successive generations of species that originate from one ancestral stem-species equally. This, he believed, would result in polytomies in the deep branches and dichotomies in the more recent, more terminal branches. The other assumption is that the species that deviate most strongly from their ancestors retain their original speciation capacity, thus suppressing further speciation of those species that deviate less from their respective ancestor (Hennig, 1950, fig. 55, bottom; reproduced in Hennig, 1966, fig. 65). This scenario would result in dichotomies in the deeper branches and polytomies in the more terminal branches. The consequence of these scenarios is that the "systematic structure will be different, and—presupposing the validity of the logistical law—will depend on how far a group has progressed towards the terminal stage at which the limit of species numbers has been reached" (Hennig, 1950, p. 334). This is a far cry from his declaration of the "principle of dichotomy" as a merely methodological one, and his passing comment on the relevant figures in his 1966 book: "figs. 64 and 65 show how in older groups a clear and appropriate picture of dichotomous differentiation (as inferred from the surviving recent species) may result from the random extinction of species or their descendants that actually

arose approximately simultaneously.” But Hennig (1950, 1953, 1957) was not the only one to root cladistic analysis (the “principle of dichotomy”) in dichotomous speciation. Many of his advocates were doing so as well. For example, in an article believed to have contributed to the broader acceptance of Hennig’s phylogenetic systematics (Schmitt, 2001, p. 341), Osche (1963, p. 862; emphasis in the original) proclaimed: “*Artaufspaltung* (‘splitting’) [...] alone is speciation in the true sense of the word.” Others (Ax, 1984, p. 60) acknowledged the possibility of multiple splitting of species lineages, yet posit the “principle of dichotomy” as an axiom of phylogenetic systematics (*ibid.*, p. 14).

It is well known that the reception of phylogenetic systematics by English-speaking systematists was mediated by Brundin’s (1966) exegesis of Hennig’s work (Nelson, 2004; Williams and Ebach, 2007). In his address delivered at the 2nd Annual Willi Hennig Society Meeting in 1981, Colin Patterson recalled how he discovered cladistics: “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*.”<sup>1</sup> Brundin (1966, p. 14) again emphasized the dichotomous splitting of species lineages as the universal pattern of speciation, from which he inferred with “necessity the following picture of the structure of phylogenetic connections which, according to evolutionary theory, must be generally valid”: a strictly dichotomous branching diagram (fig. 2 in Brundin, 1966). “There are many examples in the literature of phylogenetic diagrams demonstrating multiple splitting of ancestral species. Such a process is theoretically possible, but considering the principles of population genetics must have been a very rare phenomenon” (Brundin, 1966, p. 17). This, of course, is nothing but a *petitio principii*—but not according to Brundin (1966, p. 22; emphasis added): “The definitions and concepts [of phylogenetic systematics] are *logical* consequences of the results of population genetics; and the method and argument follows *strict rules*, thus giving reasonable guarantee for a phylogenetic system which is on the whole free of inconclusive judgment and able to function as a reliable general reference system.” As Hennig (1957) had done before, Brundin (1966, p. 22) pointed to the fact that incongruent character distribution might be suggestive of reticulated relationships. But “since it is possible to *prove* that the phylogenetic relationships *always* form a

[strictly dichotomous] hierarchy, we have to ask how they can be *deduced* from the reticular morphological relationships of the species” (Brundin, 1966, p. 22; emphasis added). The answer, of course, was Hennig’s distinction of synapomorphy from symplesiomorphy. Brundin (1966, p. 23) carried his argument forward, while addressing the deviation rule: “it is of fundamental importance to note that the speciation process must be looked upon as a splitting of an ancestral species into daughter species, and not as a branching off of a daughter species from a persisting ancestral species.” The extinction of the ancestral species upon speciation is thus “a *logical* consequence of the *definition* of phylogenetic relationship, and that definition is self-evident” (*ibid.*, emphasis added; same in Brundin, 1971, p. 118). Consider this another *petitio principii*, or else the definition of “phylogenetic relationship”, which implies the “principle of dichotomy”, if self-evident, must be considered one that cannot be further justified, nor is in need of further justification.

Brundin’s (1966) exegesis of Hennig’s phylogenetic systematics is soaked with logic: consider his appeals to universality and necessity, to proof and deduction, to strict rules and primitive (i.e. self-evident) terms. Consider how a historically contingent event such as the extinction of the stem-species is presented as a logical consequence of a definition, or how dichotomies are to be deduced from reticulating morphological relationships. But whether or not these concepts of logic are applied appropriately in this context is not the issue. The interesting question is: Why should a phylogenetic system built on logic and strict rules be the one that best captures the historical contingency of the evolutionary process?

### Logic, mind, and nature

Hennig (1950, 1966) had reduced speciation to a strictly dichotomous lineage-splitting process. For this he earned applause not only from Brundin (1966, 1971), but also from Günther (1956, 1962), whom Hennig held in high regard for a series of reviews of research on animal systematics and phylogeny: “in these he undertook the task to allocate this research [...] to its proper place in the philosophy of science and the history of philosophy” (Hennig, 1976, p. 298). Günther (1962, p. 279) backed up Hennig’s (1950) adoption of the “principle of dichotomy” with reference to the philosopher Kurt Bloch: “the dichotomy is the most adequate and logically best founded form of classification [...] The law of the dichotomy is, however, not merely subjective, but is instead grounded in the ontological reality of the polarity of all being” (Bloch, 1956, p. 71). Explicating the “law of dichotomy”, Bloch (1956, p. 73) noted: “There can be no doubt that systematics is a regulative

<sup>1</sup>Patterson’s talk, delivered at the 2nd Annual Willi Hennig Society Meeting on 3 October 1981 in Ann Arbor, MI, was transcribed and made available by D.M. Williams, Department of Botany, The Natural History Museum, London. The emphasis is mine.

principle of our reason, as was shown by KANT. This is proven by the purely logical investigations of systematics and its application in the natural sciences. The question has to be asked, however, whether systematics is nothing but a transcendental principle of reason, or whether it has some form of ontological reality, which is denied by KANT.” The broader context thus leads back to Kant, as would indeed be expected in German philosophy of science. (For an excellent introduction to Kant see Gardner, 1999, on which the following discussion is based.)

Kant is famous (and controversial) for his defence of “a priori synthetic judgments”. His argument starts with the distinction between analytical and synthetic judgments. Analytic judgments are rooted in logic, that is, the law of non-contradiction: the statement “a triangle has three sides” is analytical, as its negation results in a contradiction of terms. Analytical judgments thus do not extend our knowledge of the world, but rather explicate our concepts, and since they are not grounded in experience, they can be known a priori. In contrast, synthetic judgments are grounded in experience, and therefore do extend our knowledge of the world experienced, for which reason they cannot be known a priori. Synthetic judgments are a matter of discovery, not a matter of logical reasoning. But Kant claims that there exist a priori synthetic judgments, and these involve concepts such as space, time, and causality, but also (in his view) mathematics and Euclidean geometry.

According to Kant, pure, “unfiltered” sensation (experience) would reveal a chaotic multiplicity. Following the insights of modern physics, the chaos of sensations became the “multidimensional multiplicity” of Ziehen (1939, p. 10) and, following his lead, of Hennig (1950, p. 6; 1966, p. 4). But given such an unstructured multiplicity, how is it then possible for us to obtain knowledge of objects, their properties and relations? How is it possible to systematize this “multidimensional multiplicity”, if such a system is not immediately given to us through perception? The traditional realist assumption is one of objects existing in time and space, which are the material cause of their representations in human discourse and thought. The arrow of explanation of how the cognition of objects is possible for us runs from the object to the subject. But Kant thought such a correspondence relation between object and subject unintelligible, and consequently reversed the arrow of explanation: it is the cognizing mind that brings concepts to the experienced world, and thereby in a way constitutes the objects of perception. Such concepts are extending our knowledge of objects, so they must be synthetic. But at the same time they make the cognition of objects possible in the first place, so they must be a priori. Kant argued that we can acquire structural knowledge of the world precisely

because we constitute it. This means, however, that what is represented in our concepts, discourse, and thought are only “things as they appear to us”, not “things in themselves”. Positive knowledge about “things in themselves” is simply impossible. But neither are the “things as they appear to us” inventions of the human mind. Objects represented in human discourse and thought are, for Kant, empirically real, but transcendently ideal. “The synthetic a priori element in cognition is the object-enabling structure of experience, the set of conditions that make objects possible for us, and the a priori features of objects are those by virtue of which objects conform to that structure” (Gardner, 1999, p. 43). It is possible to imagine empty space, but it is not possible to imagine objects without spatial extension. Since representation of an outer world of objects necessarily presupposes the representation of space, the representation of space cannot have been acquired empirically, but must be a priori. The crucial point here is that Kant’s metaphysics stipulated an *isomorphy* of the extra-mental world with our synthetic a priori concepts. The outer world of objects must share the structure of our experience of it, if our experience is to be one of reality (Gardner, 1999, p. 46). But where do these synthetic a priori concepts come from?

It is, perhaps, Lorenz (1941a [1978]; at the time professor of psychology at the Immanuel Kant University in Königsberg, later Kaliningrad), who most famously once again turned the arrow of explanation around from the way Kant had oriented it. Running from subject to object for Kant, Lorenz turned Kant’s synthetic a priori into an evolutionary a posteriori. Lorenz applauded Kant for having discovered that cognition and human thought embody certain structural (conceptual) components that precede all individual experience, but differently from Kant, he interpreted these as an evolutionary adaptation of humankind to the outer world of objects: “those given structures of cognition and the concepts that precede all individual experience correspond to the outer world of objects for the same reasons that explain why the hoof of a horse fits the savannah floor even before it is born” (Lorenz, 1941a [1978, p. 86]). “The laws of our thought processes, which we recognize as being *a priori*, are no *lusus naturae* [pleasantries of nature]. We need them for our survival!” (ibid., p. 88).

In the same year, Lorenz (1941b) published an early exemplification of what was to become known as the “Hennigan argumentation scheme”, which he applied to innate movement patterns in ducks in search for “monophyletic” groups (ibid., p. 289). Theoretical considerations about the pattern of character evolution led him to postulate a dichotomously diverging model of phylogenetic trees, which he then found confirmed in his case study. In the introduction to his paper, Lorenz (1941b, p. 198) emphasized the “systematic tact” that

characterizes the work of a competent systematist, “but to turn systematics into a true science, this intuitive component must be successfully analyzed” (ibid., p. 199). In his discussion of Lorenz’s (1941b) paper, Hennig (1950, p. 189) subordinated such systematic tact “under the more general concept of intuition, which plays a role not only in systematics, but also in the most exact of all sciences”, that is, mathematics (ibid., p. 190). His analysis of this intuition lead to the recognition of the exact tools of logic that the systematist can bring to bear on his research, methods that he explicated in his own work (Hennig, 1950).

But Lorenz (1941a) was not the first to turn Kant’s synthetic a priori concepts into an evolutionary adaptation. The first to do so, according to Rensch (1968, p. 232), was the philosopher Theodor Ziehen, who again was read and much cited by Hennig (1950, 1966). The laws of logic, according to Ziehen (1934, p. 86), are a phylogenetic adaptation to the “Given”; conversely, all that is “Given” (all that exists in our perception) is structured according to the laws of logic. Rensch, a former student of Ziehen (Rensch, 1979), concurred: “human thinking developed phylogenetically by adapting itself to the universal logical laws [...] Hence logical laws as well as causal laws were also valid before man existed and before there were any organisms on the earth” (Rensch, 1960; p. 99). “How decisive for evolution the logical laws are may easily be shown by the assumption that these laws would *not* be valid”, that is, by counterfactual reasoning (ibid., p. 98). His examples included the transitivity of identity in “reduplicated” genes, or allometric growth that can be described in a mathematical formula. “The logical relations that are given in facts can be expressed in the language of mathematics, as arithmetic and algebra are applied logic. This means that mathematical theorems exist in the extra-mental world; humankind has merely come to recognize their existence and found ways to formalize them in the course of phylogeny” (Rensch, 1968, p. 232).

Rensch spent a lifetime researching “laws” or “rules” of evolution (for further comments see Rieppel, 2007). It was Rensch (1947) who first introduced the term “cladogenesis” in a discussion of its “lawfulness” (expressed in terms of regularities). One of the regularities of cladogenesis that Rensch (1933) had identified in a classic paper was allopatric speciation: interruption of gene flow between populations as a consequence of geographical isolation. This paper by Rensch was prominently cited by the architects of the Modern Synthesis (e.g. Dobzhansky, 1937; Mayr, 1942), and by Hennig (1950), who also cited Dobzhansky (1939). Although he (Hennig, 1957, p. 58) later referred to Dobzhansky in support of dichotomous speciation, Hennig could find neither in Rensch (1933, 1947) nor in Dobzhansky (1939) a “rule”, let alone a “law”, of dichotomous speciation. Instead, Rensch (1933, p. 69)

dismissed as “highly speculative” Rosa’s (1931) idea that speciation is invariably dichotomous due to an “inherent force” driving the process (on Rosa and his controversial significance for phylogenetic systematics, see Baroni-Urbani, 1977, 1979; Nelson and Platnick, 1981; Hull, 1988; Craw, 1992). Hennig (1950, 1966) discussed Rosa’s (1899) “law of the progressive reduction of variability”, but (contra Baroni-Urbani, 1977, p. 344) did not cite Rosa’s (1918, 1931) book on hologenesis that explicated the latter author’s views on lawfully dichotomous speciation.

Indeed, Hennig’s adherence to the “principle of dichotomy” has other sources, which is the logical positivists’, in particular Carnap’s (1963 [1997]), answer to Kant (for a discussion of logical positivist roots of Hennig’s phylogenetic systematics, see Rieppel, 2005, 2006, 2007). With the recognition that Euclidean geometry is not the only possible description of space, and even more so with Einstein’s special and general theory of relativity, the *synthetic* a priori concepts of Kant came under serious pressure. Evidently there are structures in the world that can be discovered, yet do not correspond to the synthetic a priori judgments identified by Kant (e.g. his conceptions of space and time). Einstein’s new theories, in particular, opened a deep divide between our common-sense perception of the world, and the mathematical structures required to describe this world theoretically (Friedman, 2007). But not only did it become clear that there are several possible geometries; Carnap also realized that different systems of logic are valid in different contexts of inquiry. He consequently adopted a logical pluralism, rejecting all extra-logical (epistemic) justification of logical laws and principles (Ryckman, 2007, p. 86). Lived experience was thought to reveal a multiplicity of sense impressions, which required to be structured in order to become relevant for objective science. For Carnap the tool to do so was logic, which he in turn took to be a priori (Friedman, 1999; p. 99). The goal of such a “logical construction of the world” was “to advance to an intersubjective, *objective world*, which can be conceptually comprehended and which is the same for all observers” (Carnap, cited by Friedman, 1999, p. 95). Logic thus structures the language that is used in scientific description of the world, yet which system of logic to choose in which context of inquiry “will be guided by the values and desiderata of the choosers” (Ricketts, 2007, p. 207). Such choice, however, imports an element of conventionalism into “the logical construction of the world”, which the logical positivists defended with an appeal to Henri Poincaré (Friedman, 1995, 1999, p. 81).

Poincaré had argued that descriptions of space in either Euclidean or non-Euclidean terms ultimately rest on the prior acceptance of different systems of *conventions* for the description of space. Carnap’s

conventionalism in particular can be traced back to his doctoral thesis *Der Raum* (Carnap, 1922; for a discussion see Mormann, 2007), a treatise on the philosophy of geometry that was cited by Hennig (1950). Carnap considered topological relations in space to be matters of fact, the metrics used to describe those relations a matter of convention. In his thesis, Carnap (1922) distinguished a “formal space”, an “intuitive space”, and a “physical space”. The theoretical space is space in the sense of mathematics, to be described as a relational structure, and it is this formal treatment of space that captured Hennig’s (1950, p. 153) attention (for further discussion see Rieppel, 2006). Species occupy different topological positions in the multidimensional space of their relational properties (*Eigenschaftsraum*: Hennig, 1950, p. 152), thus forming a multidimensional system that cannot be pictured in its totality all at once (ibid., p. 279). Different structure descriptions will capture different dimensions of that multidimensional system; conversely, all properties that satisfy the same formal requirements will also satisfy the same structure description. Among all possible structure descriptions of such a multidimensional system of species, Hennig (1950) took the phylogenetic one to be the most fundamental, because it can be expressed in a single, precise and unambiguous metric, which is time. Once that choice is made, the whole theoretical edifice of phylogenetic systematics follows logically. To mix different metrics, such as time and morphology, or time and ecology, results in a logical fallacy, which Hennig (1966, 1974, p. 280) called—following Günther (1956, p. 38)—the “violation of the metabase” (*Metabasis*). The same logical mistake is made if the critique of phylogenetic systematics (e.g. Mayr, 1974) employs a metric different from Hennig’s choice.

### The evolution of Hennig’s argument

Hennig (1953) prefaced his review of the state of the art of systematics in entomology with a brief summary of the principles underlying phylogenetic systematics. He noted that the diversity of organisms forms a “multidimensional multiplicity”, and asserted that set theory, “a branch of mathematics, or mathematical logic respectively”, is the right tool to use in the systematization, and classification, of that organismic diversity (Hennig, 1953, p. 6). Set theory, he continued to explain, shows that there are as many possibilities to classify a multidimensional multiplicity as there are different dimensions. The most important point, therefore, is to identify a dimension to which all other dimensions can be reduced—and this dimension is time (ibid.). “It is a well established fact that new species originate only through the splitting of already existing species” (ibid., p. 7). Therefore, if the “degree of

phylogenetic relationship” as expressed in the dimension of time is chosen as the “*principium divisionis*” of the natural system, the strictly dichotomous structure of the phylogenetic system follows as a “logically necessary consequence” (ibid.). Such a strictly dichotomous structure of the phylogenetic system, he continued, renders it easier to derive from it a number of definitions, in particular the “definition of phylogenetic relationship” (ibid.; emphasis in the original). Given that definition (see above), it then becomes clear that the essence of phylogenetic systematics is the “search for sister-groups” (ibid., p. 10). Turning to issues of methodology, Hennig (1953, p. 14) recognized that, given the “principle of dichotomy”, the search for sister-groups proceeds through the analysis of three-taxon statements: “in praxi, the systematist has to resolve a *Regel-de-tri*-problem” (ibid.). The “*Regel-de-tri*” is a common German abbreviation for “*Regula de tribus termini*”, which in mathematics is known as “the rule of three”. The “principle of dichotomy” is therefore recognized to be of major methodological importance, and it is ontologically grounded in dichotomous speciation.

Whereas Hennig (1953) appealed to set theory only in a general sense, he soon had delivered to him the relevant tools of symbolic logic, when he became acquainted with the work of Woodger (1952) and Gregg (1954) on the theoretical definition of “hierarchy”: “In my view the work of WOODGER and GREGG is enormously important [...] every systematist should look into it” (Hennig, 1957; pp. 55–56). Hennig (1957, p. 55) once again emphasized that the “choice of the type of system” to be used in the classification of a multidimensional multiplicity cannot be arbitrary: “the choice of the type of system has to correspond to the structure description [Strukturbild] of certain relations, which exist between the entities that are to be components of the system [...] The hierarchical type of system has most recently been investigated by Woodger and Gregg [...] We therefore have to ask the question whether there exist relations between animal species that satisfy the requirements invoked by Woodger’s definition of ‘hierarchy’; in addition, these relations that exist between animal species must exist objectively, i.e., independent of any human being that may or may not recognize them” (ibid., pp. 55, 57). Hennig (1957, p. 58) invoked modern population genetics when he reduced speciation to a dichotomous splitting of a species lineage: “As Dobzhansky and many others assume, geographic isolation plays a major role” in speciation. From this premise he concluded: “The structure of phylogenetic relations, which according to the theory of descent have to exist between species, will therefore *necessarily* be captured” by a strictly dichotomous branching diagram (ibid., p. 58 and fig. 4; emphasis added). It is in this context that Hennig (1957, fig. 3) first introduced his famous diagram

(Hennig, 1966, fig. 4) that illustrates how a species lineage-splitting event gives rise to dichotomous phylogenetic relations that satisfy the requirements of Woodger's definition of "hierarchy": "It is evident that there exists an exact correspondence between the [strictly dichotomous] structure description [Strukturbild] of phylogenetic relations and the structure description of relations that exists among elements of a set which, according to Woodger's definition, must be called a hierarchy" (ibid., p. 58). The strictly dichotomous phylogenetic system, if correctly reconstructed, would thus "deliver an exact list of all speciation events, which have played a role in the evolution of the current diversity in the animal kingdom" (ibid., p. 62).

Hennig (1957, p. 56; 1966, p. 17) must have recognized that Woodger's (1952) definition of "hierarchy" was based on the "one-many" relation, and therefore did not exclude polytomies (Gregg, 1954, fig. 2.5; Hennig, 1957, fig. 1; Hennig, 1966, fig. 2). It was Hennig who reduced the phylogenetic hierarchy to the "principle of dichotomy". While ontologically grounded in dichotomous speciation, his insistence on that principle had important methodological reasons. It reduced the "search for sister-groups" to the unequivocality of the "rule of three". The earliest application of that rule to phylogeny reconstruction might be that of Müller (1864, p. 7), who analysed crustacean relationships in terms of a "three taxon statement" as he searched for a method to "reconstruct a phylogenetic tree that implies no contradiction" in character distribution (ibid., p. 2). It is for the same reason that 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, six 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). Following that statement, Bloch (1956, p. 71) continued: "All forms of classification except for the dichotomous one are initially suspect, because they do not imply necessity." The necessity implied by the "principle of dichotomy" is rooted in the "Law of Excluded Middle". In a dichotomous classification, any species or taxon is necessarily on one or other side of the fork; there is no third place to go. The same necessity applies to Hennig's argumentation scheme for character analysis. Hennig (1957, p. 64) recognized that treating a multitude of (morphological) characters as equally informative results in reticulated relationships, an insight that was already familiar to Linnaeus. "But how is it possible to infer from the reticulated morphological relations of animal species the—as we now know—hierarchically structured phylogenetic relationships?" (ibid.). The answer is Hennig's "argumentation

scheme", character analysis within the framework of a dichotomously structured three-taxon statement: a character is, or is not, a synapomorphy—terium non datur.

## Conclusions

Unless it is argued with Ziehen (1934), Lorenz (1941a), and Rensch (1960, 1968) that the extra-mental world is structured according to the laws of logic, our capacity of logical reasoning hence being an evolutionary adaptation to this extra-mental world, the question remains why a system built on logic and strict methodological rules should be the most appropriate one to capture the contingencies of the evolutionary process. Unquestionably, the "principle of dichotomy" was for Hennig (1950, 1966) an important methodological tool in the disambiguation of systematics. It allows for unambiguous character analysis, and for precision in the expression of phylogenetic relationships. But considering the principle as only a methodological tool and nothing more, Hennig (1950, p. 332) was confronted with the problem formulated by Kant: does the systematist carry the "principle of dichotomy" into nature, or is nature dichotomously structured in the first place? Hennig's (1950, 1966) realism required an isomorphism between nature and the natural system he was seeking. He consequently could not avoid the ontological grounding of the "principle of dichotomy" in speciation: speciation is dichotomous, and nothing else. However, Hennig (1950, 1966) clearly recognized the difference between sexually reproductive species as tokogenetic (reticulating) systems, and the bifurcating phylogenetic relationships between species. He was also aware of the limitations of his approach in the study of asexually reproducing organisms (Hennig, 1966, p. 44). Hennig (1950, 1966) may well have overextended the "principle of dichotomy" by grounding it ontologically in speciation, but then again, he was happy to concede that his system may not be applicable to all forms of life. When Hennig was invited to summarize his theory for the Annual Review of Entomology, he emphasized: "The definition of the concept 'phylogenetic relationship' is based on the fact that reproduction is bisexual in the majority of organisms [...] This is especially true for the insects, with which this paper is mainly concerned" (Hennig, 1965, p. 97).

Colin Patterson, who discovered the logic of phylogenetic systematics in Brundin (1966; see above), came to the conclusion that "evolution may well be true, but basing one's systematics on that belief will give bad systematics", as also will "the belief that trees not cladograms are the proper level of analysis" (Patterson, 2002, p. 31). Such decoupling of systematics from evolutionary theory (Brady, 1985; see also Nelson and

Platnick, 1981; Brower, 2000; Williams and Ebach, 2007) was branded “pattern cladism” (Beatty, 1982), and while it rendered the “principle of dichotomy” an uncontroversial tool in the search for an inclusive hierarchy that is built not on descent, but instead on relative degrees of phylogenetic relationships, it was criticized for its ontological emptiness (Hull, 1988). While logically consistent in research into higher levels of relationships from a pattern cladistic point of view, the “principle of dichotomy” came under renewed theoretical pressure as it was applied to tokogenetic systems such as species and their populations in phylogeography (Avice, 2000). The attempt to trace the history of populations of sexually reproducing species through the application of cladistic techniques was recognized as an imposition of a dichotomous hierarchy on what are essentially reticulating systems (Goldstein and DeSalle, 2000; Goldstein et al., 2000).

Reticulation through hybridization has long been recognized to be incompatible with a strictly bifurcating hierarchy (see e.g. the discussion of hybridization in Platnick and Funk, 1983). More recently, however, and especially—but not only—at the prokaryote level, systematists have sought to base phylogenetic relationships not on the hierarchical distribution of molecular characters, but on the *transmission* of genetic material. This changes the perspective from a search for pattern to research into historical processes. The bifurcating cladogram—taken as the metaphor for the Tree of Life—thus becomes the proverbial Wittgensteinian ladder that, once climbed to see the world aright, has to be kicked away. Paraphrasing Wittgenstein’s *Tractatus* (§6.54), Doolittle and Baptiste (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” (see also Doolittle, 1999, 2009). The results are reticulating systems that depict both vertical as well as horizontal (lateral) gene transfer.

The adoption of a process view in phylogeny reconstruction does not allow the relegation of lateral gene transfer (or other mechanisms causing reticulation) to mere noise (incongruence) based on the expectation that genetic signals are predominantly passed on in vertical descent (Lienau and DeSalle, 2009b, p. 2). Even if this were, or is, the case, the reconstruction of a mere pattern of relative degrees of phylogenetic relationships—at whatever level of biological complexity—will not satisfy a processual approach. A strictly bifurcating tree “does not provide an accurate description of the processes that have shaped life’s history” (Fournier et al., 2009). Current debates about the validity of the “universal Tree of Life” metaphor need to reflect back on the

dichotomy of pattern versus process analysis in order to avoid sterility.

The Tree of Life metaphor is commonly traced back to Darwin (1837). A few pages earlier, in his 1837 Notebook B, Darwin sketched a somewhat more rudimentary diagram, noting “The tree of life should perhaps be called the coral of life, base of branches dead, so that passages cannot be seen” (De Beer, 1960, p. 44). Whereas the pattern approach to cladistics does not seek passages, the processual approach to phylogeny reconstruction considers the “dead layers of coral” to “form a richly connected network analogous to horizontal gene transfer (HGT) between species” (Fournier et al., 2009, p. 2229). It is important, then, to discern whether contemporary discussions of phylogeny reconstructions turn around “trees” (strictly bifurcating cladograms that depict trees in a graph theoretical sense; Platnick, 1977) or branching “corals” (processual networks in a genomic or phylogeographical context).

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