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## THE DEVELOPMENT OF PHYLOGENETIC CONCEPTS IN HENNIG'S EARLY THEORETICAL PUBLICATIONS (1947-1966)

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**Abstract.**—In this paper, we describe the development of Hennig's most important phylogenetic concepts, which culminated in the publication of the now famous *Phylogenetic Systematics* in 1966. Hennig proposed strict definitions of monophyly and phylogenetic relationships as early as 1950 in *Grundzüge einer Theorie der phylogenetischen Systematik*. However, in this edition of the book, the terms "apomorphic" and "plesiomorphic" were introduced for taxa and not for characters. It was not until 1952 that these terms were consistently applied to characters, hereby for the first time allowing the reconstruction of phylogenetic relationships. But this is not Hennig's sole contribution to systematics, as revealed by a comparison of his *Phylogenetic Systematics* with publications of the "new systematics" school (e.g., Huxley, 1940, *The new systematics*, Oxford Univ. Press, Oxford, England; Mayr et al., 1953, *Methods and principles of systematic zoology*, McGraw-Hill, New York). Hennig was the person who redirected the interest of systematics to the study of supraspecific taxa after years of focusing on species and infraspecific taxa. [History; phylogenetic systematics; cladistics; monophyly; Hennig; apomorphy; plesiomorphy.]

The oldest field of the biological sciences, systematics, underwent dramatic changes in the middle of this century. These changes were in part initiated by an entomologist, Willi Hennig, who clarified or, depending on your systematic persuasion, redefined the goals of phylogenetic systematics in his *Phylogenetic Systematics* (1966). The history of phylogenetic systematics sensu Hennig has not been extensively studied. Surprisingly, most contributions that deal with this subject focus on systematists that anticipated Hennig's ideas, were influential in their development, or dealt with their reception in various countries (Hull, 1988; Craw, 1992; Donoghue and Kadereit, 1992).

Our goal is to describe the development of Hennig's thought on systematic theory as documented in his own publications (see also Dupuis, 1979, 1982; Ulrich, 1985; Schmitt, 1989). We focus on the years between the completion of the manuscript for his first main theoretical contribution *Grundzüge einer Theorie der phylogenetischen Systematik* in 1945 (published in 1950) and the publication of a modified version of this book (completed in 1960) as *Phyloge-*

*netic Systematics* in 1966. We concentrate on Hennig's contributions to phylogenetic relationships of higher categories (above species level) and largely ignore relationships within species and problems with assigning ranks.

Accordingly, this paper deals mainly with three topics: (1) the goals of strictly phylogenetic systematics (cladistics) sensu Hennig, i.e., largely the definition of monophyly and of phylogenetic relationship; (2) the concept of apomorphic and plesiomorphic characters; and (3) the different methods of determining the polarity of character transformation series. We briefly compare the goals of Hennig's systematics with principles laid down in the works of contemporary representatives of the "new systematics."

### GOALS OF STRICTLY PHYLOGENETIC SYSTEMATICS

Although Hennig's *Grundzüge einer Theorie der phylogenetischen Systematik* was published in 1950, Hennig had written the manuscript without having access to a library as a prisoner of war in 1945. This book is Hennig's earliest extensive publi-

cation on systematic theory. It was preceded by 75 mostly empirical publications (mostly on Diptera and a few on lizards and snakes). However, in 1947 and 1949 he published two short theoretical papers, "Problems of biological systematics" (Probleme der biologischen Systematik) and "Clarification of some terms in phylogenetic systematics" (Zur Klärung einiger Begriffe der phylogenetischen Systematik), which are largely abstracts of the 1950 book whose printing was delayed by the post-war paper shortage (Schlee, 1978).

At this time, Hennig was mainly concerned with establishing systematics as a science "whose goals are not inferior in importance to those of any other biological field" (Hennig, 1947:279) (see Appendix, note 1, for original German text). However, according to Hennig, this importance could only be claimed for strictly phylogenetic systematics, which discovers real phylogenetic relationships. It could not be claimed for morphological or typological systematics, where organisms are classified according to similarity without any theoretical framework.

In the 1950 *Grundzüge*, Hennig laid down the main goals and principles of cladistic classification but without describing stringent methods for reconstructing phylogenetic relationships. The most important chapter of Hennig's *Grundzüge* for our discussion is undoubtedly the second one. The first part deals with "group-categories of lower order." By this, Hennig meant infraspecific taxa and biological species. The members of group categories of lower order are connected by ontogenetic and tokogenetic relationships. Ontogenetic relationships are relationships among ontogenetic stages of one individual; tokogenetic ones are netlike and exist among individuals of populations. Hennig pointed out that only the relationships among species but not the ones within species are hierarchic. Thus netlike tokogenetic relationships need to be distinguished from phylogenetic relationships that only exist among species and/or higher taxa (Hennig used "taxonomic group" instead of what would today be called tax-

on). Little space was devoted to a discussion of variability within species (cyclomorphosis, polymorphisms, etc.), but Hennig discussed in detail the differentiation of species into geographic subspecies. The discussion was motivated by his interest in phylogenetic relationships, and according to Hennig the formation of subspecies is the first step towards speciation. "With the discussion of the fragmentation of species into subspecies we have entered the field of phylogenetic relationships" (Hennig, 1950:94) (Appendix, note 2).

In the second and much longer part of the chapter, Hennig discussed "group-categories of higher order," i.e., supraspecific taxa. How higher taxonomic groups originate and whether they are "real" is central to Hennig's argument. He argued that if species are real, higher taxa can also claim something like reality ("Realität," e.g., Hennig, 1947:279 [Appendix, note 3], 1950:115) because they originate by speciation. Thus, higher taxa are real because they are in a historical sense identical to their stem species: "two species that are descendants of a common stem species thus forming a group-category of a higher order [have to be] viewed as identical with their stem species, because it continues to exist through them" (Hennig 1950:115) (Appendix, note 4). Because the reality of species is critical for this argument, Hennig had to deal with a defect of the biological species concept, whose definition does not allow the delimitation of biological species in time. Note that the delimitation of species in time was discussed in the part of the chapter on supraspecific taxa and not in the part on "species." As Günther (1956) had mentioned, the problem of how to delimit species in time becomes important when a logically stringent theory of phylogenetic systematics is developed. Hennig decided that the "methodologically best solution" (Hennig, 1974, in reference to Günther, 1962) is to consider the stem species extinct at the speciation event:

When some of the tokogenetic relationships among the individuals of one species cease to exist, the species disintegrates into two species and itself ceases to exist as a species. It is the common an-

cestor of the two daughter species. Both daughter species share a first order phylogenetic relationship. They constitute a group category of a higher order. (Hennig, 1950:102) (Appendix, note 5)

For Hennig, it followed from this discussion of how higher taxa originate that phylogenetic relationships must be defined through common ancestry or more precisely that "the relative recency of common ancestry of the ancestors is the only direct measure of phylogenetic relationship" (Zimmermann, 1937, cited in Hennig, 1950:103 [Appendix, note 6]; see Donoghue and Kaderleit, 1992). Hennig's discussion here closely follows Zimmermann's line of reasoning. Hennig explicitly refuted all definitions of relationships that are based entirely or in part on overall similarity. Instead, he recognized that reality can only be claimed for higher taxa that include stem species and all their descendants. This insight appears to necessarily have led to his redefinition of monophyly:

Only those species groups—and this applies to all group categories of higher order—can be called monophyletic which can be traced back to a common stem species. . . . It has to be added that monophyletic groups not only ought to contain species that are descendants of one common stem species, but they also must include all species that come from that stem species. (Hennig, 1950:307–308) (Appendix, note 7)

Already at this stage in the development of Hennig's ideas, the now famous case of the "Reptilia" was used as an example of a widely recognized taxon that is not monophyletic *sensu* Hennig (1950:257). However, the term paraphyletic was not used in the *Grundzüge* and was introduced as late as 1960 in the German manuscript (published posthumously in 1982) whose translation was published as *Phylogenetic Systematics*.

#### APOMORPHY AND PLESIOMORPHY

Hennig's *Grundzüge* introduced a strict concept of monophyly but contained neither the concepts nor the methods that are today considered essential for demonstrating whether groups are monophyletic. However, the initial steps towards the development of the concepts of apomorphy

and plesiomorphy can be traced back to the *Grundzüge*. He elaborated what he called the "deviation rule" (Deviationsregel): "This rule says that when an ancestral species gives rise to two daughter species, one usually remains morphologically more similar to its ancestor than the other which undergoes morphological differentiation [from the stem species]" (Hennig, 1950:106) (Appendix, note 8). Hennig called the morphologically derived species apomorphic and the other species plesiomorphic. Occasionally, he also applied the terms to higher taxa. Clearly, the terms apomorphic and plesiomorphic were introduced for taxa and not for characters. This is particularly evident in the paper where they were first published (Hennig, 1949). Here, Hennig criticized that contrary to the principles of phylogenetic systematics, in morphological taxonomy, "morphologically derived component taxa of very speciose groups are taxonomically separated, and that they are, in ignorance of the degree of phylogenetic relationships, coordinated [i.e., receive equal rank] with all of the remaining component taxa" (Hennig, 1949:137) (Appendix, note 9). He proposed the terms to facilitate the discussion of whether the apomorphic taxon is the sister group of the plesiomorphic taxon or nested within it (Hennig, 1949:137) (Appendix, note 10). In passing, Hennig sometimes used apomorphic and plesiomorphic for characters (Hennig, 1949, 1950), but he was obviously unaware of the important difference that this alternative application would make in the future.

There is another indication that Hennig himself did not realize the importance of these terms for phylogenetic systematics. He published apomorphic and plesiomorphic together with a number of rather obscure terms that never gained any significance (Hennig, 1949; e.g., "stenomer" and "eurymer," "stenochor" and "eurychor," etc.). Indeed, in their original meaning apomorphic and plesiomorphic were more or less superfluous because there was hardly a need for yet another way to refer to "advanced" and "primitive" groups. Applied to taxa, apomorphic and plesio-

morphic are still in the tradition of what may be traced back to the idea of the *scala naturae*, that whole taxa are either advanced or primitive. It was even felt by systematists of this period that the "few" cases where a taxon displayed about as many derived as primitive characters required a special term, "specialization crossings" (literal translation of "Spezialisationskreuzungen"; Abel, 1929). It is certainly interesting that Hennig first used the terms apomorphic and plesiomorphic for characters when he discussed such specialization crossings (Hennig, 1950:107):

Frequently, one group will be plesiomorphic with respect to one character . . . and apomorphic with respect to another so that a total judgment [of the entire taxon] is impossible ("specialization crossing"). Even in these cases the proposed terms remain applicable, but now for the different characters. (Hennig, 1949:137) (Appendix, note 11)

These specialization crossings apparently stimulated Hennig to think in terms of characters instead of whole taxa. Thus, the specialization crossings were important for the development of a systematics that devotes more attention to the study of individual characters.

It was not until the publication of the third volume of *Die Larvenformen der Dipteren* in 1952 that Hennig expressed the important difference between using apomorphic and plesiomorphic for taxa or characters (Hennig, 1952). In 1952 (p. 103), he stated unmistakably, "In strict phylogenetic systematics it is not the congruence of plesiomorphic (primitive), but only of apomorphic (derived) characters that count" (Appendix, note 12). In this paper, Hennig did not really elaborate these new ideas because they were tangential to the main purpose of the book. Such discussion was left to a paper on insect phylogeny (Hennig, 1953), which includes a comprehensive summary of Hennig's positions on theoretical systematics at that time. In this paper, strict monophyly and the concepts of apomorphic and plesiomorphic characters were explained in detail (although the terms were still also used for taxa). Also, the prefixes aut-, syn-, and sym- for apomorphic and plesiomorphic were intro-

duced. It was not until 20 years later that he strongly disapproved of using apomorphic and plesiomorphic for taxa and stated "that it is fundamentally wrong to speak of plesiomorphic and apomorphic groups" (cited from a book that was written in 1975 and posthumously published in 1984; it was probably intended to be an introduction to a textbook of systematic zoology [Hennig, 1984:41] (Appendix note 13.)

Thus, a character-based concept of apomorphy and plesiomorphy was derived from a taxon-based concept and is historically more recent than the strict definition of monophyly and phylogenetic relationship. Considering that these concepts are so closely related today that they are always discussed together, it is certainly surprising that they were not developed at the same time.

#### RECONSTRUCTION OF PHYLOGENETIC RELATIONSHIPS

What were Hennig's ideas on how to reconstruct phylogenetic relationships in his *Grundzüge einer Theorie der phylogenetischen Systematik* (1950)? After all, he had already adopted a strict definition of monophyly, and the reader could expect that Hennig would proceed with the description of similarly stringent techniques for its recognition.

Hennig discussed three methods for reconstructing phylogenetic relationships. He started with the paleontological method. Here, he mainly refuted the common conception that the reconstruction of phylogenetic relationships is dependent on a good fossil record. Hennig presented the arguments still in use for demonstrating that paleontology can at best be one tool in an attempt to reconstruct phylogenetic relationships. He mentioned the incompleteness of the fossil record, problems with polymorphic species, and the generally poor state of preservation of most fossil specimens. However, Hennig pointed out that the fossil record is valuable for determining the age and thus rank of taxa and reconstructing character phylogenies (a concept that was originally introduced by Zimmermann, 1937; see also Donoghue

and Kadereit, 1992). By this he meant determining the direction of change for any particular character.

For Hennig, the second, comparative holomorphological method was by far the most important tool for reconstructing phylogenetic relationships. His discussion begins with the well-known rule "the more similar, the more closely related." But in contrast to Zimmermann (1937), Hennig went further and refuted the idea that this rule will generally yield correct results. According to him, there are many different methods for determining similarity, and none can claim superiority over any other. Furthermore, the different methods often yield different results, although there can only be one underlying phylogeny. How then could measures of similarity be good measures of phylogenetic relationship? He discussed at length why protein similarities as measured by antibody reactions are no better than similarity as measured by morphological characters. He summarized:

Thus one obtains a classification of morphological characters in those that point to a very narrow and those that point to a wider degree of phylogenetic relationships, i.e., a valuation of morphological characters according to their value as indicators of various degrees of phylogenetic relationship. (Hennig, 1950:172) (Appendix, note 14)

He gave four "rules for evaluating morphological characters as indicators of the degree of phylogenetic relationship."

The first rule ("Kriterium der Häufigkeit des Vorkommens der Merkmale") is well known: (1) "characters that are shared by a larger set of species indicate a wider relationship than those shared by a smaller set" (Hennig, 1950:172) (Appendix, note 15). Hennig was aware of the fact that there are exceptions to this rule, and he gave some examples, but he considered this rule generally valid. The second rule ("Kriterium der ontogenetischen Merkmalspräcedens") was derived from Haeckel's biogenetic law: (2) character states that appear first in ontogenetic transformation series are phylogenetically older than states appearing later (p. 174). Again, Hennig discussed problems and pointed to exceptions. Rules 3 ("Kriterium der Kompl-

ziertheit der Merkmale," p. 175) and 4 ("Kriterium der übereinstimmenden Sondermerkmale," p. 178) are even more indicative of the incomplete state of Hennig's ideas about the reconstruction of phylogenetic relationships than are the first two rules: (3) in the case of character conflict, complex similarities overrule even a large number of simple similarities because simple similarities are more easily explained by convergent evolution; (4) characters that appear to have no function are better indicators of phylogenetic relationship than those that have a known function because "from experience the latter [characters] follow certain evolutionary trends" (Hennig, 1950:178).

In retrospect, only the first two criteria may be discussed as methods for determining the polarity of character transformation series. However, the "common equals primitive" rule should not be used because it can lead to incorrect results (e.g., Stevens, 1980; Watrous and Wheeler, 1981), and the ontogenetic criterion *sensu* Hennig is highly controversial (e.g., Nelson, 1973, 1978; Stevens, 1980; Kluge and Strauss, 1985; Wheeler, 1990). The third and fourth rules are of an entirely different kind and remind one of criteria that may be used to approximate the probability that structures are homologous (cf. Hennig: congruent complex and "neutral" characters are more likely to be homologous). These rules alone demonstrate how far Hennig was in 1945 from distinguishing between the two steps in character analysis: homologizing and determining polarity.

A third method that Hennig suggested for reconstructing phylogenetic relationships is the "chorological" one:

As a basic rule for the relationships between the "chorological" distribution and the phylogenetic relationships of taxonomic groups of the higher order, it may apply that groups of species which belong to a monophyletic group are also restricted to spatially circumscribed areas. (Hennig, 1950:194-195) (Appendix, note 16)

According to Hennig, this rule is as approximate as the "the more similar, the more closely related" rule as used in the holomorphological method. Nevertheless,

Hennig described a number of examples at length and developed a general rule of vicariance: "Vicariant groups of organisms, regardless of their rank, share a first order phylogenetic relationship, and thus they need to be coordinated in the system" (Hennig, 1950:198) (Appendix, note 17). Today, this rule is also judged inappropriate for reconstructing phylogenetic relationships. Even if taxa occupy adjacent geographic areas, it is still necessary to determine whether this distribution is derived or ancestral.

Although Hennig's clearly circumscribed goal in the *Grundzüge einer Theorie der phylogenetischen Systematik* in 1950 was the reconstruction of phylogenetic relationships, his methods were at that time not capable of achieving this goal.

A 1953 paper on insect phylogeny still had no discussion of methods for polarizing characters, although Hennig had already recognized that monophyly can only be based on apomorphies. However, here a clear distinction between the two steps, first determining homologies and second establishing polarity, was realized. It remains nevertheless unclear how Hennig distinguished between derived and ancestral states in the cladistic analysis of insects that he presented.

The next comprehensive discussion of methods for reconstructing phylogenetic relationships is found in Hennig's 1966 book. Compared with the 1950 *Grundzüge einer Theorie der phylogenetischen Systematik*, the methods chapter of the 1966 book was more or less rewritten and reorganized. The paleontological method now appears last and the chorological method is no longer elaborated in nearly as much detail, being shortened by more than two thirds. The first part of the chapter on reconstructing phylogenetic relationships deals with the comparative holomorphological method. It benefitted from Remane's writings on homology, and Hennig adopted criteria described by Remane (1952) for determining whether characters are similar enough to be called homologues. As in the 1953 paper, Hennig distinguished between the two steps in the

study of characters. First putative homologies are established, and then polarities are assigned. Polarity assignment belongs to what Hennig still called character phylogenetics. According to him, there are four criteria for assigning polarities. Because the 1966 book is sufficiently known, we mention these criteria only briefly: (1) the criterion of geological character precedence, (2) the criterion of chorological progression, (3) the criterion of ontogenetic character precedence, and (4) the criterion of the correlation of series of transformations (Hennig, 1966:95-96).

The one criterion most frequently used today, outgroup comparison, is not mentioned in 1950, 1953, 1966, or even the later draft of his textbook on systematic zoology (Hennig, 1984). Although he was certainly aware of outgroup comparison, Hennig's position remains unclear. However, Hennig (1953, 1966) was aware of Maslin's paper (1952) that described various methods for polarizing characters, including a method that anticipated outgroup comparison. In his taxonomic papers, polarity decisions were often not discussed. If they were, sometimes evolutionary trends were invoked. Sometimes outgroup comparison was carried out by comparing the ingroup with a close relative, e.g., character states of "lower" insects with those of the Myriapoda (Hennig, 1955).

#### DISCUSSION

Hennig's *Phylogenetic Systematics* of 1966 was not a new book. Instead, it was only a revision of the 1950 *Grundzüge*. His ideas on how phylogenetic relationships should be reconstructed had changed considerably between 1945 and 1960, and the concept of the book published in 1950 was not able to reflect his advances in the theory of systematics. But apparently Hennig was aware of this problem. In early August 1965, he wrote to the translator, Dr. Zangerl:

When I was writing the manuscript I had difficulties finding the right compromise between the original [the 1950 book] and a truly revised edition. Since a "translation" had been proposed to me, I tried to keep as much as possible of the structure and the text of the original. But the original mainly

reflected the pre-war situation. (Hennig, unpubl. correspondence) (Appendix, note 18)

Although from a theoretical point of view the 1966 book was perhaps not as important as the 1950 first edition, this second edition contained the detailed discussion of hierarchy and, more importantly, methods for the reconstruction of phylogenetic relationships. Without the methods described in the 1966 edition, all the goals of the 1950 book would have been unattainable. It was also the 1966 edition that popularized Hennig's version of phylogenetic systematics. Thus, historically the second edition was much more important because the first edition went widely unnoticed (Kühne, 1978; for conflicting views, see Craw, 1992).

The 1950 book is certainly a milestone in the history of systematics. At this early stage, Hennig already defined phylogenetic relationships through recentness of common ancestry and accordingly modified the definition of monophyly. However, the real significance of Hennig's book can only be assessed in comparison with ideas laid down by the most influential contemporaneous systematists. We briefly compare Hennig's book with other prominent contributions to systematic theory from that period: Huxley (1940); Mayr, Linsley, and Usinger (1953); and Simpson (1961).

#### *Evolutionary Systematics*

The neontologists who called themselves "new systematists" focused on species-level problems and largely neglected the study of higher taxa. Thus, Huxley (1940) and Mayr et al. (1953) mainly dealt with species and species-level problems: "In any case, the problem of species, in this dual aspect of their differentiation and their maintenance as separate groups, is at the heart of both the theory and the practice of taxonomy" (Huxley, 1940:4). "This brings us to the more strictly taxonomic aspects of our subject. These, as already noted, largely centre around the concept of species" (Huxley, 1940:16), and "the species is the most important taxonomic cat-

egory, not only for the taxonomist but also for the general biologist" (Mayr et al., 1953:23). Evolutionary systematists stress "practical convenience" (Huxley, 1940:19) as being important for classifications: "there are a certain number of exceptions where a phylogenetic interpretation is meaningless, and others where taxonomy and phylogeny cannot be made to square with each other" (Huxley, 1940:20), and "it is obvious from these examples that a compromise must often be made between the practical aims of classification and its phylogenetic basis" (Mayr et al., 1953:44). A strictly phylogenetic system was not ideal for Huxley (1940) and Mayr et al. (1953), and no definition of monophyly or phylogenetic relationships nor rules for their reconstruction were specified.

Huxley (1940) discussed whether higher taxa are "real." His argument is difficult to follow because the terms categories and taxa were used interchangeably, but the following quotation appears to apply to taxa:

Species are seen in the majority of cases to be definable as distinct self-perpetuating units with an objective existence in nature, and therefore on a different theoretical footing from genera or families or other higher categories, which are not definable in this concrete way. (Huxley, 1940:4)

Thus higher taxa are, according to Huxley, not objective, only species are. What a difference from Hennig, who concluded that higher taxa are as real as species because they are in a historical sense identical to their stem species, given, of course, that the higher taxa are strictly monophyletic.

As a paleontologist, Simpson (1961) discussed the origin and nature of higher taxa in detail. Having read the first edition of Hennig's *Grundzüge*, he actually responded to Hennig's positions. However, he reached completely different conclusions as to what the goals of systematics should be. As an evolutionary systematist, he thought that "the 'best' (most meaningful, most useful for many inductions) method of classification is by evolutionary relationships and not solely on similarity of individuals" (p. 27), but his "evolutionary relationships" are quite different from Hennig's phylo-



genetic relationships: "That classification can or should express phylogeny is an evident error" (p. 107). "It is preferable to consider evolutionary classification not as expressing phylogeny, not even based on it (although in a sufficiently broad sense that is true) but as *consistent* with it" (p. 113, emphasis in original).

Simpson's definition of monophyly is very different from Hennig's. He rejected Hennig's position that monophyletic higher taxa originate in a single stem species via dichotomous speciation:

An apparently better definition, and one usual when the word is defined at all (most taxonomists fail to define it), would be descent from a single species. That can, nevertheless, readily be shown to be undesirable in principle and usually inapplicable in practice. (p. 123)

For Simpson, the essence of "monophyly is the derivation of a taxon through one or more lineages . . . from one immediately ancestral taxon of the same or lower rank" (p. 124). This definition explicitly allows paraphyletic taxa *sensu* Hennig (1965, 1966), and possibly for this reason there was little incentive for Simpson to develop methods that can be used for reconstructing phylogenetic relationships. Accordingly, Simpson restricted his discussion of characters to general statements such as "characters in common tend to be proportional to recency of common ancestry. The distances between lower taxa in this approach are inversely proportional to characters in common" (p. 191), and promising ideas are not developed in detail:

Not only characters in common but also sequences of varying characters within groups enter into phylogenetic and other taxonomic studies. Here the main problem is to distinguish primitive from specialized characters in a sequence and to relate characters to the propinquity of the common ancestry. (pp. 67-68)

#### CONCLUSIONS

Hennig undoubtedly made a very significant contribution to systematics. It is generally acknowledged that his definitions of monophyly and phylogenetic relationships created the sound foundation

of phylogenetic systematics. But his second contribution was almost as important. After decades of discussing species-level problems, he redirected the interest of systematists to the study of higher taxa and the reconstruction of phylogenetic relationships. Kühne's (1978) conclusion that *Phylogenetic Systematics* (1966) was a publication that caused a revolution in systematics is certainly correct. Hennig undoubtedly influenced systematics like no other biologist since Linnaeus and Darwin. Moreover, ecologists and evolutionary biologists are increasingly using cladistic techniques, and Hennig's concepts have spread well beyond systematics.

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## APPENDIX

### ORIGINAL GERMAN TEXT OF QUOTATIONS

1. . . . deren Aufgaben an Bedeutung hinter denen keiner anderen biologischen Teilwissenschaft zurückstehen. (Hennig, 1947:279)
2. Mit der Besprechung der Subspeciesgliederung einer Art sind wir somit auf das Gebiet der phylogenetischen Beziehungen gekommen. (Hennig, 1950:94)
3. Die Annahme, daß auch den Gruppen höherer Kategorienstufen im phylogenetischen System im gewissen Sinne Realität und Individualität zugesprochen werden muß . . . ist darin begründet, daß eine Stammart auch nach dem Zerfall in ihre Nachfolgearten, und zwar nur in ihnen gemeinsam, weiterlebt . . . (Hennig, 1947:279)
4. . . . zwei Arten, die aus einer gemeinsamen Stammart hervorgehen und damit eine Gruppenkategorie höherer Ordnung bilden, [müssen] als mit ihrer Stammart identisch angesehen werden, denn diese besteht ja in ihnen und zwar in ihnen gemeinsam weiter. (Hennig, 1950:115)
5. Zerfällt eine Art durch Aufhören eines Teils der zwischen ihren Individuen bestehenden tokogenetischen Beziehungen in zwei Arten, so hört sie selbst auf, als Art zu bestehen. Sie ist die beiden Tochterarten gemeinsame Stammart. Beide Tochterarten stehen zueinander in einem phylogenetischen Verwandtschaftsverhältnis ersten Grades. Sie bilden zusammen eine Gruppenkategorie höherer Ordnung . . . (Hennig, 1950:102)
6. Das relative Altersverhältnis der Ahnen . . . ist das einzige unmittelbare Maß der phylogenetischen Verwandtschaft. (Zimmermann, 1937, cited in Hennig, 1950:103)
7. Als monophyletisch entstanden können demnach nur Artengruppen—und das sind alle Gruppen höherer Rangstufe—bezeichnet werden, die letzten Endes auf eine gemeinsame Stammart zurückgeführt werden können. . . . hinzugefügt werden (muß), daß eine monophyletische Gruppe nicht nur Arten umfassen darf, die von einer gemeinsamen Stammart abzuleiten sind, daß sie vielmehr darüber hinaus auch alle die Arten um-

- fassen muß, die von dieser Stammart herkommen. (Hennig, 1950:307-308)
8. Diese Regel besagt, daß von zwei Arten, die aus einer gemeinsamen Stammart hervorgehen, häufig eine der beiden Tochterarten in ihren Gestaltmerkmalen der gemeinsamen Stammart ähnlicher bleibt als die andere, die sich gestaltlich von ihr fortentwickelt. (Hennig, 1950:106)
  9. . . . morphologisch ausgezeichnete Teilgruppen artenreicher Einheiten systematisch aus diesen [herauszulösen] und der Gesamtheit aller anderen Teilgruppen, ohne Rücksicht auf den Grad ihrer phylogenetischen Verwandtschaft [zu koordinieren]. (Hennig, 1949:137)
  10. Ich möchte Gruppen, die sich durch auffällige morphologische Sonderentwicklungen von ihren nächsten Verwandten entfernt haben, und daher im Vergleich zu ihren Schwestergruppen mit einem Range eingestuft worden sind, der nicht ihren phylogenetischen Beziehungen entspricht, als apomorph bezeichnen. (Hennig, 1949:137)
  11. Vielfach wird eine Gruppe sich hinsichtlich der einen Eigenschaft . . . als plesiomorph, in anderen als apomorph erweisen, ohne daß eine Gesamtbeurteilung möglich wäre ("Spezialisationskreuzungen"). Auch in diesen Fällen bleiben die vorgeschlagenen Bezeichnungen, dann eben für die Einzelzüge der Gestalt, verwendbar. (Hennig, 1949:137)
  12. In einer konsequent phylogenetischen Systematik zählen aber nicht die Übereinstimmungen in plesiomorphen ("primitiven"), sondern nur die in apomorphen ("abgeleiteten") Merkmalen. (Hennig 1952:103)
  13. . . . daß es grundsätzlich falsch ist von plesiomorphen und apomorphen Gruppen . . . zu sprechen. (Hennig, 1984:41)
  14. Es ergibt sich auf diese Weise aber auch eine Klassifizierung der morphologischen Merkmale in solche, die einen sehr engen und solche, die verschiedene weitere Grade der phylogenetischen Verwandtschaft anzeigen, eine Wertung der morphologischen Merkmale also nach ihrem Wert als Indikatoren verschiedener Grade der phylogenetischen Verwandtschaft. (Hennig, 1950:172)
  15. Merkmale, die einem größeren Kreis von Arten gemeinsam sind, zeigen eine weitläufigere Verwandtschaft an als solche, die einer geringeren Zahl von Arten gemeinsam sind. (Hennig, 1950:172)
  16. Als Grundregel für die Beziehungen zwischen der chorologischen Verbreitung und der phylogenetischen Verwandtschaft der taxonomischen Gruppen höherer Ordnungsstufe kann gelten, daß Artengruppen, die einer Abstammungsgemeinschaft angehören, auch in ihrer Verbreitung auf einheitliche Räume von einer bestimmten Geschlossenheit beschränkt sind. (Hennig, 1950:194-195)
  17. Vikariierende Organismengruppen, gleich welcher Ordnungsstufe, stehen zueinander in einem phylogenetischen Verwandtschaftsverhältnis ersten Grades und sind im System daher einander zu koordinieren. (Hennig, 1950:198)
  18. Bei der Abfassung meines Manuskriptes habe ich überhaupt vor der Schwierigkeit gestanden, den rechten Weg zwischen dem Original und einer Neubearbeitung zu finden. Da mir an sich eine "Übersetzung" vorgeschlagen wurde, habe ich mich bemüht, möglichst viel von der Anordnung und auch vom Text des Originales unverändert zu lassen. Aber das Original setzte sich vor allem mit einer Situation auseinander, wie sie vor dem Kriege bestand. (from letter to R. Zangerl, August 1965)