



Willi Hennig (1913–1976) in his fifties.

WILLI HENNIG'S IMPACT ON TAXONOMIC THOUGHT

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The present review is neither bibliographical nor historical. I hope merely to overview the methodological strengths and weaknesses of Hennigian taxonomic thought and of some recent works devoted to theoretical questions that have been revived by an increasing interest in that thought.

A FASCINATING EPISTEMOLOGICAL VENTURE

Willi Hennig (1913–1976) was a German insect taxonomist who was known during his life time among Diptera specialists for numerous monographs assignable at first sight to alpha systematics (100). Although he published a major work on theoretical taxonomy in German as early as 1950 (74), he became famous only after the publication in 1966 of the English translation of a second book (77), which was not published in its original language until 1982 (82). Initially, his work engendered fierce attacks on his “phylogenetic systematics” by members of other taxonomic schools (41). Recently, however, Hennig's ideas have come to form the foundation of the fashionable cladistic school. The epistemological analysis of this venture will be a task for the future, provided that the original works are not forgotten.

Hennig and His Works

On this topic, we only need to supplement a previous review (41). Besides a first theoretical paper based on Diptera (70), in 1936 Hennig published works on the *Rassenkreis* and the biogeography of the lizard genus *Draco* (71, 72). A criticism of the first paper (169) led Hennig to extend his study of Diptera larvae and to refine the notion of larva-imaginal incongruence (73). From this time on,

he substituted incongruence for *Rassenkreis* as evidence of the fundamental statement that similarity alone cannot indicate genealogy. This position, a virtual break with what was to become the Mayrian school, was acknowledged as early as 1948 (176). Hennig's 1950 book was a preliminary sketch, eventually improved by introducing the word and concept of *synapomorphy* (75) and by an acquaintance (76) with Woodger's logic. The English "translation" that appeared in 1966 was, then, a new book (77). Nowadays it constitutes the main avenue into Hennigian thought. Yet this is one of the weaknesses of the cladistic school: Having been completed in manuscript form in 1961, this book is not Hennig's *ultima verba*, and its translation is far from satisfactory (see examples of necessary retranslations below and in 55). In the same year (1966), Hennig's work on the Diptera of New Zealand (78) was translated into English; it contains the first hint of Hennig's doubts about what would become biogeographical "cladism" (see 41). An excellent Spanish translation of the 1961 manuscript was published in 1968 (79), but it has been overlooked. In 1969, Hennig's treatise on fossil insects (80) opened with a chapter representing "the most complete, the most balanced, and perhaps the most felicitous expression of his thought" (41, p. 10).

Since Hennig's death, his two fundamental books have been reprinted (74, 77). His treatise of 1969 has been translated [perhaps with too many interpolations and comments (81)], and his son, Professor Wolfgang Hennig, has edited three posthumous works: the most useful authentic German text of the first American book (82), a classification of Chordata (83), and—largely echoing a 1974 polemic with Mayr—a synopsis of the problems of phylogenetic research (84).

Hennig Today, Through Words and Works

Hennig's ideas, commonly considered part of what is called cladism, continue to be discussed in many writings. Some words, such as *cladism*, have to be explained, and a choice made among the various writings.

SOME POLYSEMIC WORDS When coining the word *clade* from "cladogenesis . . . taken over directly from Rensch," Huxley intended to denote "delimitable monophyletic units" (96, p. 454) or, more precisely, "monophyletic units of whatever magnitude" (97, p. 27). He seems not to have known of an older use of this word (36) referring to a group of great magnitude possessing a particular structural type, i.e. simultaneously applied to a taxon, a higher taxonomic category, and a grade sensu Huxley!

The adjective *cladistic* has been explicitly derived from *clade* sensu Huxley by Cain & Harrison, for whom "closeness of relationship in terms of phyletic lines can be called cladistic . . . [and] similarity due to common ancestry, not to convergence, can be called patristic" (20, p. 3). Both *cladistic* and *patristic*

(20) refer to phyletic affinity and need the clarification afforded by Sokal & Sneath (159, p. 220): *Cladistic* is a relation "through *recency* of common ancestry" and *patristic*, one by common ancestry (not otherwise specified). For these authors, who rely on the relationships of Hennig's opposing types I and Ia (76, Fig. 6), *cladistic* is "the type I phylogenetic relationship of Hennig, 1957." Thus, they equate a cladistic relation with a Hennigian one.

The noun *cladist* was introduced in 1965 "in line with the terminology developed by Rensch (1960), Huxley (1958) and Cain & Harrison (1960)" (116, p. 167). Although none of these authors referred to Hennig, in coining the word *cladism* Mayr typifies *the cladist* as one who adheres to that "phylogenetic school" of which Hennig is the "most articulate spokesman" (118, p. 167).

The word *cladogram* was introduced in the same year (1965) but has two different meanings. For Mayr (117, p. 81), "the cladogram of the cladist" meant the phyletic diagram of the Hennigian school. For Camin & Sokal (21, p. 312), the term *cladogram* is used "to distinguish a cladistic dendrogram from a phenetic one which might be called a phenogram"; unfortunately, these authors built their "cladograms" by phenetic and not by Hennigian techniques. Consequently, there are two kinds of cladograms: those relying on attributes (Hennig's *Stufenreihe*; Sneath's synapomorphograms, see 125) and those relying on objects (in phenetic constructs); their inadvertent use as synonyms (e.g. in 158, p. 160) is confusing.

In Hennig's works, these words are always set off by quotation marks and appear as mere citations. In works by other authors, *cladist* and *cladism* commonly apply nowadays to the school born of Hennigian thought, whereas *cladistic* and *cladogram* have become equally popular in both the phenetic and the Hennigian schools, and consequently, their meaning remains ambiguous. Even worse, *cladogram* has become a fashionable word that is sometimes used to denote intuitive constructs and no longer refers to a definite procedure.

SOME SIGNIFICANT WORKS Under such headings as cladism, Hennigism, and phylogenetic systematics, Hennigian thought nowadays underlies many works—by both supporters and opponents—on a wide variety of topics. For example, Hennig's name appears as a key-word in the titles of numerous works: methodological essays (5, 28, 41, 45, 69, 98, 107, 108, 128, 129, 149, 150); reports of meetings (58, 162); or special works on vertebrate paleontology (13, 66, 68, 151, 168), biogeography (33, 37, 143), parasitology (15), entomology (1, 42), and biochemical or molecular taxonomy (95, 139).

Works that do not refer to Hennig—whether in their titles or their lists of references—are becoming much more common. Owing to the increasing volume of this cladistic literature, only a limited number of recent sources can be cited to supplement previous reviews (see 41; and for botany: 62, 85).

Journal papers that offer factual applications of Hennigian methods are too

numerous to cite here; those dealing with theoretical questions have also proliferated, particularly in *Systematic Zoology*, and will be considered in the ensuing discussion when necessary. Review articles are scattered in various serials; those recently published in this *Annual Review* and in others bear specifically on Hennigian procedure (161) or document the degree of Hennigian penetration into various fields (biogeography: 99; paleontology: 136; molecular biology: 170) and particular taxa (22, 110, 112).

Symposia and symposium-like volumes with a predominantly Hennigian perspective have appeared in biogeography (133) and paleontology (19), as special journal issues devoted to Hennig (51, 87, 160), and as proceedings of the Hennig Society (60, 142). Others are found in fields where Hennigian thought has only begun to penetrate (88, 126, 163). Most of these volumes, however, reflect a balance between the conflicting taxonomic methods; some are of general or methodological interest (29, 56, 61, 106, 137, 153) and others bear on special fields—e.g. paleontology (31, 115), evolutionary theory (23, 152), biogeography (10, 155), primatology (26, 27), and arthropodology (65). Books or monographs with a Hennigian background include important general treatises (46, 67, 145, 165, 178) or major specialized studies in biogeography (132), paleontology (109, 111), primatology (166, 167), and entomology (2, 12, 35).

Textbooks that discuss Hennigian views from a biological (40, 148) or a methodological (103, 157) standpoint remain scarce. Handbooks, whether historical or epistemological, are somewhat deceiving in their treatment of Hennig. Jahn et al. (101) only give biographical details and an amalgam of Hennig's and Remane's quite different views on homologies (see 69, 98). Mayr (118) reiterates his criticisms of cladism and limits his support to the synapomorphy procedure. [See however, Ross (147a).]

Since Hennig's death, as many as 1000 books and papers illustrating or discussing his thought may have been published. Comparisons of Hennig with Darwin, Mayr, Simpson—even Picasso (33)—and, more recently, with Weismann (43) have also flourished. As impressive as the numbers of works and comparisons may be, an even greater number of taxonomists have never heard of Hennig (25, 138), and some of his peers are among his most determined opponents.

Under these conditions, it is obviously impossible to be content with enumerating numbers of books and papers; the following sections are, therefore, a personal attempt to evaluate the Hennigian impact on present-day taxonomy.

DISCOURSE ON A METHOD

At the beginning of the nineteenth century—besides the phenetic Adansonian and the genealogic Lamarckian concepts, which were both far ahead of their

times—the dominant paradigm was the so-called natural method, a Linnean system amended with the ad-hoc teleological principles of subordination and correlation of characters.

Darwin, who had “two distinct objects in view” (38, p. 61), carried out two independent revolutions. His biological revolution proposed a mechanism (natural selection) to account for the amount of difference between organisms. His taxonomic revolution, founded on the inference of descent with modification, advocated genealogical taxonomic arrangements freed from categorical and typological thinking. Darwin repeatedly distinguished *ranking*, which implies amount of difference, from *arrangement*, which implies descent. He recalled (37a, pp. 457–58) that even in the absence of a known mechanism, consideration of taxonomic arrangement alone would have directed him to the concept of descent. Regretably, he carefully elaborated the theory of selection but not the practice of taxonomy. This fact explains why the majority of naturalists—among whom Haeckel holds the foremost position (see 44)—eventually retained pre-Darwinian taxonomic practices.

The genetic revolution has led to two opposing views of taxonomy that correspond to each side of the Darwinian dualism. Those taxonomists devoted to “evolution as a process”—here termed Mayrians—study variation, selection, isolation, etc. When looking at the results of these processes, however, they support the use of categories (first of all, species), as well as the principles of typology (they highly prize “grades”) and overall similarity; they discard divisive procedures only at the lower taxonomic levels. *Taxonomically speaking*, the true Darwinians are those naturalists who focus on the products of evolution, whatever its mechanisms. They praise the agglomerative methods and break with typological thinking. They represent two schools that have developed independently of the Mayrians and of one another. The phenetic school rests on similarity and neglects categories; at the beginning, it discarded any concern for genealogy. The Hennigian school rests on genealogy and discards similarity; it initially was haunted by the equivalence of categories.

Such an opposition is highly significant. Any classificatory approach usually considers *objects*—that which is being classified, e.g. biological individuals or taxa—and their *attributes*, often called characters by naturalists. The relations between objects and attributes (in biology, between taxa and characters) may be viewed as *intensional*, as if attributes make objects, or as *extensional*, as if objects make attributes (see below). According to an intensional view, classification rests on the similarity of attributes; according to an extensional view, it depends on possible intrinsic relations between objects. Among biological objects—individuals and taxa—that are linked by a history, these relations make possible an extensional view that is precisely the one expressed by the Hennigian fundamental statement. The next section presents that statement and the corresponding logic and procedure; the following one will compare Hennigism with other schools.

The Hennigian Fundamental Statement

Hennig's approach to taxonomy starts from what I have called the Hennigian fundamental statement (41), which teaches that there is no absolute coincidence between similarity of attributes and genealogy of objects. The proposition "a common origin implies some similarity" is true, while the converse, "some similarity implies a common origin," is false (177). This kind of statement dates back to the fathers of genealogical thinking in taxonomy (Buffon, Darwin, etc.) and was even expressed by some naturalists who, instead of acknowledging actual descent, believed in an ideal affinity between living beings [it was then asserted that "similarities and affinities are two astronomically [*himmelweit*] different things" (122)].

To test for the lack of an absolute linkage between similarity and genealogy, Darwin and Hennig used several kinds of empirical facts.

1. Hennig considered the *Rassenkreis* (which he studied in the genus *Draco*; see 71, 72) as a demonstration of the fundamental statement. In these cases, however, the genealogical arrangements are merely inferred from the *vollständige Übergänge* (i.e. perfect transitions) between varieties (70, p. 171). These *Übergänge* are only similarity relationships, and Hennig eventually turned away from this circularity.

2. From the 5th edition of the *Origin* . . . (1869) on, Darwin adopted Fritz Müller's discovery of incongruences between larval and adult arrangements in Crustacea as a demonstration of the lack of an absolute linkage between similarity and genealogy. Likewise, from 1943 on, Hennig consistently substantiated his fundamental statement with the example of the frequent lack of *Deckung* between larval and adult arrangements in holometabolous insects (73). After 1950 (74), he used the term *Incongruenz*, which Van Emden (171) had revived from Weismann's work.

Incongruence in supraspecific arrangements, although frequently endorsed as such (41, 117, 156, 176), is not a valid demonstration. Sokal & Sneath rightly remark:

Incongruence between larval and adult classifications shows that the cladistic relationships cannot be exactly proportional to the phenetic relationships, since the cladistic relationships of adults and larvae of the same species must be identical, while the phenetic relationships need not be. This statement is true, but the converse is not necessarily true; that is, congruence does not prove the exact correspondence of phenetic and cladistic relationships because both larval and adult features might have both undergone convergence to an equal degree, although this is unlikely (159, p. 224).

In other words, the Hennigian fundamental statement can be demonstrated using larval-adult incongruences only if the set of organisms being studied is monophyletic. This monophyly, although often probable at lower levels, is precisely the fact to be demonstrated.

3. Besides the two “demonstrations” refuted here because they are founded on merely inferred genealogies, Darwin (37a, pp. 424, 433, 456) and Hennig (70, p. 171) used a third one that validly took into account sets of more probable genealogies. They considered that if one did not know the genealogy, incongruences between characters in different instars, generations, or sexes in a species could lead one to place the variants in unrelated taxa. This demonstration can be freed from the circularity of a categorical approach by considering the various allomorphs in what I call a proved, short lineage (44)—which can be operationally observed—rather than in a “species.”

Hennigian Logic and Procedure

As just noted, the Hennigian fundamental statement and its demonstrations are not recent discoveries. What is interesting is the logical consequences that Hennig drew from such a statement and, above all, the corresponding procedure.

HENNIGIAN LOGIC From an epistemological standpoint, this topic can be most profitably treated by comparing Darwinian and Hennigian approaches.

Major logical approaches Darwin and Hennig drew the same major logical deductions from the fundamental statement: (a) in order to be stable, the arrangement of taxa must reflect their history, i.e. their unique genealogy and (b) the hierarchically nested taxa, if genealogical, are monophyletic “individuals.” When considering proved, short lineages, it appears indeed that the individuality of the taxa, i.e. their reality, relies on their homogeneity and completeness. Therefore, long lineages can be considered proven only if they simultaneously satisfy the conditions of homogeneity (Darwin’s single progenitor) and completeness.

Homogeneity is a classical condition of monophyly. Completeness means that a taxon comprises its ancestor and *all the descendants of that ancestor*. The need for this condition was already foreseen in the third criterion of De Candolle’s (39) composite “definition” of species. In the *Origin of Species* . . . , Darwin stressed no less than 20 times the importance of considering the totality of the descendants of a given ancestor; but he used merely the term *all* (listed among the “words suppressed” from a recent Concordance; see 6) to express this condition. He employed *co-descended* for the first time in the 5th edition (1869) and *co-descendants* only in the *Descent of Man* (38, 1871 edition, p. 188). This notion of completeness, which was acknowledged “early in the history of evolutionary theory” (89), occurs commonly in classical studies. It is also explicit in works concerning pure lines (104) or the logic of taxonomy (48, 103, 180). Curiously enough, since 1971 (3) completeness as a criterion for monophyly has been challenged only by criticizing Hennig, and the recent

discussions of this criterion (25, 178) continue to ignore its consistent pre-Hennigian use.

Other logical approaches Darwin and Hennig do not draw the same deductions from the fundamental statement when they consider the treatment of categories and divisive versus agglomerative procedures.

1. Darwin openly denied the reality of categories, including that of species, using them only for convenience. Hennig's constant practice was to contrast species, as a *Wirkungssystem*, and the higher taxa. Beginning in 1936 (70), he searched for many years for the objective equivalence of rank; in 1969 (80) he finally recognized that this quest was premature (see 41). Given his repeated acknowledgments (e.g. in 76) of Woodger's anticategorical thinking and the multiplicity of ranks expressed in his later works (80, 81), it is evident that Hennig's ultima ratio could only be a theoretical rejection of categories. This rejection explicitly included the category "species" (84); thus it follows that Hennig "assumes the association of evolutionary changes with speciation only for the sake of convenience" (86). Today, considering the multiple mechanisms of isolation (already foreseen by Darwin), neo-Hennigians assert that intersterility results from apomorphic acquisitions developed along with the divergence of lineages (14, 178); this implies that interfecundity is not an essential criterion of species but only a plesiomorphic condition of variable categorical significance.

2. Darwin, not having elaborated explicit procedures in taxonomy, did not provide divisive or agglomerative models. By constructing divisive or semi-agglomerative arrangements, his followers seem to have betrayed his anti-typological and anticategorical thought; this is particularly true of Haeckel (see 44). Hennigian logic, on the contrary, is plainly agglomerative. Sneath (156) emphasized that an agglomerative construct exhibits more stability than a divisive one. In fact, a reappraisal at the higher levels in a divisive construct has no more repercussions on the lower levels than a modification at the lower levels in an agglomerative construct has on the higher ones. The best argument in favor of an agglomerative procedure is perhaps that it is emancipated from the teleological principles of subordination and correlation of characters. In this sense, Mayr (118) has rightly underlined the importance of replacing the divisive procedure with the agglomerative one—a "revolution" that lasted two centuries. It is worthwhile to recall, however, that when applied to a few large, scattered taxa, there are operational uncertainties (see below).

HENNIGIAN PROCEDURE Since the Hennigian procedure is agglomerative as to attributes, it is opposed to the Haeckelian one (44) and implies the rejection of predefined objects (and therefore of categories; see above). It proceeds in

two steps: (a) the analysis of attributes, called character analysis, and (b) the clustering of attributes.

Character analysis This constitutes the first step of the procedure and requires numerous small, densely distributed taxa (as often occurs in entomology where the procedure was born; see 42). These objects allow a relative evaluation (*Wertung*) of a few states—ideally two: apomorph and plesiomorph—for each attribute. *Apomorphy* refers to an attribute (not object) that is unique among the numerous objects (*autapomorphy*) or shared by only a few of them (*synapomorphy*); *plesiomorphy* denotes the converse condition, found in most objects. These terms are necessarily relative and may vary for each attribute of an object.

Hennig identified the “frequency of occurrence” (*Häufigkeit des Vorkommens*) of an attribute state as the foremost criterion of plesiomorphy (common occurrence) or apomorphy (unique occurrence). Hennig believed, however, that it is possible to determine attribute polarity on the basis of the intrinsic criterion of ontogenetic precedence of states in a single taxon. He also thought that the extrinsic, diachronic criteria of geological precedence and chorological progression might be helpful. He disregarded all subjective criteria on principle (as presuming a functional significance or a success in evolution) but retained logical criteria such as complexity of characters (see an implicit critique in 144) and correlation of transformation series.

From the beginnings of modern descent theory, all of these criteria for evaluating states of attributes have been used in deciding between primitive and derived states. Their critical study has been enhanced by both Hennig (74, 77) and his followers (for bibliography and critiques, see 41). A prime example of such a discussion is offered by Stevens (161), who seems to be the first to have taken into account the data and opinions of both zoologists and botanists. Having carefully scrutinized all the criteria, Stevens concluded that the best assessment of the polarity of attribute states rests on out-group comparison. I would even argue that most of the criteria should be reduced to this ultimate one, which has been carefully worked out (175) and is an *R*-technique (see below).

Two kinds of criteria, however—those linked to chorological or to paleontological documentation—seem impossible to reduce to out-group comparison of attributes. In fact, the distribution, or date, of a taxon is not an attribute but a document because it depends on the extrinsic and never exhaustively explored dimensions of space and time. I use the word *document* for what, despite the Darwinian critique (see 37a, p. 486), has been frequently viewed as “armorial bearings.” Although such documents have given rise to considerable discussion, the conditionality of their use in phylogenetic taxonomy has not yet been logically formalized. It is not clear under what circumstances distributions and dates can be viewed as extrinsic but questionable documents or as having

the same significance as intrinsic attributes. The biogeographical aspect will be treated below; as for fossils, the reader is referred to Hennig himself and to numerous reviews or symposia (see, for example, 13, 19, 23, 31, 41, 59, 87, 111, 115, 136, 151, 152, 168).

Clustering of oriented attributes This second step constitutes the most original part of Hennigian procedure. Except for a few precursors, phylogenetic taxonomists before Hennig clustered objects according to a Haeckelian view of conservative evolution by searching for the most primitive ancestor and often for plesiomorphic attributes (see 44). In contrast, Hennig's principle (149, 150) requires clustering to be started using the most divergent apomorphies. The smallest objects that share the most diverging apomorphy are considered as sister objects and form a synapomorphic taxon. By continuous chaining, the successive-sister apomorphic taxa of t rank constitute in ascending order the successive taxa of $t-1$ rank. In my opinion, "the word synapomorphy expresses the full spirit of a true genealogical and Hennigian procedure" (44). Logically, synapomorphic clustering is equivalent to the single-link method advocated in phenetics (49, 103). Biologically, it corresponds to the proven fact of descent with modification. Genealogically, it affords the only conceivable way of building strictly monophyletic arrangements—i.e. in which the taxa are homogeneous and complete. Consequently, the monophyletic taxa resulting from the chained clustering of synapomorphies are defined not by attributes (similarity) but by members (genealogy); this is a requisite of the Hennigian fundamental statement and of an R -method (see below).

Obviously, such a chaining of synapomorphies—from those that substantiate the smallest taxa to those that indicate the largest ones—reflects a parsimony procedure. It could be faced with unsolved convergences and parallelisms, especially among attributes of simple pattern, e.g. molecular ones (see examples in 144). Perhaps in this case the alternative procedure of character compatibility would be appropriate (see 113, 164); its para-Hennigian value is a subject for discussion (54, 55a).

The Hennigian clustering procedure results in a multiplicity of categories (which leads to the rejection of that concept). The corresponding nomenclature of the nested taxa—if necessary at each rank—could raise practical difficulties (see 41). Yet, despite the place it is given in some phylogenetic treatises (178), nomenclature is not taxonomy; it is nothing but its servant and must consent to some compromises.

THE CHALLENGE OF METHODS AND OBJECTS

During the last 30 years, all scientific fields have been invaded by numerical taxonomy (see 157, 159). Similarly, Hennigism now seems to have come of age. The mere expansion of these methods, however, does not demonstrate

their universal value. During the eighteenth century, all kinds of objects—minerals, illnesses, etc.—were classified according to Linnean procedures, and at the end of the nineteenth century, scholars brought up on natural history and Darwinism saw genealogies in every field. Because of the evident misuses, such past generalizations aroused numerous, useful discussions among naturalists. Likewise, one must acquire a critical understanding of both objects and methods before deciding whether present-day methods can legitimately be applied to each kind of object and, conversely, if the objects are being viewed with the right method.

Various Concepts of Methods and Objects

Despite the psychogenetic relation that ultimately unites the concepts of objects and methods, logically one can only consider them as separate notions.

TAXONOMIC OBJECTS The inclination to apply a “neutral” method to the objects of taxonomy has been strengthened by the view that the historical relations between these objects can be known only by inference. It is precisely this question—theory now or theory later?—that Hull (89) raised when he recalled some biologists’ opinion that “classification should be theoretically neutral; no theoretical considerations should ever intrude during the formation stages of classification although theoretical inferences may be drawn from the classification afterwards” (90). Such a *petitio principii* reflects the major conflict between Mayrian and Hennigian taxonomists, which rests not on methods (Mayr supports the value of synapomorphy) but on objects. Mayrians emphasize the amount of difference and Hennigians, the pattern of descent.

A poor translation ascribed the following opinion to Hennig:

This is probably a lingering effect of the ancient concept of the “ladder of organisms”, expecting that a developmental series from “lower” to higher, or at least from more “primitive” to derived forms, must be expressed in the phylogenetic system. But the task of the phylogenetic system is not to present the result of evolution [sic], but only to present the phylogenetic relationships of species and species groups on the basis of the temporal sequence of origin of sister groups (77, p. 194).

If critics puzzled by this declaration (25) had read it in Spanish (79, p. 263) or German (82, p. 188), they would have understood it as follows:

The expectation that the phylogenetic system must also express an evolutionary series from “lower” to “higher” forms—or at least from “more primitive” to “more derived” forms—is probably a lingering effect of the very old concept of the “chain of beings.” In fact, the task of the phylogenetic system is only to describe the phylogenetic relatedness of the species and groups of species according to the temporal sequence of the birth of the sister groups; it is not to describe the final success [*éxito* or *Erfolg*] of the evolution.

Such a statement demonstrates that, according to Hennig’s view of phylogenetic research, the pattern of descent must take precedence over the final success (e.g. fitness, adaptation, progress) of the descendants. The distinction

corresponds to the dualism of Darwin, who asserted that independent of any explanation of process, the arrangement of products alone would have convinced him of descent with modification. It also reflects the point of contention between Hennigians and Mayrians. Hennigian taxa are strictly monophyletic lineages, i.e. complete and homogeneous, regardless of the degree of modification of the attributes of their members. Mayrian taxa may be incomplete or heterogeneous, depending upon the gaps introduced among them by the differential success of attributes in nature—or in the minds of naturalists.

This conceptual duality affects research objectives: For biologists who stress processes, models of evolution can generate heuristic taxonomies; for those who focus on the results, models of genealogies can produce heuristic views of evolution. Among the bicentenary profusion of alleged arrangements and mechanisms—whatever may by chance be the predictive value of a particular one—only the research is actually heuristic. In this sense, the analysis of object discontinuities (genetic diversity, reproductive isolation, population ecology) is as heuristic as that of attribute discontinuities (plesiomorphies, apomorphies, and incongruences at various levels of development or organization). Since all of these discontinuities are accessible to observation and experimentation, a theory of objects may be devised now or later, i.e. it may either precede or follow the development of a theory of attributes.

TAXONOMIC METHODS The use of so-called numerical methods in taxonomy has been favored not only because of the “neutrality” of mathematics and the aura of computers, but also because of the following epistemological constraints:

1. Mathematization is frequently viewed as self-justified (e.g. one refrains from examining the Hennigian principles “since they are primarily non-numerical”; see 127). Such an attitude neglects a more basic distinction than that between quantitative and qualitative thinking, i.e. that between intensional and extensional thinking (see 180, pp. 15, 23, 64), of which only a few taxonomists are aware (14, 16, 18, 105, 144).

2. The intensional methods that antedate the reception of Boolean thought [“based squarely upon the relations of extension” (180, p. 64)] have routinely been applied. Williams avows this when he says:

Purely logical considerations have played little part in clustering theory. Few problems are amenable to the “X is A or not – A” type of approach; clustering procedures have developed because so many problems involve the many-valued or continuous concept of “X is more like Y than it is like Z.” Set theory may have its place in consideration of the nature or purpose of classification . . . , but for the construction of classifications more conventional algebraic techniques are unavoidable (179, p. 304).

3. Clustering has obscured analysis, which necessarily constitutes a prior step.

4. The phenetic intensional technique usually refers to the taxonomic philosophy of Gilmour, for whom "a natural classification is that grouping which endeavours to utilize all the attributes of the individuals under consideration" (63). This postulate is even commonly substantiated by referring to the notion of information content. In fact, "classifications in the narrow sense are incapable of storing much in the way of specific information. Rather than being storage-and-retrieval systems themselves, they serve as indexes to such storage-and-retrieval systems. The information resides in the monograph, not in the classification" (89, p. 28), and perhaps not even in the monograph but in the object. This statement seems to be true for the classifications of all schools (11). Nevertheless, Gilmour's postulate has been accepted by pheneticists for whom *natural classification* means one "whose constituent groups describe the distributions among organisms of as many features as possible" (50, 52).

Obviously, the dispute between pheneticists and Hennigians is not about objects (today, pheneticists admit phylogeny) but about method. Although both advocate an agglomerative procedure, they start from opposite considerations. The functors of the phenetic analysis of objects are the attributes; those of the Hennigian analysis of attributes are the objects. Thus, phenetic taxonomy is intensional, since for appraisal of each object, it requires an intensive study of its various attributes, *Q*'s (*qualitas*). Conversely, Hennigian taxonomy is extensional since, for appraisal of each attribute, it requires an extensive consideration of various objects, *R*'s (*res*). The *Q*-procedure of the phenetic taxonomy best defines each OTU (class or exemplar) when, at the analysis step, it uses a large number of attributes, whether discrete or not. At the clustering step, three techniques can be applied: complete-linkage, average-linkage, or single-linkage; some authors recommend only the last one (49, 103). The clusters delimit the supraindividual taxa that are polythetic classes (monophyletic or not) defined by a diagnosis (not by content) and nested in continuous phenetic ranks with increasing distances between objects. The *R*-procedure of Hennigian taxonomy best defines each state of an attribute when, at the analysis step, it uses a large number of objects, whether they are of the same "rank" or not. At the clustering step, three techniques (homologous to the former ones) can be applied: sympleisiomorphy, typology, and synapomorphy; Hennig uses only the last one. The clusters delimit the supraindividual taxa that are monophyletic individuals (monothetic or not) defined by content (not by a diagnosis) and nested in discontinuous phyletic ranks of successive divergences of attributes.

The mere operability of the above methods implies, besides the intentional postulate of the *Q*-naturalness of objects as a function of attributes, the recognition of the inverse extensional postulate of the *R*-naturalness of attributes as a function of objects (which seems to have been formulated only implicitly; see 91). Ultimately such "naturalnesses" are only partial; according

to De Candolle's (39) criticism of Adanson, total naturalness would require that all the attributes of all the objects be known.

Generalizations as Empirical Tests

Various instances of expanding or interchanging procedures and objects afford the candid taxonomist an opportunity to test empirically the legitimacy of a number of inadvertent generalizations of methods.

GENERALIZATIONS OF *R*-TECHNIQUE The extensional *R*-technique of agglomerating attributes tested against objects encounters difficulties when attributes are under- or overestimated. An underestimation occurs when intrinsic, reproducible (i.e. homologous) attributes, such as those of living beings, are considered as documents independent of the descent of objects. Conversely, an overestimation occurs when documents independent of the descent of objects are viewed as intrinsic, reproducible attributes.

"Transformed cladism" The disagreement over the question of theory or no theory illustrates an underestimation of true attributes. Discarding some precursory remarks, it seems to have arisen from a polemical paper by Nelson (130) and an expanded version of this paper by Nelson & Platnick (132) expressing strictly formal views about phylogeny. Numerous attacks were launched against the authors, labeled pattern cladists (8), and against their alleged sterile enterprise (4), which was called dendronomics (120) or transformed cladism (24, 25). Platnick convincingly assumed the defense but, unfortunately, in an article whose title at first sight credited the school with a "transformation of cladistics" (140); there were numerous other advocates as well (e.g. 14, 59, 134, 138). Apparently these Nelsonians—despite a formal and unattractive treatment—strictly follow the Hennigian principles, both in terms of character analysis and synapomorphic clustering. Without any discontinuity or transformation of method, their "methodological cladistics" remains, as before, grounded on parsimony. This technique is, moreover, thoroughly defended by Farris (54).

The conflict rests ultimately on a philosophical requisite that constructs be independent from evolutionary theory (not merely from a particular one). Patterson (138) reduced the crucial point of the debate to whether homologies and monophyly must be *constructed* by an operative parsimony or *defined* by real descent from a common ancestor. Darwin resolved this problem in terms of probabilities: If there are so many homologies, they cannot be without a cause and the only scientifically conceivable one is descent with modification. Hennig explicitly adopted this solution (75, 77; see also 41), and his position on this point has been contrasted with Remane's (see 69, 98).

The consideration of objects governed by a reproducible syntax (although they are not living organisms) may demonstrate that despite the Nelsonians'

reluctance, homologies must have a cause. The significant messages (or texts) appear suitable for copying and in this respect are similar to organisms. For a long time, they have represented the field of application of a classifying *R*-technique, i.e. the Lachmann (ca. 1850) or "stemmatic" method, also called the "method of the common faults" (9, 59a, 114). Two transformed cladists have argued that this old method corresponds to Hennigian synapomorphy (141). It is notably more objective than stylistic judgment in the humanities, which is the homologue of the gradistic one in biology.

It is significant that through stemmatics one can chronologize related texts, the only possible history of which results from copying with modification. If the existence of a syntax (molecular or linguistic) makes the reproduction of organized individuals or texts possible, descent (whether repetitive or with modification) is the prime cause of their history. The descent—that of Darwin's *Descent of Man* and of *Descendenztheorie*—is real for organisms (i.e. *omne vivum e vivo*) and also for texts (i.e. no copy without a model). The modifications, whatever their mechanism (e.g. fault in autoreproduction, clerical error), are equally real. When they arise, descent with modification necessarily follows. This statement does not imply a particular theory about the mechanism involved, and consequently, Nelsonians could acknowledge evolution as an outcome of reproduction.

Use of nonhomologous attributes This type of overestimation of "attributes" is illustrated by the so-called Hennig-Brundin biogeography (37). For these authors, geographical distributions represent attributes of the object-taxa. In fact, the distributions are acquired and nonreproducible and constitute documents concerning the taxa, rather than inherited, intrinsic attributes of these objects. Such documents can be viewed as attributes characterizing the objects only for those objects whose intrinsic divergence exhibits a coincidence (parallelism) with extrinsic distribution in space. This corresponds to the "progression rule" originally enunciated by Hennig, who eventually expressed increasing doubts about its universality (see 41).

GENERALIZATIONS OF *Q*-TECHNIQUE The intensional *Q*-technique of agglomerating objects tested against attributes encounters difficulties when objects are under- or overestimated. An underestimation occurs when individual objects linked by descent with modification, such as living taxa, are considered as extrinsic assemblages of attributes. Conversely, an overestimation occurs when extrinsic assemblages of elements are viewed as true individual objects.

Numerical cladistics This field illustrates the underestimation of living taxa. Since a *Q*-matrix can be converted easily into its inverse *R*-matrix, pheneticists

have ad libitum elaborated mathematical techniques for introducing some consideration of attribute phylogeny into their intensional method. All these techniques may ultimately be "phenetic methods in disguise" (158) and generalizations of Mayrian "objects" (delimited by a posteriori gaps). In recent years, one has witnessed the phenomenal growth of an inconclusive literature concerning the comparative value of these techniques (e.g. see 123, 146, 147, 158). Such controversies have fostered a return to standard Hennigian procedures in morphological (64), biochemical (144), and karyological (174) systematics. Two recent events will accelerate this movement.

In 1979 at the 13th Numerical Taxonomy Conference, "J. S. Farris amazed friend and foe alike by rejecting as philosophically defective most previous approaches to the logical basis of phylogenetic inferences, including his own elegant statistical work" (124); the Willi Hennig Society arose from this "speciation event" (121). Later, when speaking of (molecular) distance data in phylogenetic analysis, Farris confirmed that "none of the known measures of genetic distances seems able to provide a logically defensible method" and advocated carrying out "phylogenetic character analysis directly on electromorphs" (53).

Such a return to extensional methodology, which Mickevich had long defended (e.g. 123), has recently culminated in a theoretical work by Farris (54) and an interesting factual study by Patton & Avise (139). In the latter, trees obtained directly from qualitative attribute states and indirectly from distance matrices are tested against organismal "model" (i.e. syncretic) classifications. "In each case, the qualitative cladistic trees provided fits to model phylogenies which were strong and as good or better than those resulting from phenetic clustering of distance-Wagner trees based on manipulation of quantitative values in matrices of genetic distance." Despite some weaknesses inherent to electrophoretic attributes, the Hennigian constructs retain one major strength: Any point of ambiguity in a tree may be specifically identified. In other words, "there is a potential loss of information in first generating a distance matrix," whereas such a loss is avoidable when one can "focus upon analyses of the character states themselves." The treatment of the attributes available in an *R*-matrix via the detour of a *Q*-matrix appears, therefore, "an unnecessary and hazardous manipulation because the particular characters ultimately contributing to the tree structure are first submerged in a distance matrix." (All preceding quotations are from 139.)

Vicariance biogeography This "method" illustrates the difficulties arising from an overestimation of "objects." It considers the biogeographic units (usually areas) as objects and their biogeographic elements (the taxa living therein) as attributes. In this approach (30, 132, 133), it is argued that the method allows a relative dating of areas based on the genealogy of their

attribute-taxa. Although qualitative (the homologous quantitative one would be Croizat's "generalized tracks"; see 135), this is a true *Q*-method and, therefore, the inverse of the Brundin *R*-method; such an opposition is implicit in some discussions (17, 135). The feasibility (17, 47, 154) and value (32, 34) of the method have been strongly questioned by opponents (see also 155); even sympathizers (93) have recalled incongruent examples. In fact, biogeographic units are determined by events extrinsic to their elements (if not merely by geographical assumptions); they appear as assemblages of elements rather than as objects with intrinsic attributes. Such assemblages can be viewed as objects characterized by attributes only for those elements whose intrinsic divergence exhibits a coincidence (synchronism) with the extrinsic patterning of the areas in time. Such elements are termed vicariants and their study constitutes vicariance biogeography. Sometimes an annexation of *R*-terminology to vicariance biogeography results in labeling areas geological taxa and their trees (without a syntax of reproduction) geological cladograms, as if cladograms of organisms were built by dividing preexisting sets.

The Operational and Logical Relevance of Methods to Objects

Using an agglomerative method, whether *R* or *Q*, is not always feasible. When tracing historic relations between higher taxa or between areas, technical problems can arise from gaps in the required information. The value of clusters rests on the number and the *density* of the functors (objects or attributes). When there are important gaps among objects or in the knowledge of their attributes (or both), the higher clusters—whether phyletic or phenetic—cannot be determined from a chained agglomeration of lower clusters of increasing rank. One is compelled to suppose that the few a priori high-ranked objects (i.e. higher taxa, continents) are representative of a set of lower-ranked ones or that the scattered attributes (characters or elements) are "typical" of such objects.

Among extant objects and attributes, the uncertainty depends on the "circumstantial availability of data" (44). For fossils or continents, the uncertainty depends on the same factor plus the losses and transformations of attributes accumulated over time. The higher the rank of taxa (or faunal assemblages), the more ancient their common origin and, consequently, the more insufficient the data available for tracing this origin. It follows that at the higher levels an agglomerative technique is not operationally better than a divisive one. This fact explains the slow reception of Hennigism among "higher taxonomists" (see examples in 88, 153) and the debates on the "taxonomy" of biogeographic areas.

Although such impediments are operational and not logical, they force us to recognize that the limits of the methods depend on the objects. It must be pointed out that when the founders of phenetics and the transformed cladists advocate no theory, they are in fact, advocating no theory of methods and no

theory of objects, respectively. Whatever their excuses (e.g. difficulties in circumscribing the prerequisites of the methods or the ultimate properties of objects), such attitudes may lead to misuses or misinterpretations. In intuitive terms, although the numerical cladists reintroduce *R*-considerations in their *Q*-method, in overlooking the biases of the mathematical techniques they seem to equate such distinct concepts as extension and intension. In this case, the weakness proceeds from numerical routines that disregard other ways of thinking; this elimination can be equated with a theory. Similarly, although the Nelsonians apply specific methods to objects, in denying the importance of reproduction they seem to equate such distinct objects as taxa and areas. The source of the weakness here is a rigorous philosophy (Popperian?) that is opposed to inductive thinking; this choice in itself also constitutes a theory.

GENERAL CONCLUSIONS

Its sparring with both evolutionary and phenetic approaches to taxonomy has prevented Hennigism from yielding all it might have. Today, as in 1979 (see 41), it still has not been tested either at the infra-specific level or with asexual organisms. Attempts to test conflicting procedures empirically using lineages of "known" pedigree are few and inconclusive. Some rely on simulation models (158; other references in 57) that "produce situations where phenetic methods are superior to phylogenetic methods and conversely" (102); others rely on organisms whose "pedigree" is more alleged than proved, such as cultivars (7) and natural hybrids (119). Nevertheless, hybridization and reticulate evolution remain, as in 1979, a stumbling block for the Hennigian method (94, 131, 172, 173). Likewise, incongruence remains a procedural debate (54, 123, 147) and not a biological one, despite the need for analyzing the feedback between levels of development or organization (see 145).

Such deficiencies may reflect traditional taxonomists' reluctance to enter into critical areas of biological research and may also be due to fundamental difficulties relating to the link between taxonomy and evolutionary theory. These difficulties bear on the following topics: the *three* kinds of "species" (i.e. genealogical individuals, phenetic classes, and biologic systems), homology, objects and assemblages, the value of dates and distributions as documents or as attributes, congruence, parsimony versus compatibility, and the biogenetic law. The revival of these old questions, which could not be discussed sufficiently in a short review, bears witness to the stimulating impact of Hennigian thought.

Perhaps such discussions also could not have progressed further because of the number of redundant philosophical and mathematical considerations that submerge the subject. As to philosophy, the Nelsonians have apparently been locked into one position by their Popperianism, and it is necessary to arrange a

way out (92). Doing so, however, requires a more diversified philosophical debate than is currently available in the taxonomic literature. As to mathematics, due to inconclusive disputes about the variety of "dialects" (48) applied to taxonomy, it is not surprising that naturalists share the reluctance expressed by Darwin about what is often "a parade of mathematical accuracy" [37a, 6th edition (1872), p. 168].

Authors seem to choose a philosophical or mathematical method primarily for subjective reasons—e.g. the author's training in that particular field. On the contrary, the debate should focus on the objective conditions for applying methods to a reality of which naturalists have the best knowledge. Although considerations of propositional logic remain scarce in present-day taxonomy (4), this debate can ultimately be resolved only by relying on the common ancestor of philosophy and mathematics—logic. The acceptance of one or another method or theory would be furthered more by a sound, candid examination than by polemics, cleverness, and redundancy. This concern for logic was a constant in Hennig's personal thought; it has been the leaven of the present renewal in taxonomy.

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