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Points of View

Walter Zimmermann and the Growth of Phylogenetic Theory

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Walter Zimmermann, shown in Figure 1, is well known among plant morphologists for developing the "telome theory," which accounts for the derivation of lateral appendages from undifferentiated axes (Zimmermann, 1938, 1965). Plant systematists are generally aware of Zimmermann's collaboration with Arthur Cronquist and Armen Takhtajan in classifying embryophytes (Cronquist et al., 1966), and his "hologenetic spiral" is a familiar image to many botanists, having been reproduced in texts such as Foster and Gifford (1974:48) and Stewart (1983:81).

Although Zimmermann was cited repeatedly by Willi Hennig (1966), who referred to him as "one of the best of modern theoreticians of systematic work" (p. 9) and "one of the most zealous of modern advocates of a consistent phylogenetic systematics" (p. 10), his contributions to phylogenetic theory have been largely overlooked. Here we draw attention to his seminal theoretical paper, "Arbeitsweise der botanischen Phylogenetik und anderer Gruppierungswissenschaften" ("Methods of botanical phylogenetics and other grouping sciences"), first published in 1931. In this paper, Zimmermann clearly expressed many of the underlying principles of phylogenetic systematics—ideas that were later taken up by Hennig and formed the core of his theory. Zimmermann also focused attention on several basic methodological issues, especially those concerning rates of evolution and the analysis of what he called "character phylogeny."

BACKGROUND

Zimmermann (1892–1980) received his Ph.D. from Freiburg i. Br. in 1921, and taught in Tübingen, Germany, as a private lecturer (1925–1929) and professor (1929–1980) of botany (Stafleu and Cowan, 1976). Although he published extensively on matters of interest to plant systematists (see references in Zimmermann, 1965), we have not attempted to summarize this entire body of work nor even that portion of it devoted to systematic theory. Instead, we focus more or less exclusively on his paper of 1931, which is his earliest and most comprehensive treatment of phylogenetic analysis and seems to have influenced Hennig's thinking most directly. This paper, variously modified, also formed the basis of Zimmermann's contribution to Heberer's "Die Evolution der Organismen" (Zimmermann, 1943, 1967).

The 1931 paper appeared in "Handbuch der biologischen Arbeitsmethoden," an ambitious series of review articles (edited by E. Abderhalden) that endeavored to

summarize working methods in all areas
of biological research. The paper was ap-
parently not widely available until 1937
(both dates are cited, sometimes by the same
author; e.g., Hennig, 1966). Zimmer-
mann's work appeared in an unlikely po-
sition in the series, between a treatise on
the microscopy of skin capillaries of living
humans and an analysis of methods for
detecting hidden Mendelain genes for cold
pigmentation in red albino eyes, particu-
larly in rabbits. Several other contributors
to this series are more familiar to system-
atists, including A. Remane, L. Diels, and
C. Mez.

Zimmermann's paper is a comprehen-
sive account of systematic methods, which
includes extensive commentary on various
sources of evidence (e.g., comparative on-
togeny, plant geography, hybridization
experiments, and serology). We will not
review the entire paper, as many of the
particulars are no longer of general inter-
est. Instead, we focus on issues that are
most interesting from the standpoint of
phylogenetic theory as it was developed
by Hennig and as we known it today. A
more complete analysis of Zimmermann's
thought—its origins and its influence on
later developments—would certainly be
valuable, but this task deserves the atten-
tion of historians and philosophers of sci-
ence. We hope, in fact, that our account
will stimulate a more complete analysis of
Zimmermann's contributions, as well as
those of others who laid the foundations
of modern phylogenetic theory (e.g., Plate,
1914). Unfortunately, this subject seems to
have attracted very little attention in com-
parison, for example, to the history of
the "modern synthesis" (e.g., Mayr and
Provine, 1980).

The passages from Zimmermann quoted
below were translated by us. We have not,
however, prepared a translation of the en-
tire text. Although it might be valuable to
do so, it would be a major undertaking in
view of the length of the paper, the sub-
tlety of the material, and the style of writ-
ing. Furthermore, in contrast to the trans-
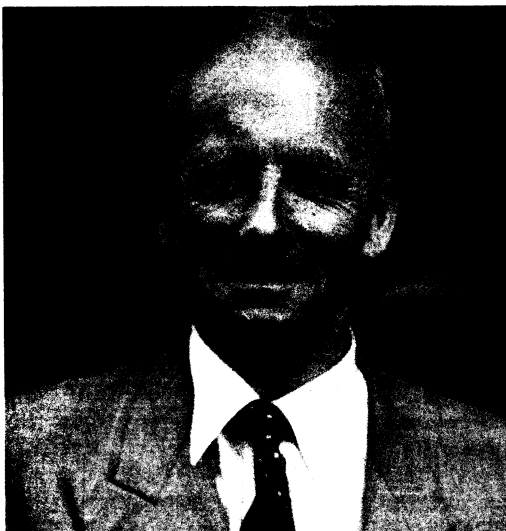lation of Hennig, which stimulated the
development of new methods in system-

FIGURE 1. Walter Zimmermann, 1959, IX Inter-
national Botanical Congress, Montreal, Canada (pho-
tograph courtesy of Arthur Cronquist, New York Bo-
tanical Garden).

atics, Zimmermann's work is now primar-
ily of historical interest.

GROUPING THEORY

The first section of Zimmermann's paper
(pp. 941–970), entitled "Die Fragestellung"
("The problem"), is devoted to the philo-
sophical underpinnings of systematic the-
ory. Although we concentrate on phylo-
genetic methods, we will outline briefly
the opening philosophical arguments, as
these provide the rationale for the remain-
der of the analysis. The general structure
of these arguments is also noteworthy, be-
cause much the same approach is evident
in the introductory sections of Hennig's
(1966) book.

Zimmermann's discussion revolves
around the comparison of three general
ways of grouping: special purpose (in
which basic forms or "types" are chosen
"randomly" for some practical purpose),
idealistic (in which the "type" is an ide-
alized form "chosen intuitively" and need
not correspond to anything that has actu-
ally existed), and phylogenetic (based on
genealogy). Phylogenetic grouping differs
fundamentally from the others in being

tied directly to objects that have a material existence in the world:

> The ancestral form [Urform] in phylogenetics once existed in reality; it is objectively characterized by the genealogical relationships, that is, by its position at the root [Wurzel] of the phylogenetic line in question [p. 949].

It is in this sense that phylogenetic grouping can be considered "objective," as compared with artificial (special purpose) or subjective (idealistic).

Having characterized these three approaches, Zimmermann expressed the central question, and his answer to it, in the following terms:

> Do we want to group phylogenetically, that is, following naturally given relationships? or do we want to group artificially? or do we want to group intuitively, following subjective impression? We do not have any other possibilities. Of course, one can do entirely without phylogenetics. One must be aware, however, that then one is forced to group artificially, or "idealistically;" phylogenetics is the only procedure which groups according to naturally given relationships, the only procedure which, through the act of grouping, directly depicts natural relationships [pp. 949–950].

Zimmermann's justification for preferring phylogenetic grouping is surprisingly subtle. After rejecting criticisms aimed at the degree of exactness of phylogenetic procedures and briefly discussing the role of intuition, Zimmermann at length discussed his main argument in favor of phylogeny. He argued that phylogenetic grouping assumes the separation of subject and object; that is, it accepts that there are objects that exist in the world outside the mind of the observer. In contrast, idealism denies any such separation and therefore can reflect only subjective ideas. Zimmermann made it clear that his position, which he referred to as "consistent [konsequent] dualism," was not strictly equivalent to "realism," which entails philosophical commitments that he clearly appreciated but preferred to sidestep. His acceptance of the existence of objects in the world was motivated instead by practical concerns. In particular, he argued that the realist/materialist position has been an eminently successful approach in other areas of sci-

ence. He adopted it, therefore, simply as an "axiom" or heuristic guiding principle. Furthermore, he contended that nondualistic approaches, which fail to sharply delimit object and subject, give rise to pseudoproblems, of which he offered several examples.

Having opted for phylogenetic grouping, Zimmermann was careful to acknowledge that the three methods can coexist and complement one another:

> It needs to be stressed that the mutual relationship between the different grouping procedures consists only in the decision which procedure we want to choose. In contrast to this, it is not true that individual results (obtained from the different grouping procedures) confirm or contradict each other. For example, a practical grouping obviously remains practical even when it is shown to be nonphylogenetic and vice versa the existence of "simpler" grouping does not contradict the correctness of a phylogenetic grouping [p. 975].

Nevertheless, he was firm in the belief that these different sorts of groups must not be confused with one another nor mixed together in a single system. This same position was adopted by Hennig (1966, e.g., p. 9), who also flatly rejected the idea that all but one method of grouping should be dismissed.

It is perhaps difficult, from our present perspective, to appreciate the need for such basic philosophical arguments. However, both Zimmermann and Hennig were forced to cope with idealism, which was at that time the dominant outlook among German scientists (Grene, 1958; Reif, 1986). Reaction to idealism is even more evident in Zimmermann's writing than in Hennig's, perhaps because some of Zimmermann's contemporaries in plant morphology were outspoken advocates of idealism, notably Wilhelm Troll (e.g., Troll, 1940; see Sattler, 1964).

Although idealism is now rarely defended as such, it is still evident in taxonomy, even in the work of those who appear to represent phylogenetic systematics. As unappealing as the prospect is to most systematists, we believe that progress in the development of systematic theory still depends critically on attention to

philosophical questions (e.g., see de Queiroz and Donoghue [1988] on "systems" versus "classes" in connection with the species problem). As Hennig (1966:78) noted, the systematist will have to come to grips with underlying conceptual issues, "if he is to avoid the justifiable charge of not knowing what he is doing or even what he is trying to do."

PHYLOGENETIC METHODS

The second part of Zimmermann's treatment (pp. 975–1048) is entitled "Die Phylogenetischen Methoden" ("The phylogenetic methods"). This section begins (as does Hennig, 1966) with an analysis of the place of systematics in biology and the special tasks of biological systematics. Regarding the analysis of the history of organisms, Zimmermann contrasted (1) description (which he equates with paleontology), (2) "historical phylogenetics," and (3) process-oriented research. The remainder of the paper is organized around the tasks he identified with these three areas: to discover whether evolution occurred, the historical course of phylogeny, and the causal factors responsible for phylogeny, respectively. This approach, which attempted to integrate microevolutionary process and macroevolutionary pattern, led Reif (1986) to conclude that Zimmermann was among a handful of German workers (including B. Rensch) who formulated a synthetic view of evolution, more or less independently of English-speaking biologists (see Mayr and Provine, 1980).

Our discussion emphasizes methods for discerning the course of phylogeny, which was Zimmermann's primary focus. He spelled out the goals of "historical phylogenetics" in the following terms:

> The task of historical phylogenetics is to find out "how it was." This task would be completely solved if we could, just by description, erect a gigantic phylogenetic tree of genealogical affinities for all organisms which ever existed and enter all transformations by which descendants are distinguished from their ancestors [pp. 981–982].

A general theme is evident in this statement and runs throughout Zimmermann's account, i.e., the distinction between a tree of taxa and the transformation of individual characters:

> Within this historical phylogenetics we can distinguish two main tasks as, so to speak, far and near aims: 1. taxon phyletics, and 2. character phyletics. Taxon phyletics is that branch of historical phylogenetics which in general can be characterized by the construction of phylogenetic trees of "species" or other taxa. . . . Character phyletics ("semophyletics"), the study of the transformation of individual characters, is, from a practical point of view, the basis of the whole of historical phylogenetics [p. 984].

Zimmermann clearly appreciated that analyses of taxon phyletics and character phyletics are closely related. Hypotheses about genealogical relationships among taxa "are deduced from the assumed relationships of characters" (p. 984). He considered character transformation series to be primary in that such ordering does not depend on knowledge of genealogical relationships, nor is it contradicted by such knowledge. However, a hypothesis of phylogenetic relationship is necessary to specify the number of originations of a trait, instances of reversal, and so on:

> one of the most important questions of taxon phylogeny is whether and when a character might have reversed; further in which sequence the different character transformation series followed each other [p. 985].

To clarify this point, Zimmermann offered two examples (modification of the foot in the evolution of equids and reduction of the gametophyte in land plants) to illustrate that although linear character transformation series are often presented, taxon phylogenies are trees, and some character modifications may have occurred only on lateral branches.

He was also careful to point out that the process of phylogenetic character transformation is continuous and does not allow a clearcut distinction between phylogeny and ontogeny. This argument foreshadowed his "hologenetic spiral," mentioned above. He also noted that for purposes of phylogeny reconstruction we are forced to select particular stages of the life cycle for comparison. Here, Zimmermann's outlook is similar to that of Hennig (1966:6), who
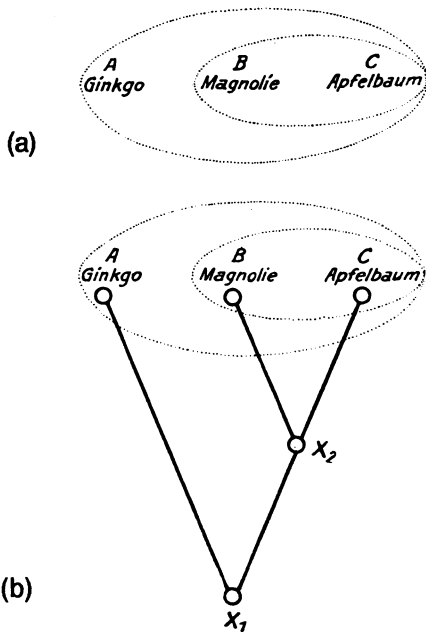
FIGURE 2. (a, b) Figure 172 of Zimmermann (1931: 990). Phylogenetic relationship as recency of shared ancestors (X1, X2).

used the word "semaphoront" for the individual organism at a particular point in its development.

Phylogenetic Relationship and the Grouping of Taxa

Zimmermann's definition of "phylogenetic relationship" is exceptionally clear. In reference to his Figure 172 (reproduced here as Fig. 2), he stated:

> We say that the plant or organs B and C are more closely related to each other than with A. The common ancestor of B and C (X2) existed more recently than the ancestor of all three plants or organs (X1). . . . The relative age relationship of ancestors X1 and X2 is the only direct measure of phylogenetic relationship [pp. 989–990].

In fact, he argued that no other representation is consistent with phylogenetic grouping:

> A statement about phylogenetic relationship which cannot be expressed in the basic scheme of Figure 172b [Fig. 2b] does not exist. . . . Whoever believes that he cannot illustrate relationships in this basic scheme . . . does not have a phylogenetic but an "idealistic" or purely systematic "relationship" in mind [pp. 989–990].

Only one exception was briefly noted, the "possible reticulate structure of a phylogenetic tree due to sexual hybridization between species" (p. 989).

For Zimmermann, knowledge of phylogenetic relationships was directly connected to phylogenetic grouping (see Fig. 2):

> In phylogenetically oriented systematics this relative grouping implies the positioning into the hierarchy of systematic categories: species, genus, family, etc. B + C, for example, might correspond to a species, and A + B + C to a genus, or B + C may correspond to a family, and A + B + C to an order or class, etc. [p. 989].

In contrast to grouping, however, Zimmermann considered ranking to be largely arbitrary: "the decision how big a group should be called 'species,' or 'family,' etc., can only be guided practically, conventionally" (p. 990).

Zimmermann also contrasted statements about phylogenetic relationship with those about the relative advancement or derivation of taxa. To say that one taxon is ancestral and another derived implies either that the former has a preponderance of ancestral features and the latter mostly derived states or that the taxon considered ancestral branched off earlier than the derived taxon. But these two meanings of ancestral and derived need not coincide. Zimmermann noted, for example, that the red algae are an ancient branch yet are highly derived in terms of many individual characters.

He also considered the derivation of coexisting taxa from one another:

> It is only in one case that such a derivation is truly possible in a taxon phylogenetic sense: Namely when the "derived" taxon is of phylogenetically smaller size than the ancestral taxon, i.e., when the derived taxon is part, an independently differentiated branch, of the (purely phylogenetically delimited) ancestral taxon [p. 1007].

In this case, although Zimmermann did not coin the term, the "ancestral taxon" would be paraphyletic (see Discussion).

Zimmermann's concept of phylogenetic relationship, which ties it directly to recency of common ancestry, represented a fundamental advance, without which, as
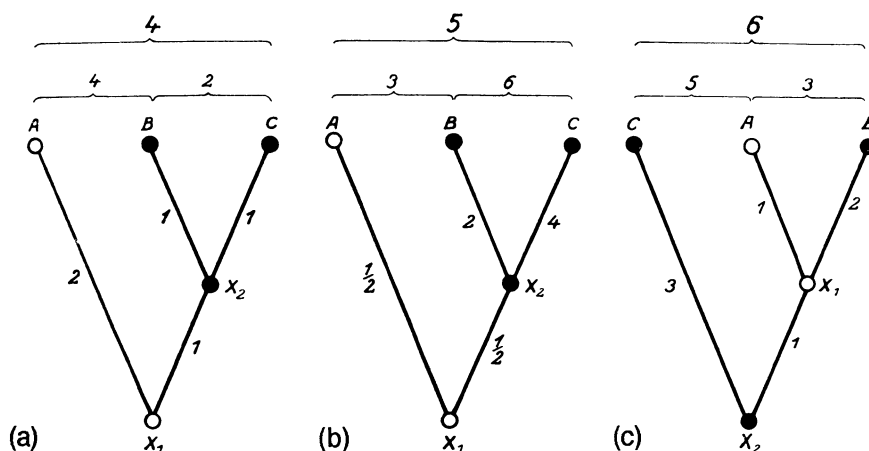
FIGURE 3.   (a–c) Figures 174–176 of Zimmermann (1931:997). The effect of unequal rates of evolution on the use of similarity in assessing phylogenetic relationship.

Hennig (1966:235) pointed out, "discussions of individual questions are useless and misleading." Indeed, Hennig reproduced Zimmermann's Figure 172 (without taxon names) in his book of 1950, and Zimmermann (1931), along with Bigelow (1956), were acknowledged by Hennig (1966:74) as sources for his definition of monophyly.

Similarity versus Relationship

Zimmermann's treatment of the practical methods of phylogenetic research begins with a discussion of the use of similarity in assessing phylogenetic relationships. He credited Plate (1912) with the recognition that similarity has often been substituted for relationship, in part because similarity and relationship were equated with one another prior to the advent of evolutionary thought. However, Zimmermann insisted that these are separate properties, with relationship referring only to recency of common ancestry. Consequently, the question arises as to the circumstances under which the use of similarity would actually lead one astray in assessing relationships. Zimmermann's answer is remarkably clear:

Degree of similarity would be an unobjectionable substitute measure for the degree of phylogenetic relationship if organisms would have become increasingly dissimilar in proportion to the passage

of time. This means that similarity is a substitute measure for degree of relationship only when the transformation of the characters studied in the phylogenetic lines in question took place 1. divergently, and 2. at an equal rate. If only one of these two preconditions does not apply, our phylogenetic claim "the more similar, the more closely related" very easily leads to mistaken conclusions [pp. 995–996].

Although Zimmermann briefly discussed convergence, parallelism, and reversal as sources of difficulty in using similarity to assess relationships, his analysis of unequal rates of evolution was especially cogent. Most of his discussion revolved around his Figures 174–176, which we have reproduced in Figure 3. In these trees, the numbers associated with the individual branches are meant to reflect the amount of change, and the difference between pairs of taxa is shown by the brackets above. Zimmermann made the point that if the amount of change in different lines (from a given ancestor to the included tips) has been equal, similarity will provide an accurate guide to relationships (Fig. 3a).

This situation differs from that in Figure 3b, in which the amount of change in different lines is unequal: A, X2, and B have not diverged very much from their common ancestor X1, whereas C has undergone a burst of evolution. Under these circumstances, similarity would be misleading, suggesting the false conclusion
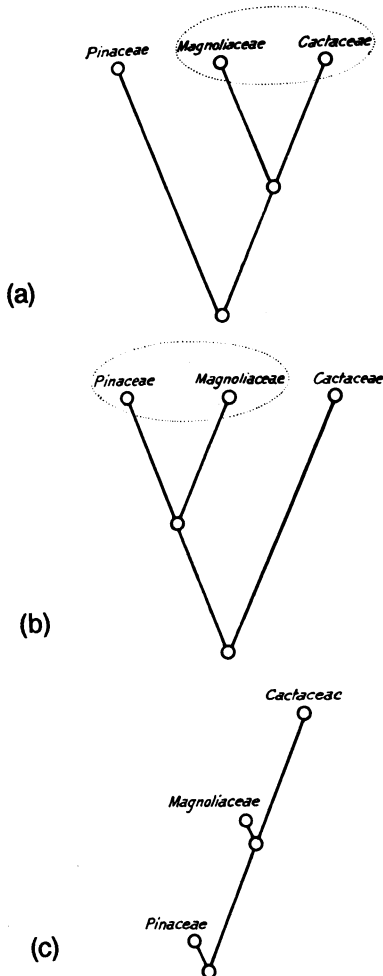
FIGURE 4. (a–c) Figures 180–182 of Zimmerman (1931:1029). The effect of unequal rates of evolution on the use of serological similarity in assessing relationships.

that taxa A and B are more closely related to one another than either is to taxon C (Fig. 3c). In this case, the branch lengths between taxa are faithfully preserved; however, the tree has been rerooted along the branch leading from X2 to C, such that the amount of evolution in different lines becomes more nearly equal.

Zimmermann recognized that unequal rates of evolution could be a very real problem in practice. He believed that such differences were characteristic of plant evolution, contrasting the "living fossil" *Ginkgo*

with some angiosperm families that evidently have generated new forms quite rapidly. He also noted that the extent of phenotypic change need not mirror the extent of the underlying genetic change. Thus, the fusion of organs, which might appear to be a major morphological change, could be brought about by a minor genetic shift.

Zimmermann provided a concrete example of the possible effects of unequal rates, referring to Mez and Ziegenspeck's (1926) tree based on serological evidence:

> Whether, as claimed by Mez and Ziegenspeck, no protein convergence occurs is doubtful, but even if the "specific" proteins would have evolved divergently throughout, the difficulty of unequally fast structural change remains. But when the protein differentiates fast in one phylogenetic line and slow in another, protein differentiation is no substitute measure for phylogenetic relationship [p. 1027].

Here he referred to his Figures 180–182, shown in our Figure 4. The serological data appeared to suggest that Magnoliaceae are more closely related to Pinaceae than to Cactaceae (Fig. 4b). Zimmermann noted, however, that it is quite likely that angiosperms are monophyletic (Magnoliaceae more closely related to Cactaceae; Fig. 4a), with rapid evolution in the line leading to Cactaceae and relatively little evolution in the lines leading to Magnoliaceae and Pinaceae (Fig. 4c).

Hennig (1966) cited Zimmermann's critique of the serological analyses of Mez but not his more general observations on rates of evolution. In fact, Hennig (1966:88) spent rather little time on the problem of rate inequality, citing only Bigelow (1958), who did not cite Zimmermann's earlier and more complete analysis.

Having specified how convergence, reversal, and especially unequal rates might lead similarity measures astray, what did Zimmermann recommend? In effect, he suggested that similarity be used but used cautiously:

> Comparison of similarity thus might be a more or less useful measure for the recognition of the degree of relationship, provided we first 1. take into account as many characters as possible; 2. limit

ourselves to large differences; and 3. take into account the diversity of the groups in question [p. 1000].

Although Zimmermann was keenly aware of the pitfalls of using similarity to measure relationship, he did not provide a method to avoid these problems. In particular, he did not arrive at anything like Hennig's principle of synapomorphy. This shortcoming is surprising in view of his emphasis on the direction of character evolution.

Character Phylogeny

Hennig's (1966:88) discussion of methods for evaluating characters as indicators of phylogenetic relationship begins with a reference to Zimmermann's view of evolution as the transformation of characters from ancestors to descendants. Hennig also credited Zimmermann with the notion of "character phylogeny" (1966:95), with its focus on determining which character condition is ancestral and which is derived. These ideas are central to phylogenetic systematics.

Zimmermann listed and discussed six methods for determining the direction of character evolution. He considered occurrence in the fossil record to be the best and most direct indicator; character conditions that appear earlier in the record are likely to be primitive. Other "auxiliary methods" are less well justified, including ontogeny, character correlation, reduction or loss of function, and "analogous conclusion" (i.e., if character state A is "known" to give rise to state B in many cases, this sequence might be assumed in an unknown case).

All of these criteria had been formulated by other authors (see Stevens, 1980). However, Zimmermann's sixth (unnamed) criterion is of particular interest, as here we can see the beginnings of what has since become known as outgroup comparison and a clear understanding of its connection to parsimony (see Watrous and Wheeler, 1981; Farris, 1982; Maddison et al., 1984). This method is based, according to Zimmermann, on the following "well-founded" assumption:
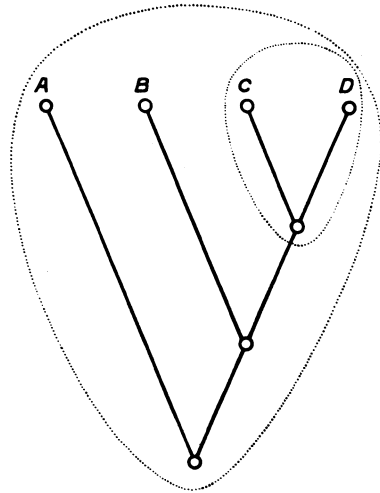

FIGURE 5. Figure 179 of Zimmermann (1931:1004). Diagram used to illustrate the use of parsimony and knowledge of related groups in assessing the direction of "character phylogeny."

characters which today are widespread in a larger taxon generally are more primitive than characters limited to only a small section of this taxon [p. 1003].

Although this method has the advantage of applying to the comparison of extant organisms, Zimmermann recognized a distinct disadvantage, namely that it requires at the outset some "secure knowledge of phylogenetic relationships."

By way of clarifying the application of this criterion, Zimmermann presented an example that relied on his Figure 179 (our Fig. 5). Here, taxa A, B, C, and D are cycads, conifers, Ranales, and composites, respectively, and the character under consideration is mode of pollination. Based on the distribution of wind and insect pollination on this tree, Zimmermann concluded that wind pollination is ancestral in seed plants (the entire group) and that a switch to insect pollination occurred in the line leading to angiosperms (the included group, consisting of C + D). The alternative, that seed plants were primitively insect pollinated and that this condition was simply retained in the angiosperm line, was rejected on the grounds that it would require the convergent evolution of wind pollination in cycads, conifers, and other "gym-

nosperm" groups (here Zimmermann explicitly assumed that cases of insect pollination in gymnosperm groups evolved within these lines):

> It is clear that such convergent evolution would be much more complicated than the course of evolution outlined above in which the common ancestor and most of the extant branches of phanerogams are wind pollinated and only some branches have acquired insect pollination. This assumption that wind pollination is more primitive has a higher likelihood [p. 1003].

In this discussion, Zimmermann focused his attention on the basal condition in all seed plants, and his determination was based, in effect, on which assignment to this node appeared to be most parsimonious. His assessment was based largely on the seed plant ("ingroup") tree rather than on a comparison of related ("outgroup") taxa, and therefore it is not outgroup analysis. Nevertheless, precisely the same reasoning—regarding nested relationships and character optimization—underlies outgroup comparison as we know it today (Maddison et al., 1984).

Hennig (1966) cited Zimmermann in connection with the use of paleontological and ontogenetic evidence but made no mention of him in connection with the method just discussed. He did, however, briefly describe a similar method as one type of correlation argument, quoting Maslin (1952:53), who made reference to "less modified members of related groups of the same rank."

The exact origins of outgroup polarity assessment are obscure. Although it was not formulated as a general principle until quite recently, something very much like it was employed by a number of early authors (see citations in Maslin [1952] and Stevens [1980]; Koponen [1968] provided an especially clear example). Regarding Zimmermann's role, he obviously did not invent outgroup analysis exactly as we know it today. Rather, he understood and clearly explained the basic elements of logic underlying the outgroup method.

DISCUSSION

As we have documented, Zimmermann presented a clear and detailed statement of several of the central ideas underlying phylogenetic systematics. His paper of 1931 is among the earliest treatments of its kind, and it presaged many later developments. In particular, some of Zimmermann's ideas appear to have been taken up more or less directly by Hennig, especially his definition of phylogenetic relationship. Hennig's methods also relied upon the distinction made by Zimmermann between "character phylogeny" and "taxon phylogeny," and he adopted many of the same strategies in responding to idealistic morphology.

Although many of the ideas expressed by Zimmermann found their way into Hennig's presentation, Hennig actually gave several elements less consideration. Thus, Hennig more or less took for granted the impact of rate inequality on the use of similarity in assessing relationship, whereas Zimmermann devoted considerable attention to this issue. Although the basic logic of outgroup comparison can be discerned in Zimmermann's paper, Hennig did not cite or elaborate on this reasoning in his discussion of methods for establishing the direction of character evolution.

In view of the elements of phylogenetic theory that are evident in Zimmermann's work, it is somewhat surprising that he did not go further than he did. Zimmermann did not, for example, formulate the concept of paraphyly. Although the distinction between monophyly and paraphyly is implicit in his work, it was never explicitly stated. Furthermore, in practice he did not appear to object to the recognition of paraphyletic groups. For example, although he realized that the "gymnosperms" are paraphyletic (e.g., Zimmermann, 1930; with Gnetales and Bennettitales most closely related to angiosperms), he continued to recognize "gymnosperms" as a distinct group, coordinate with angiosperms in his classification of seed plants (e.g., Zimmermann, 1930; Cronquist et al., 1966). In contrast, Hennig clearly distinguished paraphyly from monophyly and insisted that knowledge of phylogenetic relationships be strictly and accurately reflected in classification.

Likewise, despite his appreciation of the

importance of polarity assessment, Zimmermann did not develop the principle that only shared derived characters (synapomorphies) provide evidence of phylogenetic relationship. In the end, he failed to provide a method for reconstructing phylogeny—a method that would circumvent the evident shortcomings of similarity. He suggested only that phylogeneticists proceed with caution when using similarity and remain fully aware of its drawbacks. In Zimmermann's later work (e.g., 1966), he acknowledged Hennig's recognition that similarity might be due to the retention of plesiomorphic characters. Even then, however, he did not seem to fully appreciate the significance of synapomorphy as a substitute for overall similarity.

The concepts of paraphyly and synapomorphy awaited development by Hennig, who also extended the application of phylogenetic systematics to the study of such things as historical biogeography and the tempo of evolution. Thus, despite Zimmermann's early and fundamental contributions, it is correct in our opinion to view Hennig as the father of modern phylogenetic systematics, just as it is correct to consider Darwin the father of evolutionary theory. But Hennig's ideas did not arise de novo or fully formed, any more than Darwin's did (e.g., Hull, 1988). Rather, they are best understood as part of an intellectual tradition that developed in response to the idealism that pervaded German science at the time. The "discovery" of Zimmermann's work helps us appreciate the magnitude of this influence and also helps tease apart the sequence of events that culminated in Hennig's synthesis.

It is remarkable how little attention has been paid to Zimmermann's contributions to phylogenetic theory. The timing of his early work in relation to the onset of World War II and the associated turmoil in Germany (and elsewhere) may help account for this neglect. Yet Hennig assimilated Zimmermann's work almost as soon as it was possible to do so under the circumstances, referring to it frequently and in very positive terms in his earlier work (e.g., 1950). Of course, even Hennig's influence

was not very far reaching until he was published in English (1965, 1966). Although Zimmermann published several papers in English (including a short article in the *American Naturalist* in 1934 on character versus taxon phylogeny), these attracted virtually no attention.

Even with the renewed interest in phylogenetic systematics since Hennig's publication in English, little reference has been made to Zimmermann's contributions. Zimmermann is not cited, for example, in recent textbooks on phylogenetics (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981; Ax, 1987; Brooks and McLennan, 1991) nor is he mentioned in Dupuis's (1984) account of Hennig's ideas and their influence on taxonomic thought. This oversight may be partly a result of the fact that the first English-speaking students of Hennig's work were zoologists (e.g., Gareth Nelson, Colin Patterson; see Hull, 1988), who may have been unaware of Zimmermann's botanical contributions and had little reason to investigate his papers cited by Hennig, especially in view of the language barrier. Mayr's (1982) brief reference to Zimmermann implies that he was an idealistic morphologist. Yet even casual inspection of Zimmermann's work shows, on the contrary, that he argued consistently against idealism (Reif, 1986).

The botanist Koponen (1968), who applied cladistic methods at a very early stage (to the moss family Mniaceae), cited both Hennig and Zimmermann for the development of a "cladistic–phyletic school" of systematics. Since then, Zimmermann seems to have been forgotten even by botanical cladists, with the exception of passing references by Stevens (1980) and more recently by Humphries and Chappill (1988).

Another factor contributing to the neglect of Zimmermann's systematic theory is that Zimmermann was apparently not a very effective advocate of his own ideas about phylogeny, although he did reiterate his systematic theory in several later publications. Indeed, he devoted much more of his energy in later years to his interests in plant morphology, especially in con-

nection with the development of the telome theory (e.g., numerous publications in *Pulsatilla*; see references in Zimmermann, 1965). This case might support Hull's argument (1988:365–367) that in the absence of a certain amount of advocacy for one's own ideas, one may well become an unappreciated precursor of other more assertive scientists.

Walter Zimmermann was an extraordinarily thoughtful individual, whose contributions to systematic and evolutionary theory never attracted the recognition they deserve. We hope that by highlighting Zimmermann's contributions to phylogenetic theory more attention will be paid not only to his work but to the social and conceptual history of phylogenetic systematics.

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A Review of Estimates of Nonreciprocity in Immunological Studies

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Biochemical data are useful for inferring phylogenetic relationships. Albumin immunology represents one such type of data. With this method, the relative degree of antigen–antibody reactions is used to estimate the immunological distance between pairs of taxa. Because the reaction strength is linearly related to the number of amino acid replacements (Maxson and Maxson, 1986), this method is touted to be appropriate for phylogenetic distance analyses (following the criteria of Farris [1972]). If other assumptions are met, this method can be used to estimate divergence times and divergence patterns (Wilson et al., 1977).

The utility of albumin immunological data depends upon conformation to the assumptions of the triangle inequality (Sneath and Sokal, 1973). One assumption is that the data generated are reciprocal, i.e., the distance estimated from taxon A to taxon B is the same as that estimated from B to A. If this requirement were met consistently, then there could be a massive reduction in workload because analyses could be performed with one-way comparisons (e.g., only the distance from A to B would be needed because this would be an accurate estimate of the distance from B to A).

Many studies have demonstrated that reciprocity is rarely achieved. The only model designed to explain nonreciprocity explicitly is that of Faith (1985). According to this model, nonreciprocity results from the fact that antibodies to species A are generated by a host organism, usually a rabbit. A perfect antibody would recognize all antigenic sites in albumin proteins from A. However, because rabbits can share antigenic sites with species A, some sites may not be recognized by the antibody. Therefore, the measurable distance between species A and some other taxon (species B) is typically less than the total distance be-