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978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

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## The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Willi Hennig (1913–76), founder of phylogenetic systematics, revolutionised our understanding of the relationships among species and their natural classification. An expert on Diptera and fossil insects, Hennig's ideas were applicable to all organisms. He wrote about the science of taxonomy or systematics, refining and promoting discussion of the precise meaning of the term relationship, the nature of systematic evidence, and how those matters impinge on a precise understanding of monophyly, paraphyly, and polyphyly. Hennig's contributions are relevant today and a platform for the future. This book focuses on the intellectual aspects of Hennig's work and gives dimension to the future of the subject in relation to Hennig's foundational contributions to the field of phylogenetic systematics. Suitable for graduate students and academic researchers, this book will also appeal to philosophers and historians interested in the legacy of Willi Hennig.

DAVID WILLIAMS is a research scientist at the Natural History Museum, London specialising in diatom systematics-taxonomy. He has published over 200 journal papers and is the author or editor of nine books. His research interests include the systematics and biogeography of diatoms and theoretical studies related to advances in cladistics.

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Frontmatter

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Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

---

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Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

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Frontmatter

[More information](#)

---

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Frontmatter

[More information](#)

# The Future of Phylogenetic Systematics

## The Legacy of Willi Hennig

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Frontmatter

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Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

vii

## Contents

List of contributors	page ix
Foreword	xi
NORMAN I. PLATNICK	
<b>Introduction</b>	<b>1</b>
DAVID WILLIAMS, MICHAEL SCHMITT and QUENTIN WHEELER	
<b>1. Mission impossible: the childhood and youth of Willi Hennig</b>	<b>10</b>
WILLI E.R. XYLANDER	
<b>2. Willi Hennig: a shy man behind a scientific revolution</b>	<b>21</b>
MICHAEL SCHMITT	
<b>3. Willi Hennig's legacy in the Nordic countries</b>	<b>31</b>
OLE SEBERG, TORBJØRN EKREM, JAAKKO HYVÖNEN and PER SUNDBERG	
<b>4. Hennigian systematics in France, a historical approach with glimpses of sociology</b>	<b>70</b>
PASCAL TASSY	
<b>5. Are we all cladists?</b>	<b>88</b>
ANDREW V.Z. BROWER	
<b>6. How much of Hennig is in present day cladistics?</b>	<b>115</b>
MICHAEL SCHMITT	
<b>7. The evolution of Willi Hennig's phylogenetic considerations</b>	<b>128</b>
RAINER WILLMANN	
<b>8. What we all learned from Hennig</b>	<b>200</b>
GARETH NELSON	
<b>9. Semaphoronts: the elements of biological systematics</b>	<b>213</b>
LEANDRO C.S. ASSIS	
<b>10. Why should cladograms be dichotomous?</b>	<b>230</b>
RENÉ ZARAGÜETA BAGILS and SOPHIE PÉCAUD	
<b>11. Hennig's auxiliary principle and reciprocal illumination revisited</b>	<b>258</b>
RANDALL D. MOOI and ANTHONY C. GILL	
<b>12. Dispersalism and neodispersalism</b>	<b>286</b>
MALTE C. EBACH and DAVID M. WILLIAMS	

Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

## viii CONTENTS

<b>13. Molecular data in systematics: a promise fulfilled, a future beckoning</b>	<b>329</b>
WARD C. WHEELER and GONZALO GIRIBET	
<b>14. Hennig, Løvtrup, evolution and biology</b>	<b>344</b>
ROBIN BRUCE	
<b>15. Willi Hennig as philosopher</b>	<b>356</b>
OLIVIER RIEPPEL	
<b>16. Hennig and hierarchies</b>	<b>377</b>
CHARISSA S. VARMA	
<b>17. Chain, tree, and network: the development of phylogenetic systematics in the context of genealogical visualization and information graphics</b>	<b>410</b>
NOBUHIRO MINAKA	
<b>18. The relational view of phylogenetic hypotheses and what it tells us on the phylogeny/classification relation problem</b>	<b>431</b>
STÉPHANE PRIN	
<b>19. This struggle for survival: systematic biology and institutional leadership</b>	<b>469</b>
QUENTIN WHEELER	
Index	479

Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

ix

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Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

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X LIST OF CONTRIBUTORS

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Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

xi

## Foreword

# Willi Hennig and systematics: a personal view

NORMAN I. PLATNICK

In September of 1973, I joined the staff of the American Museum of Natural History in Manhattan. I had spent the previous five years doing graduate work on spider systematics, first at Michigan State University, then at Harvard University. At both institutions, I had taken courses on the principles of systematics and evolutionary biology; the one at Michigan State had been taught by entomologist Roland Fisher, and the ones at Harvard were given by Ernst Mayr, Steve Gould, and entomologist John Burns. Although access to the spider collections at both institutions allowed me to learn a lot about spiders, what little I learned about “how to do systematics” was actually gleaned mostly from studying the papers of my professors (Dick Sauer and Herb Levi) and colleagues, not from courses covering systematic theory.

At the American Museum, I was assigned an office that had been occupied by my two predecessors as curator of the world’s largest spider collection: Willis Gertsch, who had spent his entire career at the Museum and who was largely responsible for building the collection, and Oxford naturalist John Cooke, who spent only a few years in New York. The office next door was occupied by entomologist Pedro Wygodzinsky. Among other groups, Wygo (as he preferred to be called) worked on Diptera, and he was therefore thoroughly familiar with the work of Willi Hennig; he had met Hennig, discussed systematics with him, and had even translated into English a large paper by Hennig on the biogeography of New Zealand Diptera (Hennig 1966a). Wygo was fluent in five languages, and had prepared that translation while on his honeymoon (Schuh and Herman 1988)!

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978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

## xii FOREWORD

It was Wygo's custom to start each weekday morning with a visit to each of the curators in the department, so my first morning at the museum, Wygo came into my office for his daily chat. Among other things, that first morning, he asked me if I had read Hennig's (1966b) book yet. I replied that I had not; in fact, the only time I had ever heard Hennig's name mentioned at Harvard was in a seminar I'd attended that had been given by coleopterist Phil Darlington. Darlington's talk was about "cladism" and its shortcomings; he had made Hennig's work sound so ill-conceived and misdirected as simply to be a waste of anyone's time.

The next morning, Wygo came in again, with the tiny cup of ungodly strong coffee he favored, and he asked me again: "Have you read Hennig's book yet?" This time, I got the message!

Over the ensuing months, I discovered that although Wygo was personally rather retiring, and not one to suggest, in public, that his fellow systematists might benefit by paying attention to Hennig, the museum had others on its staff that were far less reticent. I had the great privilege and pleasure of meeting and getting to know folks like Gary Nelson, Donn Rosen, Gene Gaffney, and (some months later, when he arrived at the museum), Toby Schuh. Gary had spent time in Stockholm, and had found the work of the Swedish entomologist Lars Brundin (1966), one of Hennig's earliest "bulldogs."

I wouldn't presume to speak for any of those folks, but for me, Hennig's writings were nothing short of a revelation. Once one worked through Hennig's somewhat arcane terminology (which was perhaps even more intrusive in the English translations than in the original German) and grasped his arguments, it became easy to see "how to do systematics." In a nutshell, it became easy to see why some taxonomic groups "work" and others don't. Hennig had realized that if life has diversified over time, then there has to be a hierarchy of taxonomic characters that is an exact mirror of that history, but that not all observed similarities among organisms directly reflect that history. There are similarities that are synapomorphies – features that were acquired by the common ancestor of a given group of organisms and were therefore passed on to all the descendants of that common ancestor. There are other similarities that do not characterize a group in this way, and if a proposed group has no putatively synapomorphic character(s) that support it, then there is no evidence that the group is not simply artificial. Every synapomorphic resemblance among organisms fits at some node on the cladogram connecting them all, and it fits at only one such node. Any resemblances that do not fit in this way are just not synapomorphic.

In some cases, it quickly became obvious why a proposed group doesn't work. Vertebrata, for example, has at least one obvious synapomorphy, the presence of a vertebral column. Invertebrata, in contrast, is merely an assortment of taxa that do not belong to the Vertebrata. They have no vertebral column, but that similarity does not unite them as a group; if it did, we would have to include plants in the Invertebrata, as they also lack a backbone.

Cambridge University Press

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Frontmatter

[More information](#)

Presence/absence characters are obvious examples of what might be called Hennigian winnowing. Everything else being equal, a group united by the presence of a feature unique to them is a likely candidate to be real, natural, and monophyletic. A group united only by the absence of such a feature is likely to be false, artificial, and not monophyletic.

But Hennig's winnow went far beyond the "Greek/barbarian" dichotomy that was pointed out as early as Plato, because it also applies to character transformation. In 1973, for example, it was obvious to all that spiders (the order Araneae) form a real, or monophyletic, group; they are united by multiple unique characters, including the peculiarly modified pedipalps of males, which are used to transfer sperm to the females. However, there was no consensus about the higher classification of spiders. Some workers, for example, recognized two suborders of spiders, one in which the chelicerae, or jaws, move in an up-and-down orientation, and another in which the chelicerae move in a side-to-side orientation.

With Hennig's winnow, it quickly became evident that this classification is false. Chelicerae that move side-to-side are indeed unique to one (huge) group of spiders, but chelicerae that move in an up-and-down orientation are not unique to a subgroup of spiders; in fact, they are found in all the closest relatives of spiders (other chelicerates like whipscorpions, etc.). There turned out to be no characters which support the lumping of those spiders with the plesiomorphic state of the cheliceral character into one group; on the contrary, there were putatively synapomorphic characters indicating that some of these spiders are actually more closely related to higher spiders than they are to the liphistiids, one of the other groups with the plesiomorphic cheliceral orientation. Application of Hennig's winnow therefore supported a different cladogram, in which tarantulas and their allies (Mygalomorphae) are more closely related to typical spiders (Araneomorphae) than they are to the Liphistiidae. The group including just liphistiids plus mygalomorphs (the Orthognatha) doesn't work; it is the analog of Invertebrata within spiders (Platnick and Gertsch 1976). In other words, transformation of the cheliceral orientation – from vertical to horizontal – appears to be a synapomorphy uniting a group, but the absence of that transformation does not.

So we came to see that all characters, even the presence/absence ones, can be viewed as transformations of some other character, and that those transformations combine to produce a character hierarchy that provides the evidence for choosing one taxonomic hierarchy over another. In effect, it is only the synapomorphic presence of one or more character transformations that can delineate a group. And the task of taxonomists thus became clear: to find the synapomorphies that allow us to construct a single hierarchy uniting all taxa.

In my view, Hennig's winnow provided a clear understanding of the past (some proposed groups are supported by evidence – putative synapomorphies – whereas others are not) and an equally clear imperative for the future: our job, as systematists, is to find the synapomorphies that support every node in the cladogram of life.

Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

## xiv FOREWORD

From this, one might suspect that work done during the ensuing decades would demonstrate this clarity, but that does not appear always to have been the case. Workers like Steve Farris showed that one could construct a matrix of similarities (characters x taxa), of the sort that had been favored by pheneticists, and analyse it parsimoniously to produce the equivalent of Hennig's character schemes (cladograms), rather than simple phenograms (branching diagrams reflecting only raw, or "overall," similarity). This was an important discovery, in that it showed clearly why phenetics, and phenograms, are wrong (see, for example, Farris 1979).

However, the fascination with matrices soon became bound up with the illusory notion of "total evidence." One can certainly sympathize with the desire to include, for example, multiple morphological and molecular data sources in a single, "total evidence" analysis, but one can never actually have all the evidence, and rigorous hypothesis testing demands that newly available sources of data should have the opportunity to call into question prior results, even when considered independently from previous datasets.

The emphasis on "total evidence" unfortunately led some workers to the operational principle that the way to discover Hennig's hierarchy is simply to code every conceivable observation of specimens into a matrix, and trust that parsimony (in this case, the congruence among these close-to-random observations) will find the right cladogram (i.e. the right hierarchy), even if the signal (i.e. any synapomorphies that might happen to be included) is vastly outweighed by the noise.

Congruence among different characters is, of course, the best evidence that a group is real, and combinability of that group with other similarly supported groups into a single cladogram is the best evidence that the real hierarchy has been found, as the probability of finding congruent characters, in a random sample of characters of all organisms, or combinable groups, in a random sample of groups of all species, by chance alone, is infinitesimally small. However, real congruence (for example, between two actual synapomorphies) could easily be overwhelmed, by chance alone, given a large enough sample of noise, in any particular matrix involving just a limited number of taxa.

It is thus scarcely surprising that as matrices have grown to include more and more "characters" that are unlikely to be synapomorphies of any group, so too has the need to apply methods of character weighting that attempt to minimize the damage they do, or that as matrices have come to be dominated by such pseudocharacters, even the heaviest weighting functions may still produce results that seem patently nonsensical to anyone who knows the taxa involved. To my mind, such pseudocharacters are "evidence" mostly that some systematists desire to display the largest possible matrix, in the hopes that quantity will somehow substitute for quality, and that finding new potential synapomorphies requires vastly more work than does finding mere noise.

Nevertheless, as some of the proponents of the "stuff as much irrelevant trivia as possible into the matrix, so maybe we can find a secondary signal" approach

Cambridge University Press

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Frontmatter

[More information](#)

have indicated, they purposefully “no longer ‘group by synapomorphy’” (Nixon and Carpenter 2012: 225). That is their loss, but it is also a loss to any biologist unwary enough to use their results, under the misapprehension that they are necessarily the results Hennig would have obtained.

Hennig, although he worked on some of the most diverse groups of organisms on the planet, never used a matrix, nor needed to. He knew what he was looking for: synapomorphies, and the groups they delineate. In spiders, for example, the goal of “total evidence” has sometimes led to the construction of matrices that are dominated by similarities that Hennig would likely have scoffed at. Many of those spider gigomatrices (gigantic, garbage-in, garbage-out matrices), for example, are chock-full of “characters” involving leg spines; to date, no one has found a way to homologize individual leg spines, and without such individual homologies, observations about leg spines are about as likely to contribute real synapomorphies as are many other such superficial “similarities” in other groups of organisms (scale counts in fishes, for example).

The advent of DNA sequence data has also clouded what should have been a clear perspective. Today, those data are most often analysed by likelihood methods that no longer associate actual character state changes with nodes on a cladogram, but rather merely provide an estimate of the most likely cladogram, given a particular set of data and a particular model of evolution. Since there is seldom, if ever, any reason to believe that the chosen model actually applies across the entire gamut of taxa being considered, there is seldom, if ever, any reason to believe that the hierarchy chosen is the one that Hennigian analysis would provide. Genomics is likely to provide some outstandingly useful synapomorphies, but in my view, they are likely to be higher-order similarities, involving changes in gene order and expression, rather than low-level similarities among endless saturated, paralogous sequences of nucleotides, each of homology fully as dubious as the leg spines of spiders or scale counts of fishes.

So what does the future hold? Only time will tell, but my prediction is that the farther systematists depart from Hennig’s clear vision, the harder it will be to obtain the actual tree of life.

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Cambridge University Press

978-1-107-11764-8 - The Future of Phylogenetic Systematics: The Legacy of Willi Hennig

Edited by David Williams, Michael Schmitt and Quentin Wheeler

Frontmatter

[More information](#)

---

xvi FOREWORD

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