Introduction

David Williams, Michael Schmitt and Quentin Wheeler

There's a story concerning the 37th American President Richard Nixon and his first meeting in 1972 with the Chinese Prime Minister Chou En-Lai in Beijing. Stuck for discussion topics and recalling that Chou En-Lai was an enthusiastic student of French history, Nixon thought to ask him what he considered to be the impact of the French Revolution on western civilization. After reflecting for a while on the question, Chou En-Lai simply replied: "It's too early to tell." Whatever truth there is in the details of this story (and the details do vary from version to version), the sentiment expressed is of some general significance to most revolutions and their perceived impact. This book concerns itself with Willi Hennig, the founder of phylogenetic systematics, the impetus behind the transformation of "taxonomy to phylogenetics," more generally thought of as the "Cladistic Revolution" in biology. If asked, "What was the impact of the cladistics revolution on systematics?", replies might vary. Some might consider the revolution, if it was one, well and truly over. After 30 years or so of discussion, systematists/taxonomists, having transformed their art, George Gaylord Simpson's view of the taxonomic process (a "useful art"; Simpson 1961: 110), into a science, can get on with their job, happy in the knowledge that fundamentals have been established: data are available, and with DNA, in large enough quantities to satisfy requirements for even the most poorly known taxonomic group, criteria have been provided, computer programs written – all that one needs to do is get some specimens, follow a protocol, find the phylogeny and then get on with more interesting questions. Or maybe the best that can be said of the revolution's

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Fig I.1 Willi Hennig, 12th August, 1976, probably the last portrait. Courtesy of Gerd Hennig, Tübingen.

effect is: "It's too early to tell." While this book concerns itself with some biography and some history of that revolution, it is not a history book.

The year 2013 was the centenary of the birth of (Emil Hans) Willi Hennig (April 20, 1913–November 5, 1976; Fig I.1), who exerted perhaps one of the strongest influences on systematic (comparative) biology since the publication of Charles Darwin's *On the Origin of Species* (1859), with the publication of his book *Phylogenetic Systematics* (1966a; it has been reprinted twice, in 1979 and 1999). Hennig was an entomologist, and his primary interest was the classification of Diptera (the true flies). In his extensive *Die Larvenformen der Dipteren* (published in three volumes from 1948 to 1952), much of the groundwork for his subsequent entomological studies was laid – the first volume of that trilogy contained an essay on theoretical issues in zoological taxonomy (*Theorie der Zoologischen Systematik*, Hennig 1948: 2–22). Hennig's dedication to empirical studies forced him to consider a host of issues pertinent to biological classification in general, which resulted in a book-length treatment of the subject, *Grundzüge einer Theorie der phylogenetischen Systematik* (1950, now one of the rarest and most expensive twentieth century taxonomic texts), principles he applied to the phylogeny of insects (Hennig 1953).

Prior to the publication of *Phylogenetic Systematics*, Hennig published two other items of general interest: *Die Dipteren-Fauna von Neuseeland als systematisches und tiergeographisches Problem* (1960, translated into English by Petr Wygodzinsky as *The Diptera fauna of New Zealand as a problem in systematics and zoogeography* but not published until 1966b), a study on the union of biogeography with systematics, and a short summary of phylogenetic systematics in English published in the

Annual Review of Entomology (Hennig 1965), both are still worth reading today. But it was, of course, the book *Phylogenetic Systematics*, translated into English from a German text by two zoologists, D. Dwight Davis and Rainer Zangerl, that had the biggest impact on systematic biology, a book that presented a detailed account in English Hennig's views on systematic methodology. Here one could engage with Hennig on the meaning of taxonomic relationship and the nature of systematic evidence, and how these matters impinged on the understanding of commonly used phylogenetic terms such as monophyly and homology – matters hardly settled today and still topics of interest and discussion for some (Nelson 2011, 2014, Ebach et al. 2013, Vanderlaan et al. 2014, and the contributions in Hamilton 2014).

Reception of *Phylogenetic Systematics* was somewhat guarded and many reviewers "generally failed to perceive the possibilities in applying Hennig's approach…" (Rosen et al. 1979); reactions from those with a vested interest in alternative approaches to classification – primarily those who had created and promoted the "New Systematics" (Huxley 1940) – were outright hostile (Philip Darlington, Ernst Mayr and George Gaylord Simpson), but "That criticism was often based on unwarranted misunderstandings by those who for no good reason considered themselves experts…" (Brundin in Wanntorp 1993: 365).

Fortunately, others did see possibilities, most notably the entomologist Lars Brundin (1907–93; see Wanntorp 1993), who specialised in chironomid midges (the nonbiting midges) and their "transantarctic relationships." Brundin's efforts were realised in a 500-page monograph, which he undertook as "an attempt to deepen the understanding of a major biogeographical problem on the basis of a phylogenetic study of some holometabolous insect groups of the dipteran order" (Brundin 1966: 5), a companion, in spirit if nothing else, to Hennig's *Die Dipteren-Fauna von Neuseeland als systematisches und tiergeographisches Problem* (Hennig 1960). Like Hennig's major opus, Brundin's monograph was published in 1966. It was this monograph that exerted a major influence on ichthyologist Gareth Nelson (Schultze 2005, Nelson 2014) who discussed the ideas presented therein with a group of (palaeo)ichthyologists – among them Colin Patterson, Roger Miles, Philipe Janvier and Niels Bonde – who, in the 1960s, were at one time or another studying fossil fishes at the Naturhistoriska Riksmuseet, Stockholm, where Brundin happened to be employed as an entomologist at the time, and at the Natural History Museum in London. Years later, Colin Patterson, a palaeoichthyologist at the Natural History Museum, noted that Brundin's monograph was "at first sight an unlikely place to find enlightenment" (Patterson 2011: 124) but "The first 50 pages … are still a wonderfully clear and strong statement of Hennig's ideas."

As noted elsewhere (Williams and Ebach 2008, 2009), the remarkable century between 1866, marked by the publication of Haeckel's *Generelle Morphologie der Organismen* (Haeckel 1866, notable for the inclusion of the very first collection of phylogenetic "oak" trees, all eight reproduced in Pietsch 2010), and 1966, with the

publication of Hennig's *Phylogenetic Systematics*, bookends for a century of examining the impact and effects of Darwinian evolution on the principles and practice of systematic biology and its results (classification). In short, that period represents the long slog in which comparative biology attempted to come to terms with evolution and its role in classification, that dialogue having its beginnings with Haeckel and the search for ancestral taxa, "enlightenment" coming primarily from the fossil record (which is not the same thing as the fossils themselves, of course).

Brundin and Hennig were indeed unlikely places "to find enlightenment" as neither needed nor extensively used the fossil record, good or otherwise, to investigate and tease apart problems in systematics and biogeography (Hennig did publish extensively on the fossil flies found in amber). The challenge to Haeckel's "palaeontological phylogeny" began primarily through the recognition of the concept of paraphyly, a term coined by Hennig to broadly meaning those uncharacterisable groups of species that were often regarded to be ancestors of one kind or another; followed by the realization that searching for ancestor – descendant sequences of taxa, fossils or otherwise, was largely a futile endeavour; and that the empirical realities of searching, instead, for taxon sister groups (relationships) rather than ancestor – descendant sequences, the critical value of the homology concept (relationships) and the necessity of recognising classification (relationships) as an independent science – ideas that today seem to have been "temporarily forgotten" in the rush to acquire more and more information as if merely accumulating data will solve problems.

Cladists, cladistics and cladism received a lot of criticism over the years, some of it just (and self-inflicted), some of it not; but much of it, as Brundin noted, misguided or misunderstood, even among cladists themselves. But like all exciting scientific disciplines, they develop piecemeal, haphazardly even, some "advances" becoming momentarily fashionable, then fading into the background destined for justifiable oblivion, while other genuine advances slumber only to be re-discovered in years to come. For example, taxonomy (classification) as a valid pursuit was first recognised and discussed in biology some 200 years ago by Augustin Pyramus de Candolle (1778–1841) in his *Théorie élémentaire de la botanique*, published in 1813 (a 2013 anniversary that went largely unnoticed). *Systematics and Biogeography*, written by Gareth Nelson and Norman Platnick addressed the same issues as de Candolle from a post-cladistics, post-Hennig perspective. A few years back when trying to sum up the achievements of *Systematics and Biogeography*, Malte Ebach and David Williams wrote, in a piece as yet unpublished, "Cladistics has been seen by some as a reaction to phylogeny reconstruction, or at least Haeckel's paleontological version of it. *Systematics and Biogeography* was a detailed critique of Haeckel's legacy as well as an attempt to revive natural classification, as outlined in Candolle's *Théorie élémentaire de la botanique*." Is Hennig a bridge between Haeckel and Nelson and Platnick, with *Systematics and Biogeography* (1981) a *Théorie élémentaire* for the

twenty-first century? There are many other examples, many other perspectives, and many other books and articles written as a result of the Cladistic Revolution (for a selection of recent books see Wägele 2005, Williams and Ebach 2008, Schuh and Brower 2009, Wiley and Lieberman 2011, Wheeler 2012, Baum and Smith 2012, Wilkins and Ebach 2013), the variety of interpretations in these contributions testimony to the value of Hennig's phylogenetic systematics.

It was timely, then, that the first biography of Hennig, *From Taxonomy to Phylogenetics – Life and Work of Willi Hennig* was published in 2013 (Schmitt 2013), that the Willi Hennig Society (the Hennig Society was founded in 1980 with the expressed purpose of promoting the field of Phylogenetic Systematics, with James S. Farris, creator of Hennig86, an early parsimony computer program (Farris 1988), as its first president) organised a plenary talk at their 2013 annual meeting (given by Schmitt: "Willi Hennig's way from taxonomy to phylogenetics"), and the Systematics Association, Linnean Society and the Natural History Museum, London, hosted a daylong meeting (27 November) to celebrate Hennig's 100th anniversary – this book is the result of that symposium.

Here we wish to say a few words about the three sponsors of that meeting. The Linnean Society has been especially significant in the early dissemination of Hennig's ideas, sponsoring the first symposium to explore the implications of *Phylogenetic Systematics* in the context of a group of organisms other than insects (Greenwood et al. 1973), assisting and encouraging the first reprinting of the book *Phylogenetic Systematics* (the first reprinting in 1979 had a new preface, Rosen et al. 1979) and, in 1974, awarding Hennig their prestigious gold medal.

The Systematics Association travelled a somewhat different path when dealing with *Phylogenetic Systematics*. The Association, created in 1937, could "count[s] among its members enthusiastic exponents of what may perhaps be called 'The New Systematics' which seeks largely to supplement the traditional methods of the museum and the herbarium," as Arthur Tansley noted in his introduction to the first Systematics Association symposium, *The Reciprocal Relationship of Ecology and Taxonomy* (Tansley 1939: 401). This may be the first mention in print of the New Systematics but it certainly points to its strong link with the Association, who eventually enabled the publication of the edited book entitled *The New Systematics* (Huxley 1940). *The New Systematics* was an attempt to bring what was thought to be known about species evolution into classification, derived from new areas of study, particularly cytology, ecology and genetics; but it was almost wholly focused on species evolution and so of little use to classification in general. Nevertheless, it shifted the focus of systematics almost exclusively to species. In many ways, Hennig's methods were to tease out justification for "the traditional methods of the museum and the herbarium" and to counter the excesses of the New Systematics and its obsession with genetics and species (Wheeler 1995). In 1964, the Association published a small book entitled *Phenetic and Phylogenetic Classification* (Heywood and McNeill

1964). In the introduction Vernon Heywood noted that "Taxonomy is in an extraordinary situation today. It is poised on the edge of a far greater revolution than that promised by the New Systematics of the 1940s" (Heywood 1964: 1). Influential though *Phenetic and Phylogenetic Classification* was, there was no mention of cladistics or phylogenetic systematics, its revolution was fixed on the phenetic phase of taxonomy, which may not have entirely vanished from the numerical perspective. Still, systematists are good at promising revolutions.

A glance at the first 13 Systematics Association publications (1960–79), cladistics is not even mentioned. The Systematics Association's influence on the development of cladistics can be appreciated in some of the edited books derived from symposia held in the early 1980s, such as *Problems of Phylogenetic Reconstruction* (Joysey and Friday 1982; some papers given at that meeting were published separately in a special issue of the *Zoological Journal of the Linnean Society* as *Problems in Phylogenetic Reconstruction* (Patterson 1982), testifying to the continued good relations between these two organisations), *Evolution, Time and Space: The Emergence of the Biosphere* (Sims et al. 1983, five additional papers given at this meeting were published separately in various issues of the Linnean Society journals) and the handbook *Cladistics: A Practical Course in Systematics* (1992, the 2nd edition appearing in 1998 with a modified title and a different roster of authors, *Cladistics: The Theory and Practice of Parsimony Analysis*; a 3rd edition is on its way). The latter book stemmed primarily from a workshop organised by staff of the Natural History Museum, London, the third sponsor, whose role in the dissemination of cladistics became the most controversial during the 1980s, events that have been covered in detail by Hull (1988) and Williams and Ebach (2008), and more recently, with a focus on the controversy in the Museum's exhibitions, in Guillé (2015).

This present book can hardly do justice to every aspect of Hennig's impact on systematic biology, least of all can it do justice to his considerable body of entomological work, for which see Andersen (2001), Meier (2005), Engel and Kristensen (2013) and Schmitt (2013). Herein are 19 chapters, which cover a broad range of topics, most of a general nature: species, evolution, biogeography, networks and trees, the principle of dichotomy, alongside a few historical and biographical chapters to allow context for the development of these ideas.

The primary aim of this book is to act as a beacon to the future, as well as a light on the past.

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1

Mission impossible: the childhood and youth of Willi Hennig

Willi E.R. Xylander

1.1 Introduction

Willi Hennig, the father of phylogenetic systematics, was born on 20 April 1913 in Dürrhennersdorf, Germany, a small village in the mountain region of the Saxonian part of Upper Lusatia (Oberlausitz). He died on 5 November 1976 at the age of 63 in Ludwigsburg in Baden-Württemberg, Germany. Schmitt has recently written a comprehensive biography of Hennig (Schmitt 2013a).

Hennig was an acknowledged specialist in the taxonomy of flies and their larvae (Diptera), head of the Department for Phylogenetic Research at the Staatliches Museum für Naturkunde Stuttgart, author of several textbooks and, during the last years of his life, honorary professor of zoology at the Eberhard Karls University, Tübingen (Eberhard Karls Universität Tübingen).

This chapter provides an overview of Hennig's childhood and youth up until he started his academic studies at the University of Leipzig (1932). I will focus on the socio-economic background of his family and the fortunate circumstances that enabled his career to overcome numerous disadvantages.

1.2 The family of Willi Hennig

Willi Hennig's mother, Maria Emma Hennig née Groß, was born on 12 June 1885 in the manor Nieder-Gebelzig in Upper Lusatia, located close to Weißenberg about

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