Will Hennig's Part in the History of Systematics

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Willi Hennig's method of assessing phylogenetic relationships is sometimes termed a "revolution" (e.g., Dupuis 1990; Mishler 2000; Wheeler 2008) or at least praised as marking "a milestone in the history of systematic biology" (Richter and Meier 1994, 212) or as a new paradigm (Kühne 1978). It might, therefore, be of interest to ask what is so different in cladistics as compared to traditional systematics. And who was the man who caused that turn in this branch of biology? Here I investigate the development of Hennig's thinking about systematics, tracing the roots of his deviation from traditional methodology and evaluating his contribution to modern cladistics.

WILLI HENNIG, THE PERSON

Emil Hans Willi Hennig (fig. 2.1) was born on April 20, 1913, the first child of Karl Ernst Emil Hennig (August 28, 1873–December 28, 1947), a railroad worker, and Marie Emma née Groß (June 12, 1885–August 3, 1965), the illegitimate child of a maidservant. He had two younger brothers, Fritz Rudolf (March 5, 1915–November 24, 1990) and Karl Herbert (April 24, 1917–January 1943 [missing near Stalingrad]). Rudolf Hennig, who became a Protestant clergyman, bequeathed a handwritten autobiographical sketch that was obviously intended to become the first chapter of a more extensive autobiography (document 1). According to this sketch, Emma Hennig saw to it that her sons

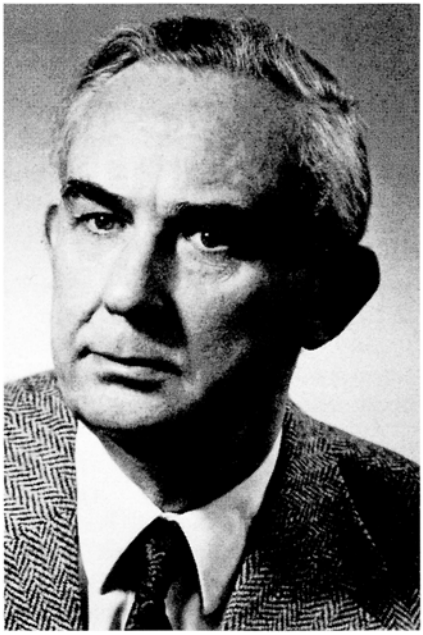

FIGURE 2.1. Willi Hennig, 1973. Courtesy of Willi Hennig Archive, Görlitz

received excellent educations, especially the eldest, Willi, who received private lessons in French while still in primary school. Rudolf describes his parents as Protestants but not especially religious. They were true Prussian patriots but not fanatics. They were not members of any political party, club, or organization.

Although the Hennig children grew up during the last years of World War I and the turbulent postwar years of the early twenties, they were only a little affected by the war and the hunger and political chaos that followed on the defeat and end of the Second German Empire. Emil Hennig did not lose his job, as so many others did, and the family was also able to maintain a small plot it owned. There the Hennigs grew potatoes and other vegetables to contribute to the family's table. Nevertheless, Rudolf recounted regular periods of financial difficulty, and also that his parents took great pains to insulate the children from these problems.

Willi Hennig seems never to have written a diary or an autobiography, or at least no such writings were preserved. Since he was two years older than Rudolf, he likely had even clearer impressions of the war and the period following it. However, it might be that he did not experience the events around him with the same sensitivity as his younger brother.

FIGURE 2.2. Willi Hennig (sitting, first row, second from right) as a primary school pupil at Oppach, ca. 1925. Courtesy of Willi Hennig Archive, Görlitz

From early childhood, Willi was described as being introverted and shy (fig. 2.2). He preferred staying at home and reading all sorts of books to playing outside with other children. He also showed an early interest in natural history, stimulated by the retired physician who taught him French. Willi's brother Rudolf mentions in his chronicle (document 1, 41; see also Vogel and Xylander 1998) that Willi was given the nickname "Orang" (after orangutan) because of his introverted nature and his overwhelming interest in natural history.

The Hennig family moved several times between 1913 and 1927, ostensibly due to Emil Hennig's relocations, but Vogel and Xylander (1998) speculate that Emma Hennig's emotional restlessness also may have played a part. Rudolf gives the impression that she was a difficult person who encountered social friction with housemates and neighbors soon after arriving at a new place (document 1).

In 1927 fourteen-year-old Willi Hennig entered a public boarding school in Klotzsche, near Dresden. There he lived in a house ("Abteilung") under the supervision of his science teacher, M. Rost, who brought the young Willi into contact with Wilhelm Meise (November 22, 1901–August 24, 2002) (see Haffer 2003; Hoerschelmann and Neumann 2003) because Willi wanted to learn more about natural history than Rost could teach him. Meise was curator of the non-insect collections at the State Museum of Zoology in Dresden. Even before Willi passed the final examination (*Abitur*) on February 26, 1932, and entered the University of Leipzig for the 1932 summer semester, he worked as a volunteer at the Dresden museum. Meise entrusted him with the task of compiling an index to the list of fishes in the British Museum of Natural History, as a kind of test of his seriousness and perseverance (document 2). Soon Meise recognized how motivated, gifted, and already well trained Hennig was, and he invited him to coauthor two papers on the "flying" snakes of the genera *Chrysopelea* and *Dendrophis* (Meise and Hennig 1932, 1935). Already as a pupil at gymnasium, Hennig had written a composition test of thirty-one pages (including tables, illustrations, and references) on the position of systematics in zoology, dated May 4, 1931 (document 3). This essay gives clear evidence of Hennig's serious interest in and profound knowledge of the subject. He received the highest score for it ("sehr gut"), although the test was on German, not biology.

Soon after meeting Wilhelm Meise, Hennig got into contact with Fritz Isidor van Emden (October 13, 1898–September 2, 1958), then curator of the entomological collections and a respected Coleoptera taxonomist. It is unclear whether Hennig already had an interest in insects before he met van Emden or received the crucial stimuli from him. At any rate, according to Meise (document 2), van Emden guided Hennig to complete a doctoral thesis on the copulatory apparatus of cyclorrhaphous Diptera, under the supervision of Paul Buchner (April 12, 1886–October 19, 1978), founder of the modern science of symbiosis. He received his doctoral degree on April 15, 1936, at the age of twenty-three. By that time he had published eight papers, including a two-hundred-page revision of the fly family Tylidae (Hennig 1934–35, 1935–36) and a sixty-eight-page revision of the agamid genus *Draco* (Hennig 1936b).

Van Emden was expelled from the public service on September 30, 1933, due to the racist Nazi laws (Hennig 1960). His successor was Klaus Günther (October 7, 1907–August 1, 1975), from Berlin, with whom Hennig from then on cultivated a lifelong friendship.

After working several months as a volunteer at the Dresden museum, Hennig received a grant from the German Science Foundation (Deutsche Forschungsgemeinschaft) to work at the Deutsches Entomologisches Institut (DEI, then in Berlin-Dahlem), which was run by the Kaiser-Wihelm-Gesellschaft, the predecessor of the Max Planck Society. There he was appointed junior research assistant (October 1, 1938; document 4) and then regular assistant (January 1, 1939; document 5).

At the University of Leipzig, Hennig had met a biology student, Irma Wehnert (August 29, 1910–April 26, 2000), who switched to the study of the history of arts after five semesters. They married on May 13, 1939. The couple had three sons: Wolfgang (b. 1941, geneticist), Bernd (b. 1943, molecular biologist), and Gerd (b. 1945, teacher of German and history).

Hennig underwent his obligatory military training in spring 1939 and was called for regular army service in September 1939, at the onset of World War II. He was deployed as an infantryman in Poland, France, Denmark, and Russia (Schlee 1978). After he was wounded by shrapnel at the Eastern Front while serving there as a private first class in 1942, he was decorated with the badge for casualties in Black. From then on, he served as a military entomologist at the Institute of Tropical Medicine and Hygiene at the Academy for Military Medicine, Berlin, and was soon sent to join the Tenth Army (Army Group C) in Italy to investigate and control malaria and other epidemics. He held the military rank of "Sonderführer Z," which corresponds roughly to platoon leader or master sergeant (document 4; document 8, 59). On March 6, 1945, he was awarded the military cross of merit, second class with swords. This decoration was bestowed for meritorious service in the homeland or behind the front lines (Klietmann 1996, 37). Until he was taken prisoner by British troops in May 1945 as a member of Malaria Training Troop 1 at Lignano (near the Gulf of Trieste, northern Italy), he was stationed at an ambulance unit in the German military hospital of Abano Terme near Padua (document 7). After a few weeks of captivity, the British troops took him out of the prisoner-of-war camp and put him into the British anti-malaria service at a former German military hospital that the British had taken over. According to short personal notes from that time, he could leave the institution but, at least in the beginning, always accompanied by a British officer. Hennig was released from captivity in October 1945. During his time as a POW, he wrote the manuscript of his *Grundzüge einer Theorie der phylogenetischen Systematik,* which was published in 1950 (see www.cladistics.org/about/hennig.html).

After his return to Germany, Hennig received a temporary appointment at the University of Leipzig as the replacement first of Prof. Dr. Friedrich Hempelmann (January 26, 1878–August 6, 1954), then, from December 1, 1945 to March 31, 1947, of Prof. Paul Buchner, Hennig's doctoral supervisor (who had left the university in 1944). Hennig gave up this appointment voluntarily because he wished to return to the DEI, where he worked from April 1, 1947, and became head of the Department of Systematic Entomology and vice-director on November 1, 1949. On August 1, 1950, he received the *venia legendi* (right to teach) following his habilitation from the Brandenburgische Landeshochschule at Potsdam and the title of professor on October 10, 1951.

The DEI was transferred to the Blücherhof manor in Mecklenburg-Vorpommern, near Waren, from 1943 to 1950. Thereafter it moved to a building in the Waldowstrasse 1 in Berlin-Friedrichshagen in the Soviet sector of the city. The Hennig family lived in West Berlin, on Opitzstrasse 3 in the district of Steglitz. During the days preceding August 13, 1961, Hennig was traveling in France with his youngest son, Gerd. When he learned of the erection of the Berlin wall on that day, he returned immediately to Berlin (on August 14), removed his personal belongings from DEI, and quit his job there (document 9).

In order to continue working at DEI he would have had to move to East Berlin, or to the German Democratic Republic, which would have meant living under difficult political and economic conditions (Peters 1995). His decision to leave the DEI was not an inconsequential one, as he was already envisaged as its future director. Quitting DEI cost him a number of privileges and opportunities, but Hennig was ardently anticommunist and already under suspicion by the East German secret police (Staatssicherheit) (document 10).

Though Hennig opposed communist ideas, he was by no means a follower of National Socialist ("Nazi") politics. Neither was he a member of the NSDAP (Nationalsozialistische Deutsche Arbeiterpartei), as documented in the official dossier on him in the records of the State Museum of Natural History, Stuttgart (SMNS) (document 6). There is also no evidence in the written documents or verbal reports of his contemporaries that he held Nazi views. Neither I nor Hennig's son Bernd have ever seen the Nazi salutation "Heil Hitler" used by him in his private correspondence. Even if a sender had written it, Hennig signed his reply using a conventional complimentary close (document 11). It seems that he added this formula only to official letters to addressees in German institutions (documents 12, 13). To make this point clear: any accusation that Willi Hennig sympathized with Nazi ideology is pure invention. This view is also strongly supported by Rieppel (2011a). Obviously, the singular source of such insinuations is a group of followers of Leon Croizat (July 16, 1894–November 30, 1982) who extensively commented on the question "Was Hennig a Nazi?" on the Internet discussion list Panbiog-L (document 14). The origin of this denunciation is, according to Platnick and Nelson (1988, 415), Croizat's unsubstantiated personal anti-German posture.

In 1961 Hennig was appointed professor at the Technische Universität Berlin, where he gave two lectures and one practical course on invertebrate zoology (Schmitt 2002). In April 1963 he became head of the Department of Phylogenetic Research (established especially for him) at the Staatliches Museum für Naturkunde, Stuttgart (SMNS). This department was housed provisionally in the city of Ludwigsburg, 15 kilometers north of Stuttgart. Here he worked and lived—at Denkendorfer Strasse 16 in Ludwigsburg-Pflugfelden—until the night of November 5, 1976, when he died suddenly from a heart attack (Schlee 1978; Schmitt 2001, 2003, 2013).

WILLI HENNIG, FOUNDER OF PHYLOGENETIC SYSTEMATICS

Hennig's basic ideas about phylogenetic research can easily be summarized. First, the only concept of relationship that can be based on an objective measure (recency of common ancestry) is that of genealogic relationship, as all other attempts to assess relationship are inevitably flawed by arbitrary emphasis on or restriction to certain characteristics of the organisms investigated. Second, focusing on the genealogical relations between species or supraspecific taxa led to the insight that Ernst Haeckel's (1866) notion of "monophyly" had to be refined to allow for nonarbitrary circumscription of taxa. Only defining *monophyletic* as "including a stem species and all of its descendants" avoids the subjectivity of the exclusion of one or some of these descendants from an accepted taxon, that is, forming a paraphyletic taxon. Third, species and supraspecific taxa can be shown to be monophyletic if they share at least one character that can be interpreted as an evolutionary novelty (a synapomorphy) in the character set of the stem species. If these ideas are accepted, the work of phylogenetic systematics is to establish a system containing exclusively species and monophyletic taxa.

Because a stem species is connected to all its immediate descendants through the same type of parent-offspring relations, it is logically unjustified to state that it survives in only one of its daughter species. Consequently, Hennig found it appropriate to state that the stem species always goes extinct when it splits into two or more daughter species. It is, however, important to note that this decision is a convention referring only to the taxonomist's need to draw boundaries within a continuum of generations. Hennig felt obliged to clarify this concept in a publication by Schlee (1971), where he wrote (p. 28) that his conceptual solution to the species boundary problem of "obligatory extinction of the stem species" does not mean that in reality organisms go extinct but simply that it is in his view the most rational way to delimit species (as taxa, not as real entities) in time.

As I have noted elsewhere (Schmitt 2001; 2003; 2013, 166), Hennig did not state or assume that species split obligatorily and exclusively into two descendant species. On the contrary: he discussed at length the possibility of polytomous splitting of species (Hennig 1966, 210ff.). But since only bifurcations can be demonstrated objectively by assessing putative synapomorphies, whereas a polytomy can never be proved positively, his "dichotomy rule" is a methodological principle that aims at resolving phylogenetic relations between the taxa of interest into dichotomies. Even in his 1950 book, where he did not explicitly claim that the "principle of dichotomy" is a methodological one, he only searched for an explanation of his empirical observation that in so many cases taxa, especially the more comprehensive ones, split into two subordinate taxa. He referred to a formal model by which he could demonstrate that even a sequence of multiple splitting can (!) result in a bifurcated tree in the long run (1950, 333). Rieppel (2011b) interprets Hennig's (1950, 332ff.) considerations as evidence that he grounded the principle of dichotomy ontologically in speciation. Although I largely agree with Rieppel's view, I emphasize that Hennig repeatedly claimed that his considerations offered *possible* explanations. I could not find any indication that he assumed bifurcation as the necessary mode of speciation.

Already in 1936, in his paper on the relations between geographic distribution and systematic classification of some Dipteran families, Hennig (1936a, 170) clearly distinguished primitive characters as "independently retained inheritance from the ancestor of all tylids" (unabhängig bewahrtes Erbe von den allen Tyliden gemeinsamen Vorfahren) from the "progressive characters" (die gemeinsamen fortschrittlichen Merkmale) shared by Tylinae and Neriinae. He emphasized that these latter characters "especially suggest" (legen ... den Gedanken ... besonders nahe) closer phylogenetic relationships of these two subfamilies. In the same paper, he stated explicitly that a systematic classification must be understood in terms of phylogenetic (which is to say, genealogical) relationship rather than morphological similarity and dissimilarity (see also Schmitt 2001, 328; 2003, 372).

From the general discussions found in his publications between 1936 and 1950 (see Anonymous 1978), it becomes clear without any doubt that the approach initially published in 1950 matured step by step over the years. It might be that Wilhelm Meise, Fritz van Emden, and—above all—Klaus Günther assisted in personal discussions from time to time, but there is definitely no evidence that they contributed more than occasional ideas.

As several authors have recognized (e.g., Hull 1988, 130; Kitching et al. 1998; Richter and Meier 1994; Schmitt 2001, 333), Hennig put remarkably little effort into elaborating a generally applicable and methodologically unobjectionable method for polarizing character states. Even his publications after 1966 remained vague and hardly useful for practical purposes in this respect. Also in personal letters (kept in the archive of SMNS), he denied even the possibility of providing a general tool for assessing character polarity. In the small book that was obviously intended to become the introductory chapter of a planned textbook on phylogenetics, later published by his eldest son, Wolfgang, in 1984, he even wondered that it is "strange to say that sometimes the phylogenetic systematics is blamed for failing to provide or develop methods for the discrimination of apomorph and plesiomorph characters" (merkwürdigerweise wird der phylogenetischen Systematik manchmal zum Vorwurf gemacht, daß sie es versäumt habe, Methoden anzugeben oder zu entwickeln, mit deren Hilfe plesiomorphe von apomorphen Merkmalen . . . unterschieden werden können; 46f.). Instead of offering a general tool or method, he referred in this booklet to lists of primitive and derived characters for insects to be found in literature (Hennig 1984, 47). Only in a joint paper with Dieter Schlee, posthumously published in 1978, did he write (or agree to) some explicit statements on this topic, among which "distribution of the characters among the taxa" comes closest to what is now known and used as the "outgroup comparison method" (Wiley 1981, 139; Watrous and Wheeler 1981).

THE HENNIGIAN REVOLUTION

If it is not a practical method for revealing genealogical relationships, what, then, is the core of the "Hennigian revolution" of 1950 and 1966? Hennig introduced the need for systematists to make clear statements of the form "A is more closely related to B than either is to C," rather than put a taxon somewhere "in between" others or allegedly solve a taxonomic problem by erecting a separate Linnaean unit for a taxon in question. Moreover, he developed a method that required explicit presentation of supporting evidence rather than statements based purely on intuition or inexplicable experience. For the first time a method was at hand that made phylogenetics a scientific enterprise comparable to the branches of investigation that fall into Popper's concept of science (although there is still an ongoing debate on the question whether this applies to cladistics, i.e., the contemporary version of Hennigian phylogenetic systematics; see, e.g., Rieppel 2007; Kluge 2009) (from Schmitt 2010).

In his own review of the *Grundzüge,* Hennig (1952) elucidates the aspects of his book that he saw as most important. The review emphasizes the relevance of systematics as a biological discipline that provides a general reference system for generalizations. This purpose can only be met, he argues, by a strictly phylogenetic system. He went on to criticize the conventional systems for mingling different concepts of "relationship," especially the type of system "often denoted by the term 'network relationship' [Netzverwandtschaft]." But he does not mention any newly introduced method. It is exclusively the concept (he called it the "theory") of systematics that he felt was noteworthy.

Jahn (1992) mentions as one of Hennig's most outstanding contributions to systematics the new concept of macrotaxonomy—meaning a focus on relations between species and monophyletic groups of species—after about fifty years of prevalence of the relations between species and infraspecific populations. Likewise, Richter and Meier (1994, 212) stated that "Hennig was the person who redirected the interest of systematics to the study of supraspecific taxa after years of focusing on species and infraspecific taxa."

This means that in pre-Hennigian systematics a focus on the phylogenetic relations between supraspecific taxa was lacking and that the ideas then current about how to form hypotheses about such relations did not meet the scientific standards Hennig demanded. That this was indeed the case is highlighted by, for instance, the handbook chapter of Kühnelt (1962), where the possibility of assessing phylogenetic relationships objectively is explicitly denied and most emphasis is put on alpha taxonomy. Richter and Meier (1994) point to a similar picture in the major English-language textbooks of that time.

From a present-day perspective, it may appear surprising how much emphasis Hennig and those who evaluated his achievements put on a "strictly phylogenetic" concept of relationship. The relevance of Hennig's thinking might be judged from a quote from J. S. L. Gilmour (1940, 461 f.): "It is even doubtful whether the real significance of the term 'phylogenetic relationship' is yet fully understood. A resolution of these differences is surely one of the greatest needs of systematic biology." The differences mentioned here are those between "taxonomic trees" reflecting "phylogenetic trees" perfectly and "logical classifications" (based on correlation or coherence of characters) not necessarily being "phylogenetic." This demand mirrors not just the personal opinion of the author, but a general understanding of that time, making clear that the publication of Hennig's *Grundzüge* marks a real innovation in biological systematics.

The actual revolution of systematics was certainly realized by the development of the practical method of polarizing characters on which modern cladistics is based. Hennig would probably have appreciated this course of history. It is, however, highly unlikely that he would have accepted the complete abandonment of the traditional view of systematics as a discipline dealing with real organisms. Consequently, he would probably have criticized Platnick's (1977) view that the sister group hypothesis "A is sister-group to B+C" is isomorphic to, for instance, the "phylogenetic tree" A→B→C (A is the ancestor of B, B is the ancestor of C). Following Hennig, each taxon, including the terminal taxa, has to be monophyletic. If taxa can be shown to be monophyletic, they must possess at least one autapomorphy and can, therefore, under no circumstances be ancestor to any other taxon of the above set (since an ancestor cannot have a character in an apomorph state as compared to its descendant). After all, the debate could only be sensible within a Hennigian framework if A, B, and C were species. There cannot be supraspecific ancestors. As Hull (1988, 137) pointed out, "The only relation represented in cladograms and their isomorphic classifications are sister-group relations."

Although the unsatisfying elaboration of a practical procedure in his fundamental books of 1950 and 1966 leaves some doubt whether it is justified to ascribe to him a new method as the turning point in the history of systematics, Willi Hennig must definitively be credited for laying the foundations for the cladistic method of phylogenetic analysis. Even if his explicit descriptions of his practical method are theoretically insufficient and of only little practical use, he gave in his empirical papers on certain animals—mostly Diptera—valuable examples that could be used as models for further refinement of the method, last but not least, in his general treatments of invertebrates (1957, 1959, 1969). But certainly more important is the fact that he outlined a framework of clear terms and concepts that allows or even compels us to reduce subjectivity and arbitrariness in biological systematics. It is in this way that he made a crucial contribution to the conversion of systematics from an art or a handicraft to a legitimate branch of science.

Willi Hennig can be seen as a rather unassertive (Schmitt 2010) scout of the cladistic revolution to follow him. He prepared the soil for the great change and made the first step but did not show any intention to walk the path to the end.

There is an amusing parallel between Willi Hennig and Carl Linnaeus: the latter is lauded for the introduction or at least the consequent use of binomial names for species, that is, establishing the combination of a genus name and a "trivial" name. Yet he did not mention this achievement when listing his major contributions to science in his autobiography (see Schmitt 2008). Thus we may prize the two of them for achievements that they themselves did not regard as their greatest ones.

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