Willi Hennig, the cautious revolutioniser[1]

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Abstract

Willi Hennig is frequently associated with the so-called cladistic revolution. However, he did neither feel nor behave as a demolitionist. He was the first born son of a railroad worker and a former maidservant. During all his life, he appeared rather shy than strong when talking publicly. Even in his writings, he claimed only in a modest way to have invented a new method of systematics.

In the present contribution, I present a short description of Hennig's contribution to modern phylogenetics, with emphasis on those aspects that were new at the time of their introduction. Also, I try to explain the psychological basis of his scientific innovations by referring to Frank Sulloway's model on the influence of birth order on the development of the human personality. This model provides a satisfying psychological explanation of Willi Hennig's revolutionary role in the history of systematics.

Keywords: History of phylogenetics, cladistics, birth order.

Zusammenfassung

Mit dem Namen Will Hennigs wird häufig die Vorstellung einer cladistischen Revolution verbunden. Er hatte jedoch keineswegs die Persönlichkeit eines Umstürzlers. Er war der erstgeborene Sohn eines Eisenbahn-Arbeiters und einer ehemaligen Magd. Sein ganzes Leben lang erschien er eher schüchtern als durchsetzungskräftig, wenn er vor einer größeren Gruppe von Menschen zu sprechen hatte. Sogar in seinen Veröffentlichungen erhob er nur in zurückhaltender Weise den Anspruch, eine neue systematische Methode entwickelt zu haben.

Im vorliegenden Beitrag gehe ich der Frage nach, was wirklich neu an Hennigs Methode war, und ich versuche die Persönlichkeitsmerkmale zu benennen, die Voraussetzungen für seine wissenschaftlichen Neurungen waren. Dabei beziehe ich mich auf Frank Sulloways Modell des Einflusses des Geburtsrangs auf die Entwicklung der menschlichen Persönlichkeit. Dieses Modell liefert eine befriedigende Erklärung für die revolutionäre Rolle Willi Hennigs in der Geschichte der Systematik: Als erstgeborenes Kind war er zwar wenig prädestiniert zu einem „Revolutionär" zu werden, sein hohes Alter beim Tod seiner Eltern und seine Schüchternheit sind jedoch Faktoren, die ihn eher „offen für Neuerungen" werden ließen.

Contents

1. Introduction

Quite frequently, the method coined by Willi Hennig for the reconstruction of phylogenetic relationships is termed a "revolution", the "Hennigian revolution" (e. g. Dupuis 1990; Mishler 2000; Wheeler 2008). Here, I pursue two questions: first, who was the man who accomplished this revolution, and second, what does "revolution" mean here?

All information on Willi Hennig's family background and childhood is taken from Vogel & Xylander (1999), whereas the data on Willi Hennig's further personal development and career were originally published in Schlee (1978) and Schmitt (2001, 2003).

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2. Hennig's family and childhood

When Emil Hans Willi Hennig (Fig. 1) was born on April 20, 1913, in Dürrhennersdorf near Löbau in Saxony (Upper Lusatia), the circumstances seemed not just favourable for the development of a newborn into a renowned scientist who is said to have caused a revolution. He was

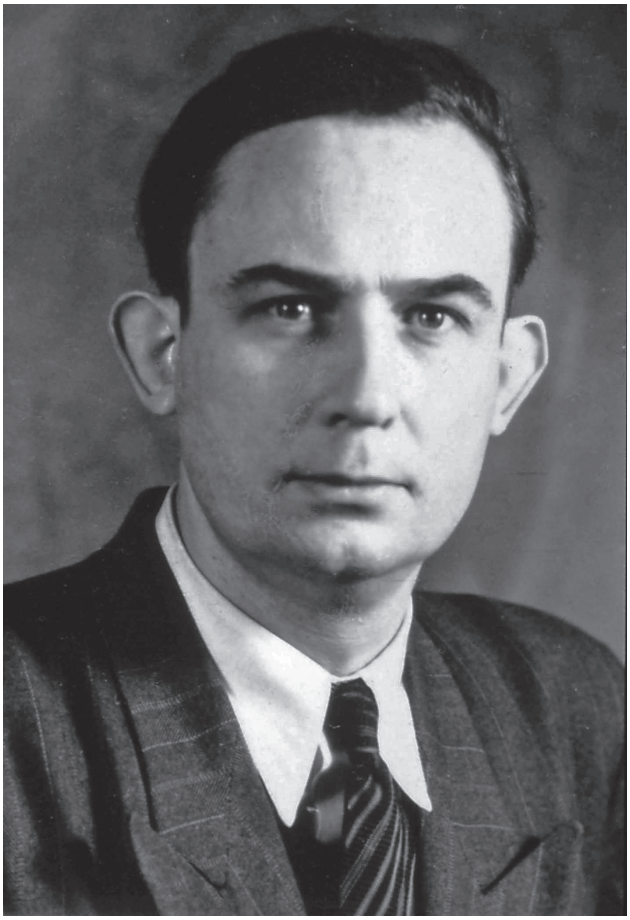

Fig. 1. Willi Hennig, ca. 1950 (courtesy of Irma Hennig).

the firstborn son of Karl Ernst Emil Hennig (28.08.1873–28.12.1947), a railroad worker, and Marie Emma, née Gross (12.06.1885–03.08.1965), who earned some money as a housemaid and later as a worker in a factory. She was the illegitimate child of a maidservant, which meant to her a social stigma from which she suffered all her life. Two younger sons were born on 05.03.1915 (Fritz Rudolf, died 24.11.1990) and 24.04.1917 (Karl Herbert, missing since January, 1943, near Stalingrad) (Fig. 2). Willi entered primary school of Dürrhennersdorf Easter 1919, but had to change school twice within three years because the Hennig family had to move several times during these years (Fig. 3). According to reports of contemporaries, Emma

Fig. 2. The Hennig family in 1923. From left: Rudolf, Emil, Herbert, Emma, Willi (Courtesy of Willi Hennig Archive, Görlitz – W. R. Xylander).

Hennig was a difficult character, nervous and unstable, whereas Emil Hennig had a calming influence on the family life. In his spare time, he relaxed at basket-weaving (Fig. 4). Vogel & Xylander (1998) speculate that not all family moves were due to the father's profession but might in part have been driven by the mother's restlessness.

Emma Hennig aimed in a very ambitious manner at providing her sons an excellent education and school training, obviously an attempt to compensate for her illegitimate birth. Already during Willi's primary school years, Emma organised private lessons in French and mathematics. The teacher was a retired military physician (Oberstabsarzt = chief staff surgeon) who not only taught the mentioned subjects to Willi but also animated him to collect insects and to build up a herbarium.

From Easter, 1927 to 1932 Willi Hennig attended a boarding school (Reformrealgymnasium der Landesschule) in Klotzsche near Dresden. He lived in the house of his science teacher, M. Rost, who brought him into contact with Wilhelm Meise (22.11.1901–24.08.2001, Fig. 5), curator of the non-insect animals at the State Museum of Zoology in Dresden.

3. Scientific education

Hennig worked at the museum as a volunteer already during his gymnasium times and was trained by Wilhelm Meise in taxonomy and morphology. Three scientific publications on "flying" reptiles (in the colubrid snake genera *Dendrophis* and *Chrysopelea* and the agamid lizard genus *Draco*), two of them co-authored by Meise and Hennig, were the outcome of this successful supervision. Even before Hennig entered the Leipzig University, he met Fritz

Fig. 3. WILLI HENNIG (circle) on the occasion of his confirmation on 10.04.1927 in Oppach (Courtesy of WILLI HENNIG Archive, Görlitz – W. R. XYLANDER).

Fig. 4. EMIL HENNIG, basket weaving (Courtesy of WILLI HENNIG Archive, Görlitz – W. R. XYLANDER).

Fig. 5. WILHELM MEISE, ca. 1935 (Courtesy of WILHELM MEISE).

van Emden (13.10.1898–02.09.1958, Fig. 6), the keeper of insects at the Dresden Museum. van Emden inspired Hennig to focus on Diptera, so that he published another five papers on flies before receiving his PhD on April 15, 1936. His doctoral thesis – under the supervision of the famous investigator of animal symbioses Paul Buchner (12.04.1886–19.10.1978) – treated the copulatory apparatus of the Diptera Cyclorrhapha.

Due to the racist Nazi laws, Fritz van Emden was expelled from the Museum on 30.09.1933. His successor became Klaus Günther (07.10.1909–01.08.1975, Fig. 7) from Berlin to whom Hennig soon established a very close relationship. One can fairly state that in the 1970s Günther was Hennig's closest friend. Although there is little written evidence, it is highly probable that the two of them discussed on Hennig's growing scientific ideas already during the Dresden times. From the correspondence accessible at the State Museum of Natural History of Stuttgart and the documents kept by the family it is clear that Klaus Günther had a considerable influence on Willi Hennig's reasoning and philosophy (Schmitt 1996). Willi Hennig died on November 5, 1976, in his home in Ludwigsburg-Pflugfelden from a sudden heart attack.

Fig. 6. Fritz van Emden (from Hennig 1960).

Fig. 7. Klaus Günther, ca. 1929 (Courtesy of Waltraut Günther).

4. Phylogenetic systematics

Already as early as 1936, Willi Hennig had begun to deviate from conventional systematics and discussed some aspects (Hennig 1936) which later became essential for his method: "relationship" should be defined in terms of phylogenetic, i. e. genealogic, relations, and only newly acquired characters are adequate arguments in favour of closer relationship. Later, when he wrote his fundamental work (Hennig 1950), he insisted that only a concept of genealogical relationship can provide a sound basis for a consistent classification, in contrast to "similarity". This strict definition of "relationship" was the first important step towards the so-called "Hennigian revolution". The next step was a concise concept of "monophyly". This term stems from Ernst Haeckel's (16.02.1834–09.08.1919) "monophyletic trees", but Haeckel (1866) left some ambiguity as to the exact meaning of "monophyletic": of course, he intended to indicate that a group of organisms stems from a single root, i. e. from a common ancestor. But he left it open whether or not there are implications other than this.

Hennig emphasised that the concept of monophyly can only lead to unambiguous phylogenetic hypotheses if it is restricted to such groups which comprise all descendants of a stem species and only these. On that concept he based the central claim of his approach that only a strictly phylogenetic system allows for unambiguous and testable hypotheses on relationship. Such a system must only contain monophyletic taxa as defined by him, and single species (which cannot be monophyletic by definition, since a single species is not "all descendants of a stem species"). The aim of phylogenetic systematics then is to hypothesize that two taxa are the exclusive descendants of an ancestor species (stem species). The immediate offspring of a stem species were called "sister groups".

A major achievement of Hennig's approach was the elaboration of a method to detect monophyletic taxa and consequently substantiate hypotheses on monophyly. From his initial finding that ancient (primitive) characters cannot prove closer relationship but only more recently acquired ones, he reached the concept of "apomorphy", meaning transformed in relation to the original state. For the – relatively – unchanged (primitive) condition Hennig coined the term "plesiomorph". In practice, to justify a hypothesis on a sister group-relationship between two taxa, at least one putative evolutionary novelty ("autapomorphy") of their stem species must be found.

As clear as this procedure sounds in principal, as obscure remained Hennig's empirical criteria or rather arguments for assessing the direction of evolutionary transformation ("Lesrichtung", "character polarity"). Also he was not quite clear on the conceptual relationship between "apomorphy" and "homology". Only in publications after 1950 he partially clarified some of the open questions. But it was not before 1981 that a convincing method for assessing character polarity was published (Wiley 1981; Watrous & Wheeler 1981; cf. Schmitt 2003).

During the 15 years following 1950, Hennig's ideas were only poorly appreciated by the scientific community. A main obstacle was certainly the fact that Hennig had published them only in German (cf. Hull 1988: 130 ff.), but even in Germany the new method was only reluctantly adopted. As pointed out elsewhere (Schmitt 1996, 2001), Hennig's sophisticated and sometimes cumbersome prose prevented a wider audience, but also that his "Grundzüge …" were published by a publisher hardly known and not experienced in science (but more in laws), and the fact that he was an entomologist who was only little perceived outside the entomological community. Things changed dramatically after the publication of "Phylogenetic Systematics" in 1966. Hennig's method was immediately accepted by a considerable number of systematists but also hotly debated by others (see Hull 1988: 130 ff.). Central conflicts were

(1) Hennig's claim that classification had to be based on a phylogenetic analysis and all non-monophyletic assemblages of species had to be excluded, which was strongly opposed by Ernst Mayr and his followers who hold the opinion that a classification should reflect more than just the sequence of cladogenetic events. Otherwise the information content of the cladogram and the system (or classification) would be identical and thus redundant. They insist that in certain cases overall similarity (caused by a high amount of plesiomorph resemblances) is biologically more relevant than monophyly based only on few characters.

(2) His view that a species goes "extinct" or rather terminates as soon as it splits into two (or more) descendants. To Hennig, this was an unavoidable consequence of the accepted circumstance that all descendants keep exactly the same type of relationship to their ancestor, so the stem species "survives" in all its offspring equally. Therefore, he insisted that "species" are delimited in time only by splitting or extinction events.

(3) Some opponents minded that there is no justification for the obligatorily dichotomous branching pattern which is regularly seen in the graphical representation of the hypotheses on phylogenetic relationships (cladograms). They stated that polytomies could not be excluded since in nature species could have split into more than two branches. However, Hennig had nowhere claimed that species could only bifurcate. It is simply a methodological postulation to aim at revealing dichotomous fissions, because only they can be proved by shared derived characters. Any polytomy can be composed of several undetected dichotomies, but a proved dichotomy can hardly be anything else.

These arguments have been extensively published, summaries can be found in Hull (1988) and Schmitt (2001).

5. Hennig as a revolutioniser

Wikipedia defines a revolution as "a fundamental change in power or organizational structures that takes place in a relatively short period of time" (checked 25.03.2010). If what Hennig presented caused indeed a revolution, then a "fundamental change" should be recognisable. Of course it is always a matter of taste what one accepts as "fundamental". But just that there was and still is such a long and fervid argument about Hennig's systematics shows that there must be a fundamental disagreement between his approach and some earlier schools of science. When checking the methods and outcomes of traditional systematics and comparing them to the analyses done under the new paradigm, it becomes evident that there are indeed differences that could induce a feeling in traditional systematists of being threatened by the new style. Hennig introduced the necessity to systematics to make clear statements in 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 opening a separate Linnean unit for a taxon in question. Moreover, he elaborated a method which 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 which fall into Popper's concept of science (although there is still an ongoing debate on the question whether or not this applies to cladistics, i. e. the contemporary version of Hennigian phylogenetic systematics, see, e. g., Rieppel 2007; Kluge 2009). Thus, one can firmly accept the expansion of the Hennigian method of systematics ("cladistics" for that matter) as a scientific revolution.

Then, the question might stand to reason if Willi Hennig as a person was a revolutionary. This means, did he intentionally threaten the taxonomic establishment of his days? To consider this possibility I find it useful to follow Frank J. Sulloway's approach of estimating human personality. In 1996, he published his comprehensive analysis of more than 6000 biographies with respect to the factors that make a person a "rebel", i. e. someone who is open to innovations and prone to transcend traditional limits. Sulloway found that of all factors taken into the meticulous statistical analysis only one explained consistently and significantly the probability of someone to become a "rebel": birth order. His study revealed clearly that laterborns are definitely more receptive to scientific innovations than firstborns, while firstborns tend to be more conforming and traditional.

Willi Hennig was the firstborn of three sons. According to Sulloway (1996), we would not expect him to purposefully revolutionise a branch of science, since for that "receptiveness for innovations" would be a prerequisite, while a "more conforming and traditional" attitude would be a hindrance (Fig. 8). As all contemporaries witness, Hennig was not at all a "rebel" personality. He was unconfident, especially when confronted with an audience of more than three people, he did not write or behave demanding, he did not try to convince someone in personal encounters. Instead, he reiterated what he saw as improvements of systematic in quite a number of taxonomic publications. In letters, he stated that his new method could only be propagated through examples, given by experienced taxonomists. With very few exceptions (1965, 1966, 1971, 1974), he did not address a general scientific readership outside entomology. Obviously, he had planned to publish a textbook of phylogenetic systematics, the introduction of which was published posthumously (1984) by Willi Hennig's eldest son Wolfgang.

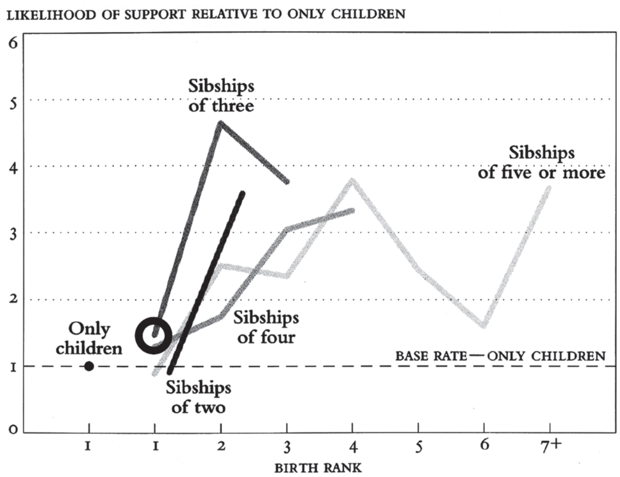

Fig. 8. Receptivity for innovations in relation to birth order and sibsize (from Sulloway 1996; circle: Willi Hennig).

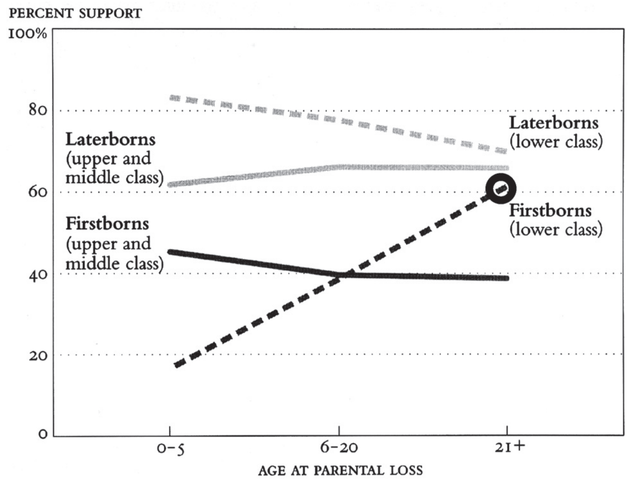

Fig. 9. Receptivity for innovations in relation to birth order, loss of parents, and social class (from Sulloway 1996; circle: Willi Hennig).

How, then, could it be that Hennig did not end as an extremely specialised – however highly respected – taxonomist but became known as the founder of a fundamentally new scientific school? Sulloway's analyses revealed some interesting interactions of birth order and other biographic and social parameters. He found that firstborns of lower social classes were nearly as open to innovations as laterborns of all classes if they were older than 21 when their parents died. This is exactly the case with Willi Hennig (Fig. 9). He was 24 when his father died, and 52 when he lost his mother. Thus, this factor could clearly compensate for his status as firstborn.

Sulloway found an additional influence that contributes to the receptiveness to innovations of firstborns: shyness, which interacts in a non-additive manner with birth order. He could demonstrate that the receptiveness of lat-

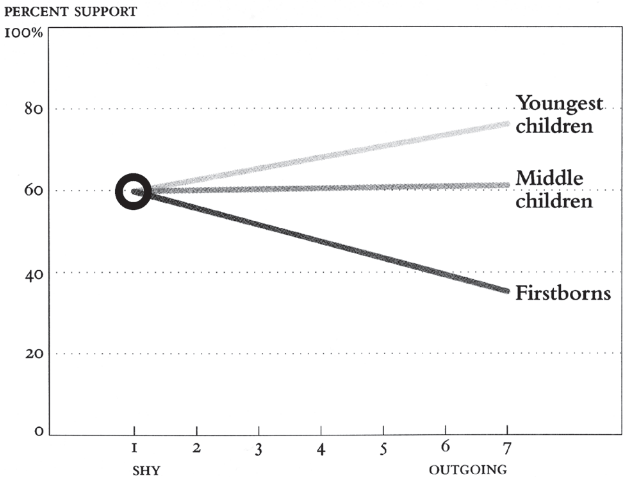

Fig. 10. Receptivity for scientific innovations in relation to birth order and shyness (from Sulloway 1996; circle: Willi Hennig).

erborns for scientific innovations was the higher the less shy they were, whereas shy firstborns are as open for innovations as shy laterborns and lose receptiveness for innovations when they lose shyness. Willi Hennig was definitively a shy person (Fig. 10). He regularly avoided occasions where he had to talk to several people he was not familiar with (let aside publicly). Hull (1988: 132) described him as "very shy and self-effacing", which is in complete concordance with all reports I received from numerous interview partners (see Schmitt 2001).

Consequently, it is most probably exactly his shyness and modesty that made Willi Hennig – although a firstborn – a scientific "rebel".

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