

## The impact of W. Hennig's "phylogenetic systematics" on contemporary entomology

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**Abstract.** Phylogenetic systematics comprise the principles and methods by which we reconstruct the evolutionary history (phylogeny) of organisms and transform this reconstruction into a biological classification of these organisms. The most important progress in designing the tools for phylogenetic reconstruction was initiated by the German entomologist Willi Hennig (1913–1976), who clarified or redefined the goals of phylogenetic systematics in a book published in 1950: *Grundzüge einer Theorie der phylogenetischen Systematik*. An extensively revised, English translation was published in 1966: *Phylogenetic Systematics*. W. Hennig's "phylogenetic systematics" undoubtedly was a very significant contribution to systematics, by some systematists and philosophers even characterized as a "revolution". Hennig's redefinition and clarification of the concepts of monophyly and phylogenetic relationships created a sound foundation for systematics in general. After decades of focussing on species-level problems, Hennig redirected the interest of systematists towards the study of higher taxa and the reconstruction of phylogenetic relationships between them. A phylogenetic system is now almost universally accepted as the most useful general reference system for biology. It has been able to accommodate new developments in systematics (such as quantitative cladistics and molecular systematics), evolutionary biology (such as ecological phylogenetics), and historical biogeography.

### INTRODUCTION

Biological systematics has been one of the most rapidly changing fields of science during the past few decades. There has been an almost explosive development in molecular systematics stimulated by the invention of new tools for generating DNA-sequences. During the same period of time, morphological or "traditional" systematics has gone through an equally impressive development emerging from a debate amongst systematists concerning the merits of different approaches for phylogeny reconstruction and classification. Whereas the contingency between classifications of organisms and their evolutionary history had been known since Darwin, it was not until the middle of the last century that real progress was made in designing the tools for phylogenetic reconstruction. This important progress was in part initiated by the German entomologist Willi Hennig (1913–1976; biography, see Anonymous, 1978; Schlee, 1981, who clarified or redefined the goals of phylogenetic systematics in a book published in 1950: *Grundzüge einer Theorie der phylogenetischen Systematik* (Hennig, 1950).

Willi Hennig's "phylogenetic systematics" comprise the principles and methods by which we reconstruct the evolutionary history (phylogeny) of organisms and transform this reconstruction into a biological classification of these organisms. Whereas most contemporary systematists are familiar with the principles and methods of phylogenetic systematics, many biologists working in other fields of evolutionary or comparative biology may not yet have achieved such familiarity. The purpose of this paper is to provide an overview of W. Hennig's "phylogenetic

systematics" and, in particular, its impact on contemporary entomology. This is done by way of examples drawn from many fields of systematic entomology. The following account, however, does not in any way pretend to be an exhaustive review of the subject.

Willi Hennig was born on April 20th, 1913, in the village of Dürrehennersdorf, east of Dresden, East Germany. He studied Zoology, Botany, and Geology at the University of Leipzig from 1932–1936 and received already at an age of 22 his promotion to Doctor of Philosophy based on a thesis on the copulatory apparatus of cyclorrhaphan Diptera. With the beginning of the World War II, in 1939, Hennig was called for military service. He was severely wounded in Russia in 1942, and was subsequently placed in the Military Medical Services, mainly in the malaria prevention program in Italy. When the war ended he became a prisoner-of-war between May and October 1945. During this time he wrote down the hand-written draft of the manuscript for his 1950-book.

After the war Hennig was employed at the Deutsches Entomologisches Institut, Berlin, in 1947, where he became head of the entomological department in 1949. After the rise of the Berlin Wall in 1961, Hennig moved to West Germany, and was in 1963 offered an attractive position at the Staatliches Museum für Naturkunde, Stuttgart, as head of a department for phylogenetic research located in Ludwigsburg. Although Hennig had the title of Professor, he did not teach any students or supervised doctoral work until he became an Honorary Professor at the Eberhard-Karls-Universität in Tübingen in 1970. Willi Hennig was a modest, almost shy person, and due to health problems rarely attended international meetings

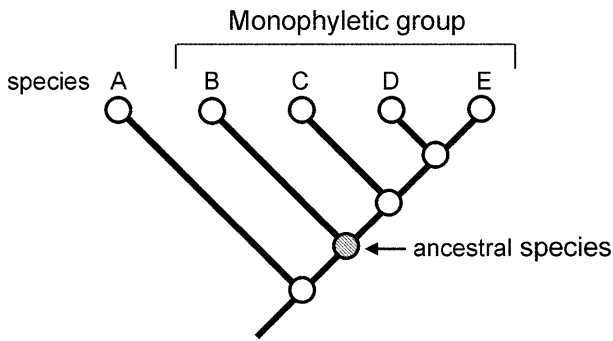


Fig. 1. W. Hennig's definition of a *monophyletic group* as "a group of species that contains all descendants of a single ancestral species".

and conferences. He died of a heart infarct in Ludwigsburg on November 5th, 1976, only 63 years old.

For various reasons did Hennig's 1950 *Grundzüge* remain virtually unknown outside German-speaking countries. One of few exceptions was Lars Brundin, a Swedish entomologist of high international standing, who was among the first to apply Hennig's phylogenetic systematics in works written in English (e.g. Brundin, 1966). An extensively revised version of the 1950 *Grundzüge*, translated into English by D. Dwight Davis and Rainer Zangerl of the Field Museum of Natural History in Chicago, was published in 1966: *Phylogenetic Systematics* (Hennig, 1966) and soon became the main reference to Hennig's "phylogenetic systematics" although Hennig himself in 1965 published a short review-paper in English (Hennig, 1965a). The original, German text of the 1966-book was published in 1982 (Hennig, 1982).

During his scientific career, Hennig earned a high reputation as systematic entomologist and first and foremost as a specialist on Diptera. He published about 100 original papers and books of which his *Die Larvenformen der Dipteren* (Hennig, 1948–1952) and his contributions to Lindner's *Fliegen der paläarktischen Region* are outstanding. He also became interested in fossil insects embedded in amber and believed - unlike many contemporary neontologists - that knowledge of extinct insects also is important to understanding relationships among living insects. This view penetrates Hennig's most important contribution to insect phylogeny, the book *Die Stammesgeschichte der Insekten* (Hennig, 1969) which was translated into English in 1981.

In recognition of his scientific accomplishments, Hennig received numerous awards, including membership of the Swedish Royal Academy of Sciences and the gold medals of the Linnean Society, London, and the American Museum of Natural History, New York. Shortly before his death, in 1975, Hennig became honorary member of the Society of Systematic Zoology. A society named after him was formed in 1980, The Willi Hennig Society, which organises annual meetings on biological systematics, phylogenetics, and biogeography, in

countries throughout the world and has published its journal, "Cladistics", since 1985.

## PHYLOGENETIC SYSTEMATICS

Hennig (1950, 1966) argued that the most useful general reference system in biology should be phylogenetic, that is a classification that exactly reflects the genealogical relationships among organisms. The last point was not agreed upon by contemporary systematists during the 1950s and 1960s, but is faithful to the view expressed by Charles Darwin (e.g., *The Origin of Species*, 6th edition, 1872, p. 346): "- that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, all true classification being genealogical; - . . .". Hennig considered the hierarchic classifications long produced by systematists to be adequate for the purpose, but emphasised that the utility of those classifications could only be maximised if they accurately reflected the phylogenetic relationships of the organisms involved. Thus, W. Hennig's "phylogenetic systematics" was originally conceived as the principles and methods by which we reconstruct the phylogenetic (genealogical) relationships among organisms and transform these relationships into a hierarchic classification.

Richter & Meier (1994) provide a useful analysis of the development of phylogenetic concepts in W. Hennig's early theoretical publications (1947–1966). Although Hennig recognised the shortcomings of the biological species definition when it comes to delimiting species in time, he nevertheless regarded species to be "real" organisms. In discussing group-categories of higher order by which he meant supraspecific taxa (genera, families, orders, etc.), Hennig argued that if species are real, higher taxa can also claim some reality because they originate by speciation. Thus, higher taxa are real because they are in a historical sense identical to their stem species. Hennig decided that the methodologically best solution is to consider the stem species extinct at the speciation event. Following this view of how higher taxa originate, phylogenetic relationships must be defined through the recency of common ancestry. This led Hennig to redefine the term "monophyly" (Fig. 1): "Only those species groups - and it applies to all group categories of higher order - can be called monophyletic which can be traced back to a common stem species. . . It has to be added that monophyletic groups not only ought to contain species that are descendants of one common species, but they must also include all species that come from that stem species." (Hennig, 1950: 307–308, translated from German). As an example of a widely recognised taxon that is not monophyletic in the strict sense, Hennig used the now famous case of "Reptilia" (Hennig, 1950: 257). The term "paraphyletic" for this kind of non-monophyletic group was not used in the 1950 *Grundzüge*, but first appeared in the 1965-review and the 1966-book.

After having introduced a strict concept of monophyly, Hennig took the initial steps towards designing methods for reconstructing systems exclusively composed of

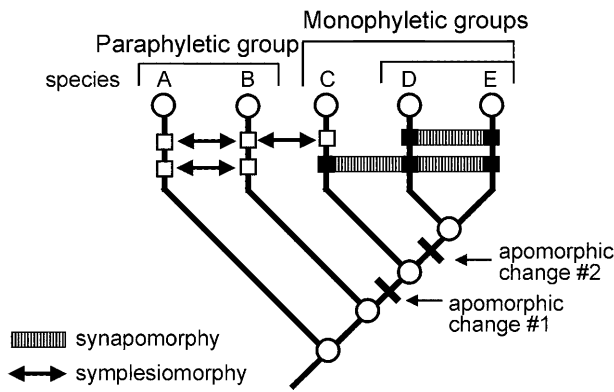


Fig. 2. W. Hennig's definition of a *synapomorphy* as "a derived character state shared by two or more species" and a *symplesiomorphy* as "an ancestral character state shared by two or more species".

monophyletic groups. He introduced the terms "apomorphic" for relatively derived species and "plesiomorphic" for relatively primitive species and occasionally also applied these terms for higher taxa. Hennig soon realised, however, that the concept of apomorphy and plesiomorphy only have meaning when applied to characters instead of taxa. The most important tool in phylogeny reconstruction was the differentiation of ancestral or primitive similarity, which Hennig called "symplesiomorphy", from advanced or derived similarity, which he called "synapomorphy" (Fig. 2). Only the last kind of similarity can be taken as evidence of phylogenetic relationship. When applied to a group of species or higher taxa, synapomorphies are identified and used to join sister-groups into more comprehensive, monophyletic

groups as presented in Hennig's well known "argumentation plan of phylogenetic systematics" (e.g., Hennig, 1965a: Fig. 3).

The basic methodology of Hennig's "phylogenetic systematics" can be illustrated by way of a small example of how to reconstruct the phylogenetic relationships between a springtail, silverfish, dragonfly, cockroach, beetle, and fly (Fig. 3). First we may consider the different modes of life cycles in these insects. All but the beetle and the fly have an incomplete metamorphosis, with a more or less gradual transition from the juvenile to the adult stage. This state is considered to be the ancestral or plesiomorphic one whereas the complete metamorphosis, comprising a distinct larval stage, as observed in the beetle and the fly, is treated as the derived or apomorphic state. Thus, the beetle and the fly can be joined by at least one synapomorphy which also characterise the higher taxon Holometabola (= Endopterygota). Among the winged insects, the cockroach shares with the beetle and the fly an overall outfit of axillary sclerites, one of which (3rd axillary) accomodates the insertion of a wing-flexing muscle. This synapomorphy joins these three insects into a monophyletic group which is the Neoptera. The presence of wings is a synapomorphy for the dragonfly, cockroach, beetle, and fly which form the monophyletic taxon Pterygota. Finally, among the wingless insects the silverfish shares an elaborate type of cuticular tentorium with the winged insects. This is one of several synapomorphies delimiting the Insecta as a monophyletic group. Hexapods outside this group (like the springtail) have the plesiomorphic state of all characters. Thus, the reconstruction of the phylogenetic relationships among these insects is completed and can be summarised by a phylogenetic diagram (Fig. 3). In contrast, the groups "Apterygota" and "Hemimetabola" are examples of paraphyletic groups sensu W. Hennig. In both cases are the supporting characters -

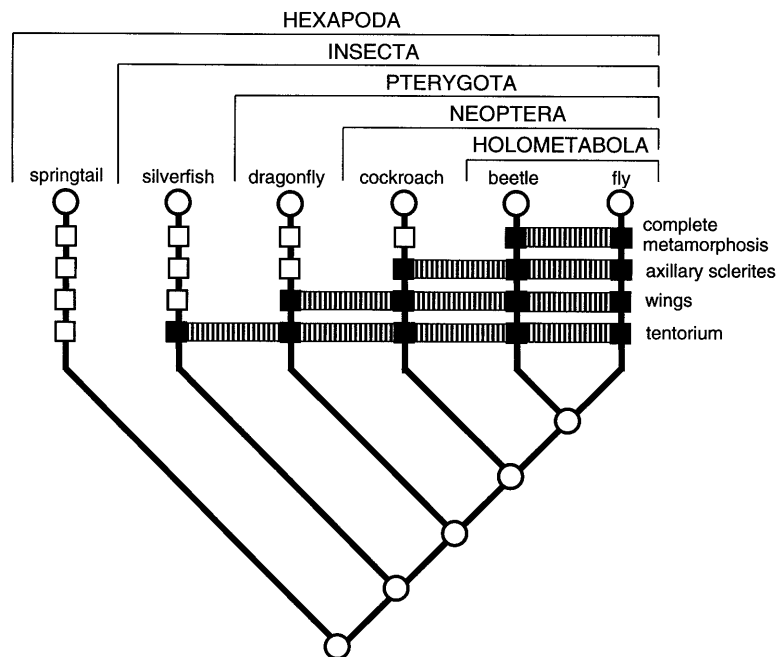
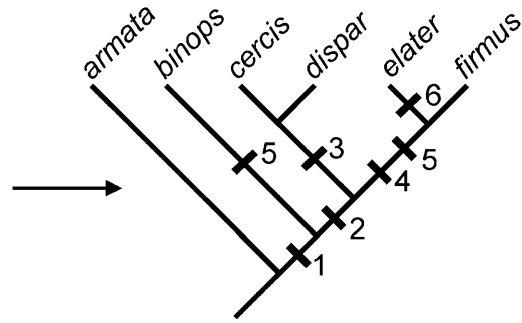


Fig. 3. W.Hennig's argumentation plan of phylogenetic systematics applied to the reconstruction of the phylogenetic relationships between a springtail, silverfish, dragonfly, cockroach, beetle, and fly. Further explanation in the text.

Characters	1	2	3	4	5	6
Taxa						
<i>armata</i>	0	0	0	0	0	0
<i>binops</i>	1	0	0	0	1	0
<i>cercis</i>	1	1	1	0	0	0
<i>dispar</i>	1	1	1	0	0	0
<i>elater</i>	1	1	0	1	1	1
<i>firmus</i>	1	1	0	1	1	0

Taxon - character matrix



Cladogram with inferred character state changes

Fig. 4. Quantitative cladistics. Taxon-character matrix for six taxa (species) and six characters (1–6) and cladogram with inferred character state changes. Further explanation in the text.

absence of wings and incomplete metamorphosis – plesiomorphies.

#### EARLY OPPONENTS

The reception of Hennig’s “phylogenetic systematics” in the world community of systematists and other evolutionary biologists was slow and reluctant, especially in North America. During the 1950s and 1960s, biological systematics was dominated by the “new systematics”, named after a book edited by Julian S. Huxley (1940) and forcefully promoted by a group of Harvard systematists headed by Ernst Mayr. The new systematists, or evolutionary systematists as they commonly are called, mainly focused on species-level problems and largely neglected the study of higher taxa which, in their opinion, are not objective in the same sense as species are. Hennig took a completely different position and concluded that higher taxa are as real as species because they are in a historical sense identical to their stem species, given, of course, that the higher taxa are strictly monophyletic.

Ernst Mayr assumed a critical attitude towards Hennig’s “phylogenetic systematics” which he called “cladism” or “cladistics” to emphasise that Hennig’s phylogenetic system only conveys information about the splitting events in evolution (cladogenesis), but not about the changes that take place in between splitting (anagenesis) (Mayr, 1969; Mayr & Ashlock, 1991). Mayr’s major point of criticism concerned the conversion of phylogenetic relationships into classifications by recency of common ancestry or the position of branching points on phylogenetic trees. In an exchange of views with Mayr in 1974 (Mayr, 1974; Hennig, 1974), Hennig carefully addresses and refutes the arguments presented, in particular the notion that a phylogeny cannot be transformed into a hierarchic classification, that monophyly cannot be defined precisely and is unimportant for reconstructing phylogenies, that a system primarily based on adaptogenesis (= anagenesis) has a much higher information content than a phylogenetic system, and that strict

dichotomous branching is a necessary principle of cladistics.

Today, W. Hennig’s “phylogenetic systematics” is almost universally accepted as the most useful general reference system in biology and Hennig’s terms “apomorphic”, “plesiomorphic”, “synapomorphy”, and “sympleisomorphy” are understood by a majority of systematists. In contemporary literature, the term “cladistics” is used more or less interchangeably with “phylogenetic systematics”. Despite differences in opinion about how to reconstruct phylogenies, Hennig’s primary goal - the identification of monophyletic groups - is universally accepted by evolutionary biologists. Monophyletic groups are commonly referred to as “clades”, and the branching diagram that is the result of a phylogenetic reconstruction is called a “cladogram”.

#### NEW DEVELOPMENTS: QUANTITATIVE CLADISTICS

Almost simultaneously with the publication of Hennig’s 1966-book did a new field of systematics arise, numerical taxonomy or “phenetics”, which took the advantage of the rapid development in computer-assisted techniques for analysing large data sets. Numerical or phenetic taxonomy, as proposed by Robert Sokal and Peter Sneath (Sokal & Sneath, 1963; Sneath & Sokal, 1973), was based on the precept that a classification incorporating the maximum number of equally weighted characters would be superior to any classification based on characters weighted according to their “evolutionary” information content. The phenetic approach was said to be “operational” in the sense that the process of data gathering was unbiased and possibly amenable to quantitative analysis.

Through the inventive work of James S. Farris (e.g. Farris et al., 1970; Farris, 1972), it soon became obvious that Hennig’s “phylogenetic systematics” could be formalised in a way that is well suited for quantification and computerisation. From this amalgamation of cladistics and numerical taxonomy emerged an approach to phylogenetic reconstruction that most appropriately can be

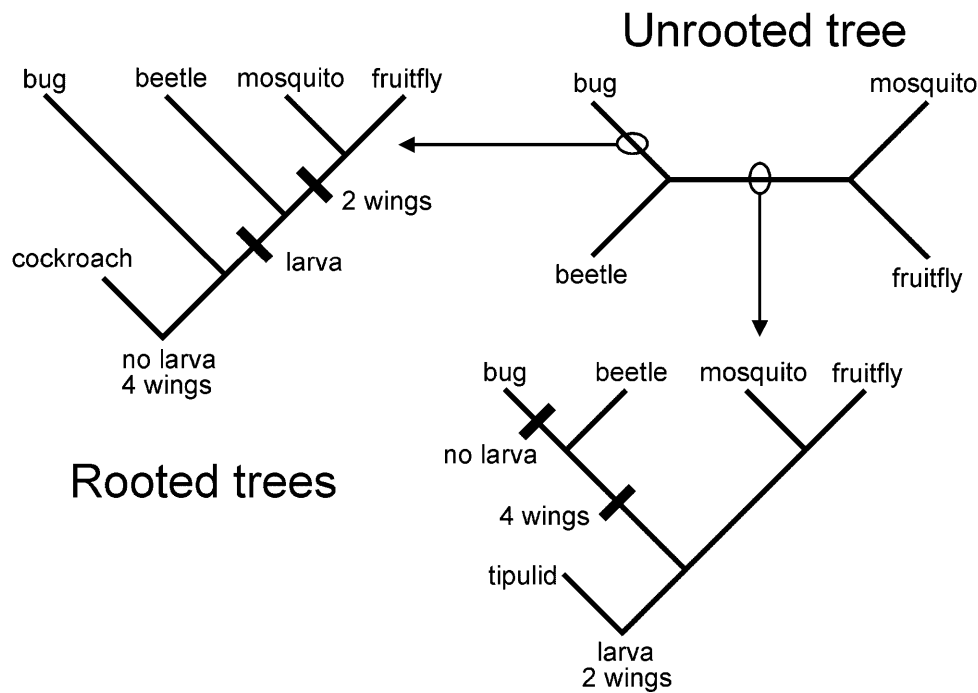


Fig. 5. An unrooted tree (or network) and two of five possible rooted trees for four ingroup taxa (bug, beetle, mosquito, and fruitfly) and one outgroup taxon (cockroach or tipulid). The effect of rooting (and outgroup choice) is illustrated for two characters: the absence/presence of a larval stage and the number of wings (2 or 4). Further explanation in the text.

called *quantitative cladistics* (Andersen, 1999; Schuh, 1999). Along with this development, the theoretical and methodological foundation of cladistics was elaborated and modified through the 1980s and 1990s (Nelson & Platnick, 1981; Maddison & Maddison, 1992; Kitching et al., 1998; Schuh, 1999). In quantitative cladistics phylogenetic relationships are reconstructed from a taxon-character matrix (Fig. 4) composed by character states scored for all taxa under study (e.g., species). The resulting cladogram can be used to infer character state changes along the branches (or internodes) of the reconstructed phylogeny.

Quantitative cladistics invariably adopts the principle of strict methodological parsimony, that is the approach that minimizes the number of *ad hoc* assumptions that must be made to explain a set of observations. In this context, the characters are the observations and the assumptions are that observed similarity of characters have arisen as a result of homology, not homoplasy (convergence, parallelism, reversal). Thus, parsimony is an analytical procedure for grouping taxa that minimizes the number of putative homoplasious similarities. Although small data sets can be analyzed mentally and cladograms drafted by hand, any reasonably-sized data matrix requires a computerized parsimony program to ensure that the cladogram(s) best supported by the character data is found. During the past couple of decades the methods of quantitative cladistics have been implemented in a number of programs for personal computers which are routinely used in modern systematics (Farris, 1988; Maddison & Maddison, 1992; Goloboff, 1993; Swofford, 1998).

One of W. Hennig's greatest achievements was to point out that similarity in ancestral (plesiomorphic) states of characters could not be used as an indication of strict monophyly for a group of organisms that share these character states. This led to an early belief that phylogenies could not be reconstructed without *à priori* knowledge of the direction of evolutionary change of character states. This is also known as the problem of character polarisation. Quantitative cladistics does not make the polarisation of characters a precondition for the success of the cladistic analysis. Instead, character polarisation is treated as an integral part of the cladistic analysis and is intimately associated with the concept of rooting (e.g., Nixon & Carpenter, 1993).

The effect of different tree rooting on character polarity is illustrated by way of a small example (Fig. 5). The unrooted tree (sometimes called a network) for four taxa (bug, beetle, mosquito, and fruitfly) can be rooted in each of its five branches. Rooting can be performed either by way of a hypothetical ancestor (with ancestral character states determined *à priori*) or by way of one or more outgroups. Placing the root on the branch leading to the bug implies the topology of the left hand tree. The tree at the bottom shows the topology when the root is placed in a position that divides the taxa into two groups (bug + beetle, mosquito + fruitfly). This type of rooting is called "midpoint rooting". When characters are assigned to unrooted trees, the states of any character may be ordered while the transformation series itself is left without polarity. By placing a root on the tree, the character states are automatically polarised. Different ways of rooting may have a profound effect on character polarisation. The

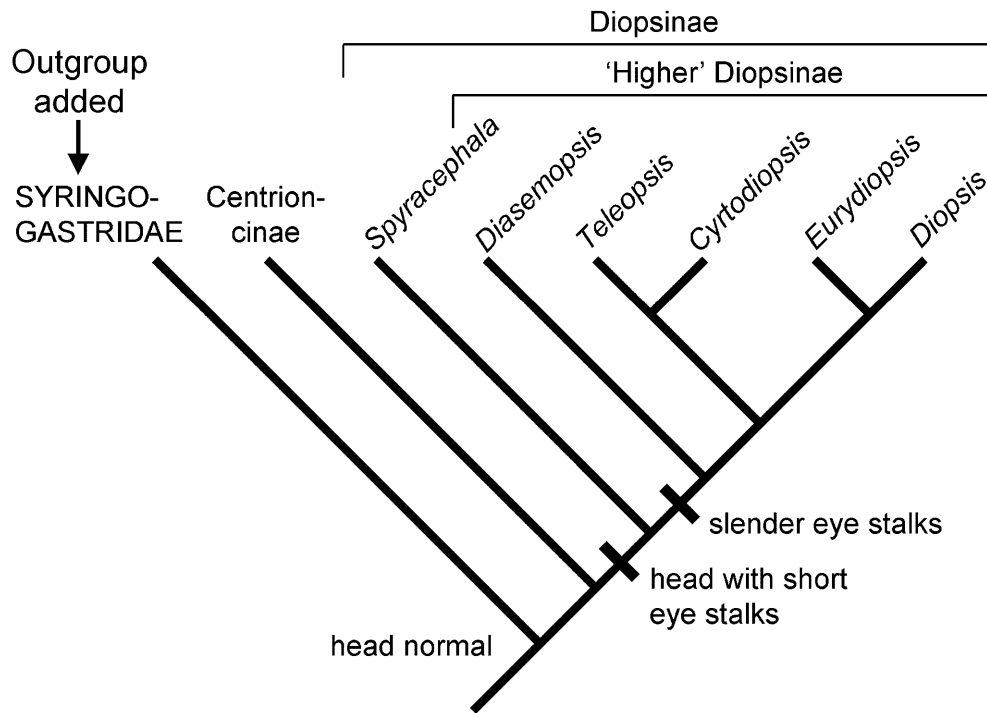


Fig. 6. Phylogeny of genera of the family Diopsidae (Diptera, Cyclorrhapha) with the family Syringogastridae added as outgroup. Evolutionary changes in head structure shown on the branches of the cladogram. (Based on Meier & Hilger, 2000).

length of the tree (as measured by the sum of character state changes along internodes) is not affected. Fig. 5 shows the effect of rooting on the polarity of two characters, the absence/presence of a larval stage and number of wings (2 or 4). It also shows the effect of outgroup choice.

As an example of application of quantitative cladistics, I will use a recently published study of the phylogeny of stalk-eyed flies, Diopsidae, a small family of acalyptrate flies (Diptera, Cyclorrhapha). Almost all of the approximately 160 described species occur in the Old World with the Afrotropical region inhabited by the majority of species. The Diopsidae are best known for their spectacular eye stalks which are found in both sexes and can be longer than the body of the adult fly. The eyestalks of Diopsidae are unique in that not only the eyes but also the antennae are located at the end of the lateral projections of the head capsule. After having been neglected for many years, studies of physiology and sexual behaviour of diopsids have recently been taken up by biologists from many disciplines. A thorough understanding of the evolution of this remarkable group requires a robust phylogenetic hypothesis for the generic relationships within the Diopsidae.

In a paper on acalyptrate flies from Baltic amber, Hennig (1965b) described a fossil diopsid, *Prospyracephala succini* (Loew), and placed it in his phylogenetic "argumentation scheme" together with a number of extant diopsid genera. He used 20 morphological characters for his analysis, each with two states. The plesiomorphic and apomorphic alternatives of each character were decided *à priori*, without comparison with any outgroup taxa.

Hennig included the fossil species in a stem-group (see below) within the subfamily Diopsinae which is the sister-group of the subfamily Centrioncinae, now containing at least 21 valid species with normal head structure. According to Hennig's phylogeny, eyestalk length increased from the stemgroup, through a series of extant forms comprising *Sphyracephala*, *Pseudodiopsis*, and the remaining diopsine genera.

Most recently, a phylogenetic study of the Diopsidae by Meier & Hilger (2000) based on 44 characters of adult morphology and 10 egg characters tells a slightly different story (Fig. 6). In this analysis character states are polarized by including outgroup taxa representing other acalyptrate families. The genera *Pseudodiopsis* and *Sphyracephala* are synonymised and placed as sister-group of the remaining Diopsinae which is firmly established as a monophyletic group. A phylogeny based on yet unpublished molecular data is remarkably congruent with this morphological phylogeny (R. Meier, personal communication). Since eye-stalks are not found in the diopsid superfamily Nothyboidea, it is not possible to decide whether the short and stocky eye-stalks of the extant genus *Sphyracephala* (as well as the Baltic amber fossil) are the ancestral or the derived state. The reconstructed phylogeny for the Diopsidae (Fig. 6) allows further inferences about the evolution of the remarkable eye-stalks of "higher" Diopsinae. For example, Gerald Wilkinson and coworkers (e.g. Wilkinson & Dodson, 1997) found that diopsids exhibiting sexual dimorphism in eye-stalk length most likely evolved from species with eye-stalk monomorphism.

## NEW DEVELOPMENTS: MOLECULAR SYSTEMATICS

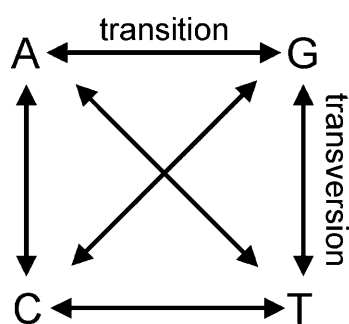
The past two decades or so have witnessed an enormous development in *molecular systematics*, including studies of the evolutionary history of organisms as inferred from molecular data (Hillis et al., 1996). Whereas early methods in molecular systematics estimated genetic distances between organisms (and therefore are essentially phenetic), the Polymerase Chain Reaction (PCR) technique yields sequences of nucleotides in strands of DNA and RNA. Following the principles of phylogenetic systematics, molecular data can be treated as a set of characters, each with four states (A, G, C, T or U), or triplets of nucleotides can be translated into amino acids using the genetic code (Fig. 7). Such data can then be used to reconstruct phylogenies in the same way as morphological characters. Furthermore, by applying the methods of quantitative cladistics, molecular data from different genes may be combined with each other and with morphological characters to yield phylogenies based on so-called “total evidence” (Andersen, 1999).

As an example of the application of molecular characters in phylogeny reconstruction, I will use a study of a small group of water striders (Hemiptera-Heteroptera, Gerridae) which has been extensively studied by John Spence and Felix Sperling, University of Alberta, Edmonton, in cooperation with Jakob Damgaard and myself from the Zoological Museum, University of Copenhagen (Andersen & Spence, 1992; Sperling et al., 1997; Damgaard, Andersen & Sperling, unpublished). The genus *Limnoporus* only comprises six species confined to the Holarctic region. Four species belonging to the *L. rufoscutellatus* (Latreille) group are difficult to separate morphologically, yet show clear behavioural isolation, postzygotic incompatibility, or both. Two species, *L. dissortis* (Drake & Hottes) and *L. notabilis* (Drake &

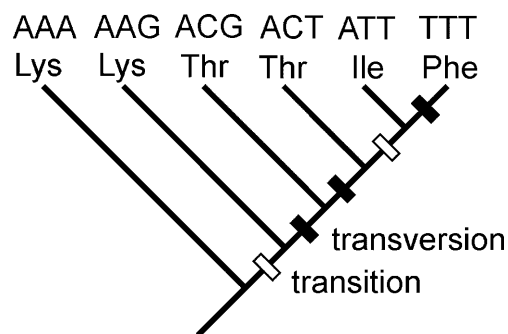
Harris), hybridize extensively in western Canada with demonstrated introgression in nature (Spence, 1990; Sperling & Spence, 1991).

We performed cladistic analyses on data sets composed by a 515-bp region of nuclear DNA (Elongation factor 1 $\alpha$ ), a 820-bp region of mitochondrial DNA (3' half of the cytochrome oxydase subunit 1), and 46 morphological characters (Fig. 8). We used *Aquarius remigis* (Say) and three species of the genus *Gerris* as outgroups. Separate analyses of the three data sets yielded cladogram that are highly congruent except for relationships within the *L. rufoscutellatus* group and relationships among outgroup species as apparent from a strict consensus cladogram. We also performed cladistic analyses on different combinations of the morphological data set and the two molecular data sets as well as all three data sets combined (total evidence; Fig. 9). Generally, the resulting cladograms are well resolved and highly congruent, lending strong support to the reconstructed phylogeny. There have been concerns that the relatively few characters normally applied in morphological analyses should be swamped by the numerous characters normally found in molecular analyses, but this and several other studies have failed to demonstrate such an effect.

The generation of molecular data and their use in systematic studies have generated many controversies about the relative value of molecular versus morphological characters for estimating phylogenies, the neutrality of molecular variants, the constancy of evolutionary rates, and the meaning of “homology” in relation to molecular characters. The bottom line of a survey of these conflicts is that both kind of characters have their merits and weaknesses. Studies that combine the two approaches can maximize both information content, reliability, and usefulness of phylogenetic hypotheses generated by the prin-



DNA nucleotides and substitutions



Cladogram, DNA-triplets and amino-acids

Fig. 7. Molecular data can be treated as characters, each with four states (the nucleotides A, C, G, and T). The left hand diagram shows the nucleotides and possible substitutions between them (either transitions or transversions). The right hand cladogram shows the relationships between six taxa, each characterized by a unique triplet of nucleotides (AAA, AAG, ACG, etc.). These can be translated into amino acids using the genetic code (Lys, Lys, Thr, etc.).

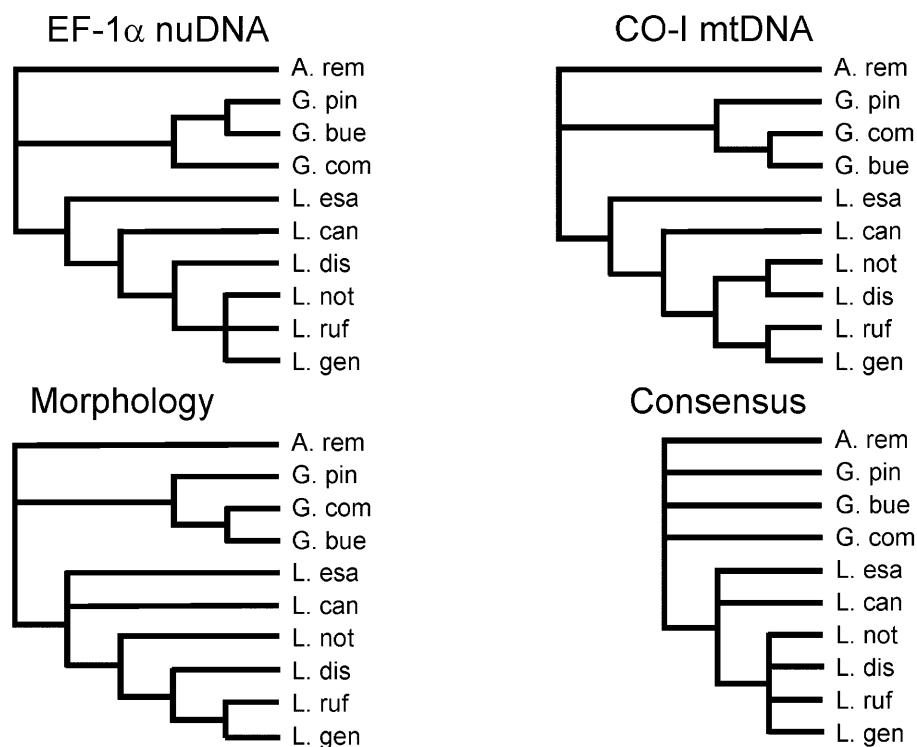


Fig. 8. Phylogeny of six species of *Limnopus* water striders (Hemiptera-Heteroptera, Gerridae) and four outgroup taxa. Cladograms based on the nuclear gene Elongation factor 1 $\alpha$  (EF-1 $\alpha$ ; top left), the mitochondrial gene Cytochrome oxidase I (COI; top right), and morphological characters (bottom left). A strict consensus cladogram for all data set is also shown (bottom right). Abbreviations for taxa: A. rem, *Aquarius remigis* (Say); G. bue, *Gerris buenoi* Kirkaldy; G. com, *Gerris comatus* Drake & Hottes; G. pin, *Gerris pingreensis* Drake & Hottes; L. can, *Limnopus canaliculatus* (Say); L. esa, *L. esakii* Miyamoto; L. dis, *Limnopus dissortis* (Drake & Harris); L. gen, *L. genitalis* Miyamoto; L. not, *L. notabilis* (Drake & Hottes); L. ruf, *L. rufoscutellatus* (Latreille). Further explanation in the text.

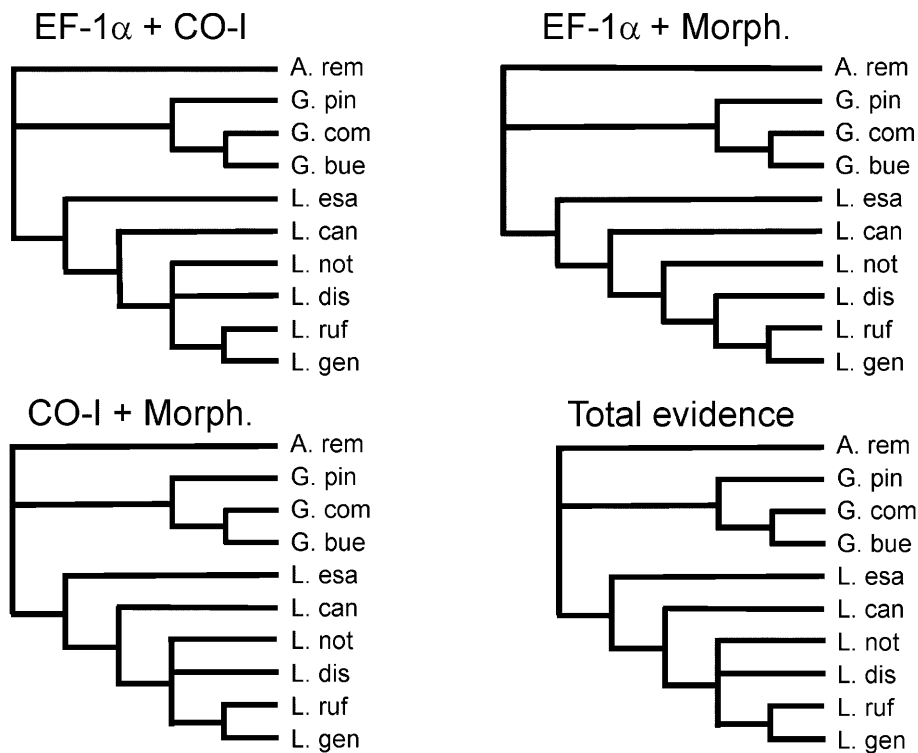


Fig. 9. Phylogeny of *Limnopus* water striders (Hemiptera-Heteroptera, Gerridae). Cladograms based on various combinations of data sets: EF-1 $\alpha$  + COI (top left), EF-1 $\alpha$  + morphology (top right), COI + morphology (bottom left), and EF-1 $\alpha$  + COI + morphology (bottom right). Abbreviations for taxa as in Fig. 8. Further explanation in the text.



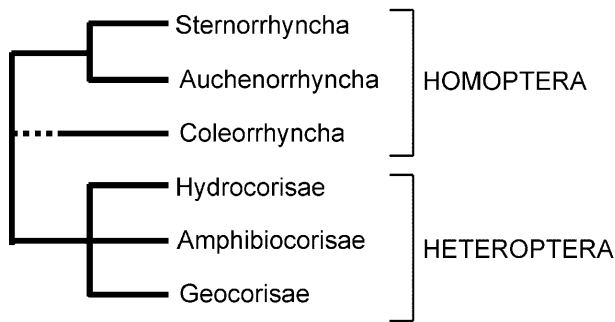


Fig. 10. Typological, pre-hennigian classification of the order Hemiptera.

ciples and methods of W. Hennig's "phylogenetic systematics".

### CLASSIFICATION

One of the main goals of biological systematics is to construct a general reference system or classification. Hennig forcefully advocated that only a phylogenetic system can achieve that goal: "Making the phylogenetic system the general reference system for special systematics has the inestimable advantage that the relations to all other conceivable biological systems can be most easily represented through it. This is because the historical development of organism must necessarily be reflected in some way in all relationships between organisms". (Hennig, 1966: 22–23). The structure of phylogenetic relationships is hierarchic and consequently a hierarchic classification is an adequate form for representation for the phylogenetic relationships between species. The phylogenetic system only recognises strictly monophyletic groups, that is groups containing an ancestral species and all of its descendants. The most important task of phylogenetic systematics is therefore to recognise and possibly eliminate non-monophyletic groups in classification.

Hennig's paper *Kritischen Bemerkungen zum phylogenetischen System der Insekten* (Hennig, 1953) was the first major publication in which he applied his "phylogenetic systematics" outside his own special group (Diptera). In a recent review, Niels P. Kristensen of the Zoological Museum, University of Copenhagen (Kristensen, 1995) evaluated the status of the systematics of insects (or hexapods) and, in particular, the impact of Hennig's "phylogenetic systematics". No one questions that groups like "Apterygota", "Thysanura", Hemimetabola, "Orthoptera", "Hemiptera-Homoptera", "Microlepidoptera", and "Hymenoptera-Symphyla" are non-monophyletic. The monophyly of the "Entognatha", "Psocoptera", "Hemiptera-Auchenorrhyncha", "Diptera-Nematocera", and "Mecoptera" has also been seriously questioned. In general, phylogenetic studies have led to a better understanding of the evolution of insects and to more "natural" classifications. This is particularly the case in the Hemiptera-Heteroptera, Lepidoptera, social

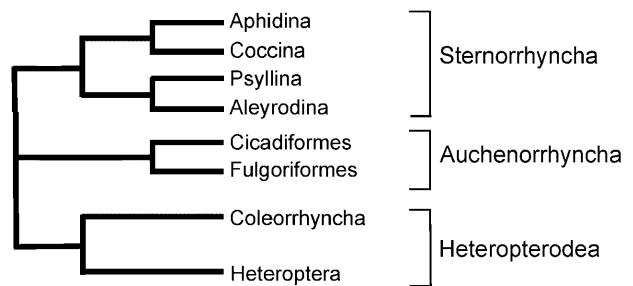


Fig. 11. Phylogenetic classification of the order Hemiptera (Hennig, 1969).

Hymenoptera, so-called higher Diptera, and in the Coleoptera. This trend is likely to continue through the united efforts of taxonomists, comparative morphologists, and molecular systematists, applying methods developed within the framework of Hennig's "phylogenetic systematics".

As an example of the impact of W. Hennig's "phylogenetic systematics" on higher classification, I will use the classification of the order Hemiptera. This order has for many years been divided in two suborders, Homoptera and Heteroptera (Fig. 10). The Homoptera comprised aphids, psyllids, coccids, and whiteflies (division Sternorrhyncha), and cicadas, leafhoppers, and planthoppers (division Auchenorrhyncha); the Heteroptera comprised true bugs which were subdivided according to habitats into land bugs (Geocorisae), water bugs (Hydrocorisae), and semiaquatic bugs (Amphibiocorisae). The division Coleorrhyncha, composed by a single family, the Peloridae, of aberrant hemipterans confined to South America, New Zealand, and Australia, was assigned an intermediate position between the two suborders. This classification is "typological" in the sense that it divides hemipterous insects into subgroups based upon very few characters, and definitely does not reflect phylogeny.

Hennig (1969) presented a classification of the Hemiptera based upon his evaluation of the phylogenetic relationships between the major groups of the order (Fig. 11), questioning the monophyly of the suborder Homoptera and placing Coleorrhyncha and Heteroptera as sister groups (division Heteropterodea). A modern, phylogenetic classification of the Hemiptera is based upon both morphological and molecular characters (Fig. 12; Carver et al., 1991; Wheeler et al., 1993; Sorensen et al., 1995). The monophyly of the Sternorrhyncha is confirmed whereas that of the Auchenorrhyncha is seriously questioned. Some hemipterists have suggested that the Fulgoromorpha are more closely related to Heteroptera than they are to other Auchenorrhyncha. Notice also the modern subdivision of the Heteroptera into eight infraorders, in particular the disruption of the old division "Geocorisae" (Fig. 11).

A cladogram can be translated to a nested or hierarchical set of relationships between taxa and groups of taxa. Ideally, only monophyletic taxa should be recog-

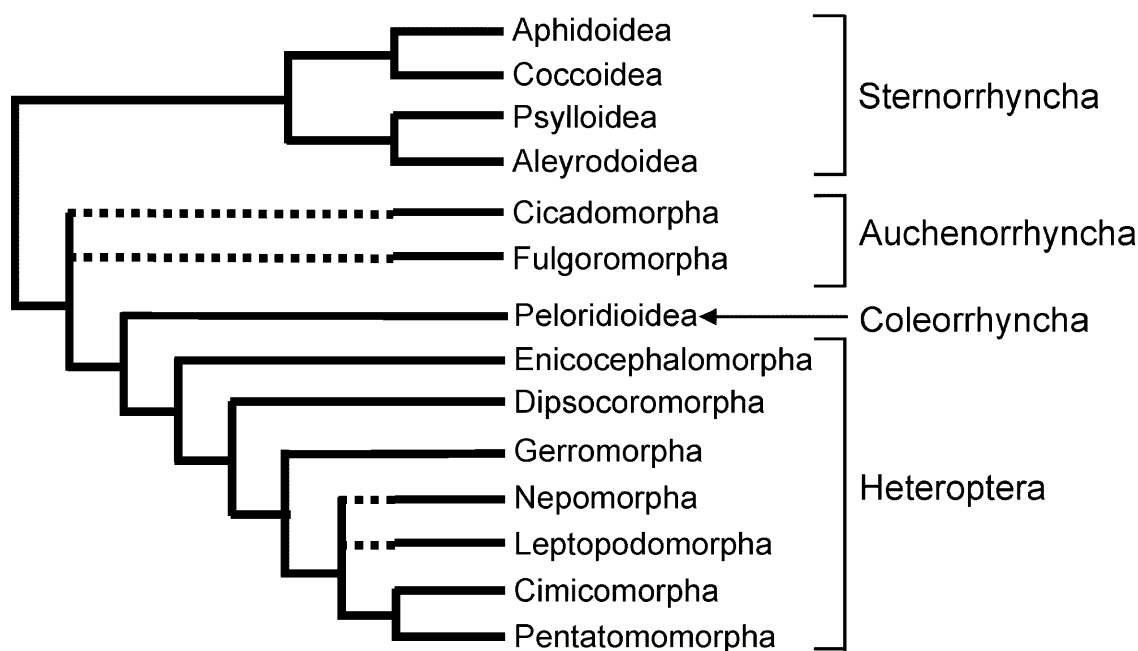


Fig. 12. Phylogenetic classification of the order Hemiptera (based on Carver et al., 1991; Wheeler et al., 1993; Sorenson et al., 1995).

nised in cladistic classifications. Originally, W. Hennig required that every monophyletic group is recognised and named in the classification and that sister groups should be given the same taxonomic rank Hennig (e.g. 1966: 154ff) also proposed that that same rank should indicate the same age across all groups (e.g. insects and mammals). For any sizeable number of taxa, however, the number of higher taxon names will increase dramatically as illustrated by the following translation of the phylogenetic relationships within the Hemiptera (Fig. 12) into a hierarchic classification:

- Order Hemiptera
  - Suborder Sternorrhyncha
  - Suborder Euhemiptera
    - New rank 1 Auchenorrhyncha
    - New rank 1 Neohemiptera
      - New rank 2 Fulgoromorpha
      - New rank 2 Heteropterodea
        - New rank 3 Coleorrhyncha
        - New rank 3 Heteroptera

An alternative (and less radical) approach to pure subordination is based on the principle of *phyletic sequencing* which does not require that every monophyletic group is formally named (e.g., Wiley, 1980; Schuh, 1999). Instead it is prescribed, that taxa of the same taxonomic rank are listed in sequence so that each taxon is the sister group of all following taxa together:

- Order Hemiptera
  - Suborder Sternorrhyncha
  - Suborder Auchenorrhyncha
  - Suborder Fulgoromorpha
  - Suborder Coleorrhyncha
  - Suborder Heteroptera

Ax (1984) and, more recently, de Queiroz & Gauthier (1992) have proposed a “phylogenetic taxonomy” which abandon the Linnean system of biological nomenclature and replaces taxon names with apomorphy-based definitions without Linnean types and ranks. The merits of such a system are currently under debate and only the future will show if it is viable.

Another example of the impact of W. Hennig’s phylogenetic systematics on higher classification of insects is the order Lepidoptera (butterflies and moths). Hennig (1953, 1966) paid much attention to the subdivision of the order Lepidoptera, which he found to be of particular interest because the basal differentiation exemplifies a pattern of diversification which he expected for many taxa following his own “deviation rule”: “. . . when a species splits, one of the two daughter species tends to deviate more strongly than the other from a common stem species” [or from the common original condition (Hennig 1966: 207)]. The majority of the extant members of the group (in this case Lepidoptera) belong to a subordinate clade (in this case Ditryisia) characterised by many apomorphies. The other extant clades within the group, all relatively poor in species, can be arranged into a sequence according to the proportion of the ditryisian apomorphies which they have acquired by what Hennig called “additive typogenesis” (Fig. 13). Early classifications of the Lepidoptera invariably included basic dichotomies, for example Monotryisia/Ditryisia, Jugatae/ Frenatae, where the first group were paraphyletic with respect to the other.

Hennig’s (1953) work stimulated further inquiry into the basal branches of the Lepidoptera phylogeny, and his principal conclusions have now been fully confirmed, chiefly through the work by Niels P. Kristensen and his co-workers. This includes exciting recent discoveries of additional small basal moth taxa (Fig. 14), as well as

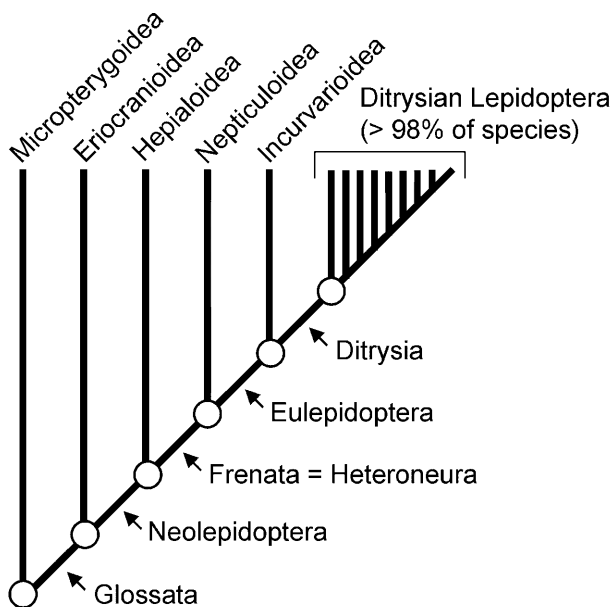


Fig. 13. Phylogenetic relationships between major groups of Lepidoptera (based on Hennig, 1953, 1966).

refined analyses of the basal taxa previously recognized. The results of this work, recently summarized by Kristensen and co-workers in the first volume of the "Handbook of Zoology: Lepidoptera" (1999), have led to the recognition of an even more richly pectinate base of the lepidopteran phylogenetic tree: as many as seven splitting

events are now recognised below the one leading to Hennig's hepialoid assemblage.

#### PHYLOGENETIC SYSTEMATICS AND FOSSILS

Fossils supply the only direct evidence of the evolutionary history of any group of organisms and we might therefore assume that phylogenetic relationships among species and higher taxa can only be inferred from the study of fossils or palaeontology. W. Hennig challenged this assumption arguing: "that the palaeontological method does not make possible direct determination of the phylogenetic relationships, but promises results only in cooperation with other methods of phylogenetic systematics." (Hennig, 1966: 141-142). Thus palaeontologists basically are limited to the same methods as neontologists when it comes to reconstructing the phylogeny of a group comprising fossil taxa, or by placing extinct species in a reconstructed phylogeny of extant species. In addition, fossils are most often too incompletely preserved to reveal the entire structure ("holomorphy" sensu Hennig) of the organism. This is especially the case with insect fossils preserved in rocks, petrified or as casts or moulds whereas insects enclosed in amber usually reveal more details.

The impact of Hennig's "phylogenetic systematics" on modern palaeontology is very obvious in a recent text book by Andrew B. Smith (Smith, 1994) and a case study by the present author (Andersen, 1998). When reconstructing the phylogenetic relationships of a group, fossils should not be treated as different from extant organisms.

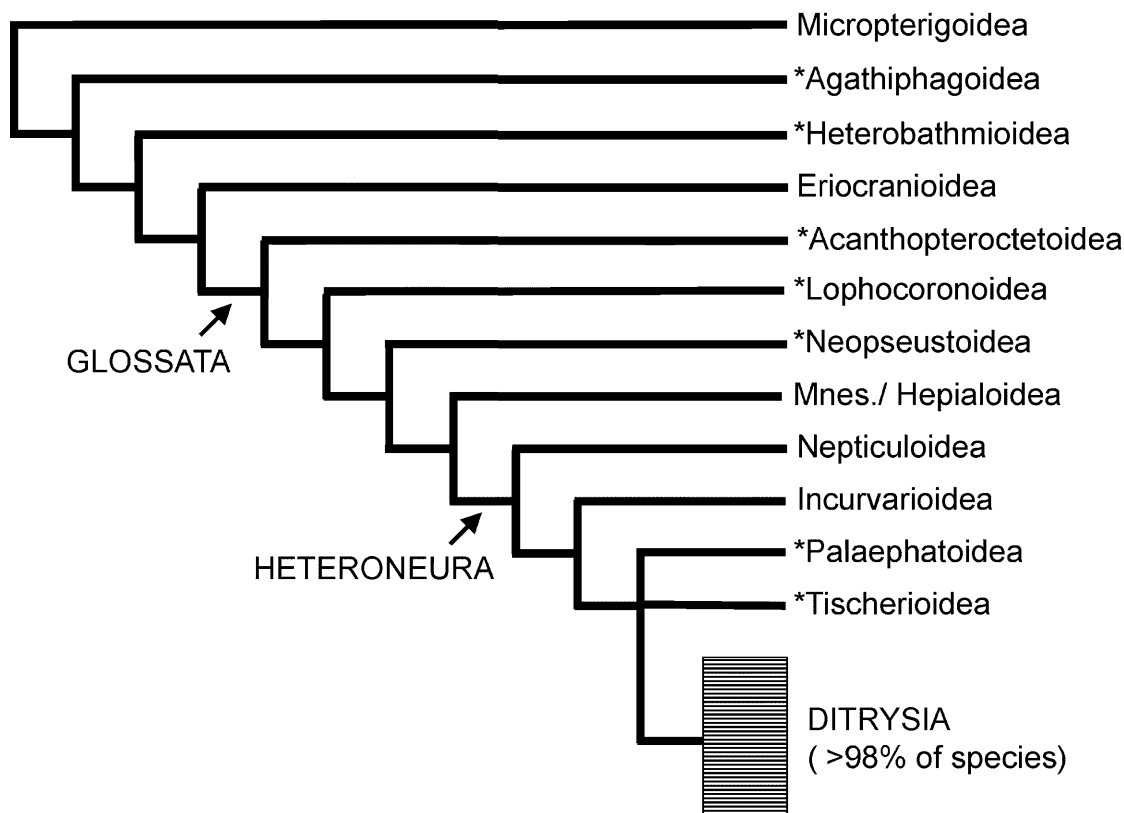


Fig. 14. Phylogenetic relationships between major groups of Lepidoptera (based on Kristensen, 1999). Taxa not known to Hennig, or considered by him to be subordinate in other taxa are marked with an asterisk (\*).

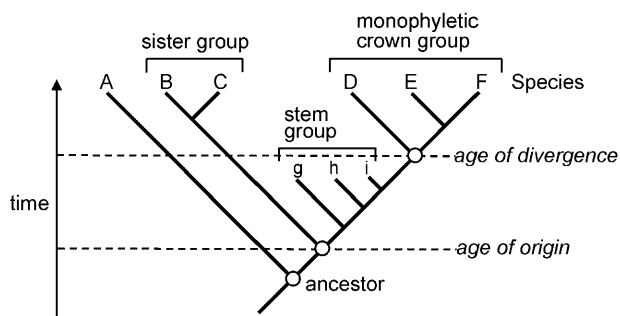


Fig. 15. A resolved phylogeny between six extant species (A-F) and three fossil species (g-i) with relative positions on a time scale. Further explanation in the text.

When it comes to translating a cladogram into a phylogenetic classification, however, fossils may pose a special problem. This problem was addressed by Hennig (1969) by introducing the concept of *stem group* (“Stammgruppe”) which is a group of extinct species possessing one or more of the diagnostic characters of an extant, monophyletic group, but not including all descendants of a common ancestor (Fig. 15, species g + h + i). A stem group is therefore paraphyletic in a phylogenetic context. In contrast, a *crown group* (Fig. 15, D + E + F) is an extant monophyletic group that also may include extinct species with all the diagnostic characters (synapomorphies) of that group, or can be shown to have secondarily lost such characters.

The distinction between stem groups and crown groups is also important for decisions on the time of origin or divergence of monophyletic groups (clades) and for comparisons between such groups. In the cladogram (Fig. 15) there are two monophyletic groups of extant species, the group composed of species D + E + F and its sister group composed of B + C. The time of origin of both groups is unequivocally determined by the splitting of their most recent common ancestor. Adding the fossil species g, h, and i to the crown group D + E + F does not change the time of origin of the group composed by all living or extinct descendants of their most recent common ancestor.

In a phylogenetic system, the word *extinction* cannot be used without specification. Only monophyletic groups can go extinct because these are the only groups that consist of all descendants of a common ancestor. By definition, a paraphyletic group cannot go extinct since it excludes at least some descendants of its ancestor. For example, even if the extant species B-D (Fig. 15) ceased to exist, their most recent common ancestor still has living descendants (E and F).

### ECOLOGICAL PHYLOGENETICS

W. Hennig repeatedly referred to the phylogenetic system as the most useful general reference system in biology and also recognized the importance of phylogenies in studies of ecology and behaviour. The American entomologist Herbert H. Ross was one of the first sys-

tematists to describe an explicit “phylogenetic method” of deciphering ecological diversification, for example in his text-book *Biological Systematics* where he writes: “After the phylogeny of the group is derived on basis of heritable characters, then the different ecological character states can be “hung on the phylogenetic hat rack” and certain inferences can be made. The crux of determining direction of ecological diversification is to find out the ecological state occupied by the ancestral species (the hypothetical ancestor) of the group, then the ecological states occupied by subsequent species. These ecological states we can call ancestral and derived.” (Ross, 1974: 246). In one of the first applications of this method, the present author (Andersen, 1979, 1982) hypothesised the sequence of evolutionary changes between habitat zones leading to the diversification of semiaquatic bugs (Hemiptera, Heteroptera: Gerromorpha).

Thus, by integrating phylogenetic and ecological information we can infer the evolutionary history of ecological traits through an approach most appropriately referred to as *ecological phylogenetics* (Spence & Andersen, 1994). Phylogenetic information can be used in two ways: (a) ecological and behavioural data about extant taxa are placed on phylogenies to reveal probable patterns of evolution and to determine the sequence of changes that generated these patterns (Fig. 16); (b) comparative analyses may be corrected for effects of phylogeny to explicitly measure so-called phylogenetic constraints. These methods have been applied successfully to ecological and behavioural problems in many insect groups as reviewed by Miller & Wenzel (1995).

Let me illustrate the application of “ecological phylogenetics” by an example from my own research on marine water striders. Although insects are unparalleled among animals in their evolutionary success on land and in freshwater, relatively few insects have invaded marine environment and only five species of the hemipterous family Gerridae have successfully colonised the open ocean. They all belong to the genus *Halobates* or sea skaters. In these ocean striders, adults and juveniles spend their entire life on the sea surface, always at some distance from land. They feed on other animals belonging to the pleustonic community and are themselves preyed upon by seabirds and pelagic fish. Their eggs are deposited on various floating objects.

There has been much speculation about the origin and evolution of sea skaters, in particular how the oceanic species of *Halobates* achieved their unique way of life. A meaningful discussion of such problems requires reliable hypotheses of relationships between species and/or monophyletic species groups. In recent years, the evolution of *Halobates* and their allies have been extensively studied by Lanna Cheng, Scripps Institute of Oceanography, San Diego and Felix A. H. Sperling, University of Alberta, Edmonton, in cooperation with Jakob Damgaard and myself. A phylogenetic hypothesis based upon a combination of molecular and morphological data (Fig. 17) suggests that ancestral halobatines were freshwater insects. Species belonging to the genus *Asclepios* invaded coastal

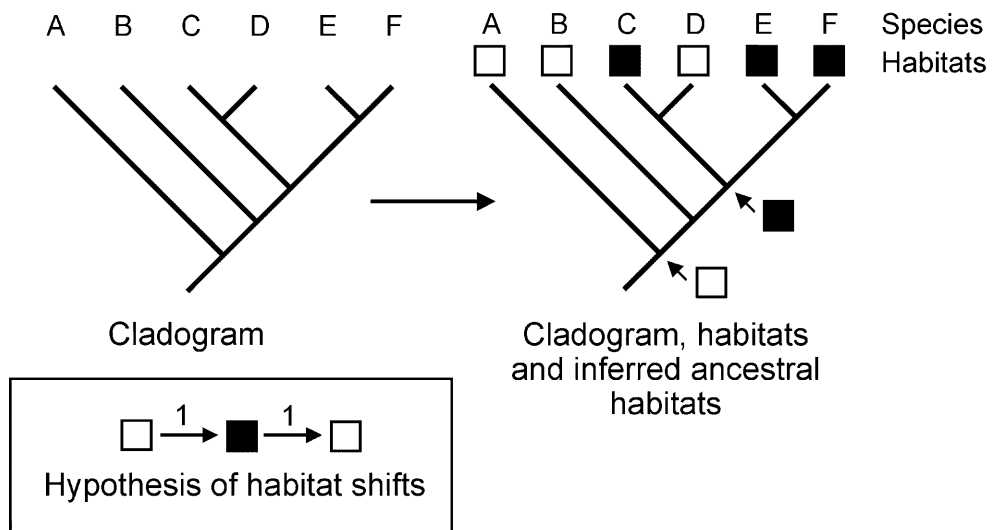


Fig. 16. Ecological Phylogenetics: mapping ecological traits on cladograms. The cladogram of relationships between six species (top left hand; A-F) is used to infer ancestral habitats (top right) as well as the evolutionary sequence of habitat changes (bottom left).

marine habitats whereas species of *Austrobates* and *Halobates* probably evolved from euryhaline ancestors to inhabit limnic and marine habitats, respectively. The oceanic way of life in some *Halobates* species probably evolved at least twice. First, at the base of the clade composed by the oceanic species *H. germanus* and *H. sericeus* and the nearshore species *H. hayanus* (and possibly a few other nearshore species). Second, at the base of the

clade composed by the oceanic species *H. sobrinus*, *H. splendens*, and *H. micans* and the nearshore species *H. flaviventris* and *H. hawaiiensis*. This hypothesis is at least more parsimonious than one including only one transition to the open ocean, and two independent reversals to nearshore habitats.

Firmly based phylogenetic hypotheses are significant in answering questions on the evolution of ecological and

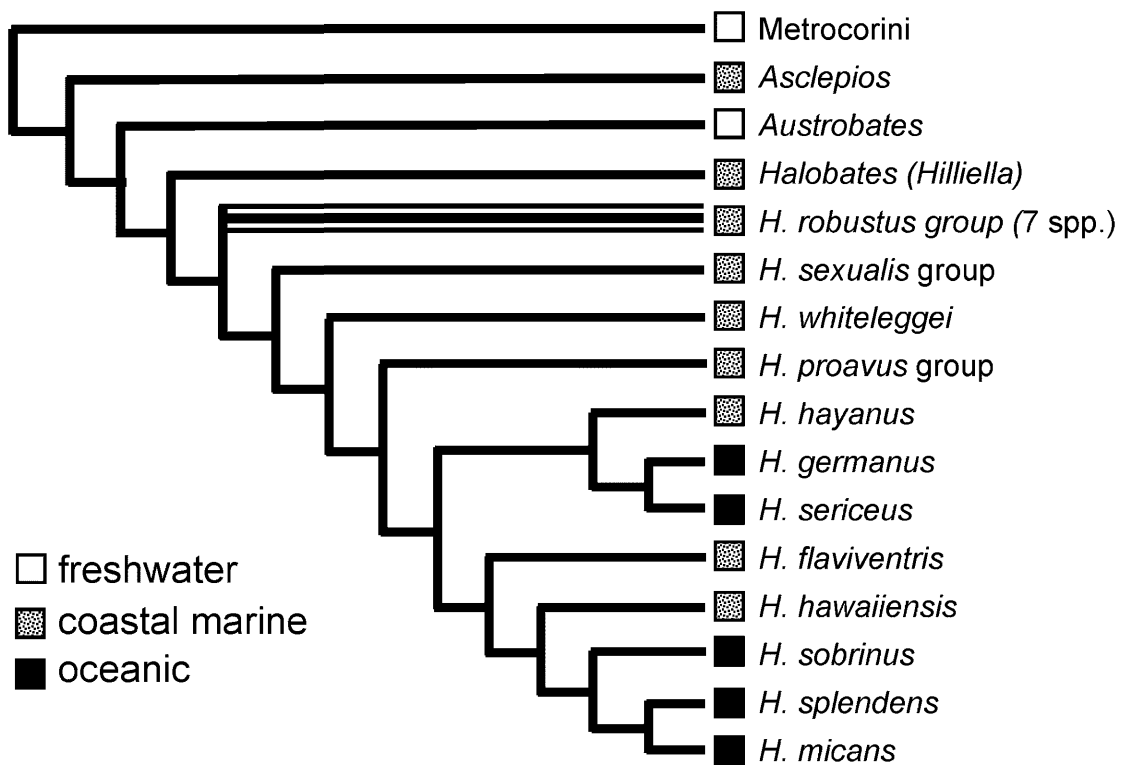


Fig. 17. Ecological evolution of sea skaters, *Halobates* (Hemiptera-Heteroptera, Gerridae). The cladogram shows different kinds of habitats superimposed upon a cladogram of relationships between the genera and species groups of sea skaters with the tribe Halobatinae-Metrocorini as outgroup. (Based upon Damgaard et al., 2000 b).

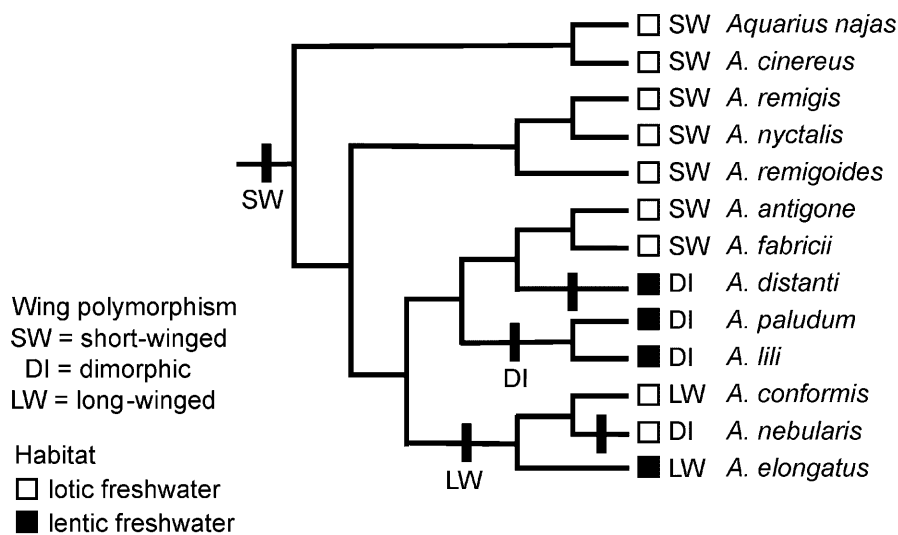


Fig. 18. Cladogram of relationships between species of *Aquarius* water striders (Hemiptera, Gerridae; based upon Damgaard et al., 2000 a) with habitats and states of wing polymorphism superimposed. Inferred changes in wing polymorphism indicated on the branches. Further explanation in the text.

behavioural traits in insects. In a phylogenetic system, sister-groups by definition have the same age of origin (but not necessarily the same age of differentiation) which allows meaningful comparisons (Fig. 15). In one of the first studies of this kind, Mitter et al. (1988) tested the widely invoked hypothesis that “diversification is accelerated by adoption of a new way of life, that is movement into a new adaptive zone”. The feeding habits of major clades of insects were mapped onto cladograms of those groups and the number of species of adjacent clades were compared. In 11 of 13 comparisons, the phytophagous lineage was significantly more diverse than its non-phytophagous sister group.

A recent collection of papers edited by Philippe Grandcolas of the Natural History Museum, Paris, reports several case studies where phylogenetic inference tells us a different story than expected (Grandcolas, 1997). For example, Halictine bees (Hymenoptera: Apidae) include several genera comprising both social and solitary species and seem ideal to test the selective advantage of eusociality in insects. However, phylogenetic analyses performed by Laurence Packer, University of York, Canada, indicate that in most genera it is the solitary behaviour that is the evolutionary novelty and eusociality is ancestral (Packer, 1997). In primarily winged insects, wing polymorphism is usually treated as a derived trait which has evolved in species using the most stable habitats. However, in northern temperate pondskaters (Hemiptera: Gerridae), phylogenetic inference has shown that the polarisation must be reversed, and that obligatorily winged species most probably have evolved from wing polymorphic species (Andersen, 1997, 2000). This is illustrated in Fig. 18 where wing development have been superimposed upon a reconstructed phylogeny for *Aquarius* water striders (Damgaard et al., 2000 a). The diagram also indicates a strong association between the most stable type of habitats (lotic freshwater habitats =

streams, rivers) and the loss of flight capacity. Finally, a study of European *Polistes* (Hymenoptera: Vespidae) tests Emery’s rule stating that social parasites are more closely related to their hosts than to each other. Cladistic optimisation of traits associated with social parasitism on a reconstructed phylogeny leads to the rejection of Emery’s rule (Carpenter, 1997).

Cladistic inference is also a powerful tool in studying co-evolution of phytophagous or parasitic insects and their hosts. For example, Hennig (1966: 112) referred to the case of the flamingoes and their mallophagan parasites which are most closely related to those found on ducks and geese, thus contradicting the hypothesis that flamingoes are aberrant storks.

#### CLADISTIC BIOGEOGRAPHY

Hennig’s “phylogenetic systematics” has also had a significant impact on the study of historical biogeography. Hennig’s major contribution to biogeographic analysis (Hennig 1960) dealt with the Diptera of New Zealand as an example problem. It relied heavily on Hennig’s own “progression rule” – the idea that if an insect has migrated to a new area, developing new characters as its distribution expands, the progression of migration is marked by sequentially more-derived characters (Hennig, 1966: 232). Figure 19 is reproduced from Hennig’s 1966-book (fig. 68) and shows a phylogeny of a group of seven species superimposed on their areas of distribution. The occurrence in South America of a partial subordinated group of a monophyletic group that is otherwise confined to New Zealand and Australia is taken as argument for a former existence of direct connection between these areas.

It was, however, the pioneering work by the Swedish entomologist Lars Brundin on the phylogeny and biogeography of southern hemisphere chironomid midges (Diptera: Chironomidae) that most forcefully demon-

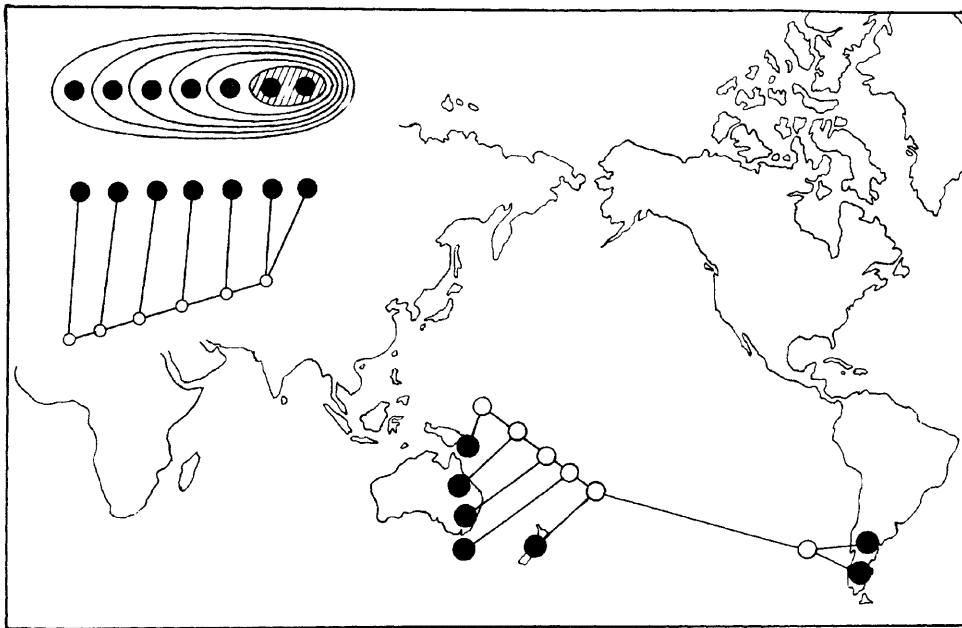


Fig. 19. Phylogeny and distribution of a hypothetical group of species on the southern continents (after Hennig 1966: fig. 68).

strated the potential use of Hennig's "phylogenetic systematics" in studies of historical biogeography (Brundin, 1966). Through the use of phylogenetic methods, Brundin demonstrated repeated patterns of intercontinental connection within lineages of chironomid midges in the southern end of the World. Figure 20 shows phylogenies for three genera of chironomid midges of which *Podoclus* and *Podomus* have species found in South America, New Zealand, and Australia whereas *Podonomopsis* only has species found in the two last mentioned areas. The three taxon-area cladograms (upper row) are congruent with a hypothesis about former land connections shown as an "area cladogram" where the faunas of South America and Australia are more closely connected than each are with the fauna of New Zealand (Fig. 20, bottom right). The appearance of Brundin's work coincided with the

increasing acceptance of Wegener's theory of continental drift and the emergence of plate tectonics as the major paradigm of historical geology. Suddenly, it all made sense: disjunct biotic patterns and geological patterns are due to the same events in earth history.

Fused with cladistics, historical biogeography has now become *cladistic biogeography* which holds great promise as an equal partner to palaeontology and palaeogeography in explaining the historical causes of the present distribution of insects (e.g. Humphries & Parenti, 1999). As principles of biogeography have a permanent place in conservation biology, phylogenetic systematics also has impact on issues related to the "biodiversity crisis", for example in providing phylogenetic information about regional biotas as one of the criteria for choosing which areas to preserve.

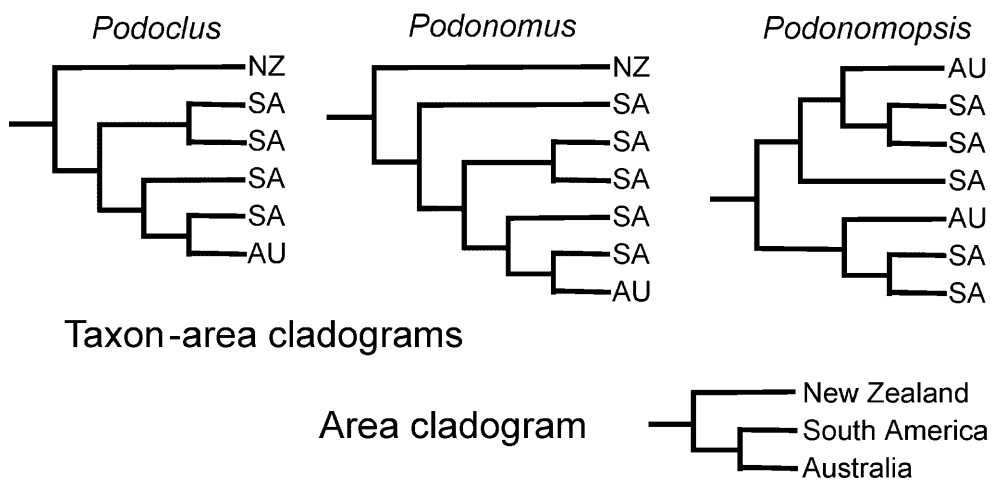


Fig. 20. Taxon-area cladogram for three genera of chironomid midges (top row) and a cladogram of relationships between three areas (bottom right). Abbreviations: AU, Australia; NZ, New Zealand; SA, South America. (Based upon Brundin, 1966).

## CONCLUSIONS

Hennig's "phylogenetic systematics" undoubtedly was a very significant contribution to systematics, by some systematists and philosophers even characterised as a "revolution".

Although most of Hennig's theoretical and methodological ideas can be traced back to earlier authors, including Charles Darwin, it was Hennig who was the first to place these ideas in a coherent theoretical and methodological framework (Richter & Meier, 1994; Kitching et al., 1998; Schuh, 1999). Thus, W. Hennig's phylogenetic systematics:

- (1) Redefines phylogenetic relationships and monophyly in terms of recency of common ancestry. It is now widely recognised that Hennig's redefinition and clarification of the concepts of monophyly and phylogenetic relationships has created a sound foundation for systematics in general.
- (2) Provides tools for reconstructing phylogenetic relationships by derived character similarity (= synapomorphy).
- (3) Redirects the interest of systematists into the study of higher taxa and their phylogeny. Hennig's third contribution was perhaps equally important. After decades of focussing on species-level problems, Hennig redirected the interest of systematists towards the study of higher taxa and the reconstruction of phylogenetic relationships between them.
- (4) Installs the phylogenetic system as the most useful general reference system in biology. W. Hennig's "phylogenetic systematics" has a significant impact on contemporary entomology. A phylogenetic system is now almost universally accepted as the most useful general reference system for biology.
- (5) Interacts forcefully with new developments in systematics, evolutionary biology, historical biogeography, and biodiversity studies. W. Hennig's "phylogenetic systematics" has been able to accommodate new developments in systematics, evolutionary biology, historical biogeography, and information technology, and has also been suggested as a basis for a new practise in classification and nomenclature.

In a recent historical review of systematic entomology in America, Charles Mitter of the University of Maryland, predicts the return of a "golden age" in systematics (Mitter, 1999). This optimism is based on significant advances over the past couple of decades in systematic theory, computing power, and new data from molecular techniques. In particular, Mitter mentions the impact of W. Hennig's "phylogenetic systematics" in the revival of systematic entomology. I concur with Mitter in the realistic postulate that the next generation of entomologists in about 20 years will inherit a "tree of life" that is robustly resolved to the family level across the insect orders, and to a much finer degree in the majority of these.

With this review, I hope to have given some insights into the state of art in phylogenetic systematics and to have encouraged the reader to share a optimistic view upon the future of systematic entomology.

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