

# The metamorphosis of traditional into advanced phylogenetic systematics and its impact on nematode systematics

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Accepted for publication 20 December 1995

**Summary.** Phylogenetic systematics as proposed by Hennig has become very successful. However, since its beginning, it has suffered from a fundamental mistake which appears inconsequential at first glance: the *relative* concepts of synapomorphy and symplesiomorphy were employed as if they were *absolute*. Closer inspection reveals the full impact of this mistake which has resulted in the exclusion of "symplesiomorphies", once recognized as such, from further analysis, and to transforming phylogenetic systematics into a form of nonphylogenetic systematics named cladistics which is not based in any way on the theory of evolution. By re-establishing the relativity of the concepts analysed, *advanced phylogenetic systematics* is achieved in which, by employing the so-called *loss tracing method* and knowledge ultimately inferred from the theory of evolution, traditional "symplesiomorphies" become exploitable for recognizing holophyletic species sets. Therefore, advanced phylogenetic systematics is superior to traditional phylogenetic systematics and cladistics. A nematological example is provided which demonstrates the new approach.

**Key words:** Phylogenetic systematics, cladistics, parsimony, outgroup analysis, loss tracing method, theory of evolution, nematodes, Enoplida.

## Why did phylogenetic systematics become so successful?

Willi Hennig, a German entomologist, became well-known for his introduction of phylogenetic systematics. His first book on the subject, written in German (Hennig, 1950), was not well received. Even his second book (Hennig, 1966), completely rewritten in English, was initially adversely criticised (Kühne, 1978), but subsequently became accepted and very successful. A comparison of Hennig's work with other contemporary authors reveals that the success of phylogenetic systematics is essentially based on the advance of the following four essential points of premises:

1) *Hennig's union of taxonomy and phylogenetics into a single discipline named phylogenetic systematics.*

Prior to Hennig, taxonomy (= systematics at that time) and phylogenetics were two largely separate disciplines. Taxonomy was independent from the theory of evolution and was merely aimed at describ-

ing and clearly ordering species diversity; a good and widely accepted taxonomic system was denoted a natural system. In contrast, phylogenetics is based on the theory of evolution, i.e. Darwin's theory of natural selection and descent, and is aimed at recognizing principles, pathways and vestiges of evolution. Among the problems dealt with are those on specialization and reversibility in phylogenetic developments, connections between ontogenetic and phylogenetic development, impact of genes and environmental factors on the phenotypic appearance of organisms and, of course, interrelationships between sets of species. Taxonomists and phylogeneticists concurred that a natural system must conform with essential phylogenetic findings; particularly, polyphyletic taxa were rejected. One of the most famous phylogeneticists, the German zoologist Adolf Remane, a very experienced taxonomist on marine gastrotrichs, thoroughly elaborated the methods of phylogenetics (Remane, 1956). Nevertheless, he did not unite taxonomy and phylogenetics into a single discipline.

In contrast, Hennig no longer accepted the separate states of taxonomy and phylogenetics. He united them into a single scientific discipline which he

<sup>1</sup>This paper is an expanded version of an invitational Plenary talk presented at the First English Language International Symposium of the Russian Society of Nematology held in St. Petersburg, Russia, 23rd to 30th September 1995.

called phylogenetic systematics. This union was necessary, as the theory of evolution is generally accepted by biologists, taxonomists included. Important potentials emerged from the union for substantiating hypotheses on interrelationships between species sets.

2) *Hennig's requirement for the acceptance of only monophyletic taxa as valid and his restrictive redefinition of "monophyly"*.

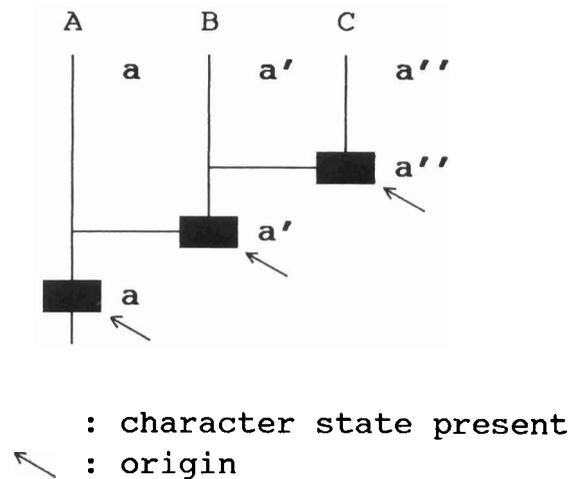
Essentially, Hennig achieved the union by his restrictive demand for the acceptance of only monophyletic taxa as valid and by rejection of all non-monophyletic ones. He even reinforced his demand by suggesting a very restrictive redefinition of *monophyletic*: Single origin is no longer accepted as the only criterion of *monophyletic*, but additionally, a monophyletic species set must include *all* known species which are hypothesized to have descended from an ancestral stem species. According to the new definition, the Reptilia are no longer monophyletic, but instead are paraphyletic, because their hypothetical ancestral stem species gave rise not only to reptiles, but also to birds and mammals, i.e. to all species of Amniota. As no further species are known to have descended from this stem species, the Amniota are denoted monophyletic.

Ashlock (1971) replaced *monophyletic sensu* Hennig with the new term *holophyletic*. This term is superior to the former and, hence is used throughout the remainder of this paper.

3) *Hennig's introduction of the new concepts of synapomorphy and symplesiomorphy*.

Hennig (1953) introduced and later (1966) defined the concepts of *synapomorphy* and *symplesiomorphy*. According to Hennig, and by common usage, these concepts refer to derived and ancestral homologous character states, respectively. That is, each of them combines the concept of homology with that of polarizing sequences of character states. Prior to Hennig, no term was available for uniting both concepts. In its simplest case, a sequence of character states comprises only two states: primary absence, and presence, of a character. Further states may refer to modifications of a character and even to its complete loss; in the latter case the character is said to be secondarily absent in the respective species. Figure 1 and its accompanying legend is Hennig's illustration and original definition of the concepts of *synapomorphy* and *symplesiomorphy*.

According to Hennig's opinion, which has been widely accepted, the holophyly of any species set is substantiated by at least one "synapomorphy", while the paraphyly of any species set is substantiated by at least one "symplesiomorphy". As Hennig and subsequent authors accepted only holophyletic taxa



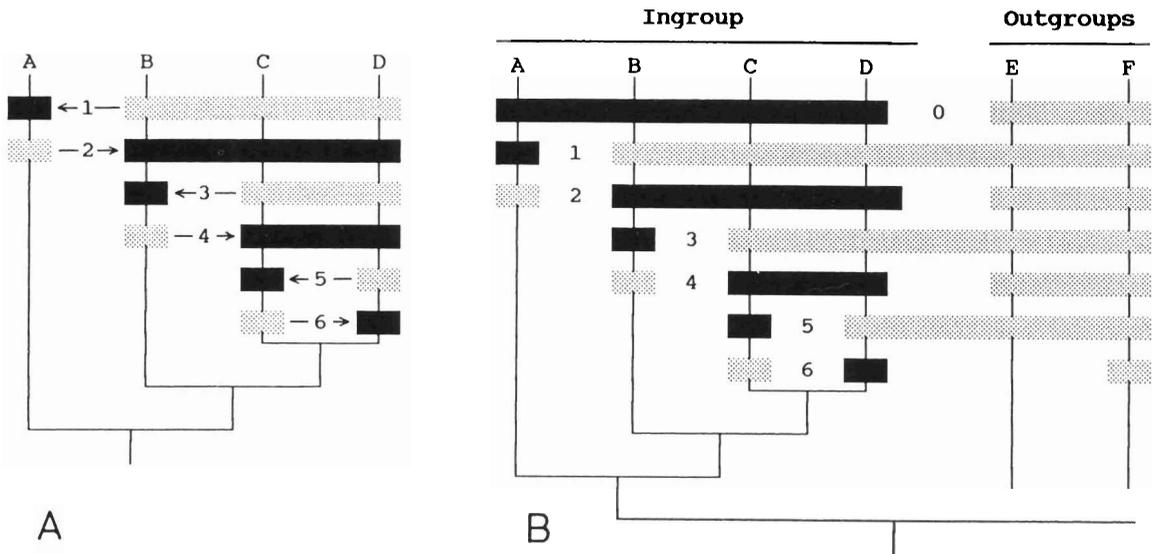
**Fig. 1.** Hennig's (1966) diagram redrawn which illustrated his explanation of the concepts of symplesiomorphy and synapomorphy: "Simple reflection shows that these [plesiomorphous and apomorphous] are relative concepts: the characters *a'* and *a''* are both apomorphous compared with *a*, but *a'* is plesiomorphous compared with *a''*. ... We will call the presence of plesiomorphous characters in different species **symplesiomorphy**, the presence of apomorphous characters **synapomorphy**, always with the assumption that the compared characters belong to one and the same transformation series." Hennig (1966) further stated: "The apomorphous features characteristic for a particular monophyletic group (present only in it) can be ignored in discussing its relationships to other groups; we will call such characters the **autapomorphous characters** of a monophyletic group." Throughout this paper, the rectangular shape of the diagrams is due to practical, rather than to theoretical, reasons.

as valid, "synapomorphies" became very important, whereas "symplesiomorphies" became completely unimportant. Hennig demonstrated this diagrammatically as redrawn in Figure 2A.

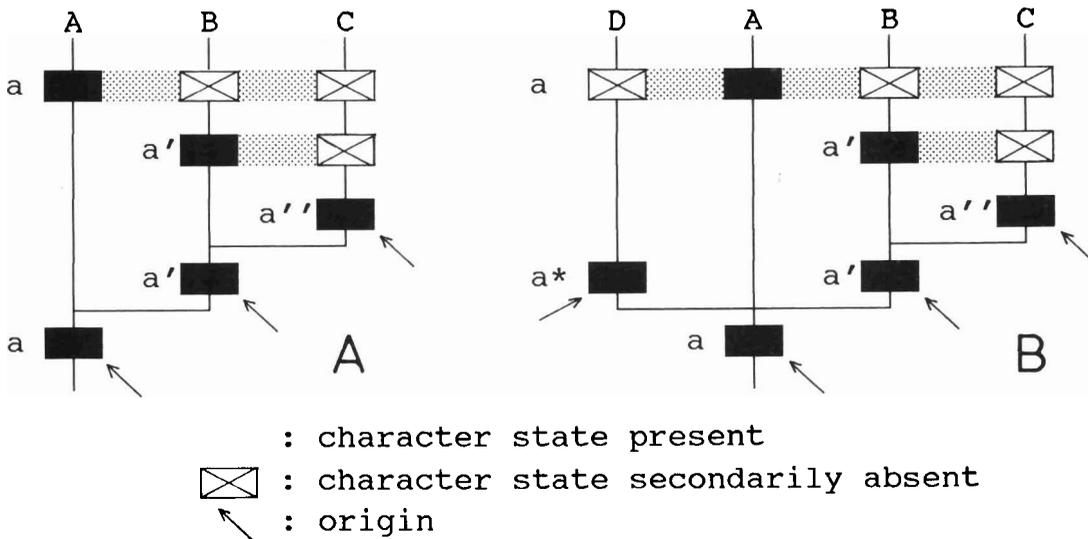
Hennig (1953) also introduced the concept of *autapomorphy*, first defining it in 1966 (see original definition cited in Fig. 1 legend). Like "synapomorphies", "autapomorphies" are exclusively used for substantiating the holophyly of species sets. Both concepts do not differ in any respect and therefore it is proposed here that the concept of autapomorphy should be abandoned.

4) *Hennig's vision of the phylogenetic system*.

Hennig (e.g. 1966) proposed a system of exclusively holophyletic taxa to be *the* (rather than a) *phylogenetic system* of the respective set of species; like a natural system, it is hierarchic or - in the words of Hennig - *encaptic*, as any taxon is either completely included in or completely excluded from any other taxon. However, for theoretical and practical reasons, *the* phylogenetic system cannot be achieved because splitting of original species into two daughter species does not *necessarily* imply that *every* daughter



**Fig. 2.** Hennig's (1966) preferred "argumentation scheme of phylogenetic systematics". **A:** Redrawing of Hennig's original scheme, which did not include all information on which its interpretation is based. **B:** The missing information added to Hennig's scheme. Holophyletic are A, B, C, D, CD, BCD, and ABCD.



**Fig. 3.** An unbranched (**A**) and a branched (**B**) sequence of character states. The unbranched sequence corresponds to that of Figure 1. In contrast to the latter, both presence and secondary absence of character states are now expressed explicitly to clearly illustrate the hypotheses of holophyly, which may be inferred from the diagrams. If the character states are exclusively present in the species sets displayed and if no further states have originated from **a**, ABC, BC and C of the left diagram, and DABC, BC, C and D of the right diagram are holophyletic.

species differs from its original species by at least one new character state. Therefore, Hennig's strict demand must be replaced with a more moderate one: *a* (rather than the) phylogenetic system must contain a maximum amount of holophyletic and a minimum amount of paraphyletic taxa, whereby both types of taxa must be clearly labelled.

Essentially, Hennig's suggestions on the method of substantiating phylogenetic hypotheses (i.e. hypotheses of synapomorphy, symplesiomorphy,

holophyly and paraphyly) are identical to the method commonly employed by phylogeneticists and thoroughly discussed by Remane (1956). Even evolutionary systematists fully concur with these suggestions as, for example, Mayr (1974), their most influential spokesman, has clearly stated. The only difference between phylogenetic and evolutionary systematics is that paraphyletic taxa are accepted as preliminary results in the former and as valid results in the latter.

## Why was phylogenetic systematics formed into a form of non-phylogenetic systematics named cladistics?

The most important offshoot of phylogenetic systematics is a form of *non*-phylogenetic systematics known as transformed cladistics or, simply, cladistics. The last named term is used in this paper. Cladistics was created around 1980 (see Platnick 1980, Patterson 1980, Nelson & Platnick 1981) and is explicitly stated to be independent from any part of the theory of evolution. That is, regardless of whether the theory of evolution is accepted or rejected, cladistics can be fully used in either case. Cladists regard themselves as legitimate intellectual successors of Hennig and to honour him founded the Willi Hennig Society in 1980.

Because of its independence from the theory of evolution, a cladistic system is nothing more than a natural system in its pre-Darwinian sense. However, in contrast to classical taxonomists, cladists are very rigid in employing an important principle which is generally accepted in science, i.e. the principle of parsimony. Applied to systematics, this principle obliges biologists to infer the most parsimonious hypothesis of relationships from a pattern of characters and character states observed in a species set being studied. Additionally, cladists have created the so-called outgroup analysis which they use for polarizing sequences of character states. Neither the principle of parsimony nor the outgroup analysis depend on any part of the theory of evolution.

Can phylogenetic systematics really be performed by employing nothing other than the two tools indicated? Is phylogenetic systematics in reality non-phylogenetic? Did Hennig make a fundamental mistake? Or, conversely, did the cladists make a fundamental mistake? The answer is that both are partly right and partly wrong as indicated here:

A) Results achieved in both phylogenetic systematics and cladistics may be identical if, and only if, a *single* most parsimonious hypothesis of relationships can be inferred from a pattern of characters and character states.

B) Hennig and subsequent authors, cladists included, made a fundamentally important mistake by using the *relative* concepts of synapomorphy and symplesiomorphy as if they were *absolute*.

C) The outgroup analysis does not deserve the label *analysis*; at best it is a technique for sampling data by taking test samples.

D) In contrast to the belief expressed by cladists, the theory of evolution can be employed as a tool in phylogenetic systematics.

The arguments for these answers are:

A) *The only cases in which results achieved in*

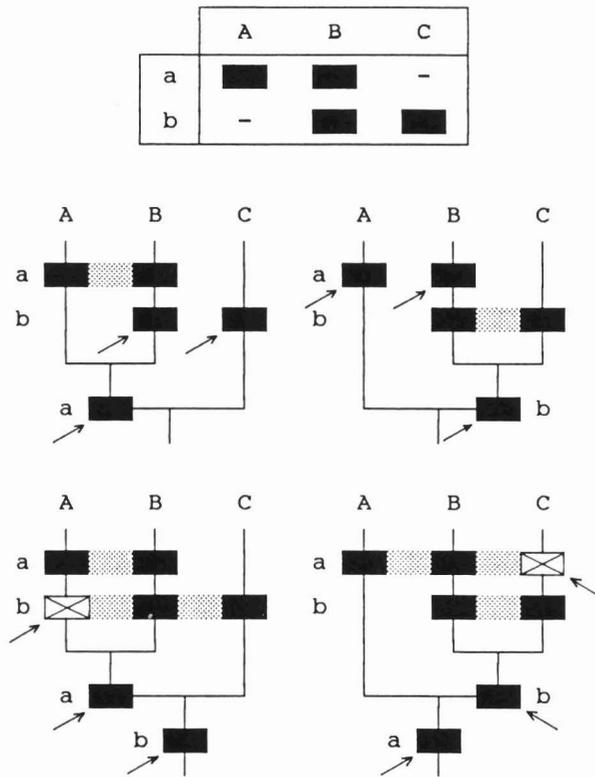
*phylogenetic systematics and cladistics are identical.* Among the patterns of characters and character states, which each may be explained by a single most parsimonious hypothesis of relationships, is that preferred by Hennig and redrawn in Figure 2A. As this pattern does not display all essential information on which its interpretation is based, the missing information must be added. The result is presented in Figure 2B. According to cladistic nomenclature, the species set ABCD (i.e. composed of A, B, C and D) may be denoted an *ingroup*, and species sets outside ABCD, for instance E and F, may be denoted its outgroups. Within the diagram of Figure 2B, all character states marked by black bars occur exclusively within the ingroup and, therefore, are denoted "synapomorphies" of their corresponding species sets. As the latter are arranged encaptically, their holophyly becomes immediately evident. A single hypothesis of relationships explains their arrangement most parsimoniously; this hypothesis is identical to that proposed by Hennig. The character states marked by stippled bars occur either within and without the ingroup or exclusively without the ingroup and, therefore, are referred to as "symplesiomorphies" of their corresponding species sets which are arranged non-encaptically and are paraphyletic.

According to earlier results (Lorenzen, 1993), results of phylogenetic systematics and cladistics are *always identical* if only a single hypothesis of relationships may be inferred from a particular pattern of characters and character states.

The surprising success of achieving identical hypotheses of relationships in phylogenetic systematics and cladistics may have tempted cladists to believe that the theory of evolution is generally not needed as a tool in phylogenetic systematics. This belief is wrong, see below.

B) *Hennig's fundamentally important mistake and its implications:* Involuntarily, by making a mistake, Hennig gave rise to the belief just stated and, therefore, to the transformation of phylogenetic systematics into cladistics. This is shown in the hypothetical example in Figure 3A, in which the ancestral character state **a** of the stem species of ABC is transformed into **a'** of the stem species of BC and further into the most advanced state **a''** of the stem species of C. Let **a**, **a'** and **a''** each be present as a homologous character state exclusively in the present day species of the sets A, B and C, respectively.

According to traditional phylogenetic systematics as advanced by Hennig and adopted by subsequent authors, **a** and **a'** are "symplesiomorphies" of A and B, respectively, while **a''** is a "synapomorphy" of C. Notations like these are incorrect, because *synapomorphy* and *symplesiomorphy* are used as if they were



**Fig. 4.** A nonencaptic character pattern used in the loss tracing method. The pattern may be explained most parsimoniously by four hypotheses of relationships. If the homology of characters *a* and *b* can be proven, *a* or *b* must be *secondarily* absent in C or A, respectively. Symbols as in Figure 3.

*absolute* concepts. As Hennig (1966) correctly stressed (cited here in the Fig. 1 legend), *plesiomorphy* and *apomorphy* are *relative* concepts. Therefore, the concepts of *symplesiomorphy* and *synapomorphy* must also be relative, as the prefix "syn" stands merely for the notion that a "plesiomorphy" or "apomorphy" is present in *several* species rather than in only one. Whenever the common but nevertheless incorrect usage of the concepts is demonstrated in the present paper, the terms are marked by quotation signs.

Apparently Hennig's mistake does not become evident if only the most advanced character state (like *a''* in Fig. 3) of any transformation sequence is denoted a "synapomorphy" of the corresponding species set and if all lesser advanced states (like *a* and *a'* in Fig. 3) are denoted "symplesiomorphies" of the corresponding species sets. This view seems to be rather widespread and is supported by all redefinitions of the concepts which suggest evaluating *the presence* of a character or character state in species sets studied.

In the following manner, Hennig's mistake may have favoured the removal of the theory of evolution from the base of phylogenetic systematics. Consider the character states of the transformation sequence

of Figure 3A: states *a'* and *a''* are *primarily* absent in more ancestral parts of the sequence, whereas states *a* and *a'* are *secondarily* absent in more advanced parts. These notions are included in the statements of synapomorphy and symplesiomorphy, respectively. If the theory of evolution is accepted, no problem arises in accepting secondary absence of characters and character states as common features of species. If, however, the theory of evolution is rejected, even secondary absence of characters and character states in species may be rejected. Any exclusion of "symplesiomorphies" from systematic analyses eliminates the problem of dealing with secondary absence of characters and character states and makes this kind of systematics attractive even to antievolutionists.

C) *The outgroup analysis is merely a technique of sampling data.* The outgroup analysis is commonly used for polarizing sequences of character states. Its technique was demonstrated above, paragraph A. The case considered (Fig. 2) was simple, as each character was represented by only two states and as the complete set of character states could be subdivided into an encaptic and a nonencaptic subset marked by black and stippled bars, respectively. In this and in all equivalent cases, the outgroup analysis can be employed unambiguously. However, it is not needed, as the same result can be achieved by exclusively employing the principle of parsimony.

In many cases, a complete set of character states can only be subdivided into non-encaptic subsets. The outgroup analysis cannot then be achieved unambiguously, as contradictory choices of in- and outgroups are possible. An example is provided by the character pattern of Figure 4, in which the outgroup analysis cannot yield any conclusion on whether characters *a* and *b* are primarily or secondarily absent in C and A, respectively.

At its best, the outgroup analysis serves for estimating the extent to which characters and character states are present not only within a taxon under study, but outside this taxon as well. Such study refers to the common exercise of seeking data needed by taking adequate test samples.

For a more detailed evaluation of the outgroup analysis see Lorenzen (1993).

D) *The theory of evolution as a tool in phylogenetic systematics:* Whenever a pattern of characters and character states can be explained most parsimoniously by various hypotheses of relationships, arguments for rejecting at least one of them can only be inferred from the theory of evolution. This was demonstrated recently (Lorenzen 1993). Perhaps, some uncertainty may exist in how to employ the theory of evolution in systematics. This aspect will be dealt with below.

## The key for metamorphosing traditional into advanced phylogenetic systematics

Undoubtedly, all character states which each comprise the most advanced state of a sequence are highly important to any kind of systematics and identification keys, because the corresponding species sets are holophyletic, are arranged encaptically, and may be accommodated most parsimoniously within a single hypothesis of relationships. Basically, the "synapomorphies" of traditional phylogenetic systematics and of cladistics refer to these important character states. The technique of their recognition and of their employment for substantiating phylogenetic hypotheses needs hardly any improvement.

If any improvement of phylogenetic systematics is to be achieved, "symplesiomorphies" (as understood traditionally) need to be included adequately in the methods for recognizing holophyletic species sets. In contrast to the belief expressed by various authors (e.g. Patterson, 1982; Ax, 1987) a "symplesiomorphy" at a certain taxonomic level cannot be denoted a "synapomorphy" at any other taxonomic level, because every "symplesiomorphy" of a species set is replaced with at least one further advanced state in another species set. That is, every "symplesiomorphy" can only be present or *secondarily absent* in a holophyletic species set.

This aspect provides the key for adequately exploiting traditional "symplesiomorphies". Traditional phylogenetic systematics has focused too much on the *presence* of characters and character states in species sets. By focusing on both the *presence and secondary absence* of characters and character states in species sets, an improved type of phylogenetic systematics emerges for which I propose the name ***Advanced Phylogenetic Systematics***.

The suggestion that cladistics is independent from any theory on the origin of species diversity implies the claim that the requirements of both anti-evolutionists and evolutionists must be fulfilled. Secondary absence of characters and character states is not an important topic for anti-evolutionists, whereas it is essential to evolutionists. This is because evolution is a highly dynamic process by which new species evolve from existing ones and in turn may even become extinct. Combined with such species dynamics is a structure dynamics, which leads to the emergence of new structures from previous ones and to modifications, and even loss, of structures. In these cases, character states of ancestral species are *secondarily absent* in subsequent species. For instance, according to evidence available, tetrapods must have descended from fishlike ancestors which implies that gills must be *secondarily absent* in adult tetrapods, and as zooparasitic nematodes must have

descended from microscopically small free-living ones, microscopic size and a free-living life style must be *secondarily absent* in large zooparasitic nematodes.

Extremely helpful for understanding the dynamics of species and their structures is the theory of evolution or, more strictly, its core, the theory of natural selection. This theory does not offer an overall explanation of any particular evolutionary phenomenon of the biotic world but, instead, describes a natural law - the principle of natural selection - and makes it responsible for evolution. According to contemporary knowledge, this natural law applies not only to organisms but, additionally, to all other things of the biotic and abiotic world which are capable of reproduction regardless of whether this occurs by division, autinduction, autocatalysis or whatever. In all cases, resources are needed for reproduction, whereas access to resources may be hindered by diverse environmental adversaries which partly depend and partly do not depend on population densities of conspecifics. According to the principle of natural selection, only those organisms and those other things capable of reproduction can reproduce themselves successfully which, by overcoming the environmental adversaries, can get access to sufficient resources needed. Commonly, conspecifics do not only resemble each other but are also different from each other. These differences may enhance or diminish their capability, *viz.* their fitness, of getting access to resources needed. In evolution, long lasting selection pressures may favour preservation, modification and even loss of structures. Emergence of new structures depends on the favourable coincidence of various genetic and environmental events and, therefore occurs rather rarely. In many cases, vestiges of evolutionary development are still present and may be interpreted by searching for evidence of their cause. Whenever such a search leads to a convincing hypothesis, the latter may serve for substantiating a hypothesis of phylogenetic relationships. Therefore, advanced phylogenetic systematics is firmly based on the theory of evolution and, as the principle of parsimony is generally valid, the latter also is incorporated into the scheme.

### Explication of the concepts of synapomorphy, symplesiomorphy and holapomorphy

The transformation of traditional into advanced phylogenetic systematics will be initiated by re-evaluating the concepts of synapomorphy and symplesiomorphy. If their relativity is fully taken into account, **a** and **a'** of Figure 3A can no longer be referred to as "symplesiomorphies" of A and B,

respectively, and **a''** can no longer be referred to as a "synapomorphy" of C but, instead, the information to be inferred from the example must read as follows:

- **a** is a symplesiomorphy of A and any subset of A relative to **a'** in B and to **a''** in C;
- **a'** is a synapomorphy of B and any subset of B relative to **a** in A and a symplesiomorphy of B and any subset of B relative to **a''** in C;
- **a''** is a synapomorphy of C and any subset of C relative to **a'** in B and to **a** in A.

Note that according to the correct usage of the concepts, statements of synapomorphy do no longer refer exclusively to holophyletic species sets but, rather, may refer to non-holophyletic ones (like B in Fig. 3A and 3B) as well. Therefore, contrary to common belief, the concept of synapomorphy is not related exclusively with that of holophyly but, instead, with that of monophyly in its pre-Hennig sense.

In many cases, an ancestral character state may give rise to more than one transformation series, e.g. two series as displayed in Figure 3B. In this case, **a'** and **a''** are neither plesiomorphic nor apomorphic relative to **a\*** in D. Instead, **a'** and **a''** are *primarily* absent not only in A, but in D as well. Additionally, **a** is *secondarily* absent not only in B and C, but also in D. As any holophyletic species set must include all known species in which a particular homologous character or character state is hypothesized to be either present or *secondarily* absent, and as such species set must be distinct from all known species in which this character or character state is *primarily* absent, the concepts of synapomorphy and symplesiomorphy may best be redefined by exclusively referring to presence, primary absence, and secondary absence of homologous characters and character states in species sets. Such redefinition will read as follows:

*Any homologous character or character state **a** of a species set A is denoted a **synapomorphy** of A relative to its primary absence in other species sets and a **symplesiomorphy** of A relative to its secondary absence in even other species sets.*

This redefinition applies even to sets containing only one species. Whenever a character or character state is analysed completely with respect to the concepts of homology, synapomorphy and symplesiomorphy, the corresponding species set is holophyletic. I introduced the concept of *holapomorphy* some years ago (1981), as no term was available for adequately expressing such a result. Its original definition is still valid but may be improved as follows:

*If a set B of known species is composed exactly of all known species in which a homologous character or character state is shown to be either present or secon-*

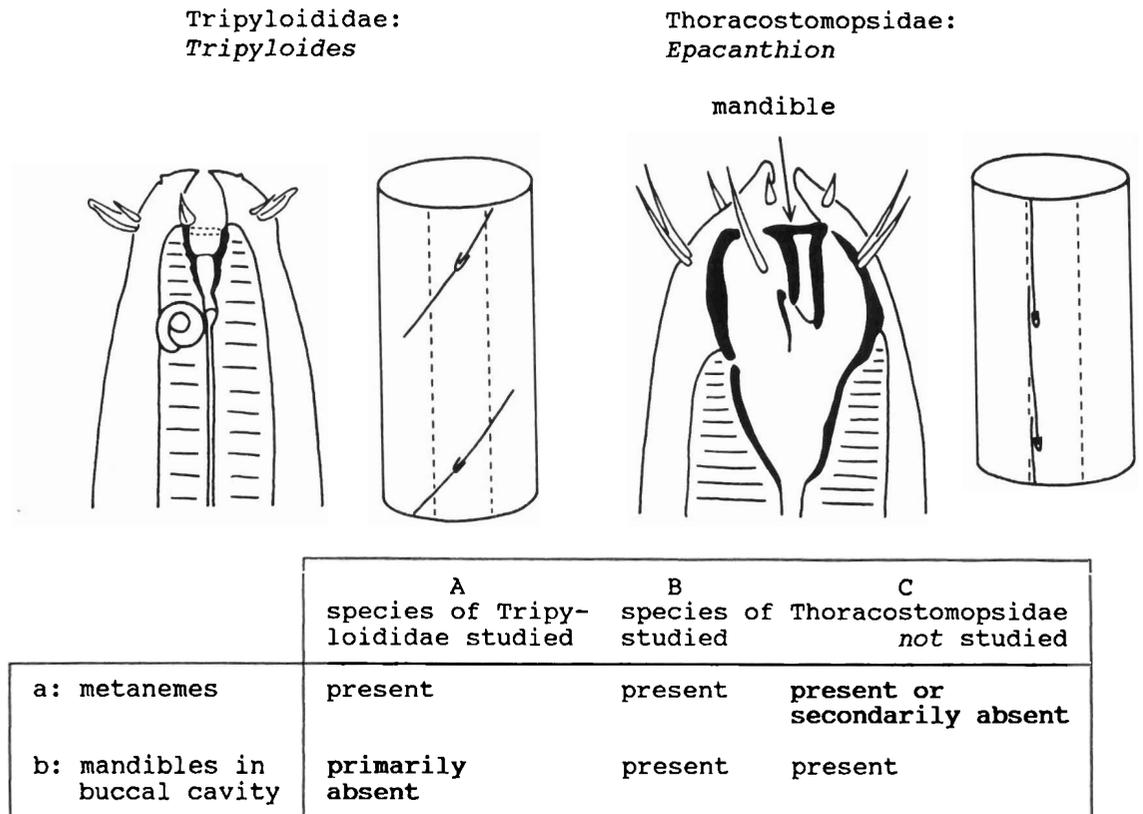
*darily absent, this character or character state is denoted a **holapomorphy** of B which, therefore, is holophyletic.*

The concept of holapomorphy is absolute, is firmly related with that of holophyly, and may be applied even to sets containing only one species. Apparently any statement of holapomorphy is the final summary of all statements of homology, synapomorphy and symplesiomorphy, which refer to the evaluation of a single character or character state. In the example of Figure 3A, the character states **a**, **a'** and **a''** are holapomorphies of the holophyletic taxa ABC, BC and C, respectively.

At various times, Hennig (1980, 1984) tried to incorporate the aspect of holapomorphy into phylogenetic systematics. He proposed to express it by the concepts of synapomorphy, "derived ground plan character (= autapomorphy)" and "derived ground plan character (an 'archapomorphy')". The term *archapomorphy* was new. Hennig did not succeed in expressing his aim by an unambiguous definition of any concept or in providing a stringent method for adequately including "symplesiomorphies" in the process of substantiating the holophyly of species sets. Therefore, the concept of holapomorphy is superior to Hennig's concepts of aut- and archapomorphy and will be retained.

### Introduction of the loss tracing method

A stringent method of selectively seeking cases of secondary absence of characters was lacking in traditional phylogenetic systematics. Recently (Lorenzen 1993), such method was presented. It makes use of the non-encaptic character pattern displayed at the top of Figure 4, where characters **a** and **b** are present in the species sets AB and BC, respectively. By exclusively employing the principle of parsimony, this character pattern may be explained most parsimoniously by four hypotheses of relationships. They clearly demonstrate the following points: 1) As the principle of parsimony was used for achieving them, it cannot be used for rejecting any one of them. 2) A first step to reject any one of them may be performed by evaluating the hypotheses of homology and analogy included in them. If arguments inferred from evolutionary biology, and hence from the theory of evolution, can be used to demonstrate that each character has evolved only once in the species sets analysed, then the upper two hypotheses of Figure 4 must be rejected and the lower two must be accepted as worthy of further analysis. The latter hypotheses deal with both primary and secondary absence of characters. That is, either must character **a** be *secondarily* absent in C, or character **b** must be *secondarily* absent in A. 3) Again, argu-



**Fig. 5.** Metanemes were found in all species studied of the Tripyloididae (left) and Thoracostomopsidae (right). By considering further characters, for example the form of the buccal cavity, a non-encaptic character pattern can be achieved from which, by employing the loss tracing method, it can be concluded that metanemes must be present or secondarily absent in the species of the Thoracostomopsidae not studied.

ments inferred from evolutionary biology may help to reject one of them and to accept the other as finally valid. 5) In contrast to traditional phylogenetic systematics, advanced phylogenetic systematics not only deals with the tentative holophyly of the species sets A, B, C, AB and BC but, additionally, with that of ABC. To fully appreciate this difference, look at Figure 4. According to the instructions of traditional phylogenetic systematics, the presence of **a** in AB and of **b** in BC would merely be "symplesiomorphies" or homoplasies (more than one origin per character or character state within a species set) of the respective species sets. 6) Any hypothesis of secondary absence of a particular character can only be substantiated by analysing it *in conjunction with other characters*.

Let the lower right hypothesis of Figure 4 be finally accepted, according to which **a** is secondarily absent in C. Character **a** may be tested against further characters, for instance against **c** present in AD. This new pattern becomes identical with that of Figure 4

and may permit the conclusion that character **a** is secondarily absent even in the species set D. The process of finding all known species in which the homologous character **a** is evidently present or secondarily absent will only be completed, when the species set achieved is encaptic relative to all other *holophyletic* species sets recognized. The species set achieved is then substantiated to be holophyletic.

The method described proved to be of such importance that it deserves a proper name and here I propose the term: *loss tracing method*. This name is new but the method was previously explicitly used in outlining a phylogenetic system of free-living nematodes (Lorenzen, 1981).

The loss tracing method is very different from the methods of traditional phylogenetic systematics which was not aimed at converting a maximum number of characters and character states into homoplasies. The loss tracing method can be applied not only to morphological characters, but to molecular ones as well.

## Advanced phylogenetic systematics applied to a nematological problem

The effectiveness of the loss tracing method can be demonstrated by applying it to a nematological example (for more details see Lorenzen, 1981): After having discovered metanemes (filamentous, serially arranged proprioceptors beneath the cuticle along the lateral chords) in the free-living marine nematode *Triodontolaimus acutus* (Triodontolaimidae, Enoplida), I proposed to identify the complete species set in which metanemes are either present or secondarily absent. After using the loss tracing method with about 150 nematode species from many families of all nematode orders, the result was finally achieved: Metanemes were recognized as a holapomorphy of the re-arranged and then holophyletic order Enoplida (Lorenzen, 1981). The analytical steps performed according to the loss tracing method were as follows (Fig. 5):

The buccal cavity of Thoracostomopsidae is provided with mandibles and they do not occur in the peculiar buccal cavity of Tripyloididae. Metanemes were found in species of both families. Are metanemes present or secondarily absent in the species of the Thoracostomopsidae not studied? This problem precisely fits the non-encaptic character pattern of Figure 4. The mandibles and the metanemes must be interpreted as homologies of the respective species sets. Therefore, hypotheses fitting the upper two patterns in Figure 4 must be rejected. As there is no evidence that the rather simple buccal cavity of Tripyloididae could have evolved from a precursor resembling the highly elaborated one of Thoracostomopsidae, metanemes *must be present or secondarily absent* in the thoracostomopsid species not studied. As Thoracostomopsidae and Tripyloididae are each evidently holophyletic, metanemes must be present or secondarily absent even in the tripyloidid species not studied because, otherwise, either the hypotheses on the holophyly of the two families or the hypothesis on the homology of metanemes were wrong. Many further steps were completed similar to those described here. The process of precisely determining the species set in which metanemes are either present or secondarily absent was completed when the species set achieved was encaptic with all the other holophyletic species sets. The species set closely resembled the previous order Enoplida which, at that time, included even the Prismatolaimidae, Monochromadorinae, Cryptonchidae, Alaimidae, Trefusiidae, Onchulidae, Lauratonematidae and Rhabdithyridae. Metanemes were not observed in species of these families and subfamilies. As no homology was found to be present in any of these families and in only *some* (rather than in all) nematodes provided with metanemes, that is, as the loss tracing method did not provide any evidence that metanemes are

secondarily absent in these families, it was concluded that metanemes must be primarily absent in them. Therefore, they were removed from the order Enoplida which then was substantiated as being holophyletic.

Further cases still await an analysis to be achieved by using the loss tracing method. For instance, an introvert is absent in nematodes, whereas it is present in larvae of Nematomorpha and in all life stages of Priapulida, Loricifera and Kinorhyncha. The taxa provided with an introvert were united into the taxon Cephalorhyncha by Malakhov in 1980 (for a discussion see Adrianov & Malakhov, 1995). Mermithoidea (nematodes) and nematomorphs share striking similarities (Lorenzen, 1985). Are they homoplasies or homologies? If the latter, an introvert could be shown to be secondarily absent in nematodes which then must be included in the Cephalorhyncha. As nematodes and gastrotrichs also share several striking similarities arguments could arise for the inclusion of the latter in the Cephalorhyncha.

## Concluding remarks

The development of traditional into advanced phylogenetic systematics is in fact a metamorphosis, because it requires breaking with the familiar, but nevertheless incorrect usage of the concepts of synapomorphy and symplesiomorphy. In turn, the metamorphosis provides the prospect for tracing present-day species back to hypothetical ancestral species. Non-encaptic character patterns, which have caused problems in traditional phylogenetic systematics and in cladistics, are now acceptable for use in the loss tracing method. Holophyletic species sets may now be recognized more precisely than formerly. The theory of advanced phylogenetic systematics is still being developed. The theory of evolution, particularly the theory of natural selection, is now recognized as an essential tool in systematics. By employing the method of advanced phylogenetic systematics, more phylogenetic problems may be solved than by employing any other systematic method currently available.

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**Lorenzen S.** Переход от традиционной к усовершенствованной филогенетической систематике и его влияние на таксономию нематод.

**Резюме.** Успех филогенетической систематики, предложенной Хеннигом, ныне совершенно очевиден. Однако, с самого начала эта концепция страдала фундаментальным, хотя и малозначительным, на первый взгляд, недостатком: относительные концепции синапоморфии и симплезиоморфии применялись так, как если бы они представляли собой *абсолютные понятия*. Изучение современной систематики позволяет выявить всю глубину последствий этой ошибки, повлекшей за собой исключение случаев, рассматривавшихся ранее как “симплезиоморфии”, из таксономического анализа и в результате трансформацию филогенетической систематики в форму нефилогенетической систематики, именуемую ныне кладистикой. Последняя уже ни в коей мере не связана концептуально с теорией эволюции. С осознанием и утверждением относительности базовых понятий становится возможным переход к *усовершенствованной филогенетической систематике* и на основе предлагаемого метода *отслеживания утерянных звеньев* и принципов теории эволюции, традиционные “симплезиоморфии” становятся пригодными к использованию для выявления групп голофилетических видов. Именно поэтому усовершенствованная филогенетическая систематика рассматривается как высшая форма филогенетической систематики и кладистики. Приводится пример из области нематологии, иллюстрирующий новый подход.

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