Stuttgarter Beiträge zur Naturkunde
Serie A (Biologie)

Herausgeber:

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart

Stuttgarter Beitr. Naturk.	Ser. A	Nr. 613	11 S.	Stuttgart, 31. 8. 2000

Mainstream Cladistics versus Hennigian Phylogenetic Systematics

By Günter Bechly, Stuttgart

Summary

Mainstream cladistic methods are shown to be fundamentally different from traditional Hennigian phylogenetic systematics, and indeed seem to have more in common with phenetics. Like phenetics, the general approach of mainstream cladistics has to be regarded as being rooted in formalism rather than realism. It is explained that parsimony implies more than the minimization of steps in cladograms, and that a priori homologization, polarization, and weighting are inevitable procedures of phylogenetic systematic analysis. Consequently it is concluded that genuine phylogenetic systematics should be preferred over mainstream cladistics.

Zusammenfassung

Es wird aufgezeigt, dass sich die moderne kladistische Methodik grundsätzlich von der traditionellen HENNIG'schen Phylogenetischen Systematik unterscheidet und tatsächlich mehr Gemeinsamkeiten mit der Phänetik besitzt. Ähnlich der Phänetik gründet sich der allgemeine Ansatz des modernen Kladismus eher in Formalismus als in Realismus. Es wird erläutert, dass das Sparsamkeitsprinzip mehr beinhaltet als nur die Minimierung der Schrittlänge von Kladogrammen, und dass die a priori Homologisierung, Lesrichtungsermittelung und Merkmalsgewichtung unverzichtbare Schritte bei der phylogenetisch systematischen Analyse sind. Es wird daher festgestellt, dass die ursprüngliche Phylogenetische Systematik dem modernen Kladismus zu bevorzugen ist.

Contents

1. Introduction

With the publication of WILLI HENNIG's (1950) *"Grundzüge einer Theorie der phylogenetischen Systematik"* (English translation: HENNIG 1966) a new era of biosystematic research began, and after some early years of vivid theoretical debates between so-called "cladists" and the proponents of evolutionary systematics and phenetics, nowadays most systematic biologists would agree that Hennigians finally succeeded in the form of modern cladistic analysis, which was recently elaborated for a broader audience in Germany with the pocket-book of RIEPPEL (1999). However, in this paper I argue that indeed phenetic reasoning has secretly "undermined" phylogenetic systematics and is now dominating biosystematic research around the globe, and that the methods that are generally known as "mainstream cladistics", "modern cladistics", "pattern cladistics", or "computer cladistics", rather represent a particular variety of non-Hennigian phenetic methods.

2. Why mainstream cladism is not phylogenetic systematics

Mainstream cladism is claiming to be just a further development and improvement of Hennigian phylogenetic systematics (PLATNICK 1979; RIEPPEL 1999). Many of its proponents maintain that a hierarchical order of organisms can be discovered from the pattern of their characters alone, without any necessity for a recourse to the theory of evolution (PLATNICK 1979; RIEPPEL 1999). This separation of "pattern and process" that are regarded as two opposite aspects of nature that cannot both be considered in the biological system, shall avoid an alleged circular reasoning between evolutionary theory and biological systematics, which shall occur if the former is postulated as basis of the latter as it was done by WILLI HENNIG with full intention and good reason. The discovery procedure of mainstream cladistics was recently summarized again by RIEPPEL (1999) and mainly consists of a computer-aided parsimony analysis of the character pattern, using a data matrix of (preferably numerous) equally weighted and unpolarized characters. Only that cladogram is accepted that requires the smallest number of character transformations or steps (most parsimonious tree). The computer is primarily calculating an unrooted tree, which is a posteriori rooted by choice of one of the analysed taxa as outgroup, and by designating the root between this outgroup and the remaining part of the tree. Only by this procedure of so-called outgroup-rooting (not to be confused with an a priori character polarization by an outgroup comparison) and a subsequent most parsimonious optimization of the characters on the resulting cladogram, the character states finally become polarized and homologized (as so-called secondary homologies), and are then interpreted in terms of symplesiomorphies and synapomorphies. If an analysis is leading to multiple most parsimonious trees of different topology, a consensus-tree is calculated that includes all dichotomies ("strict consensus") or all nestings ("Adams consensus") that are common to all most parsimonious trees, or at least occur in the majority of them ("majority rule consensus"). The resulting cladograms are generally not regarded as phylogenetic trees or pedigrees, but only as graphical representations of the most parsimonious interpretation of the character pattern ("synapomorphy-schemes").

Even a dedicated cladist could not but acknowledge that this methodology, which dominates current phylogenetic research, is strikingly free of any biological or evolutionary connotations, except that the used characters are biological characters and the analysed objects are biological entities. There is no biological foundation why this method should be the method of choice for biosystematics, and indeed many cladists only endorse formalistic arguments like "maximization of information content". Mainstream cladists often claim their methodology as superior, because of its inherent theory-neutrality and the alleged falsifiability of the results (cladograms) (PLATNICK 1979; RIEPPEL 1999). Unfortunately both goals are dubious and misleading. Theory-neutrality is not desirable at all within natural sciences, since it necessarily implies a strong loss of explanatory power. Especially the independence of any evolutionary theories, that is strongly endorsed by many mainstream cladists, cannot be regarded as a desirable property of biosystematic reasoning, since it boils down to ignorance of reality (it should go without saying that "reality" here has to be understood in the sense of a very well-corroborated and generally accepted theory, not as an absolute fact per se). The alleged falsifiability, which would be desirable indeed, since scientific hypotheses have to be falsifiable according to the philosopher KARL POPPER *("The Logic of Scientific Discovery"),* is far beyond reach, since hypothetical reconstructions of singular historical events (like phylogeny) can never be falsifiable in a Popperian sense. Systematical biology and evolutionary research are rather historical science than strict natural science in the sense of POPPER, and therefore imply hermeneutic procedures (or "mutual enlightenment" sensu HENNIG) rather than falsificationism (HOFFMANN & REIF 1988).

If is rather surprising that most mainstream cladists do not seem to be aware that their formalistic methodology is much more similar to numerical systematics than to genuine phylogenetic systematics of WILLI HENNIG. The only significant difference between mainstream cladistics and numerical systematics (phenetics) appears to be the use of different clustering algorithms (parsimony versus maximum similarity), which has the consequence that cladists only use one of the states of a given character as group-defining similarity (the one that is most parsimoniously interpreted as synapomorphy), while pheneticists generally accept all states (symplesiomorphies, as well as synapomorphies, and even convergences) as group-defining similarities. However, since mainstream cladists reject a priori polarization (RIEPPEL 1999), and some even reject a priori homologization, in practice they also do accept non-homologies and symplesiomorphies as group defining similarities! The resulting parsimony-phenograms that include non-Hennigian groupings are afterwards used to assign Hennigian properties to the characters (interpretation as symplesiomorphies or synapomorphies) and groupings (interpretation as monophyletic groups). However, the mere use of Hennigian terminology does of course not transform a basically phenetic approach into a Hennigian method.

The mainstream cladistic approach described above indeed conflicts with the three most fundamental assumptions of Hennigian phylogenetic systematics:

- 1.) A (mainly) hierarchical order or organismic diversity has to be postulated a priori, based on the generally accepted synthetic theory of evolution, because otherwise there would be no scientific foundation and justification at all for the solution of the common problem of conflicting evidence by use of parsimony arguments. If a hierarchical order of life is not a priori postulated, conflicting evidence could not be recognized as such, since all non-encaptic hypotheses of homology and relationship could indeed be correct rather than conflicting. However, the a priori postulation of a hierarchical order of life can only be justified in the framework of natural sciences if and only if it is based on a well-corroborated scientific theory that explains the process that leads to such a hierarchical order. The theory of evolution fulfils this goal and it is a theory that is generally accepted and basically undisputed by scientists today. Curiously only some biologists seem to be very anxious to accept such a theory as a methodological foundation for modern biosystematic research, while no physician ever was anxious concerning the use of the theory of relativity or the theory of quantum mechanics as methodological foundations for further research in modern physics. I have never heard of an astronomer who studies stars as "lights in the sky" only because the theory that they are distant suns is just a theory, and basing research methods on this theory would render the results to be based on circular reasoning. If all scientists would only accept hypotheses as explanations for certain observations, but would generally reject the use of well-corroborated hypotheses as foundations for new methodological approaches, then natural science would indeed cease to proceed. Accepting an organismic evolution and a resulting hierarchical order of life as foundations for phylogenetic research cannot be considered as circular reasoning, since no one ever intended to use the results of the analysis as evidence for the truth of these basic assumptions, but only to study the particular phylogenetic relationships of a particular group of organisms. If the basic assumptions of evolution and hierarchy are true, which every biologist seems to believe, then the results of phylogenetic systematic research matter, while they would be irrelevant anyway if the basic assumptions would be incorrect (e.g. if god would have created life or the evolutionary pattern would basically be non-hierarchic), which nobody (hopefully including mainstream cladists) seems to believe.

● 2.) Based on the theory of evolution only homologous and derived characters can be used as group defining characters within a phylogenetic approach to systematisation. Consequently, a priori homologization and polarization are inevitable procedures that have to precede any reconstruction of phylogenetic relationship. Therefore, the counter-argument that a priori homologization and polarization should be avoided because they are ad hoc hypotheses is irrelevant, since the principle of parsimony only refers to unnecessary ad hoc hypotheses and not to those ad hoc hypotheses that are necessarily required as justification and foundation for a research program, which would not make any sense without these ad hoc hypotheses. A methodology that generally avoids all ad hoc hypotheses may be most parsimonious, but certainly will have to be regarded as senseless.

● 3.) Different hypotheses of homology, polarity, and relationship are backed by different quantity and quality of evidence. Therefore, a weighting of the plausibility of conflicting hypotheses, based on the concerning evidence, is necessary if the final goal is recognition of a reality of nature.

Like phenetics, mainstream cladistics ignores evolutionary theory, does not a priori postulate a hierarchical order of nature, does not a priori homologize and polarize the characters, and does not consider weighting as a legitimate procedure. Consequently mainstream cladistics is rather rooted in phenetic reasoning than in Hennigian views. Since the phenetic and modern cladistic methods prefer formalistic and reductionist foundations rather than realistic scientific foundations, the results cannot be regarded as an approximation towards the recognition of a true phylogenetic order of life. Mainstream cladistics should therefore be dismissed in favour of a revival of traditional Hennigian methods. It would also be desirable that mainstream cladists start to realize and acknowledge that their approach is fundamentally different from Hennigian methods and by no means a more modern and improved variety of phylogenetic systematics.

3. Why non-weighting of characters is a misconception of mainstream cladistics

Character weighting represents a procedure that allows a choice between conflicting hypotheses of homology and monophyly, according to certain weighting criteria, by assigning higher weight to some characters than to other conflicting characters. The primary object of weighting is not the character itself, but the amount and quality of the available evidence for the correctness of the homology hypotheses that are involved in any character definitions. If we would know for sure that all persumed synapomorphies are indeed correct, they would of course all have the same value and weight. However, the common incongruence of potential synapomorphies proves that some must indeed be incorrect. All putative synapomorphies involve homology hypotheses that can either be correct, or wrong. Since statements of similarity are the foundation for any assumptions of homology, the very different degree of complexity of these statements of similarity implies a different faith in the correctness of the resulting homology hypotheses, and consequently a different weight of the concerning characters. The basic rational behind this statement can be easily explained by the following example: if there are two different pieces of paper found at two very remote localities, each with an identical single letter written with a typewriter on it, one would not necessarily assume that they were written by the same person or copied by one person from another, because the probability that two people independently type the same letter is relatively high (1:26). On the other hand, if there would be an identical poem written on these two pieces of paper, one would of course be quite sure that they were derived from the same source, simply because it is unlikely that two persons independently write the very same poem. Another example could be a judge at court who likewise has to estimate the relative weight of the evidence and the trustability of the witnesses to reconstruct the past events, rather than just counting the pieces of evidence and the number of witnesses and then using PAUP to decide who will have to go to jail. Weighting does not mean that some synapomorphies are better than others, but only takes into account that we can and must have stronger faith in the correctness of those homology hypotheses that are backed by better evidence, than in others that are backed by less good evidence (since no real probability is involved in statements about past events, the alternative expression “different truth probabilities of the homology hypotheses” should be avoided!). Please note that this kind of weighting does not need any knowledge about a particular evolutionary process, and it does not make any assumptions about it either, since it is exclusively based on the results of the characters analysis.

The most important criteria for an a priori weighting (a weighting that is preceding the phylogenetic analysis) of conflicting synapomorphy hypotheses are the compatibility (incl. uniqueness and congruence) and the structural complexity of the characters. Compatibility refers to the number of conflicting characters (or rather implied grouping hypotheses), which means that those characters that conflict with many other characters are regarded as less good evidence than characters that conflict with few or no other characters. Weighting on the basis of structural complexity means that simple structures that might easily evolve by convergence, or superficial similarities that might be based on an insufficient analysis, are regarded as weaker evidence, than characters that are so complex that they could hardly be non-homologous, and that are so well-investigated that the proposed similarity is not just superficial. Since there can be no complexity whatever in the mere absence of something (negative similarities), reductions are usually regarded as rather weak evidence. It is obvious that the criterion of complexity can never provide precise numerical weights, but only a somewhat vague greater trust in certain characters rather than in others. This may be one of the reasons for the strong disapproval of this important criterion by most mainstream cladists, since counting steps and favouring or rejecting certain cladograms because of insignificant differences in step-length, would not make much sense in this context. Anyway, a preliminary indication for the complexity of a character can be the simple linguistic complexity of its description: a less complex character needs less words to describe it than a more complex character. In molecular biology there is sometimes a further criterion available for a priori weighting, since the different probabilities of certain mutations are known in some cases (e.g. transitions are much more frequent than transversions, which was considered in the algorithm of transition-transversion-parsimony). The most important criterion for a posteriori weighting (weighting on the basis of the result of a phylogenetic analysis) is the homoplasy of a character on a given cladogram, which again involves the principle of parsimony. Characters that are less homoplastic in the resulting cladogram (characters with a CI closer to 1), are regarded as stronger evidence than characters that are more homoplastic (CI closer to 0) and thus imply many convergent origins or many convergent losses. All available weighting criteria should be used to estimate the relative weight of a character. This may also include conflicting evidence from the biogeographical or stratigraphical range of certain taxa, or the circumstance that some phylogenies may imply more complicated evolutionary scenarios than others.

The representatives of mainstream cladism mostly reject character weighting (Rieppel 1999), or at least any sort of a priori weighting, because it shall be a much too subjective procedure and/or based on circular reasoning. Nevertheless, their dogma of (alleged) non-weighting is nothing but a beautiful dream, since the choice of characters and the delimitation of characters already involves so many subjective decisions, that these characters are already strongly weighted as soon as they are chosen and formulated. Furthermore, the alleged non-weighting indeed represents an equal-weighting. This is even more problematic, since an exactly equal support for all involved homology hypotheses certainly represents one of the least likely cases one can think of. The issue of character weighting of course has most important consequences for the application of the principle of parsimony.

4. Why "Ockham's razor" implies more than cladistic parsimony

The well-known principle of parsimony (also known as "Ockham's razor") requires that ad hoc assumptions should be minimized as far as possible in scientific explanations of natural phenomena. This means for phylogenetic systematics that from the millions of theoretically possible trees only those should be preferred that minimize all biological assumptions that are implied by the concerning trees (e.g. assumptions of non-homology). The principle of parsimony is a basic epistemological principle, and thus should be viewed as a tool, not as a claim that evolution always took the most parsimonious way. This principle is just taking into account that there is no other possibility than parsimony to choose between different alternative hypotheses that explain singular historical happenings, which can only be reconstructed, but not repeated and tested like scientific experiments. Nowadays there are several software-packages (e.g. PAUP, Hennig-86, Phylip, and MacClade) available for the computer-aided calculation of most parsimonious trees from large data sets (numerous taxa and characters). The biggest problem of this computer-cladism is the circumstance that characters are either regarded as unweighted (which boils down to "equally weighted"), or that more or less arbitrary discrete weights have to be assigned to the characters. Since there is no rational way to decide whether a character should have the weight 0.3, 1, 17, or 16345, the preference of a most parsimonious tree (in the mainstream cladistic sense) that is only some steps shorter than other possible trees appears to be ill-founded.

The restriction of parsimony to a mathematical analysis of the character pattern with a mere numerical minimization of homoplasies ("cladistic parsimony") is not only over-reductionistic, but even appears to be untenable regarding the highly subjective impact of character choice and delimitation. Since nearly every character complex can be either lumped into a single character (e.g. "vertebrate eye"), or splitted into dozens of characters (retina, cornea, iris, ciliary muscle, etc.), a most parsimonious tree can be simply overturned by a different choice and delimitation of the characters, unless there is no conflicting evidence at all. Character choice and delimitation always imply a (often unreflected) weighting procedure. This renders quite unlikely that all characters have the same weight (i.e. that we can have the same faith in the correctness of each involved homology hypothesis), and it also prohibits the assignment of discrete weights to the characters. Objective criteria for the delimitation of characters do not exist and almost certainly never will, because they are impossible out of theoretical reasons, since every subdivision of a continuum like a body always will have to be rather artificial and subjective, and thus more or less optional. Regarding the unavoidable subjective impact on character selection and character delimitation, the preference of cladograms which are only a few steps shorter than alternative cladograms is untenable, since it lacks any scientific justification. Most parsimonious trees in the realm of mainstream cladistics are much more likely artifacts of the applied methods than representations of true phylogenetic relationship. Consequently, the over-reductionist view of the principle of parsimony, in terms of a mere minimization of the step-length of cladograms, has to be dismissed as unwarranted formalism that is inappropriate for a science that is striving for the recognition of truth.

This does of course not mean at all that I generally reject parsimony as a principle of choice between competing phylogenetic hypotheses. I only reject the reduction of parsimony to a simple search for shortest trees. The principle of parsimony must be understood in a much broader context, in such a way, that a cladogram that is some steps shorter than other cladograms, but has to interpret complex similarities as non-homologies, is regarded as less parsimonious than a cladogram that is a few steps longer, but treats these complex similarities as homologies, since the additional steps concern only weak characters which obviously have a higher risk of convergence.

Furthermore, if the topology of certain cladograms implies much more complicated evolutionary scenarios for certain structures, or certain biogeographical patterns, these ad hoc hypotheses should perhaps be considered in a true parsimony analysis as well, and not only the number of steps that is minimally necessary to explain the character pattern.

Considering these arguments, the elaborate and sophisticated discussions about parsimony algorithms (e.g. the pro and contra of three-taxon-parsimony), homoplasy indices, consensus procedures, islands of trees, and statistical tests (e.g. bootstrapping, jack-knifing, PTP, etc.) can be regarded as more or less irrelevant for phylogenetic research, even though such issues currently still constitute a large portion of the publications in journals like *Systematic Biology* and *Cladistics.*

5. Why computer-cladistics is not objective

Dedicated computer-cladists often maintain, that an analysis by "hand" should only be possible in cases of few characters without significant conflicts, while a computer-aided parsimony-analysis shall be far superior in cases of numerous characters with many conflicting evidence (Trueman 1996). This is of course true, if the only goal of the analysis is the discovery of the shortest tree. However, this goal is ill-founded out of the reasons already explained above. Besides, a phylogenetic-systematic analysis is not done by hand anyway, but by brain. The apparent objectivity of computers is misleading (Wägele 1994), since the most important procedure is not the parsimony-analysis, but the character-analysis (careful study, choice, and delimitation of the characters) in which no computers are involved anyway. The well-known computer wisdom "garbage in – garbage out" also applies in this case. Dubious phylogenetic hypotheses that are based on computer analyses of numerous equally weighted characters are quite common in cladistic literature. A general problem of computer-cladism is the fact that a parsimony-algorithm can even generate a fully resolved most parsimonious cladogram from an uninformative data set that is only containing very weak and extremely homoplastic characters. This "ability" has even been cherished by computer-cladists as "extraction of a cladistic signal from a noisy data set", while it is in reality just an unwarranted transformation of noise into apparent information (even the best alchemists failed to make gold out of plumb). If one cannot find convincing evidence for a phylogenetic tree in a "manual" analysis of a data set, the latter simply does not seem to contain any useful phylogenetic information! Even if a correct tree could be calculated from this data set with a parsimony-analysis, the result would not be very useful, since the branchings would not be supported by convincing evidence, what is often the case in published cladograms. Maybe the most fundamental difference between mainstream cladistics and Hennigian phylogenetic systematics is, that the ultimate goal of mainstream cladistics is calculation of a maximally resolved minimum-length tree from the available data, while the goal of phylogenetic systematics is the reconstruction of well-corroborated phylogenetic trees, based on a careful search for convincing evidence (strong characters), which can form the sound basis for other disciplines of evolutionary biology (historical biogeography, co-evolution, evolutionary scenarios; etc.).

6. Conclusion

The complex problems of phylogeny and evolution can neither be reduced to pseudo-objective computer algorithms that can only calculate with precisely quantified values, nor can they be formulated as strictly falsifiable hypotheses. However, the concerning hypotheses and arguments can well be rationally discussed on the basis of the total available evidence and background knowledge. Hennigian phylogenetic systematics offers the biological justification, theoretical foundation, methodology, and terminology for such rational discussions; nothing more and nothing less. Mainstream cladistics on the other hand is a formalistic and over-reductionistic method that is agnostic to biological reasoning and evolutionary thinking and thus should be abandoned, since it does not contribute to our knowledge about biodiversity and evolution.

7. Acknowledgements

I am very grateful to Dr Gerhard Mickoleit (Tübingen); Dr Erich Weber (Tübingen), Dr Michael Kühnapfel (Stuttgart), Prof. Dr Wolf Ernst Reif (Tübingen), Dr Rainer Schoch (Stuttgart), and Dr Martin Lindeboom (Tübingen) for most stimulating discussions on the theory and practice of phylogenetic systematics.

8. References

Hennig, W. (1950): Grundzüge einer Theorie der Phylogenetischen Systematik. – 370 pp.; Berlin (Deutscher Zentralverlag).

– (1966): Phylogenetic Systematics. – 263 pp.; Urbana (Univ. Illinois Press).

Hoffmann, A. & Reif, W.-E. (1988): The methodology of the biological sciences: From an evolutionary biological perspective. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **177** (2): 185–211; Stuttgart.

Platnick, N. (1979): Philosophy and the transformation of cladistics. – Systematic Zoology, **28** (4): 537–546; Washington.

Rieppel, O. (1999): Einführung in die computergestützte Kladistik. – 112 pp.; München (Pfeil).

Trueman, J. W. H. (1996): A preliminary cladistic analysis of odonate wing venation. – Odonatologica, **25** (1): 59–72; Bilthoven.

Wägele, J. W. (1994): Review of methodological problems of 'Computer cladistics' exemplified with a case study on isopod phylogeny (Crustacea: Isopoda). – Zeitschrift für Zoologische Systematik und Evolutionsforschung **32:** 81–107; Hamburg & Berlin.

Appendix: List of issues and criteria involved in character weighting

1.) The first subjective part in each phylogenetic analysis is the choice of studied taxa (OTUs) and the choice and delimitation of characters which are both also influenced by the previous knowledge and expectations of the researcher.

2.) The compatibility of chosen characters is a very important issue, since only incompatible characters impose a problem that requires weighting at all.

3.) Complexity is one of the most important weighting criteria, based on the assumption that phenotypical complexity mostly reflects genotypical complexity. Indications for complexity can be the number of identifiable functional substructures and their degree of specialisation, or the number of assumed independent homology criteria. Even the mere semantical complexity of the character description (how many words does one need for a detailed description of the character) could be a useful indication of character complexity.

4.) Parsimony of course can be used for weighting as well. It is generally desirable to shift further homoplasy into weak characters that are homoplastic anyway, thus maximising the number and weight of non-homoplastic characters.

5.) The amount and quality of background knowledge about a given character (function, ontogenesis, genetics, amount and selection of the studied sample, etc.) is important, too, because the homology hypotheses that are based on characters that are better understood can be regarded as more likely to be correct than conflicting hypotheses that are based on less well understood characters.

6.) Likewise, similarity, being the base of all homology assumptions, plays an important role in weighting, since homology hypotheses that are backed by stronger similarities have to regarded as more likely correct than conflicting homology hypotheses that are backed by less specific similarities. By the way: The use of the terms "primary homologies" for similarities and "secondary homologies" for tested homology hypotheses by some cladists, is as ill-founded as would be the terms "primary verdicts" for evidences and "secondary verdicts" for the sentences at court.

7.) The similar or different function of compared characters can be used in the estimation of convergence, since similar functions imply higher liability for convergence in many cases, especially if there is only a limited set of possible biological solutions.

8.) Problems with evolutionary scenarios that are resulting from certain assumptions of homology and polarity can also be used in character weighting, but since this criterion is rather based on theoretical considerations than on real evidence, it should only be applied in cases of conflicting hypotheses that are backed by an equal amount of strong evidence. A good example could be the case of the phylogenetic relationships of Myxini, Petromyzonta and Gnathostomata: In this case there are two reasonable alternatives, Cyclostomata (Myxini + Petromyzonta) versus Myopterygii (Petromyzonta + Gnathostomata), that are both supported by numerous strong putative synapomorphies. This dilemma could be solved by choosing the Myopterygii hypothesis and adopting an evolutionary scenario in which gnathostomes evolved from neotenic petromyzontoid "Ammocoetes" larvae, since the latter do not yet posses the conflicting similarities that are shared by adult Petromyzonta and Myxini.

9.) Biogeographical and biostratigraphical evidences can be useful, even though they have to be taken with great care due to numerous possibilities for errors (e.g. apparent vicariance patterns caused by correlated extinction events or the incomplete fossil record). A suitable example could be the cladistic analysis of Odonata by TRUEMAN (1996) who proposed a cladogram that is strongly conflicting with the fossil record: It implies that 15 branches of crown-group Zygoptera were already separated in the Triassic or even Permian, while no crown-group Zygoptera are known from any pre-Cretaceous deposits at all, although there are numerous localities with an excellent fossil record of Permian and early Mesozoic odonates. This contradiction is much too significant to be simply explained as sampling artifact, due to an incomplete fossil record.

10.) Finally, the likelihood for convergences in some genetic characters can be directly studied, e.g. the frequency of transitions versus transversions.

Author's address:

Dr Günter Bechly, Staatliches Museum für Naturkunde Stuttgart (Museum am Löwentor),
Rosenstein 1, D-70191 Stuttgart, Germany;
e-mail: bechly@gmx.de.

ISSN 0341-0145

Schriftleitung: Dr. Wolfgang Seeger, Rosenstein 1, D-70191 Stuttgart
Gesamtherstellung: Gulde-Druck GmbH, D-72072 Tübingen