POINT OF VIEW

Neglecting evolution is bad taxonomy

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"Nothing in biology makes sense except in the light of evolution" T. Dobzhansky (1973).

In a recent letter to the editor, Ebach & al. (2006) argue for monophyly as a sole criterion for grouping of taxa. Since their argumentation does not address the main points of previous advocates of paraphyletic taxa, I would like to (1) respond to their letter, and (2) provide a brief outline of strength and weaknesses of different concepts of classifications, and (3) give a plea for the here proposed evolutionary classification (in the sense of Mayr & Bock, 2002).

Ebach & al. (2006) wonder why the theoretical issues of paraphyly, that have been intensively discussed in the late 1970s and 1980s, are nowadays raised again. This is simply because in the meantime extensive empirical data resulting from cladistic and molecular phylogenetic studies have been accumulated, and the resulting classifications provide an empirical "test" of usefulness of Hennigian principles. Several systematists (e.g., Nordal & Stedje, 2005; Brummitt, 2006) and evolutionary biologists (e.g., Mayr & Bock, 2002; Hörandl, 2006) have expressed the opinion that a concept of strict monophyly results in unsatisfactorily classifications. The difficulties of including extinct taxa have been outlined by palaeontologists (see e.g., Kitching & al., 1998; Reif, 2005a, b). The reasons are (1) conceptual problems, (2) frequently observed discrepancies with pre-cladistic classifications, and the (3) nomenclatural consequences (e.g., Stevens, 2006). I will address here the first two items; the third one and some thoughts on practicability will be presented in a forthcoming paper.

Conceptual problems of Hennigian classifications. — Accepting paraphyly is not just a result of "inaccurate" definitions, as seen by Ebach & al. (2006). In the past, several definitions of monophyly and paraphyly have been proposed (reviews e.g., Wiley 1981; Reif, 2005a). Hennig (1966) and almost all later authors include two components in the definition of a monophyletic group: common ancestry and inclusiveness (all descendants of a common ancestor). The former is an evolutionary component, the latter just a logical one. This has been best recognized by Ashlock (1971) who defines "monophyly" in a broader sense, i.e., solely by common ancestry, and subdivides it into *holophyletic* = inclusive groups ("A holophyletic group is a monophyletic group that contains all of the descendants of the most recent common ancestor of that group (= monophyly of Hennig)" and *paraphyletic* = non-inclusive-groups ("a paraphyletic group is a monophyletic group that does not contain all of the descendants of the most common recent ancestor of the group"). That is, this hierarchy of terms separates the two components and places the evolutionary one over the logical one.

Inclusiveness is the main argument of Ebach & al. (2006) and other authors for accepting only monophyletic groups (sensu Hennig) as taxa. Inclusiveness per se is just a logical term; inclusive groups can be based on pure similarity as well (a classification that would be based on colors of petals would create, e.g., also an "inclusive" group of yellow flowered species—even if this would group buttercups and dandelions together). Inclusiveness is not necessarily connected with evolution. In fact, the majority of speciation processes are probably *not* inclusive, because they are not necessarily connected with extinction, as outlined in the review of Hörandl (2006). In principle this applies to higher taxa as well. The problem of monophyly is that it requires inclusive entities derived from non-inclusive processes.

If Ebach & al. (2006) reject to include a particular evolutionary model into classification, they are not aware that common ancestry *is* a model of evolution, and monophyly just a particular model for a certain type of branching, i.e., the one of dichotomous splits. Without inclusion of an evolutionary model, taxonomy is no more a biological discipline, but just a logical construct—a concept that I would not regard as desirable. Basically, the discussion on monophyletic and paraphyletic taxa can be reduced to the question whether inclusiveness should be regarded as a criterion for grouping. Application of monophyly sensu Hennig *alone* does include a concept of descent, but by clinging to "inclusiveness", a couple of evolutionary processes cannot be recognized in classifications, simply because evolution is not inclusive.

Some authors have defined terms just by character-state distributions. As a pure character-related approach, monophyly and paraphyly are relative, context-based

terms, depending on how the direction of change is defined by the researcher (Kitching & al., 1998; the problems of the commonly used outgroup methods are, e.g., discussed in Crisci & Stuessy, 1984). Only if the character-state change is connected with a time component, character-state changes get a direction that is informative about evolutionary histories. The relative character of all cladistic terms in the context of time has been recently comprehensively illustrated by, e.g., Kitching & al. (1998) and Reif (2005b).

The inclusion of time is indeed a main problem for Hennigian classifications because they include common ancestry as a time-related component but shift origins of all extant taxa to the same time level. By inclusion of extinct taxa, Reif (2005b) expresses the opinion that groups classified according to Hennigian principles can be applied only within a certain level of time because he regards taxa as synchronous and clades as diachronous groups. After reviewing previous definitions the author offers new time-related operational definitions:

"A taxon is monophyletic if its time of divergence is older than its time of differentiation.

"A taxon is paraphyletic if its time of differentiation is younger than its time of divergence from its plesiomorphic 'sister group' and older than its time of divergence from its apomorphic sister group.

"A taxon is polyphyletic if the time of divergence of its elements is young compared to the times of the divergence of the groups from which its elements are derived."

The strength of these definitions is that they overcome the inappropriate criterion of "inclusiveness", and include explicitely the time-component; moreover, paraphyletic groups are clearly distinguished from polyphyletic ones by the inclusion of the direct relationship to both the apomorphic and the "plesiomorphic" (parental) group, which does not apply to polyphyletic taxa. Reif's argumentation highlights a drawback of Hennigian classification: it is basically designed for extant taxa only and does not permit inclusion of different levels of time into classifications. Reif (2005a) concludes that two parallel systems are needed, one for biologists working with extant (synchronous) groups and one for palaeontologists working with extinct and extant (diachronous) groups (which I would not regard as desirable).

A simpler solution would be to accept diachronous groups, i.e., both paraphyletic and monophyletic ones, as taxa. In my example in Hörandl (2006) it would mean that the progenitors A and B should be regarded as a taxon before *and* after the speciation process of the derivative D. In a Hennigian classification only the recent time level is regarded (the group B and D)—for a grouping of A and B we would have to shift them to an earlier time level (which is unfortunately not possible if they still exist). If D has many autapomorphies and is thus distinct from A and B, this cannot be recognized in a Hennigian classification because A and B is a paraphyletic group. In evolutionary classifications, diachronous groups are acceptable as taxa, which would allow to address the different evolutionary processes involved. The raise of a new group would not affect the older group which reflects evolutionary reality of coexistence of lineages of different ages and divergence times.

The alternative classification after Hennigian principles also does reflect natural groups, but implies in both cases a loss of information: (1) grouping of (A, B, D) looses the information of the speciation event of D, and forces species together that are results of different evolutionary processes and time levels; (2) grouping of A (B, D) looses information about the sister relationship of A and B and may force highly divergent taxa together (depending on the divergence of D). The former approach is often preferred, resulting in considerable lumping and a loss of information about evolutionary processes within the resulting large taxa.

Advocates of monophyly have often stressed the difficulty of distinguishing paraphyletic and polyphyletic taxa. In fact, also polyphyletic groups do have a common ancestry, but divergence times may go back so far into the past, that they become uninformative for evolutionary history and thus meaningless for classifications (if one would group all species with yellow flowers together, they would still have a common ancestor, at least that of all angiosperms; depending on the degree of homoplasy of the character used, this ancestry may go back to the origins of life). But, the difference to paraphyletic groups is not just a gradual one – polyphyletic groups were never monophyletic before the rise of a derivative group out of it. One may use also the definition of Mayr & Bock (2002): "Paraphyletic—a taxon that includes the stem portion of clades that evolved into new taxa."

Paraphyletic groups can be characterized by symplesiomorphies, which are homologous characters as well as synapomorphies. In a cladogram, they will often appear as a gradual series of branches basal to a monophyletic group, and should form a clade if the putative derivative group is pruned from a cladogram. Indirectly, recognition of paraphyletic groups will also make it easier to reflect anagenetic change, i.e., autapomorphies for classification, because if a novel taxon with autapomorphies arises, it will turn the contemporary progenitors into a paraphyletic group; if the latter are accepted, it is not necessary to sink the taxon with autapomorphies into the progenitor group (as it is usually done with single species if one accepts only monophyletic groups). Criteria for recognition of autapomorphies themselves would require a completely different methodical approach (e.g., Stuessy, 1997).

Polyphyletic groups also do have a common ancestry, but include species that have neither a sister relationship, nor a progenitor-derivative relationship to each other; they are based on homoplasious characters and taken from different clades or distant branches of a cladogram. I agree with Mayr & Ashlock (1991) and Mayr & Bock (2002) to reject the recognition of homoplasy and consequently polyphyletic taxa.

Discrepancies of Hennigian and pre-cladistic classifications. — These discrepancies are due both to conceptual and methodical differences. Conceptual ones concern the relational approach of Hennigian classification, as discussed above. Methodical differences relate to (1) the different strategies of sampling of both taxa and characters in pre-cladistic and Hennigian classifications (which is perhaps more important as the much disputed use of DNA vs. morphology); and (2) the almost exclusive and direct use of cladograms as a basis for classification.

Hennigian classifications are usually based on a character-related sampling, with a focus on selection of "informative" characters (potential synapomorphies) and "representative" taxa, in practice without aiming at completeness ("this applies also to the present practice of phylogenetic studies using DNA sequences). With this selection, usually a grouping of the "remaining species" is tried (whereby, ironically enough, taxonomists often use similarity to assign the non-analyzed species to a group). Because of the relational concept of cladistics, both sampling designs and the kind of dataset selected will strongly affect tree topologies, and consequently clade-based classifications. Simple adding of taxa can result in dramatic changes of tree topologies (see, e.g., examples in Mayr & Ashlock, 1991).

The selection of datasets is even more crucial for tree topologies and thus classifications. DNA sequence data are the most reliable approach for reconstructing phylogenies; but, a phylogenetic analysis based on some DNA regions *alone* cannot be informative about branching patterns, that are not directly connected to the sequences used (i.e., other regions of the genome, karyology, or more adaptive features such as morphology, physiology, etc.; see e.g., Stace, 2005). DNA data may give insights into evolutionary processes, e.g., hybridization—but will reconstruct relationships correctly only if the right set of markers is used (see, e.g., examples in Seehausen, 2004). As pointed out by Alexander (2006), DNA is optimal for the recognition of descent and evolutionary history, but not of modification—recognition of the latter as the second important component of evolutionary processes requires the inclusion of more adaptive characters (e.g., morphology).

Groups that appear as paraphyletic in a phylogenetic analysis (e.g., based on DNA sequences), but with a high number of shared or unique characters outside the dataset used (e.g., morphology), can be thus also seen as indicators of incomplete datasets, simply requiring addition of *other* datasets to those used for analysis. One should then refrain from taxonomic conclusions and try to find additional characters to detect potential synapomorphies. A prominent example of the effect of incomplete sampling might be provided by extant gymnosperms, which appeared in early cladistic analyses as a paraphyletic group, but were resolved as monophyletic and sister to angiosperms after analyses of more comprehensive datasets; the various tree topologies retrieved for gymnosperms using different datasets demonstrate how strongly sampling of characters affects tree topologies, and thus classifications (see survey in Soltis & al., 2005). If datasets are not yet fully available, e.g., accepting paraphyletic groups as taxa is then the best compromise of available data and the necessity of a taxonomic decision for large scale-classifications (as, e.g., argued by Smith & al., 2006, for their recent classification of ferns, including some paraphyletic taxa). Such an approach might be also the best solution for groups of extinct taxa, where comprehensive datasets (e.g., molecular data) are simply not available (see, e.g., Hilton & Bateman, 2006, on pteridosperms). Non-inclusive sampling of taxa and characters, as it is current practice, will consequently result in highly unstable clades and, consequently in highly unstable classifications, if a principle of inclusiveness is followed.

Nevertheless, the optimistic view of Ebach & al. (2006), that a more comprehensive sampling will solve all problems, is not necessarily justified—if a progenitor group has no synapomorphy compared to a younger derivative group, it will never be resolved in a cladogram as a sister group to the derivative group. Moreover, addition of terminal taxa may break up nice monophyletic groups or turn characters into symplesiomorphies. An example might be provided by the prominent feature of double fertilization and formation of a biparental endosperm, which is usually seen as a key innovation for the origin of angiosperms (e.g., Stuessy, 2004; whether forms of double fertilization in *Ephedra* and *Gnetum* are homologous to that of angiosperms is under discussion; see Friedmann & Floyd, 2001; Raghavan, 2003). But, in fact, some rather advanced taxa have skipped double fertilization and develop either a purely maternal endosperm (e.g., *Taraxacum* and other diplosporous Asteraceae; Spielman & al., 2003) or do not form a polar nucleus (Podostomaceae; Raghavan, 2003). Thus, with a *comprehensive* sampling of taxa, both double fertilization and thus formation of endosperm is in cladistic terms a symplesiomorphy, and angiosperms are, with respect to this character, a non-inclusive, i.e., a paraphyletic group. This example shows that it is quite useful to consider symplesiomorphies for classifications—if we exclude this character, we loose a

lot of information about evolutionary history of angiosperms, because as a symplesiomorphy of angiosperms it is quite an important character for large-scale classifications. It is quite likely, that more comprehensive samplings of taxa and characters will increase the number of such cases, because more evolutionary changes will be included; this may potentially also increase conflicts of different datasets.

Pre-cladistic classifications (following the survey of Stuessy, 1990, and leaving here early artificial classifications aside) are based on more or less comprehensive datasets of morphological characters (often supported by karyological, biogeographical and other information, depending on the state of research). In general, complete sets of taxa (species) were used, based on monographic work and Floras. The taxonomic decision was either done by a posteriori intuitive selection and weighting of characters (natural classifications in the terminology of Stuessy, 1990). This was also the basic methodical approach of phyletic classifications of the 20th century, but just with an attempt to understand evolutionary history of groups as a background, not as explicit grouping criterion. Comprehensive sampling of characters is also the principle of phenetics, but with a criterion of overall similarity for grouping. These approaches are more organism-related and have necessarily a higher probability to detect large numbers of shared characters that are potentially symplesiomorphies, and also of course more autapomorphies. Groups based on such datasets are necessarily more stable because of the inclusion of a high number of symplesiomorphies (which will reflect in many cases also overall similarity), and the non-relational principle (a group is mainly defined by its own properties). The main conceptual drawbacks of these methods are: subjective weighting of diagnostic characters and degree of similarities; overemphasizing of evolutionary novelty because of visual "distinctness" of, e.g., rapidly evolving morphological characters. Because of the lack of molecular data in pre-cladistic times, classifications have often selected homoplasious morphological characters as diagnostic ones for grouping. This historical methodical drawback should not be misused to justify Hennigian classifications. By including a broad range of characters into classification, pre-cladistic classifications did have a potential to recognize natural groups, but with the drawback to lack an explicit analytical approach.

Principles of evolutionary classifications in the sense of E. Mayr. — I do not give a plea for returning to pre-cladistic classification—progress in research should be reflected in classification. I suggest an evolutionary approach as recently proposed by Mayr & Bock (2002), aiming at usage of cladistic methods for recognition of genealogy, but with recognition of taxa based on a broader range of criteria (see also Table 1). The following procedure is recommended: (1) test provisional taxa for monophyly with as many different kinds of datasets and taxa as possible, in separate and combined analyses; (2) examine putative cases of non-dichotomous branching with alternative methods, and try to find out ancestor-descendant relationships; (3) sort out homoplasious characters and thus polyphyletic taxa; (4) base natural taxa on either a) synapomorphies, b) symplesiomorphies or c) autapomorphies, decided case by case. Evolutionary classifications would use cladograms just as a tool for recognition of relationships and processes, but not primary basis for definition of taxa. In the proposed procedure monophyly and paraphyly are *features* of taxa (as,

Table 1. Main differences and features of cladistic classifications (sensu Hennig) and evolutionary classifications (sensu Mayr).

	Cladistic	Evolutionary
Kind of branching regarded	dichotomous only	budding, reticulate, anagenetic change, dichotomous
Main principle	pattern-orientated, character-related	process-orientated, organismic-related
Time levels	recent only	includes various time levels
Characters used	synapomorphies	synapomorphies, symplesiomorphies, autapomorphies
Monophyly/ paraphyly	criteria for recognition of taxa	features of taxa
Methods for reconstruction	cladograms	cladograms, phylograms, networks, patristic methods; to be developed further
Main level of subjectivity	selection of tree topology and clades	selection of criterion (symplesiomorphies/ synapomorphies/ autapomorphies)
Main source of error	incomplete sampling of characters and taxa; misinterpretation of branching pattern	misinterpretation of evolutionary process
Main advantage	simplicity (because of a single criterion)	reflects best complexity and diversity of evolutionary
Main disadvantages	reflects only a part of existing natural groups, context-dependent, problem of different time-levels, subject of rapid change	requires more comprehensive sampling and analytical approaches, and application of different criteria

e.g., practiced by Smith & al., 2006), not criteria to define taxa. In Table 1, I have tabulated the features of the two concepts of classifications, outlining their strengths and weaknesses. Evolutionary classifications require application of different criteria in different cases, a broader basis of characters, and more sophisticated analyses, but will provide a more informative system with respect to evolutionary history than Hennigian classifications.

If Ebach & al. (2006) regard evolutionary approaches as "bad" taxonomy, then they just express a dogmatic view without really thinking what a "good" taxonomy should aim at. To my opinion, taxonomy should be the synthetic outcome of systematic work, which comprises recognizing phylogenies and evolutionary process in a conceptualized way (see also Stuessy, 1990). Many authors put emphasis on reconstruction of phylogeny, i.e., evolutionary history, as a primary goal of systematics (e.g., Judd & al., 2002; Simpson, 2006). Judd & al. (2002) state "A phylogeny-based classification, such as the one followed in this book, attempts to arrange organisms into groups on the basis of their evolutionary relationships." Fine, but how can evolutionary relationships be reconstructed without recognition of the diversity of evolutionary processes? Monophyly alone neglects the *diversity* of evolutionary relationships, which would be better reflected by evolutionary classifications as presented here.

In conclusion, accepting monophyletic *and* paraphyletic taxa is not bad taxonomy, but a first step to a *better* taxonomy.

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